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FEEDBACK BETWEEN PLANTS AND THEIR SOIL COMMUNITIES IN AN OLD FIELD COMMUNITY[1]

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Abstract. The nature of the interaction between plants and their soil community was investigated by testing for differential responses of four old-field perennial plant species to inocula derived from soil communities that had been grown with ("cultured by") one of these four plant species. The differentiation of the soil communities was evident in measurements of plant survival, phenology, growth, and root–shoot ratios. Effects on survival and growth suggest negative feedbacks between these species and the soil communities that they culture. Survival rates of *Krigia dandelion* were significantly reduced when grown with their "own" soil community. Considered as a whole, the three other species (all grasses) had significantly lower growth and root–shoot ratios when grown with soil communities started with their own inocula compared to soil communities started with the inocula of other species. However, the significance of this effect on growth rate and root–shoot ratios was due primarily to the pairwise comparison of *Anthoxanthum odoratum* and *Danthonia spicata* and of *Anthoxanthum* and *Panicum sphaerocarpon,* respectively. Pairwise comparisons of *Danthonia* and *Panicum* do not suggest differential responses to each other's soils in growth rate or root–shoot ratios nor do soil communities appear to affect the relative competitive ability of these two species. While the components of the soil community responsible for these effects have not been identified, similar although less pronounced patterns were observed in experiments using inocula consisting of washed live root segments as compared to experiments using whole soil as inoculum, suggesting that root pathogens are one important agent.

Key words: feedback; grasses; negative feedback; old field; plant community dynamics; plant–soil community interaction; soil community; soil microbial ecology; soil pathogens; vesicular-arbuscular mycorrhizae.

INTRODUCTION

Interactions between plants and soil organisms have long been recognized for their importance in plant mineral nutrition and nutrient cycling (Marschner 1986, Richards 1987, Allen 1991). Historically, experimental work on plant–soil organism interactions has focussed largely on the effect of specific soil organisms on plant growth (examples reviewed in Hayman 1987, Turkington et al. 1988). However, little is known about the consequences of changes in the species or genotypic composition of soil organisms on the dynamics of plant populations, or vice versa.

Recently, several investigations have demonstrated the integral role of the soil community in the population and community ecology of plants. The presence of mycorrhizal fungi has been found to significantly influence plant competitive ability (reviewed in Allen and Allen 1990 and Brundrett 1991), in some cases reversing the outcome of plant competition (Sieverding and Leihner 1984, Allen and Allen 1990). Furthermore, the presence of mycorrhizal fungi has been demonstrated to change the relative abundance of plants in artificial communities (Grime et al. 1987, Allen and Allen 1990) and in secondary succession in the field (Medve 1984). Chanway et al. (1989) suggested that *Rhizobium* may mediate an apparent coevolutionary response between the legume *Trifolium repens* and a grass, *Lolium perenne.* Further investigations (Chanway et al. 1990, Turkington 1992) suggested that *Lolium perenne* and another grass, *Holcus lanatus,* influence the growth of *T. repens* by changing the composition of the soil community.

These studies demonstrate that interactions between plant species may be mediated by the soil community, a suggestion that has frequently been considered by agriculturalists (Bruehl 1987) but rarely investigated explicitly in an ecological context (Turkington et al. 1988, Chanway et al. 1991). The study of the interaction between plants and their soil communities has been carried out somewhat idiosyncratically and has lacked a hypothesis-generating theoretical framework. This is in contrast with the bulk of recent work on plant competition (Austin 1986, Grace and Tilman 1990), which has focussed on testing hypotheses generated by the competing theoretical frameworks of Grime (1979) and Tilman (1982).

The concept of ecological and genetical feedback may provide a fruitful framework with which to investigate the interaction between plants and their soil community (Bever 1992). This feedback involves two steps:

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the plant or population of plants must change the composition of the soil community and this change must then in turn affect the rate of growth of the plant or population. It is well documented that plants can affect the density and composition of the soil community (Turkington et al. 1988, Chanway et al. 1991). For example, the density (Howeler et al. 1987, Harinikumar and Bagyaraj 1988) and composition (Schenck and Kinloch 1980, Dodd et al. 1990, Johnson et al. 1991) of the vesicular-arbuscular mycorrhizal (VAM) fungal community has been found to be altered by crop rotations as well as by the immediate vicinity of a particular plant species in an old field (McGonigle and Fitter 1990, Johnson et al. 1992*a*, Sanders and Fitter 1992). Furthermore, as described in the preceding paragraphs, the soil community has been shown to affect the plant community (Turkington et al. 1988, Allen and Allen 1990, Brundrett 1991, Chanway et al. 1991). Thus, through its effect on the composition of the soil community, a given species or genotype of plant may either increase its own growth rate relative to other types of plants (i.e., positive feedback) or decrease its own growth rate (i.e., negative feedback).

The nature of the feedback on plant growth rates through the soil community is not well characterized and there is evidence for both positive and negative feedback. Mytton (1975) demonstrated positive feedback between cultivars of white clover and the composition of *Rhizobium* genotypes in experimental communities. Such positive feedback between legumes and their nitrogen-fixing bacteria is supported by the observation that locally coexisting bacterial genotypes are more effective at promoting plant growth than noncoexisting genotypes (Nutman and Read 1952, Robinson 1969, Lie et al. 1987, Chanway et al. 1988). However, work on agricultural systems has also demonstrated negative feedback in plant growth through the soil community. For example, Olsson and Gerhardson (1992) demonstrated that repeated cropping with barley changed the soil community in a manner that substantially decreased the growth rate of barley relative to wheat or oats. Similarly, Kollmorgen et al. (1985) found that pre-cropping with any plant species besides wheat would reduce the density of *Gaeumannomyces graminis,* the causative agent of "take-all" disease in wheat. Furthermore, Johnson et al. (1992*b*) found a positive correlation between changes in the composition of arbuscular mycorrhizal fungi due to repeated cropping of corn and soybeans and the decreased productivity of these crops. In fact, the frequency with which crop rotation is practiced is testimony to the importance of negative feedback in agricultural systems (Shipton 1977, Cook 1981). In a unique case where feedback through the soil community was tested in a natural community, strong differential effects were observed which suggest that changes in the soil community are responsible for the succession of grass species in coastal dunes (Van der Putten et al. 1993).

In this study, the nature of feedback processes between four old-field plant species and their soil communities was evaluated using experimental microcosms. Specifically, replicates of an experimental soil community were allowed to differentiate over a period of 15 mo in response to association with each of these four plant species. The response of the four plant species was evaluated when grown individually in a common sterile soil inoculated with either roots or whole soil from the four differentiated soil communities. Given that plants grown in competition often provide a more sensitive test of differential responses to soil parameters (e.g., nutrient status: Snaydon 1962, McGraw and Chapin 1989; and mycorrhizal fungi: Allen and Allen 1990), a competition experiment using two of the four plant species and soil cultures from the previous experiment is also reported.

Methods

Study system

The plants and soil used in these experiments were obtained from an old field in Durham, North Carolina. The field has been mowed annually for nearly 50 yr. The site has been the subject of intensive investigation over the last 20 yr (Fowler 1978, Alexander 1984, Antonovics et al. 1988, Moloney 1988, Kelley 1989, Ronsheim 1992). The plant community in the field is diverse and lacks any distinctly dominant species. The soil is a sandy loam of the White Store series and consists of a 10–20 cm deep sandy layer overlying a sand/clay hardpan (Fowler 1978, Fowler and Antonovics 1981).

Three grasses, *Anthoxanthum odoratum* L., *Danthonia spicata* (L.) Beauv., and *Panicum sphaerocarpon* Ell., and a composite, *Krigia dandelion* (L.) Nutt., were used in this study. These species will hereafter be referred to by their generic name alone. These species were chosen because of the ease with which they could be cloned. The grasses can be cloned by separating plants into component tillers and *Krigia* can be cloned by separating tubers. Furthermore, populations of *Anthoxanthum, Danthonia,* and *Panicum* from this field have been used in a number of previous studies (*Anthoxanthum*: Antonovics and Ellstrand 1984, 1985, Ellstrand and Antonovics 1985, Schmitt and Antonovics 1986, Kelley et al. 1988, Kelley 1989; *Danthonia*: Clay 1982, 1983; *Panicum*: Felber and Antonovics, *unpublished data*).

The experimental soil communities: establishment of "culture pots"

Replicates of the four plant species were grown in separate pots of a mixture of fresh and autoclaved soil. The soil communities were initially similar and were allowed to differentiate while the plants were grown in the greenhouse during the next 15 mo. Tillers from each of the three grass species were collected from a

single individual of that species in the field in December of 1988. Single genotypes of each species were used to maximize the probability of detecting effects by decreasing the error. However, such sampling limits generalization of the results to the level of the population or species. *Krigia* tubers were collected by separating them from soil collected from a 200-cm^2 region of the field and therefore are likely to be mixtures of several clones. The tillers and tubers were cleaned of microbial contaminants by removing all roots, washing, and then surface sterilizing by immersion in 5% solution of chlorox (itself 5.25% aqueous NaOCl) for 10 min. For each species, three or four tillers (or tubers) were planted into each of four replicate 15 cm diameter pots. The pots were filled with a mixture of two-thirds chopped, sifted, and autoclaved soil and one-third fresh homogenized soil (including chopped roots) from the field site. The plants were kept in the greenhouse for 15 mo and were watered, but not fertilized, as needed.

Experiments 1 and 2: tests of differentiation of soil and root communities

After 15 mo, I tested for differentiation of the soil community cultured by the four plant species using whole soil as inocula and washed roots as inocula. For both types of inocula, the test experiments were full factorial designs with the four plant species grown in five treatments: the inocula from the four plant species and a sterile control. Plants grown in their own soil or in the sterile control were replicated nine times; plants grown in other soil communities were replicated six times. The greater replication of plants in their own soil communities allowed greater confidence in the contrasts of plant growth in their own soil against that in other soils.

The tillers, tubers, roots, and soil from the culture pots were used in these test experiments. Tubers of *Krigia* were separated from the soil, the grasses were separated into individual tillers, and all roots were clipped off. The tillers and tubers were then washed and surface sterilized by immersion in a 5% Chlorox solution for 10 min to decrease the microbial carryover into the test experiment. The soil and roots from the replicates of each species were thoroughly mixed by hand and divided into two equal portions for preparation of the soil and root inocula.

Soil inoculum for each plant species was prepared by dicing the roots and crumbling the soil until it passed through a 1.16-cm mesh. The soil was then mixed and divided into two portions: one stored at 4°C (for <1 wk) for use as living inoculum and one autoclaved for use as pasteurized inoculum. The effect of differences between mineral soils was minimized by inoculating treatments with small quantities of soil inoculum (1 part inoculum to 30 parts sterile background mix) and mixing equal quantities of all four soil inocula into each pot such that treatment pots received three pasteurized inocula and one fresh inoculum and the control treatment received all pasteurized inocula. The background soil was made up of a homogenized mixture of two parts diced, sieved, and autoclaved soil from the field and one part autoclaved sand. While all methods of soil pasteurization alter the physical properties of the soil, this soil does not appear to be severely changed by autoclaving. Analyses of this soil before and after the pasteurization treatment did not reveal significant changes in its mineral content. Furthermore, another perennial from this field, *Allium vineale,* was found to respond similarly to soil pasteurized by autoclaving or irradiation (Bever 1992). Populations of *Allium* were also found to grow best with autoclaved portions of their local soil rather than other soils, demonstrating that this pasteurization process does not change the soil in such a manner that local adaptation is disguised (Bever 1992).

The comparison of root inocula was designed to isolate the effect of vesicular-arbuscular mycorrhizal fungi, a component of the soil community known to exert large effects on plant growth (Brundrett 1991). Roots were removed from the soil by passing the soil–root mixture through 58-mm mesh. The root inoculum of each plant species was then prepared by washing the remaining soil from the roots with water and cutting the roots into segments of <1 cm. These roots were not surface sterilized as in Meredith and Anderson (1992). A portion of each root inoculum was autoclaved and was used to make the physical effect of the roots consistent across the treatments, as described for the soil inocula. The bacterial community in this experiment was homogenized by inoculating the autoclaved background mix with a common bacterial inoculum. This inoculum was made by mixing the rinse water from the four root types and then passing this slurry through a 35-μm mesh to remove spores of mycorrhizal fungi. This method has been found to give an inoculum of the major components of the soil community exclusive of mycorrhizal fungi (Ames et al. 1987).

The surface-sterilized tillers and tubers for these two experiments were weighed and planted into 10-cm square pots on 14 and 15 March 1990. The pots were placed in three randomized blocks arranged to minimize the error due to a suspected gradient of moisture and temperature in the greenhouse. The soil inocula experiment abutted the root inocula experiment on the same greenhouse bench. The plants were watered as needed, with care taken to minimize the splashing of soil between pots.

Plants began flowering on 4 April and inflorescences were collected from all flowering plants approximately every 10 d until the plants were harvested during the 1st wk of August 1990. A portion of the root systems of a subsample of the plants in each treatment was preserved in a 5% formalin, 70% ethanol solution for microscopic examination. These roots were cleared in KOH and stained in trypan blue as described in Koske

and Gemma (1989) and examined for presence of mycorrhizal fungal infection.

The remaining roots, live shoots, and dead shoots of each plant, along with the previously harvested inflorescences, were dried at 70°C to constant mass before being weighed. For the plants with sampled root systems, the total dry root mass was calculated from the total wet mass, wet mass after sampling, and dry mass after sampling.

Data analysis.—Survival of the plants to the end of the experiment was analyzed using chi-square tests. *Krigia* suffered high mortality and was therefore not included in analyses of plant growth. For the grass species, the effect of plant species, inoculum, and the species × inoculum interaction on total inflorescence production, plant biomass, and root–shoot ratios were analyzed with analyses of covariance using the general linear models procedure of SAS (SAS Institute 1990). Several individuals of grasses that died back near the experiment's end because they inadvertently did not receive a watering treatment were outliers and were therefore excluded from the analyses of plant mass and root–shoot ratios, although the results were not substantially affected by their exclusion.

Inflorescence biomasses were summed monthly and the values were log transformed ($\log[1 + x]$) to increase the homogeneity of variance. However, these efforts did not adequately improve the nonhomogeneity and the nonnormality of variance because of the large numbers of zeros in the data set. Nevertheless, the data were analyzed using the parametric repeated-measures profile analysis (Simms and Burdick 1988) because of the lack of any good nonparametric alternative. Although the F tests from these analyses are unbiased, because we do not know the appropriate weighting for the variances, the tests are not the minimum variance unbiased estimates and thus significance values from these analyses should be regarded as approximate. The measures of plant biomass and root–shoot ratio adequately met the parametric assumptions and were analyzed using an analysis of covariance. Initial fresh biomass was used as a covariate in all analyses.

Positive or negative feedback was detected using "home vs. away" or "leading diagonal" (Turkington and Harper 1979) contrasts. The three-species "home vs. away" contrast was constructed by subtracting the average measure of plant types grown with inocula derived from other types of plants (away) from the average measure of plant types grown with inocula derived from their own type of plants (home). The three-species "home vs. away" contrast was partitioned into three pairwise contrasts (Bever 1992), the overall significance of which was tested using a three-degrees-of-freedom (3 df) contrast. If this 3 df was found significant, individual pairwise home vs. away contrasts were then tested with the significance values adjusted for multiple comparisons by the Dunn-Sidák method (Sokal and Rohlf 1981).

The overall effect of live soil was tested by contrasting the average measure with live soil inocula against the measure with sterile inoculum. Differential responses of the grasses to sterile soil were also examined with contrasts. Since difference between specific pairs of species was not of interest a priori, the general significance of the species × sterility interaction was tested with a conservative F test constructed from the sums of squares of only the largest contrast of the differential response of two species to live soil as the treatment sums of squares with 2 degrees of freedom (Scheffé 1959).

Experiment 3: competition between Danthonia *and* Panicum

To test whether competitive ability is influenced by the soil community, *Danthonia* and *Panicum* were grown in a full factorial experiment with three competition treatments (one tiller per pot, two tillers of the same species per pot, and two tillers of different species per pot) and three soil inocula (live soil from *Danthonia* and from *Panicum,* and a sterile control). The two tillers were planted in opposite corners of the 10-cm pots separated by 5 cm. The tillers were derived, prepared, and weighed as described above. The soil inocula and background soil were also prepared as described above with the exception that 1 part inoculum was mixed with 50 parts background soil. The experiment was planted on 3 April 1990. Plants began to flower on 25 April and inflorescences were collected approximately every 10 d until plants were harvested during the last week of August 1990. Only shoots were harvested because of the difficulty of separating the roots when two plants were grown together.

Data analysis.—The variance of shoot mass was significantly greater between plants within pots containing two plants of the same species than among these pots, as tested by the "folded form F statistic" in the TTEST procedure of SAS (1987). Therefore, averaged values for the two plants were used in further analyses. The variance of live shoot mass was not significantly different among the three competition treatments of each species after removing the effect of initial mass by regression. The experiment was analyzed using a full factorial analysis of covariance (two levels of species, three levels of competition, and three levels of inoculum, with initial mass as a covariate).

The significance of intraspecific and interspecific competition, overyielding, and differences in competitive ability were tested as linear hypotheses using contrast statements. Overyielding and competitive ability are often measured as ratios or sums of ratios (relative yield total and yield suppression ratio, respectively; Aarssen 1983), which are not amenable to analysis using linear models (Vandermeer 1989). In this study, overyielding was tested as the difference in plant size with interspecific competition and with intraspecific competition (Bever 1992). Difference in the competi-

tive ability of the two species was tested by contrasting the difference in growth with interspecific and intraspecific competition of the two species. The presence of intraspecific competition was tested by contrasting growth in the absence of competition against growth with intraspecific competition (Bever 1992). Of particular interest was whether the estimate of competitive ability depended on the soil community.

Results

Experiment 1: comparison of soil inocula

There was high mortality of *Krigia* in this experiment (50%). In fact, *Krigia* were significantly more likely to die when planted with their own soil inoculum than with inocula from soil of the other species ($P < 0.04$, $\chi_1^2 = 10.57$, Fig. 1). Of the grasses, only one individual (a *Danthonia* in its own soil community) died during this experiment.

Total inflorescence biomass of the grasses differed significantly among species ($P < 0.05$, $F_{2,65} = 3.33$) but was unaffected by inoculum or the species × inoculum interaction. This was also true of the slopes of inflorescence biomass over time as tested by contrasting the first-order coefficients. However, the species × inoculum interaction significantly influenced the curvature of the profiles as tested using the second-order coefficients ($P < 0.03$, $F_{8,65} = 2.33$). The significance of this interaction was due largely to the differential response of each species to its own soil community vs. all other soil communities. Inflorescence production of grasses grown with their own inoculum declined in May relative to production when grown with other inocula but was increased in April and June (Fig. 2). This "home vs. away" effect was significant for the grasses overall ($P < 0.001$, $F_{1,65} = 11.99$) and for the pairwise comparison of *Anthoxanthum* and *Danthonia* ($P < 0.02$, $F_{1,65} = 8.74$); however, note that the values must be used as approximations because of the nonhomogeneity of variance. The absence of a difference in overall inflorescence production is not surprising because the

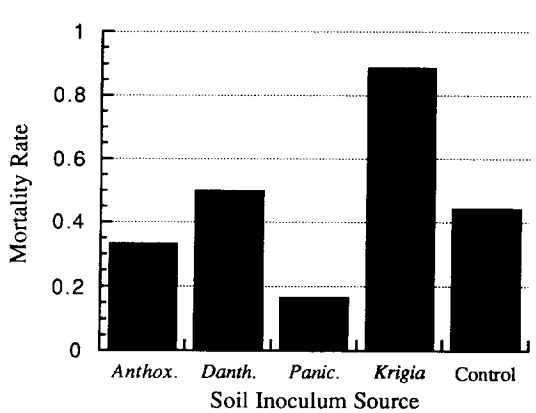

FIG. 1. Mortality rates of *Krigia dandelion* when grown with soil inocula from cultures of different plant species.

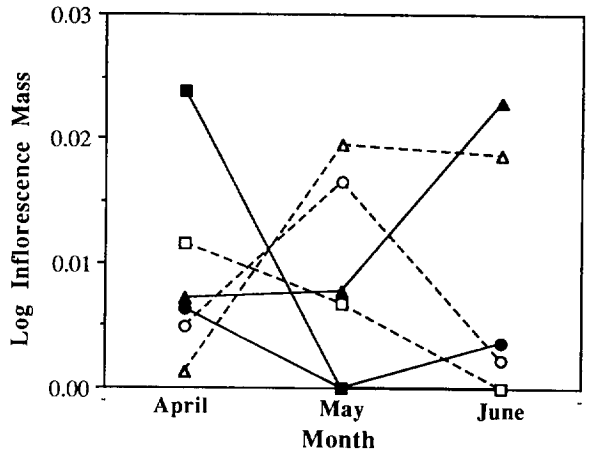

FIG. 2. Profiles of inflorescence production of the three grasses in their own soil inocula and the average of the other grass soil inocula. Profiles of the log of the inflorescence production of *Anthoxanthum, Danthonia,* and *Panicum* over a 3-mo period are represented by squares, circles, and triangles, respectively. Production in their own soil inocula and the average production in the other two grass soil inocula are represented by the solid and dashed line, respectively. Each point is a total of all inflorescences produced that month.

propensity of the tillers to flower is determined prior to the planting of the experiment. The delay in flowering of the grasses when grown with their own soil inocula reflects their altered, possibly weakened, physiological state.

Both plant biomass and root–shoot ratio were significantly affected by the inoculum and the species × inoculum interaction (Table 1). The plants were larger and had significantly higher root–shoot ratios when grown with sterile inoculum vs. live inocula (Table 1, Fig. 3). Furthermore, the effect of living soil on the root-to-shoot ratios differed among the three species ($P < 0.025$), particularly between *Danthonia* and *Panicum* (Fig. 3). In the "home vs. away" contrasts, the grasses were significantly smaller when grown with their own soil community than with other soil communities. This was true for the grasses overall ($P < 0.03$), for the pairwise comparisons of grasses in general, and for the pairwise comparison of *Anthoxanthum* and *Danthonia* in particular ($P < 0.01$) (Table 1, Fig. 4). The three grasses overall and the pairwise comparisons in general also had lower root–shoot ratios when grown with their own soil community than when grown with other soil communities ($P < 0.002$); the significance of these comparisons is due largely to the highly significant pairwise contrast of *Anthoxanthum* and *Panicum* ($P < 0.0004$) (Table 1, Fig. 4).

Microscopic examination of the roots revealed that roots from plants inoculated with live inoculum were all infected with mycorrhizal fungi while 90% of the sterile controls were free of mycorrhizal fungal infection at the end of the experiment. At harvest, the roots of *Danthonia* and *Panicum* that were inoculated with

TABLE 1. Analyses of covariance of plant masses and root–shoot ratios from treatments using soil inocula (Experiment 1).*

Source of variation	df	Plant masses		Root–shoot ratios	
		ss	*P*	ss	*P*
Block	2	0.144	NS	0.142	NS
Initial mass	1	0.552	0.06	0.201	0.04
Species	2	20.366	0.0001	19.130	0.0001
Inoculum	4	3.863	0.0002	4.756	0.0001
Species × Inoculum	8	3.589	0.006	3.858	0.0001
Error	88	13.504		3.985	
		Contrasts			
Effect of live soil	1	0.601	0.05	2.618	0.0001
Species × Live soil†	2	0.729	0.05	0.355	0.025
		Home vs. away‡			
Three species	1	0.698	0.03	0.442	0.002
Pairwise overall	3	2.914	0.004	2.304	0.0001
Anthox. and *Danth.*	1	1.464	0.01	0.000	NS
Anthox. and *Panic.*	1	0.606	NS	2.133	0.0004
Danth. and *Panic.*	1	0.061	NS	0.004	NS

* All tests were performed using the Type three sums of squares (ss) from SAS (SAS Institute 1990). Initial mass was used as a covariate. The significance levels of the pairwise "home vs. away" contrasts have been adjusted for multiple comparisons using the Dunn-Sidak method (Sokal and Rohlf 1981). Plants that died back from lack of water near the experiments' completion were excluded from the analyses. However, analyses including these plants gave the same conclusions.

† This effect was tested conservatively using an *F* statistic constructed with the ss from the most significant pairwise contrast (*Anthoxanthum* vs. *Danthonia* and *Danthonia* vs. *Panicum* for plant masses and root–shoot ratios, respectively) as the treatment ss.

‡ Comparison of plants grown in soil inoculated with the soil community developed in the root environment of the same plant genotype, vs. plants grown in soil inoculated with the soil community developed around the roots of a different species.

living *Danthonia* and *Panicum* soil were visibly different from roots of *Danthonia* and *Panicum* from other inoculation treatments. Sections of roots of *Danthonia* and *Panicum* grown with soil inoculated with live soil from *Danthonia* and *Panicum* were not white to tan-colored, as were the roots from other treatments, but ranged from brown to translucent and easily disintegrated upon washing—apparently from necrosis. Microscopic examination of the stained roots showed evidence of a diversity of structures from saprophytic or pathogenic fungi, including oospores, hyphae of microdocium, and hyphae of other nonmycorrhizal fungi, which were common when *Danthonia* and *Panicum* were grown in their own or each other's soils but much less so when these plants were grown with other treatments or in other plant species.

Experiment 2: comparison of root inocula

As in the previous experiment, *Krigia* experienced high mortality (50%). A greater proportion of the grasses, particularly *Danthonia*, died or did not grow in this experiment than in the previous one. However, in neither case did the distribution of mortality with respect to inoculum differ significantly from that expected by chance.

As in the previous experiment, the species differed in total inflorescence production ($P < 0.007$, $F_{2,68} = 5.47$), but overall inflorescence biomass was not affected by inocula. However, inoculum treatments did affect flowering phenology. Inflorescence production declined with time significantly more quickly in treatments with sterile roots than in treatments with live roots ($P < 0.007$, $F_{1,68} = 7.78$; Fig. 5). Furthermore, the effect of living roots on the curvature of inflorescence production was species dependent ($P < 0.01$, $F_{2,68} = 9.71$); between April and May, the inflorescence production of *Anthoxanthum* in pots inoculated with sterile roots declined sharply while that of *Panicum* increased (Fig. 5). There was no evidence from analyses of profiles of inflorescence production that the grasses responded differently to the various live root inocula.

As in Experiment 1, root–shoot ratios were significantly larger in plants grown with sterile roots than in plants grown with live roots ($P < 0.02$); however, overall plant size was not significantly affected (Table 2, Fig. 6). The three grasses were significantly smaller when grown with root inocula from their own species than from other species, however the pairwise comparisons were not significant (Table 2, Fig. 7a). Furthermore, *Anthoxanthum* and *Panicum* had significantly lower root–shoot ratios when grown with their own root inocula than when grown with each other's root inocula (Table 2, Fig. 7b). The patterns in this experiment were similar to, but less significant than, those observed in the experiment using whole soil inocula.

As in Experiment 1, plants inoculated with live soil were infected with mycorrhizal fungi and 90% of the sterile controls were free of mycorrhizal fungi. Furthermore, as in Experiment 1, necrotic roots and an abundance of internal nonmycorrhizal fungi were observed when *Danthonia* and *Panicum* were grown with their own or each other's live root inocula, but not in other treatments.

Experiment 3: competition between Danthonia *and* Panicum

Analysis of the inflorescence profiles showed that *Danthonia* and *Panicum* differed in their overall inflorescence production ($P < 0.0001$, $F_{1,88} = 20.03$) and in their flowering phenologies ($P < 0.03$, $F_{1,88} = 5.16$ and $P < 0.002$, $F_{1,88} = 11.07$ for the first- and second-degree coefficient contrasts, respectively). Furthermore, analysis of the overall inflorescence production and the curvature of inflorescence production both showed that *Danthonia* and *Panicum* differed in their response to intraspecific competition ($P < 0.006$, $F_{1,88} = 8.07$ and $P < 0.04$, $F_{1,88} = 4.85$, respectively), with *Panicum* being more negatively affected than *Danthonia*. However, in the analysis of inflorescence profiles, there was no evidence that the grasses responded differently to inoculum source.

Analyses of plant biomass clearly demonstrated that growth of *Danthonia* and *Panicum* was reduced by intraspecific competition ($P < 0.0001$, Table 3, Fig. 8). However, there was no significant overyielding or underyielding (Fig. 8). The biomass variance was greater within pots with two *Danthonia* plants than between them ($P < 0.05$, folded form F test), but this effect was not significant in *Panicum*. However, *Panicum* was a stronger competitor than *Danthonia* ($P < 0.0004$, Table 3). That is, the mass of *Panicum* was greater when grown with *Danthonia* than when grown with another *Panicum* and, conversely, the mass of *Danthonia* was smaller when grown with *Panicum* than when grown with another *Danthonia* (Fig. 8).

Inoculum source did not have strong effects on plant growth (Table 3, Fig. 8). Overall growth rate, yield total, and competitive ability were not significantly affected by the presence of live soil in general or by each species' own soil community specifically.

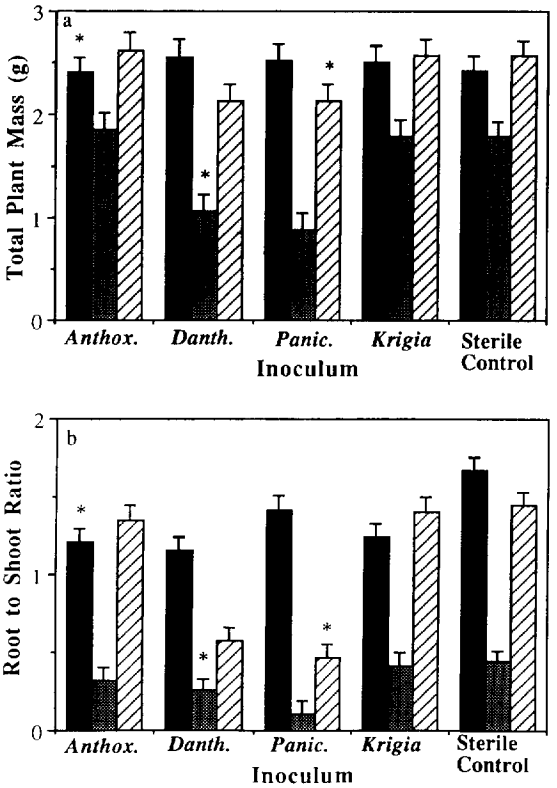

FIG. 3. Total plant biomass and root–shoot ratios of three grasses grown with different soil communities. Total plant biomass (a) and root–shoot ratios (b) of *Anthoxanthum*, *Danthonia*, and *Panicum* are represented by solid, shaded, and striped bars, respectively. Error bars represent 1 SE. Asterisks signify the grasses in their own soil inocula.

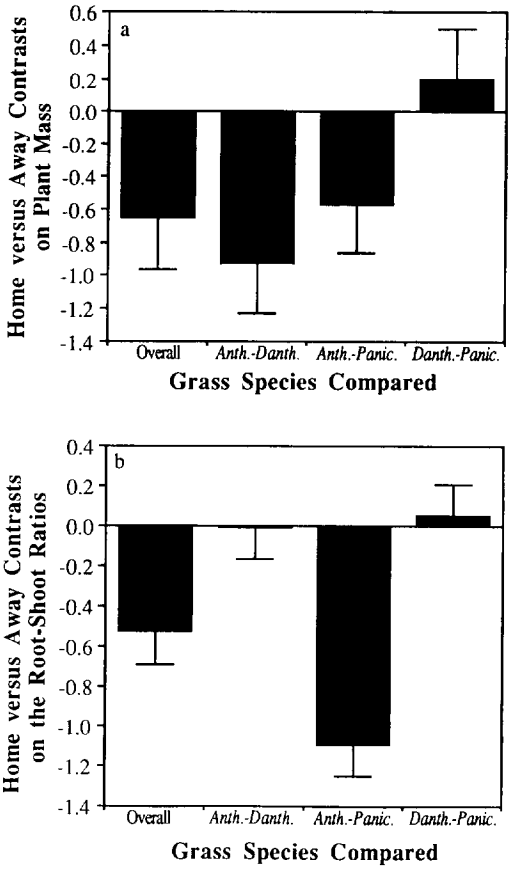

FIG. 4. "Home vs. away" contrasts from the comparison of soil inoculum treatments. The home vs. away contrasts estimate the difference between growth of plants in treatments with their own soil inocula and growth in treatments with other soil inocula. These estimates are plotted with 1 SE for the overall comparison of the three grass species and the three pairwise comparisons of grasses. (a) and (b) present the magnitudes of these home vs. away contrasts for plant biomass and root–shoot ratios, respectively.

DISCUSSION

The soil and root inocula test experiments provide an abundance of evidence that the experimental soil communities have differentiated as a result of being "cultured" on different plant types. Measures of plant

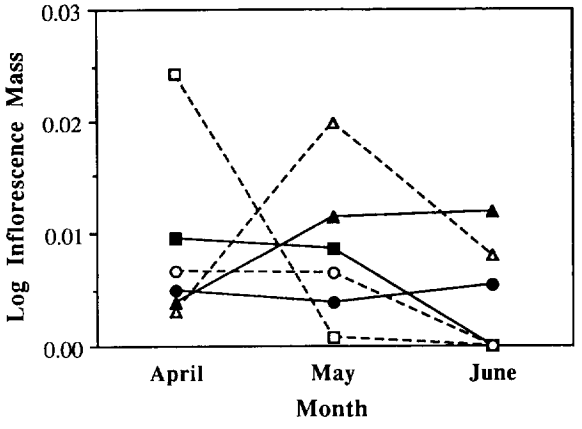

FIG. 5. Profiles of inflorescence production of the three grasses under live and sterile root inocula. Profiles of the log of the inflorescence production of *Anthoxanthum, Danthonia,* and *Panicum* over a 3-mo period are represented by a square, circle, and triangle, respectively. The production in sterile and average production in the four live inocula are represented by the dashed and solid line, respectively. Each point is a total of all inflorescences produced that month.

survival, plant growth, root–shoot ratios, and flowering phenology were all significantly affected by the source of the inoculum. Furthermore, for all of these measures, the plant species responded differentially to the inocula. Given the precautions taken to minimize any possible influences of differences in the mineral soil or of possible allelochemicals, these effects are presumed to be due to differences in the soil biota. This substantial differentiation of the soil communities occurred relatively quickly, over a time period of 15 mo.

Furthermore, this differentiation of the soil communities appears to have caused a negative feedback on plant survival and growth. Survival of *Krigia* (Fig. 1) and growth of the grasses (Fig. 4) were reduced as a result of being grown in association with live soil inoculum that was previously cultured by that same species. Furthermore, the delay in flowering of the grasses when grown with their own soil inocula (Fig. 2) may reflect the plant's weakened physiological state.

Negative feedback on plant growth and survival through their soil communities could result from an accumulation of specific pathogens (Burdon 1987) or a change in composition of the community of mutualists (Bever 1992). While the experiments discussed here were not designed to identify the members of the soil community that caused these effects, root pathogens seem to be the most likely agents. In these experiments, no overall growth advantage due to live inoculum was observed, in spite of the presence of mycorrhizal fungi. A beneficial affect of mycorrhizal fungi may have been minimized by the fertility of the soil, light intensity, or genotypic identity of the mycorrhizal fungi (Bethlenfalvay et al. 1982, Hetrick et al. 1984, Bever 1992). Alternatively, the beneficial effect of mycorrhizal fungi may have been negated by the presence of pathogens or other soil microbes as had been observed for *Andropogon* by Hetrick and Wilson (1991). The root inoculum experiment was expected to highlight effects attributable to mycorrhizal fungi.

TABLE 2. Analyses of covariance of plant masses and root–shoot ratios from the comparison of root inocula (Experiment 2).*

Source	df	Plant masses		Root–shoot ratio	
		ss	*P*	ss	*P*
Block	2	0.284	NS	0.251	0.03
Initial mass	1	0.549	NS	0.207	0.02
Species	2	9.183	0.0001	12.804	0.0001
Inoculum	4	1.174	NS	0.344	0.05
Species × Inoculum	8	1.336	NS	0.796	0.009
Error	76	12.159		2.672	
		Contrasts			
Effect of live soil	1	0.374	NS	0.223	0.02
Species × Live soil†	2	0.046	NS	0.070	NS
		Home vs. Away‡			
Three species	1	0.664	0.05	0.068	NS
Pairwise overall	3	0.692	NS	0.630	0.001
Anthox. and *Danth.*	1	0.205	NS	0.000	NS
Anthox. and *Panic.*	1	0.346	NS	0.536	0.0008
Danth. and *Panic.*	1	0.379	NS	0.016	NS

* All tests were performed using the Type three sums of squares (ss) from SAS (SAS Institute 1990). Initial mass was used as a covariate. The significance levels of the pairwise "home vs. away" contrasts have been adjusted for multiple comparisons using the Dunn-Sidak method (Sokal and Rohlf 1981). Plants that died back from lack of water near the experiments' completion were excluded from the analyses. However, analyses including these plants gave the same conclusions.

† This effect was tested conservatively using an *F* statistic constructed with the ss from the most significant pairwise contrast (*Anthoxanthum* vs. *Panicum* and *Anthoxanthum* vs. *Danthonia* plant masses and root–shoot ratios, respectively) as the treatment ss.

‡ Contrast defined in Table 1.

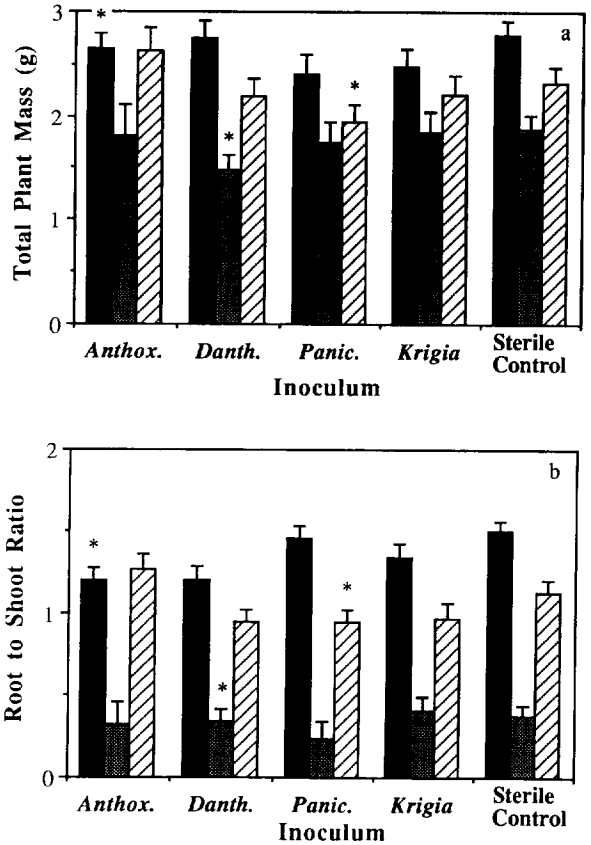

FIG. 6. Plant biomass and root–shoot ratios of three grasses grown in soils with different root inocula. Plant biomass (a) and root–shoot ratios (b) of *Anthoxanthum, Danthonia,* and *Panicum,* are represented by solid, shaded, and striped bars, respectively. Error bars represent the standard errors. Asterisks signify the grasses in their own soil inocula.

However, the results were parallel to those observed when using whole soil as inocula (specifically, no growth advantage of live inocula and decreased growth and root–shoot ratio when grown with their own soil community). The observation of an abundance of nonmycorrhizal fungi in the roots of *Danthonia* and *Panicum* when grown in their own or each other's inocula, suggests that the root inoculum study was not successful in isolating the effect of beneficial mycorrhizal fungi from that of other root-inhabiting fungi. The saprophytic or pathogenic nature of the nonmycorrhizal fungi is uncertain; however, several fungi have been subsequently isolated from these roots including species of *Fusarium* and *Pythium* (J. D. Bever, *unpublished data*), genera that are commonly pathogenic. The observation of necrosis and the presence of potentially pathogenic fungi in the roots of *Danthonia* and *Panicum* when grown in their own and each other's inocula suggests that pathogenic fungi are responsible for the large negative feedback in growth rate observed in the grasses. Furthermore, these pathogens may also be responsible for the reduced root–shoot ratio in grasses grown with their own inocula. Root death and decreased root growth due to an accumulation of a barley-specific fungal root pathogen (a species of *Fusarium*) was found by Olsson and Gerhardson (1992).

Regardless of agent, this evidence of strong negative feedback on the growth of plant individuals and populations through their soil communities suggests the action of a rarely considered mechanism for maintenance of plant species and genetic diversity. Levins (1974, 1975) argued that negative feedback is an essential requirement for community stability. The important mechanism for negative feedback and maintenance of species diversity has traditionally been thought to be the partitioning of resources during competition (reviewed in den Boer 1986, Grace and Tilman 1990). The validity of this view for plant communities has recently been strongly questioned (Aarssen 1983,

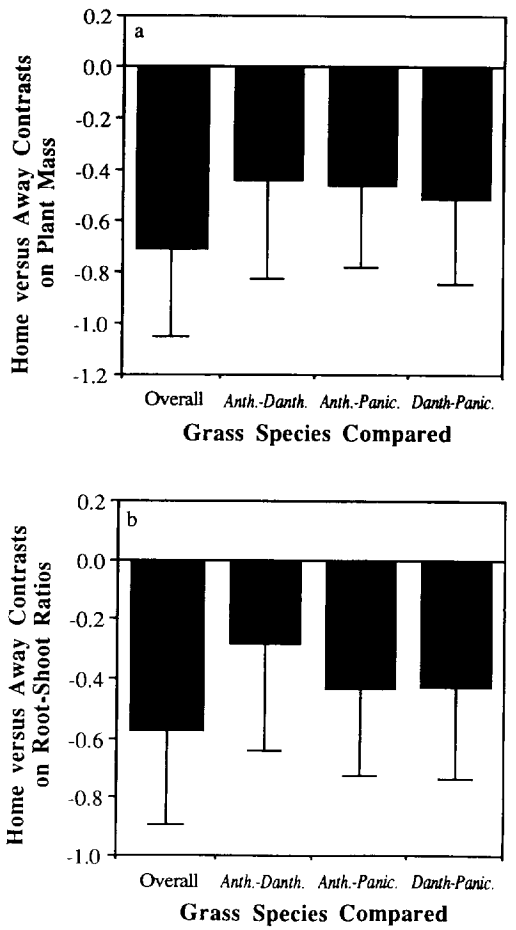

FIG. 7. "Home vs. away" contrasts from the comparison of root inocula. The home vs. away contrasts estimate the difference between growth of plants in treatments with their own root inocula and growth in treatments with other root inocula. These estimates are plotted with their standard errors for the overall comparison of the three grass species and the three pairwise comparisons of grasses. (a) and (b) present the magnitudes of these home vs. away contrasts for plant biomass and root–shoot ratios, respectively.

TABLE 3. Analysis of covariance of masses of live plants from the competition experiment (Experiment 3).*

Source of variation	df	ss	*P*
Block	4	0.244	NS
Initial mass	1	0.620	0.0001
Species	1	0.505	0.0002
Competition	2	1.832	0.0001
Species × Competition	2	1.064	0.0001
Inoculum (i.e., soil community)	2	0.029	NS
Species × Inoculum	2	0.026	NS
Competition × Inoculum	4	0.009	NS
Species × Competition × Inoculum	4	0.151	NS
Error	82	2.765	
	Contrasts		
Overyielding	1	0.014	NS
Intraspecific competition	1	1.021	0.0001
Different competitive abilities	1	0.452	0.0004
Effect of live inoculum	1	0.021	NS
Species × Live inoculum	1	0.008	NS
Diff. comp. abil. × Live inoc.	1	0.057	NS
	Home vs. away		
Overall growth	1	0.017	NS
Competitive abilities	1	0.004	NS

* All tests were performed using the Type three sums of squares (ss) using SAS (SAS Institute 1990). Initial mass was used as a covariate. The contrasts provide linear tests of the significance of the effects listed. That is, these contrasts are constructed as differences or as differences of differences. For example, the contrast for different competitive abilities tests whether the species differ in the difference between growing with intraspecific and interspecific competition.

den Boer 1986, Silvertown and Law 1987, Goldberg and Barton 1992) and a variety of alternative mechanisms for species coexistence have been suggested (reviewed in Aarssen 1989). The demonstration of strong negative feedback between plants and their soil communities in these experiments suggests that it may be an important mechanism for the coexistence of plant species and genotypes. Specifically, an increase in the density of a given plant type may change the soil community in a way that causes the density of that type to decrease and the density of a rare type to increase.

However, the results of the three experiments reported here do not suggest that a plant's soil community always exerts negative feedback on that plant's growth. *Danthonia* and *Panicum* did not respond differentially to each other's soil or root communities in comparisons of growth responses (Experiments 1, 2, and 3) or in comparisons of competitive ability (Experiment 3). The competition experiment demonstrated that the *Panicum* genotype studied here is a stronger competitor than the *Danthonia* genotype regardless of soil communities.

The differences in feedbacks and competitive abilities observed in this study should not be interpreted as characteristic of the species studied. Since these experiments were conducted on single genotypes of each species, inference about the ecology of the specific species studied here would be unwarranted. Ecologically important traits have been found repeatedly to vary among genotypes of a single population as was demonstrated for competitive ability with populations of *Danthonia* and *Anthoxanthum* from this site (Kelley and Clay 1987), as well as in other systems (e.g., McNeilly 1984, Taylor and Aarssen 1990). The feedbacks or competitive abilities of single genotypes do not necessarily represent the feedbacks or competitive abilities of entire species.

Empirical and theoretical work on plant competition has focussed almost exclusively on the mineral component of the soil in spite of the important role of the soil community in plant nutrition (see Grace and Tilman 1990). While the soil community treatments did not significantly influence the outcome of competition between the *Danthonia* and *Panicum* genotypes, the negative feedback between these two genotypes and that of *Anthoxanthum* through the soil community in the first two experiments suggests that the soil community does play an integral role in plant–plant interactions. Such negative feedback may generate indirect mutualistic effects between different species or genotypes similar to those discussed by Vandermeer et al. (1985) wherein a given plant type changes the soil community in a way that increases the growth rate of competing plant types relative to its own.

Given that both the response and the effect of the soil community are likely to be highly local, the rapid response of this community to its vegetative host could generate a highly nonuniform and nonrandom distribution of soil communities. Such patterns have been observed in the distribution of genotypes of *Rhizobium* (Chanway et al. 1989) and a species of *Bacillus* (Chanway et al. 1990) as well as in the composition of soil bacterial communities (K. M. Westover and S. E. Kelley, *personal communication*) and arbuscular mycorrhizal communities (J. D. Bever, *unpublished data*) in this field. This suggests that the soil community may

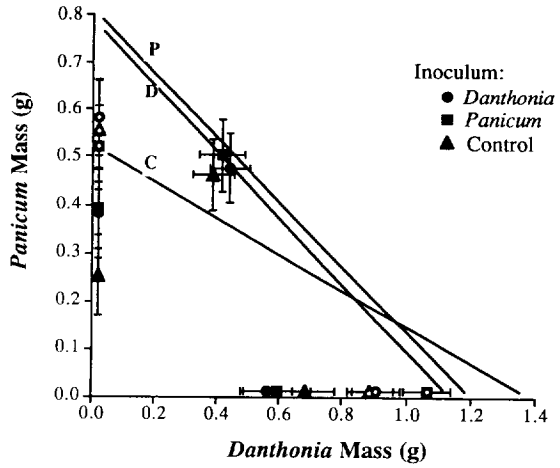

FIG. 8. Biomass of *Danthonia* and *Panicum* grown without competition, with intraspecific competition, and with interspecific competition. The aboveground live biomasses of individual plants of *Danthonia* and *Panicum* are presented on the x axis and y axis, respectively (as is common in plots of land equivalency ratios, Vandermeer 1989). Biomasses of plants grown without competition are represented by open symbols, and biomasses of individual plants grown with intraspecific and interspecific competition are represented by the solid symbols near the axes and in the interior, respectively. That is, the interior points represent the masses of *Danthonia* and *Panicum* plants under interspecific competition on the x and y axes, respectively. Plants grown with the *Danthonia* soil community, *Panicum* soil community, and the sterile control are represented by circles, squares, and triangles, respectively. The lines indicate where the relative yield total equals one for the three soil inocula as indicated by the adjacent letters (representing the genus of the plant in whose root environment the inoculum soil community developed). These lines intersect the axes at the total biomass of the two individuals grown in intraspecific competition (twice the biomass of individual plants grown with intraspecific competition). The combined yields in mixture did not differ significantly from those in monoculture. The *Panicum* genotype was a superior competitor to the *Danthonia* genotype ($P < 0.0004$), as is illustrated by the biomass of *Danthonia* and *Panicum* being greater when grown with *Danthonia* than when grown with *Panicum*. Neither growth nor competitive ability was significantly affected by soil inoculum source.

play an important role in the spatial as well as the numerical dynamics of plant populations and communities.

The soil community may also play an important role in the evolution of breeding systems. If the negative feedback observed among genotypes of different species in this experiment was observed among genotypes of the same species, the interaction of plants with their soil communities would result in negative frequency-dependent selection. Frequency-dependent selection has been suggested as an explanation for the maintenance of sexual reproduction (Price and Waser 1982), and such a "minority type advantage" has previously been demonstrated in the population of *Anthoxanthum* in this field (Antonovics and Ellstrand 1984, Ellstrand and Antonovics 1985, Schmitt and Antonovics 1986, Kelley et al. 1988, Kelley 1989). While some evidence suggested that aphids were involved, possibly as viral transmitters (Schmitt and Antonovics 1986), the results of this study suggest that the soil community may also be important.

The results reported here suggest that plants can "culture" a soil community which has strong negative effects specific to that plant type. This in turn raises a number of crucial issues: How general is negative feedback with respect to taxonomic and genetic levels of plants? Will the nature of the feedback differ in an undisturbed field soil? At what spatial and temporal scale are these feedbacks manifest? And finally, what components of the soil community (as distinguished by ecological guild or taxonomic level) are principally responsible for these effects?

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