LETTER

Evaluating plant–soil feedback together with competition in a serpentine grassland

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Abstract

Plants can alter biotic and abiotic soil characteristics in ways that feedback to change the performance of that same plant species relative to co-occurring plants. Most evidence for this plant–soil feedback comes from greenhouse studies of potted plants, and consequently, little is known about the importance of feedback in relation to other biological processes known to structure plant communities, such as plant–plant competition. In a field experiment with three C_4 grasses, negative feedback was expressed through reduced survival and shoot biomass when seedlings were planted within existing clumps of conspecifics compared with clumps of heterospecifics. However, the combined effects of feedback and competition were species-specific. Only *Andropogon gerardii* exhibited feedback when competition with the clumps was allowed. For *Sorghastrum nutans*, strong interspecific competition eliminated the feedback expressed in the absence of competition, and *Schizachyrium scoparium* showed no feedback at all. That arbuscular mycorrhizal (AM) fungi may play a role in the feedback was indicated by higher AM root colonization with conspecific plant neighbours. We suggest that feedback and competition should not be viewed as entirely separate processes and that their importance in structuring plant communities cannot be judged in isolation from each other.

INTRODUCTION

A plant species can alter the soil in which it grows in ways that feed back to affect the relative performance of that species compared with other plant species (Reynolds *et al.* 2003; Ehrenfeld *et al.* 2005). This feedback can occur through a variety of abiotic and biotic processes, including changes to the physical, chemical and biogeochemical properties of soils and the community structure of soil microbes and invertebrates (Reynolds *et al.* 2003; Brinkman *et al.* 2005; Ehrenfeld *et al.* 2005). Plant–soil feedback is negative if the performance of that plant species decreases relative to other plant species (Van der Putten *et al.* 1993; Packer & Clay 2000) and positive if the opposite is true (Callaway *et al.* 2004). Changes in relative performance can happen both through direct effects on the species that modified the soil and indirectly through effects on other plant species.

Plant–soil feedback has the potential to influence the species composition (Bever 1994; Klironomos 2002), spatial structure (Packer & Clay 2000) and temporal dynamics (Van der Putten *et al.* 1993; Kardol *et al.* 2006) of plant communities. By increasing the probability that a plant is replaced by an individual of the same species, positive feedback can lead to an increase in the abundance of that species and, potentially, a decrease in species diversity (Klironomos 2002; Reynolds *et al.* 2003) and is one factor contributing to exotic plant invasions (Klironomos 2002; Reinhart *et al.* 2003; Callaway *et al.* 2004). In contrast, negative feedback could either be a stabilizing force maintaining diversity (Bever 2002, 2003) or contribute to successional changes in plant communities (Van der Putten *et al.* 1993; Kardol *et al.* 2006) because it increases the probability that a plant is replaced by an individual of a different species (Reynolds *et al.* 2003; Bonanomi *et al.* 2005a).

Studies of microbial-mediated feedback have been a particularly active area of research (Van der Putten *et al.* 1993; Packer & Clay 2000; Klironomos 2002; Reynolds *et al.* 2003; Callaway *et al.* 2004; Reinhart & Callaway 2006). These microbes may range from pathogens, to potential mutualists, such as mycorrhizal fungi or nitrogen-fixing bacteria, to free-living microbes that alter nutrient cycles (Reynolds *et al.* 2003; Hawkes *et al.* 2005). Their action as agents of feedback depends on some plant specificity on the part of the microbes as well as differences among plant species in how they are affected. Even mutualistic microbes can function in negative feedback if they provide different levels of benefit to different plant species and if they confer the least benefit to the particular species on which they are most prolific (Bever 2002; Klironomos 2002). Arbuscular mycorrhizal (AM) fungi can also act as parasites if the benefits they provide fail to compensate for demands on plant carbon (Johnson *et al.* 1997; Klironomos 2003; Jones & Smith 2004).

The need to evaluate the importance of plant–soil feedback in relation to other ecological factors influencing plant community composition is frequently discussed (Reynolds *et al.* 2003; Bonanomi *et al.* 2005b; Ehrenfeld *et al.* 2005; Kardol *et al.* 2006), but there are few relevant data. The majority of feedback studies have been conducted in the greenhouse in the absence of such important biological processes as service by pollinators and seed dispersers, aboveground and belowground herbivory (Van der Putten 2003) and natural levels of competition (Grace & Tilman 1990; Keddy 2001), which is the focus here. The few outdoor tests of feedback (e.g. De Rooij-Van der Goes *et al.* 1995; Bonanomi *et al.* 2005b) have not included competition as an experimental factor.

Like feedback, competition can be an important stabilizing factor in the maintenance of species diversity. Niche-based models show that species coexistence is promoted when intraspecific competition is stronger than interspecific competition or when a species consumes relatively more of its own limiting resource(s) than do co-occurring species (Chesson 2000). This leads to the prediction that in a stable system, intraspecific competition should reduce plant performance more than interspecific competition, and therefore, we would expect intraspecific competition to exacerbate the effects of any negative feedback.

In this field study, we examined the combined effects of feedback and plant–plant competition on three native C_4 bunch grasses in a serpentine grassland. A previous greenhouse study, without competition, provided evidence that AM fungi contribute to negative feedback in the system (Castelli & Casper 2003). Current conceptual models predict negative feedback in well-established, late successional communities (Bever 2003; Reynolds *et al.* 2003; Ehrenfeld *et al.* 2005) such as this. Thus, we test two specific hypotheses that: (1) negative plant–soil feedback, expressed through lower plant performance in soils previously occupied by conspecifics, occurs in the natural plant community and (2) the added component of intraspecific competition strengthens the performance differences caused by negative feedback.

METHODS

The experiment was conducted in the Nottingham Serpentine Barrens, consisting of prairie and savannah vegetation, located within Nottingham County Park in Chester Co., PA, USA, 39°44′ N, 76°02′ W (120–130 m a.s.l.). The native C_4 bunchgrasses studied here are dominants in the grassland, which is interspersed with stands of *Pinus rigida* Mill. Grassland management and restoration practices, including prescribed burns, are somewhat sporadic, but the areas used in this study have not burned since the 1960s when wildfire suppression was established. The total mean annual precipitation of 115 cm is evenly distributed throughout the year, and temperatures ranging from a mean (low) of −6.9 °C in January to a mean (high) of 30.6 °C in July; Octoraro Lake weather station, 39°48′ N, 76°03′ W (NOAA 2002). The soils are Alfisols, classified as fine-silty or fine-loamy, mostly serpentinic, mesic Typic Hapludalfs or Lithic Hapludalfs, depending on the depth to bedrock (Rabenhorst *et al.* 1982). Serpentine soils are characteristically high in metals such as Fe, Mg, Ni and Cr and low in major plant nutrients and water availability (Brady *et al.* 2005).

The grasses are among the dominant species at the site, where they grow as distinct, monospecific clumps: *Andropogon gerardii* Vitman, *Sorghastrum nutans* L. (Nash) and *Schizachyrium scoparium* (Michx.) Nash. They are also major components of the once extensive, tallgrass prairie of the central USA (Great Plains Flora Association 1986). The most common AM fungal species in the Nottingham soils are *Gigaspora gigantea* (Nicolson & Gerdemann) Gerdemann & Trappe, *Scutellospora calospora* (Nicolson & Gerdemann) Walker & Sanders and several morphotypes in the genus *Glomus*, including *G. etunicatum* Becker & Gerdemann and *G. intraradices* Schenck & Smith (Castelli & Casper 2003).

The experiment involved planting the three target grasses as seedlings into artificial gaps created within large (> 50 cm diameter), naturally occurring clumps of the same three grasses in a complete factorial design, resulting in nine different combinations of target and clump (neighbour) species. One of the two seedlings planted into each clump experienced both belowground and aboveground competition from the clump while competition was prevented for the other.

Spatially, the experiment was set up in 20 separate blocks, widely dispersed throughout the 263 ha park. A block covered an area of roughly 20 × 20 m and encompassed

one replicate of each target species × clump species combination, except that *Sorghastrum* was not found in six blocks. In those blocks, *Sorghastrum* was also omitted as a target species, leaving only the four possible combinations of *Andropogon* and *Schizachyrium* as target and neighbour species. Within a block, clumps of the different grass species were typically interspersed, and those used in the experiment were all at least a meter apart.

Two 12 cm diameter gaps, separated by at least 10 cm, were created in each clump by pounding a pipe into the soil to a depth of 15 cm. The soil was extracted from the hole and all aboveground plant parts, major roots and large rocks discarded. The soil was then homogenized and replaced. In the gap designated as the no competition treatment, the sides of the hole were lined with a cylinder of 30 μm nylon mesh (Cahill 1999) before the soil was replaced; this allows lateral water movement and access by fungal hyphae but excludes neighbour roots. The shoots of the grass clump were held back from this gap using large mesh nylon netting. In the second gap, designated the competition treatment, the holes were not lined before the soil was replaced, and the shoots were allowed to overtop the seedlings.

The seedlings were started in sterile sand in the University of Pennsylvania greenhouse from seed collected within the park the preceding autumn. In early May 2001, when foliage on the established clumps was < 20 cm tall, one 2-week-old seedling of the appropriate species was planted into each gap and watered over the first week to encourage establishment. After 4 months, survival was assessed, and shoots and roots were harvested and dried to constant mass before weighing. Because it was impossible to recover all of the fine roots, only shoot biomass is reported here.

Because AM fungi had shown feedback with these grasses in a prior greenhouse study (Castelli & Casper 2003), root colonization by AM fungi was assessed. Approximately 0.1 g wet mass of roots was collected from five randomly selected replicates of each neighbour species × target species combination in the no competition treatment only. The root pieces were cleared in 10% KOH for 7 days and stained in 0.1% Trypan blue in lactoglycerol (Phillips & Hayman 1970). Colonization was measured under a dissecting microscope using the gridline intersect method (Giovannetti & Mosse 1980).

Shoot biomass (ln transformed) was analysed as a function of target plant species, neighbour identity (conspecific or heterospecific) and competition treatment (all treated as fixed effects) using a generalized linear mixed model ANOVA (PROC MIXED) in SAS (v9.1) with block as a random factor. Target species were treated as a fixed effect; because of our ongoing interest in these particular, common grasses (Castelli & Casper 2003) they were not chosen at random from among the species available. The same model was applied to survival using PROC GLIMMIX with a binomial error distribution (SAS 9.1). Root colonization (arcsine transformed) was examined for each target species separately as a function of neighbour identity and block using ANOVA (PROC MIXED). Planned comparisons among competition treatments and neighbour identity combinations were made using differences in least squares mean.

RESULTS

Consistent with negative plant–soil feedback, shoot biomass was lower in the presence of conspecific neighbours compared with heterospecific neighbours ($F_{1,197} = 20.71$, $P < 0.001$). Shoot biomass was also reduced by competition ($F_{1,197} = 7.47$, $P < 0.01$) and differed among target plant species ($F_{2,197} = 4.86$, $P < 0.01$).

Although there were no significant two-way or three-way interactions in the overall ANOVA ($P > 0.10$), planned comparisons reveal that the three species responded quite differently to the competition treatments and neighbour identity. For *Sorghastrum*, shoot biomass was much lower in the presence of conspecific neighbours but only in the absence of competition (Fig. 1). For *Andropogon*, shoot biomass was lower with conspecific neighbours and unaffected by competition. For *Schizachyrium*, there was no significant effect of neighbour identity within either competition treatment, although shoot biomass was still greater in heterospecific soils without competition than with competition in either soil type. None of the three species showed reduced shoot biomass in conspecific soils with intraspecific competition compared to conspecific soils without competition.

Again, consistent with negative plant–soil feedback, survival was lower with conspecific neighbours than with heterospecific neighbours (Fig. 2), across all target plant species ($F_{1,289} = 34.10$, $P < 0.001$) but was unaffected by competition treatment. Survival also differed among target species ($F_{2,289} = 4.54$, $P < 0.02$), with a significant interaction between the identity of the target species and whether neighbours were conspecific or heterospecific ($F_{2,289} = 9.49$, $P < 0.001$). The feedback effect on survival was very strong for *Andropogon* and non-significant for the other two species.

Root colonization data gathered for plants in the no competition treatment (Fig. 3) show that root colonization was higher with conspecific neighbours for all three target plant species: *Sorghastrum* ($F_{2,5} = 6.029$; $P < 0.05$), *Andropogon* ($F_{2,5} = 12.67$; $P < 0.01$) and *Schizachyrium* ($F_{2,5} = 5.90$; $P < 0.05$).

DISCUSSION

Collectively, the three grass species showed negative plant–soil feedback in a field setting, but when each is examined separately, there are large differences among species in the
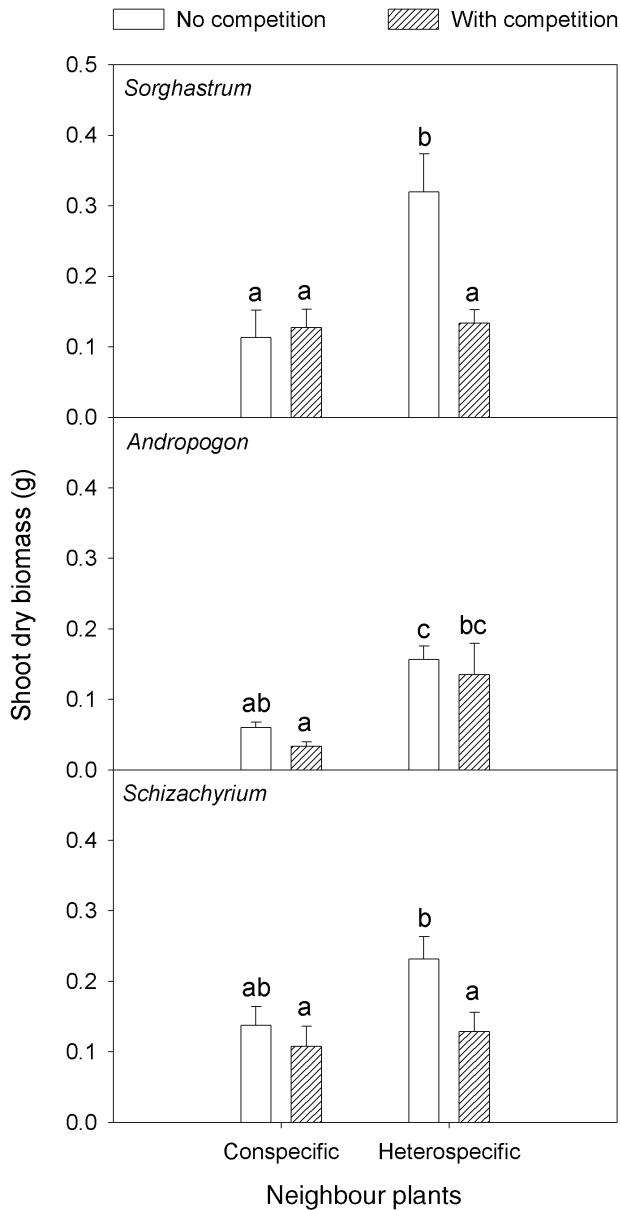
Figure 1 Biomass for seedlings grown with conspecific vs. heterospecific neighbours for each of the three target species, with and without competition (+SEM). Planned comparisons were made within species, with different letters indicating significant differences at the $P < 0.05$ level.

Figure 2 Survival data with conspecific vs. heterospecific neighbours and with and without competition for each of the target species. Letters indicate significant differences among treatment combinations for *Andropogon* as shown in Fig. 1. There were no differences among treatment combinations for *Sorghastrum* and *Schizachyrium*.

strength of the feedback and in the combined effects of feedback and competition from neighbours. Only *Andropogon* exhibited strong negative feedback that was unchanged by competition, expressed as both smaller shoot biomass and much reduced survival in soils previously occupied by *Andropogon*.

That the success of both *Sorghastrum* and *Schizachyrium* was independent of neighbour identity in the presence of
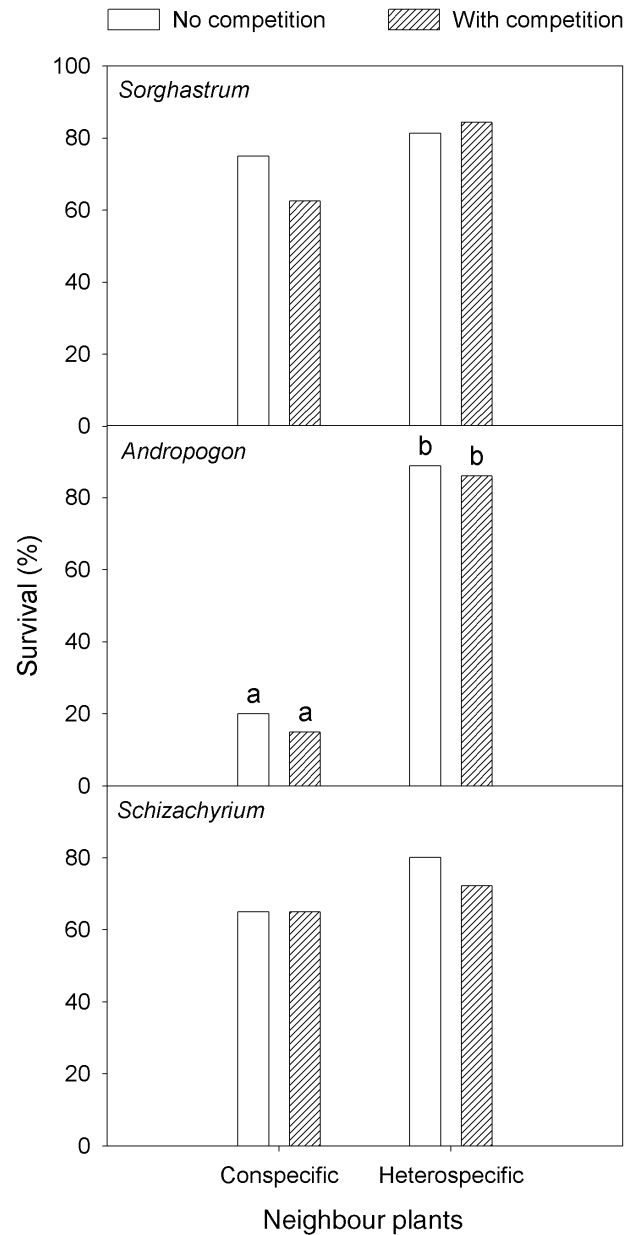
competition was an important result. First, it does not support our hypothesis that intraspecific competition enhances negative feedback. Second, for the particular niche dimensions compared here – conspecific soils with intraspecific competition vs. heterospecific soils with interspecific competition – neither species appears to
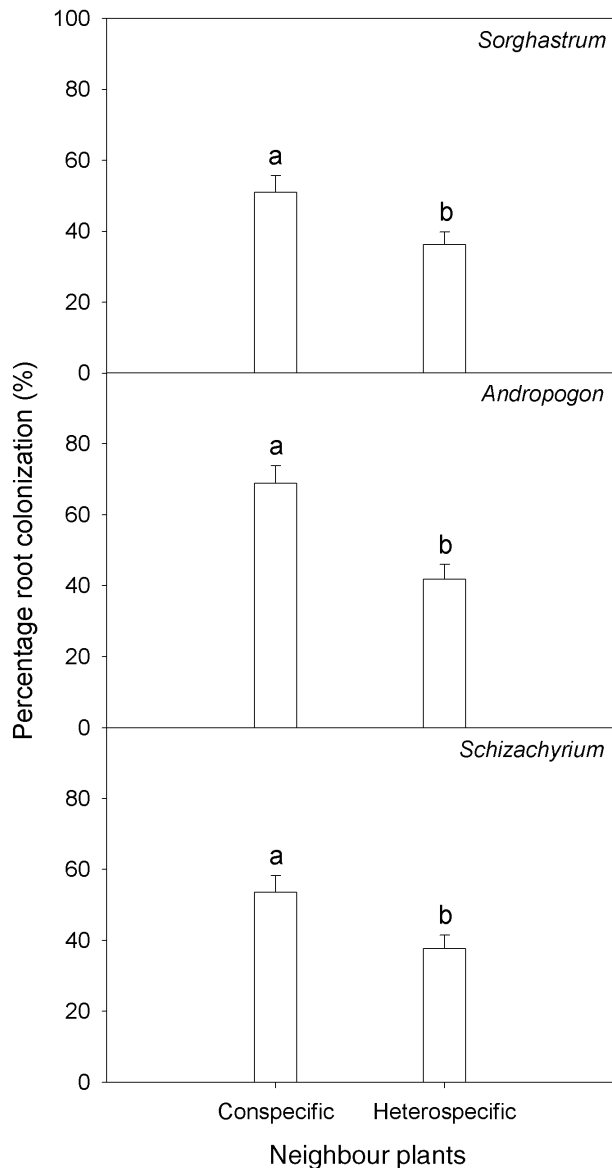
Figure 3 Percentage arbuscular mycorrhizal fungal root colonization for target plants in the no competition treatment (+SEM). Letters indicate significant differences as shown in Fig. 1.

specialize in niche space. This means that neutral models (Bell 2000; Hubbell 2001) could explain their coexistence as well as competition models. In the case of *Sorghastrum*, the lack of niche differentiation occurred despite strong but opposing effects of negative feedback and interspecific competition.

Our field experiment incorporating both feedback and competition from established plants well illustrates the difficulty of extrapolating from pot experiments of feedback to natural communities and of generalizing to other grasslands. The plant–soil feedback previously demonstrated for *Sorghastrum* without competition in the greenhouse

(Castelli & Casper 2003) does not predict the performance of *Sorghastrum* with competition in the field. Additionally, in the greenhouse, *Andropogon* exhibited negative feedback in field-collected Nottingham soils only if nutrients are added and positive feedback in soils collected from a different serpentine barren (Gustafson & Casper 2004), indicating entirely different dynamics between the plants and soils.

The fact that feedback was expressed through seedling mortality, especially for *Andropogon*, suggests more attention should be paid to soil effects on the early life stages of plants as has been argued for studies of competition (Aarssen & Keogh 2002). Host-specific soil pathogens can have severe consequences for seedlings (Packer & Clay 2000), and seedling emergence and performance can sometimes respond negatively to AM fungi even though those fungi benefit adult plants (Koide 1985; Harnett *et al.* 1994). The presence of AM fungi can also differentially affect seedling responses to older interspecific and intraspecific competitors (Moora & Zobel 1996). Studies employing seed additions to natural plant communities (Zobel *et al.* 2000), where mortality is always likely to be greater than in the more benign greenhouse environment, could better illuminate the extent that feedback operates on early life cycle stages and influences seedling establishment (Bonanomi *et al.* 2005b).

Arbuscular mycorrhizal fungal colonization in these grasses is often highest in particular soil treatments or plant–fungal combinations that produce the least plant growth (Castelli & Casper 2003; Gustafson & Casper 2004), just as it was here for *Andropogon* and *Sorghastrum* in conspecific soils. This implicates the fungi as an agent of feedback both in the field and when plants are isolated in pots (Castelli & Casper 2003; Gustafson & Casper 2004). Further study would be needed to understand the specific role of the fungi, although the patterns of infectivity suggest they might simply present more of a carbon drain in conspecific soils.

Our current knowledge about the combined effects of competition and plant–soil feedback is based on a few greenhouse studies framed in the context of how feedback influences the competitive ability of even-aged plants. Those studies show negative feedback (Van der Putten & Peters 1997) and positive feedback (Reinhart & Callaway 2006) can influence the outcome of interspecific competition. Similarly, negative feedback enhanced density-dependent, intraspecific competition in greenhouse monocultures of black cherry seedlings (Reinhart *et al.* 2003). In contrast, soil origin did not affect competition between two species from a North Carolina grassland (Bever 1994). None of these experiments ask how competition from established plants might reduce or exacerbate the expression of feedback.

It may not be possible to fully separate the effects of feedback and competition on plant performance. In our no

competition treatment, the extraradical mycorrhizal network might have accessed the target seedlings through the mesh fabric and mediated resource competition with neighbours (Giovannetti *et al.* 2004; Simard & Durall 2004), thereby contributing to the smaller shoot biomass in conspecific soils. On the other hand, feedback may take place when competition occurs through root–root interactions. Neighbours can affect the AM fungal community infecting a plant (Mummey *et al.* 2005; Hawkes *et al.* 2006) and alter soil properties through root exudates and effects on other soil microbes (Schenk 2006), beyond reducing nutrients and water (Casper & Jackson 1997). Thus, apparent competition may be a combination of competition for resources and other feedback processes (Schenk 2006). In this case, feedback is happening in real time and not through legacy effects from a previous soil occupant. In fact, for all three species studied here, intraspecific competition could be largely an expression of feedback as the combination of intraspecific competition and conspecific soils did not reduce shoot biomass over conspecific soils alone.

Therefore, we think that feedback and competition cannot be viewed as strictly separate forces and that their importance cannot be evaluated in isolation from each other. Competition studies should incorporate the full potential for feedback, and studies examining feedback should be conducted in the presence of naturally occurring, competing neighbours, which could influence seedling establishment. This calls for field experiments that control for both previous soil occupants and current neighbour identity. Researchers should be prepared for species-specific responses to these two factors (Bonanomi *et al.* 2005b; Bezemer *et al.* 2006; Schenk 2006), just as we found here.

For this particular system, the next logical experiment would combine soils vacated by conspecifics with heterospecific neighbours and vice versa. Further work is also needed to determine the source(s) of the feedback. While AM fungi may play a role, that possibility does not preclude the action of other biological agents such as soil pathogens or invertebrates or changes to abiotic soil components.

ACKNOWLEDGEMENTS

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