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Can community composition be predicted from pairwise species interactions?

E. Cayenne Engel · Jake F. Weltzin

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Abstract Plant communities are often structured by interactions among species, such as competition or facilitation. If competition is an important factor that controls the presence and absence of species within intact communities, then a competitive hierarchy, a ranked order from competitive dominant to competitive subordinate, should predict the composition of intact communities. We tested whether a competitive hierarchy derived from pairwise comparisons accurately predicts species abundances within a constructed polyculture community consisting of seven species common to old-field plant communities. We first conducted a pot experiment in field conditions wherein we grew the species in all possible combinations, then created a competitive hierarchy derived from both competitive effect and competitive response for each species. Concurrently, at the same site in native field soil, we constructed polycultures consisting of the same seven species and calculated an abundance hierarchy based on foliar cover, biomass, and an index of species performance. The

competitive hierarchy was not concordant with the abundance hierarchy, indicating that simple pairwise comparisons may not account for other factors that influence the abundance of species within relatively complex communities.

Keywords Abundance hierarchy · Competitive hierarchy · Field experiment · Old-field · Species composition

Introduction

The number and relative abundance of species within plant communities may be determined by the relative strength, their competitive abilities, as well as other biotic factors, and abiotic factors (e.g., herbivory, availability of resources; Grime 1977; Connell 1983; Huston and Smith 1987; Keddy 1990; 2001; Goldberg and Barton 1992; Callaway and Walker 1997; Howard and Goldberg 2001). If a community of species is exposed to constant environmental conditions, species with a greater competitive ability should inhibit those with lower competitive ability. Such a pattern of species interactions should lead to a predictable rank order of dominance within the community (Keddy 2001). A competitive hierarchy, i.e., a ranked order from competitive dominant to competitive subordinate, may be derived to explain the composition and structure of communities (Miller

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and Werner 1987; Goldberg and Barton 1992; Keddy 2001).

Competitive hierarchies are often determined by comparing how plants both affect and are affected by the growth of other plants (Goldberg and Landa 1991; Connolly et al. 2001; Keddy et al. 2002). Further, they are typically derived from experiments that examine pairwise comparisons among species, and that quantify the relative competitive effect (i.e., the ability of a species to suppress other species) and competitive response (i.e., the ability of a species to withstand suppression by other species) (Norrington-Davies 1967; Fowler 1982; Moore and Williams 1983; Mitchley and Grub 1986; Miller and Werner 1987; Goldberg and Landa 1991). However, these hierarchies are rarely developed in field situations that reflect environmental conditions similar to those experienced by intact communities. For example, many experiments are conducted in pots with artificial substrate, and are often conducted in glasshouses as opposed to field conditions. Hierarchies derived in artificial situations may less accurately predict field abundances than hierarchies constructed from conditions comparable to the field environment (Wilson and Keddy 1986; Karez 2003).

Competitive hierarchies are typically assumed to predict the relative abundance of constituent species in polyculture. However, hierarchies developed from pairwise interactions are limited in their ability to describe competition at the community level because individuals in nature often compete with those from several species simultaneously (Connell 1983; Schoener 1983). Although these higher-order interactions may be important predictors of relative abundance in more complex communities, there have been few theoretical or empirical tests of the utility of competitive hierarchies as tools for predicting abundance within natural plant communities (Shipley and Keddy 1994; Paul Keddy pers. comm. 2003). Howard (2001) determined that total competitive effect was not correlated with relative abundance within a natural field community. Taking a slightly different approach, Aarssen (1988) used a series of greenhouse experiments to determine that rank orders derived from pairwise interaction experiments were not identical to rank orders based on four-species mixtures. Mitchley and Grubb (1986) compared the rank order of pot and field experiments as part of their

investigation of controls on the relative abundance of perennials in grassland ecosystems.

In this article, we describe an empirical study consisting of two complementary field experiments designed to determine whether a competitive hierarchy based on pairwise interactions could be used to predict the abundance of plant species in more complex communities. First, we derived a competitive hierarchy from a field-based pot experiment, wherein we grew inter- and intra-specific pairwise combinations of seven species common to old-field communities in the southeastern United States for an entire growing season. Concurrent with the pot experiment, and at the same field site, we established and monitored polycultures of all seven species in native field soil. We then compared the competitive hierarchy derived from the pot experiment to abundance rankings derived from the polyculture (community) experiment for one and two growing seasons. We used data from each experiment to derive independent competitive rankings for each species based on relative yield (for the pot experiment) or abundance (for the community experiment), and to test the concordance of the rankings for the two experiments. Concordance of ranks suggest that pairwise experiments could be used to predict community abundance, whereas non-concordance of ranks suggest that other factors, or higher-order interactions among species, would better explain individual abundance within complex field communities.

Methods

Site description

Research was conducted at the Oak Ridge National Laboratory (ORNL) Environmental Research Park in Oak Ridge, Tennessee (25°54' N; 84°21' W). This site was abandoned from agriculture in 1943, and was converted to a managed fescue field in 1964 (Kelly 1975). The soil is derived from floodplain alluvium deposited by the nearby Clinch River, and is classified as Captina silt loam—fine-silty, siliceous, mesic typic fragiudult, well drained, and slightly acidic (Soil Conservation Service 1967; Edwards and Norby 1998). Mean annual precipitation is 1322 mm; mean

annual temperature is 13.9°C (Norby et al. 1999). Old-fields nearby are dominated by the seven species selected for this study: *Andropogon virginicus* L., a C₄ grass, the C₃ grasses *Dactylis glomerata* L. and *Festuca pretense* L., the nitrogen-fixing legumes *Lespedeza cuneata* (Dum. Cours.) G. Don and *Trifolium pratense* L., and the herbaceous dicots *Plantago lanceolata* L.—a weak biennial at this site—and the perennial *Solidago Canadensis* L. Nomenclature follows NRCS (2007).

Pot competition experiment

The pot competition experiment was conducted at the ORNL field site using pots sunk partially into the soil to minimize pot edge effects. The bottom of each 8.8 l pot was first lined with geotextile cloth to minimize movement of roots into and out of the pot. Soil excavated from depths between 4 cm (to minimize the seed bank) and 30 cm was homogenized by sifting through a 1-cm sieve, and was then placed into the pots at a bulk density equivalent to undisturbed soil. At the field site, we used a soil augur to drill a grid of holes at 60 cm spacing in otherwise undisturbed field soil, to a depth 2 cm less than the height of the pots; we then placed the soil-filled pots into the holes at randomly assigned locations. We constructed a 2.5 m tall fence around the experimental site to exclude larger mammalian herbivores.

We established each of the seven plant species from seed, within soil collected from the field site, at the University of Tennessee greenhouse in February 2003; seedlings were out-transplanted into pots in the field in May 2003. Individual seedlings of each species were planted within each pot in all possible inter- and intra-specific combinations (i.e., 21 inter-specific pairs and 7 intraspecific pairs); seedlings were planted in the geometric center of each half of each pot ($n = 4$, for a total of 112 pots). Immediately after planting, pots were watered with a solution of 4-12-4 NPK liquid fertilizer; thereafter, pots were watered occasionally during July and August as necessary to prevent wilting. In October 2003, 6 months after outplanting, pots were destructively harvested: aboveground biomass for each plant was clipped, and belowground biomass was collected by wet flotation. Plant samples were dried in an oven at 60°C for 48 h.

We assessed the response of a species to competition by calculating the relative yield per plant (RYP) derived from whole plant biomass for each individual,

$$\text{RYP}_{ij} = Y_{ij}/Y_{ii} \quad (1)$$

where RYP_{ij} is the relative yield per plant of species i grown with species j , Y_{ij} is the yield of an individual of species i grown with an individual of species j , and Y_{ii} is the yield of an individual of species i grown in monoculture. Values of $\text{RYP}_{ij} > 1$ indicate that species i has greater yield when grown with species j than when grown in monoculture; thus, species j is less competitive than species i . Conversely, when $\text{RYP}_{ij} < 1$, j is a better competitor than i .

We formed a matrix of RYP scores for each combination of species grown together, and then calculated a target score (analogous to competitive effect) and a neighbor score (analogous to competitive response) for each species (cf Wilson and Keddy 1986; Goldberg and Landa 1991; Keddy 2001). *Target scores* are defined as the RYP of target plants averaged across all combinations of a species grown with each neighbor species, i.e., the mean across each column of the matrix. The *neighbor score* is the mean RYP of each species functioning as a neighbor to each target species, i.e., the mean across each row of the matrix. Greater target scores, and lower neighbor scores, denote the better competitor. We assigned ordinal ranks to target scores and neighbor scores separately; ranks were summed, and the sums again ranked to produce a competitive hierarchy. Tied ranks were assigned equal positions.

Community experiment

At the same site, we created polycultures of all seven species in three blocks of two plots each. Construction of plots was initiated in summer 2002, when existing vegetation within each plot was killed with an application of glyphosate herbicide. We constructed three 12.6 m² circular whole-plots, each of which was trenched to a depth of 75 cm along its diameter and perimeter to create two 6.3 m² experimental units per whole-plot. Trenches were lined with insulating foam and 4-mil polyvinyl chloride (PVC) film to minimize lateral flow of water on the soil surface and subsurface. Dead plant biomass and

aboveground meristems were eliminated by removing the top 1 cm layer of soil with a hoe. Field soil within each plot was otherwise left intact.

Seedlings of the seven plant species were established from seed in a 1:1 mix of field and potting soil within a greenhouse at the University of Tennessee in Month, year, and were out-transplanted into the field plots in August 2002. A set of 25 seedlings of each species was planted in an identical, predetermined array (at 18 cm spacing) within each plot, in a manner such that no individual neighbored a conspecific. Plots were watered as necessary for the first three months after transplanting to ensure establishment of seedlings. The few plants that died within 4 weeks of transplanting were replaced with individuals of the same species maintained in the greenhouse for that purpose. All plants not in the original planted array were removed by hand-weeding until spring 2003; thereafter, we weeded only those species not included in our list of seven planted species. Within each plot we designated two 0.49 m² permanent subplots from which we collected data throughout the experiment. At treatment initiation, each subplot contained 16 individual plants, with at least one, but no more than three individuals of each of the seven planted species. Each subplot had identical initial species composition and layout.

We estimated foliar cover of each plant species within each subplot at the peak of the growing season (in early September) in 2003 and 2004 using a modified Domin-Krajina scale (Mueller-Dombois and Ellenberg 1974). In 2003, we determined species-specific biomass in late September by clipping at 2 cm all plants within a 0.37 m² subplot separate from those used to track foliar cover; plant samples were dried in an oven at 60°C for 48 h. In 2004 we used non-destructive techniques to estimate biomass using algorithms developed for each species (with coefficients of determination $\geq 61\%$). For each year, we determined an importance value (IV) for each species calculated as the sum of relative foliar cover and relative biomass.

Statistical analysis

Target and neighbor scores for the pot competition experiment were analyzed with separate one-way ANOVA models (Proc GLM, SAS Institute 1999). Foliar cover, biomass, and IV data for each year of

the community experiment were analyzed with one-way mixed-model ANOVAs in a block design (Proc Mixed, SAS Institute 1999). Data were log-transformed or arcsine-square root-transformed as appropriate to meet assumptions of normality (Shapiro-Wilk W-statistic; Shapiro and Wilk 1965). Equality of variance was assessed using Levene's test (Levene 1960). Non-transformed means are presented in tables.

We used Kendall's coefficient of concordance for multiple comparisons (Kendall's *W*) to determine concordance of (1) the competitive hierarchies derived from target, neighbor, and target and neighbor scores combined, all derived from the pot competition experiment, and (2) the abundance hierarchies derived from foliar cover, biomass, and IV for each year of the community experiment (Sokal and Rohlf 1995). Finally, we used Kendall's tau (Kendall and Gibbons 1990) to determine concordance of the competition hierarchy and the abundance hierarchy from each year.

Results

Competitive hierarchy derived from the pot competition experiment

When grown in pairwise combinations with all species, *Andropogon* produced most biomass when grown with *Festuca*, *Lespedeza* or *Solidago*, and least biomass when grown with *Dactylis*, *Plantago*, or another *Andropogon* (Table 1). Production of biomass by *Dactylis* was clearly greatest when grown with *Andropogon* and least when grown with *Plantago*; biomass of *Dactylis* was intermediate in all other species combinations. Biomass of *Lespedeza* was greatest when grown with *Dactylis*, *Solidago*, *Trifolium*, or another *Lespedeza*; in contrast, biomass of *Lespedeza* was least when grown with *Andropogon*, *Festuca*, and *Plantago*. *Festuca*, *Plantago*, *Solidago*, and *Trifolium* responded little to neighbor identity in terms of biomass production.

Based on target scores, *Andropogon* ranked as the most competitive species, whereas *Festuca* ranked as least competitive species (Table 2). In contrast, *Plantago* had the strongest competitive effect (i.e., it had the lowest neighbor score), whereas *Festuca* had the weakest competitive effect; *Dactylis*,

Table 1 Mean (± 1 SE) biomass (g plant^{-1}) of each target species (in columns) grown with each neighbor species (in rows) within the pot competition experiment.

Neighbor species	Target species						
	<i>Andropogon</i>	<i>Dactylis</i>	<i>Festuca</i>	<i>Lespedeza</i>	<i>Plantago</i>	<i>Solidago</i>	<i>Trifolium</i>
<i>Andropogon</i>	19 \pm 2 ^{de}	14 \pm 5 ^a	2.3 \pm 1.4 ^a	13 \pm 5 ^c	18 \pm 7 ^a	8 \pm 6 ^a	1.5 \pm 0.5 ^a
<i>Dactylis</i>	21 \pm 5 ^{cde}	9 \pm 1 ^b	1.4 \pm 0.6 ^a	33 \pm 3 ^a	23 \pm 2 ^a	11 \pm 3 ^a	2.5 \pm 0.7 ^a
<i>Festuca</i>	44 \pm 6 ^a	6 \pm 2 ^b	1.6 \pm 1.3 ^a	17 \pm 4 ^{bc}	16 \pm 6 ^a	13 \pm 5 ^a	7 \pm 5 ^a
<i>Lespedeza</i>	32 \pm 5 ^{abc}	10 \pm 1 ^b	1.3 \pm 0.9 ^a	26 \pm 3 ^a	12 \pm 5 ^a	16 \pm 9 ^a	6 \pm 4 ^a
<i>Plantago</i>	16 \pm 3 ^e	4 \pm 1 ^c	1.1 \pm 0.2 ^a	16 \pm 5 ^{bc}	13 \pm 3 ^a	6 \pm 1 ^a	1.7 \pm 0.7 ^a
<i>Solidago</i>	35 \pm 8 ^{ab}	7 \pm 2 ^b	1.7 \pm 0.5 ^a	29 \pm 3 ^a	17 \pm 5 ^a	8 \pm 2 ^a	4.2 \pm 2.3 ^a
<i>Trifolium</i>	29 \pm 4 ^{bcd}	9 \pm 2 ^b	1.4 \pm 0.0 ^a	25 \pm 6 ^{ab}	13 \pm 6 ^a	12 \pm 2 ^a	2.6 \pm 0.7 ^a

Within a column, means with the same letter do not differ ($P > 0.05$)

Table 2 Mean (± 1 SE) target score (competitive response) and neighbor score (competitive effect) for each species within the pot competition experiment.

Species	Target score	Target score rank	Neighbor score	Neighbor score rank	Overall competitive hierarchy
<i>Andropogon</i>	1.67 \pm 0.19 ^a	1	0.72 \pm 0.17 ^{ab}	2	1
<i>Dactylis</i>	0.68 \pm 0.10 ^{bc}	6	1.19 \pm 0.11 ^a	4	5
<i>Festuca</i>	0.47 \pm 0.09 ^c	7	1.53 \pm 0.34 ^a	7	7
<i>Lespedeza</i>	0.72 \pm 0.13 ^{bc}	5	1.24 \pm 0.19 ^a	5	6
<i>Plantago</i>	1.24 \pm 0.15 ^{ab}	4	0.41 \pm 0.08 ^b	1	2
<i>Solidago</i>	1.37 \pm 0.26 ^{ab}	3	1.24 \pm 0.19 ^a	5	4
<i>Trifolium</i>	1.46 \pm 0.41 ^{ab}	2	1.14 \pm 0.15 ^a	3	2

The competitive hierarchy was determined by ranking the numerical sum of the target score rank and the neighbor score rank. Within target and neighbor score columns, means with the same letter do not differ ($P > 0.05$)

Festuca, *Lespedeza*, *Solidago*, and *Trifolium* had intermediate neighbor scores. However, the simplicity of these rankings based on raw scores was compromised by the statistical equivalence of all but the most extreme target and neighbor scores. In terms of an overall competitive hierarchy (determined by ranking the sums of the target and neighbor score ranks), *Andropogon* ranked highest whereas *Festuca* ranked lowest (Table 2). We compared the competitive hierarchy to the abundance hierarchy derived from the community experiment.

Abundance hierarchies derived from the community experiment

At the peak of the 2003 growing season, *Dactylis* was the dominant species in the community experiment, with greater cover, biomass, and importance value (IV) than all other species (Table 3). In contrast, *Solidago* and *Trifolium* were least-dominant, with the

lowest cover, biomass, and IV. *Andropogon*, *Festuca*, *Lespedeza*, and *Plantago* were intermediate in terms of dominance. In 2004, *Andropogon* and *Dactylis* had the greatest cover, biomass, and the highest IV, whereas *Festuca* and *Solidago* were the least dominant species.

We used the rankings of IV as an abundance hierarchy for comparison to the competitive hierarchy derived from the pot experiment. However, because the rank order of IV differed between 2003 and 2004 (Kendall's tau = 0.43; $P = 0.18$), we compare the abundance hierarchy for each year to the competitive hierarchy.

Competitive hierarchy versus abundance hierarchy

The competitive hierarchy and the abundance hierarchy were not concordant for either 2003 (Kendall's tau = 0.03; $P = 0.94$) or 2004 (Kendall's tau = 0.39;

Table 3 Mean (± 1 SE) foliar cover, biomass, and importance value (IV, i.e., sum of relative foliar cover and relative biomass) for each species within the community experiment in 2003 and 2004.

Year	Species	Foliar cover (%)	Cover Rank	Biomass (g m ⁻²)	Biomass Rank	IV (%)	IV Rank
2003	<i>Andropogon</i>	6 \pm 1 ^{cd}	4	122 \pm 31 ^b	2	25 \pm 6 ^{bc}	3
	<i>Dactylis</i>	35 \pm 6 ^a	1	425 \pm 106 ^a	1	94 \pm 7 ^a	1
	<i>Festuca</i>	7 \pm 1 ^{bd}	3	71 \pm 18 ^b	5	17 \pm 1 ^d	5
	<i>Lespedeza</i>	6 \pm 2 ^{cd}	4	74 \pm 24 ^b	4	19 \pm 4 ^{cd}	4
	<i>Plantago</i>	12 \pm 2 ^b	2	109 \pm 37 ^b	3	32 \pm 6 ^b	2
	<i>Solidago</i>	4 \pm 1 ^{cde}	6	11 \pm 4 ^c	7	8 \pm 2 ^e	6
	<i>Trifolium</i>	2 \pm 1 ^e	7	21 \pm 15 ^c	6	5 \pm 2 ^e	7
2004	<i>Andropogon</i>	23 \pm 6 ^a	2	237 \pm 62 ^a	1	77 \pm 10 ^a	1
	<i>Dactylis</i>	24 \pm 8 ^a	1	98 \pm 26 ^b	2	53 \pm 10 ^b	2
	<i>Festuca</i>	8 \pm 0 ^c	6	0.6 \pm 0.3 ^d	6	0.4 \pm 0.2 ^e	7
	<i>Lespedeza</i>	17 \pm 5 ^{ab}	3	25 \pm 20 ^c	4	39 \pm 9 ^{bc}	3
	<i>Plantago</i>	11 \pm 3 ^b	4	24 \pm 5 ^c	5	22 \pm 4 ^{cd}	4
	<i>Solidago</i>	1 \pm 1 ^c	5	0.1 \pm 0.1 ^e	7	2 \pm 1 ^e	6
	<i>Trifolium</i>	1 \pm 1 ^c	7	40 \pm 30 ^c	3	8 \pm 5 ^{de}	5

Within foliar cover, biomass, and IV columns, means with the same letter do not differ ($P > 0.05$)

$P = 0.22$). In 2004, *Andropogon* ranked first in both the competitive hierarchy and the abundance hierarchy, whereas *Festuca* ranked last in both hierarchies; this suggests these two species have similar competitive effects on—and responses to—neighbors in terms of both pairwise and higher-order interactions. However, the species in the middle ranks were entirely non-concordant.

Discussion

Relationship between the competitive hierarchy and community composition

The competitive hierarchy that we derived from pairwise comparisons did not predict the structure of an intact community grown in the same environmental conditions in either its first or second season of development. This suggests that competitive hierarchies derived from pairwise interactions may have limited utility for explaining the structure of more complex communities. Although competitive interactions and hierarchies are often invoked to explain species coexistence and relative abundance (e.g., Panetta and Randall 1993; Shipley and Keddy 1994; Zamfir and Goldberg 2000; Bigelow and Canham 2002), there have been few studies designed to

explicitly compare experimentally derived competitive hierarchies with field abundances (e.g., Mitchley and Grubb 1986; Aarssen 1988, Howard 2001). Thus, though the derivation of competitive hierarchies may provide insight into the structure and composition of communities (Miller and Warner 1987; Goldberg and Barton 1992), inferring relationships among many species from interactions among pairs of species may not directly translate into field abundances.

Community composition through time

The relative abundance of species in the community changed between 2003 (the first year of community establishment) and 2004. We allowed the communities to mature, senesce, and re-establish during this time, but the relative abundance of species within the communities did not become concordant with the competition hierarchy. However, between 2003 and 2004, there were some important shifts in species dominance within the communities that may have been linked to species interactions. For example, *Andropogon*, the top competitor in the competitive hierarchy, became the most dominant species in the community by 2004.

Plantago ranked second in the competitive hierarchy, but it performed better at suppressing other individuals than it did at resisting suppression from

neighbors. This may explain why it dominated the community in 2003, but then dropped positions in the abundance hierarchy during the second year, when canopy architecture within the community changed and individuals of other species grew tall enough to overtop it. *Plantago* is considered an early-successional herb that is displaced as succession progresses (Van der Putten et al. 2000.) In this example, the ability to negatively affect other species may be a more important determinant of the ability to survive in a multi-species community than resistance to suppression.

Although we excluded seedling and plant recruitment and mortality from the pot experiment, these demographic forces are active in structuring plant communities and are ignored by most competition studies. In many successional communities, light can become a limiting factor, thus contributing to the displacement of relatively low-statured plants, or affecting rates of seedling emergence and early establishment. In our pot competition experiment, where we purposely limited the potential for such diffuse competition by preventing the establishment of non-target plants, we may have inadvertently maintained light at levels greater than would have been available in the intact communities.

Controls on community composition

Within our multi-species community there was a breadth of growth forms that provide a variety of resource utilization mechanisms. However, we should not ignore the influence of niche overlap within our communities. For example, *Dactylis* and *Festuca*, two of our three grass species, are bunchgrasses with similar size and morphologies, and they both grow quickly and produce reproductive structures early in the growing season. The classical competition theory states that species with perfectly overlapping resource requirements cannot coexist indefinitely because of competitive exclusion (MacArthur and Levins 1967; Schoener 1983; Pacala and Tilman 1994). *Dactylis* and *Festuca* have similar morphology and phenology; thus, if *Dactylis* is a better overall competitor (as suggested in our pairwise experiment), we should expect *Festuca* to eventually be excluded from the system. We found that neither *Festuca* nor *Dactylis* were greatly suppressed by each other in our competition

experiment, therefore we assume that they utilize resources differently, or that resources were not limited in our pot experiment. Because we chose species common to existing communities in east Tennessee, and because most of the species that we used in our experiment had different growth forms and physiological pathways, competitive exclusion due to niche overlap in this system may be only exhibited in the form of the quintessential “ghost of competition past” (Connell 1980).

Pairwise assessments of species interactions are capable of detecting positive interactions between plants (Callaway and Walker 1997; Hacker and Bertness 1999). For example, nitrogen-fixing species, such as *Trifolium* and *Lespedeza*, both present in our experiments, could potentially facilitate the growth of neighbors by increasing the availability of soil nitrogen (Hunter and Aarssen 1988; Richardson et al. 2000; Carino and Daehler 2002). However, we did not observe facilitation between either of the legumes in our experiment and any other plant species. It is possible that beneficial associations may develop with time, but we did not observe them within our experimental framework. Further research is needed to isolate the relative roles (if any) of competitive ability, niche overlap, and positive interactions on community development and the trajectory of the communities in this system.

Competition among members of ecological communities, especially plants, is highly localized and thus is dependent on conditions that arise from spatial and temporal heterogeneity in biotic and abiotic factors (Keddy and Shipley 1989). For example, competitive abilities demonstrably shift along environmental gradients, with ramifications for community composition (Keddy and Wisheu 1989; Silvertown and Dale 1991; Gurevitch et al. 1990; Goldberg et al. 1999; Novoplansky and Goldberg 2001; Suding and Goldberg 2001). Given sufficient availability of propagules, community composition may further be affected by stochastic processes, differential abiotic tolerance of constituent species, indirect interactions within and between trophic levels (e.g., Callaway and Walker 1997; Lortie et al. 2004). By planting seedlings of equal size at the same time into experimental plots at a single site, we were able to standardize a number of variables that could ultimately be responsible for controlling species composition in natural ecosystems.

Ultimately, community composition and biodiversity are defined by interactions among species traits and spatiotemporal variation in the availability of resource and species resource-use that drive patterns of species invasion, competition, and coexistence. Keddy (2001) provides detailed descriptions of the many tools and approaches that can be used to investigate species interactions and to determine the contribution of said interactions to community structure.

Finally, extrapolations from pairwise interactions may be limited in their ability to describe competition at the level of the community because individuals in nature often interact with several species simultaneously (e.g., Connell 1983; Schoener 1983). For example, consideration of multiple-species interactions can better account for additive competitive effects, which may disrupt patterns produced by pairwise competition experiments. Thus, our understanding of the structure of multi-species communities may benefit from derivation of competitive interactions from multi-species comparisons, though this will be limited to all but the most simple communities (e.g., Perkins et al. in press).

Conclusions

The pot experiment considering both competitive effect and competitive response of species in pairwise comparisons produced a clear hierarchical ranking of competitive abilities. However, the hierarchical ranking from the pot experiment was not concordant with the relative abundance of the same suite of species growing in community over the course of one or even two growing seasons. This suggests that hierarchies derived from pairwise pot experiments may be insufficient predictors of community composition in intact communities. Other factors held constant, multi-species assemblages may be controlled by higher order interactions or resource limitations internal or external to the community proper; thus, adequate prediction of community composition may require consideration of additive interactions among species coupled with availability of potentially limiting resources.

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