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MAINTENANCE OF DIVERSITY WITHIN PLANT COMMUNITIES: SOIL PATHOGENS AS AGENTS OF NEGATIVE FEEDBACK

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Abstract. The effect of soil pathogens on plant communities was investigated using four old-field perennial plant species and five isolates of a pathogenic oomycete in the genus *Pythium.* These *Pythium* strains were isolated from the roots of two of the plant species, *Danthonia spicata* and *Panicum sphaerocarpon,* used in a previous experiment on the consequences of changes in the soil community on plant growth. In this previous experiment, *Danthonia* and *Panicum* changed the soil community in a manner that reduced their growth relative to that of a third plant species, *Anthoxanthum odoratum.* In the current experiments, we found that inoculation with *Pythium* reduced overall plant mass and root : shoot ratios, but *Danthonia* and *Panicum* were more susceptible to the presence of *Pythium* than the other two plant species, *Anthoxanthum* and *Plantago lanceolata.* In addition, *Pythium* accumulates at different rates on different plant species, with a greater than tenfold higher population observed in association with *Panicum* compared to *Anthoxanthum.* The results of these experiments suggest that the accumulation of species-specific soil pathogens could account for the previous observation of negative feedback on plant growth through changes in the soil community. As negative feedback may act to maintain plant species diversity within a community, these results suggest that soil pathogens may themselves contribute to the maintenance of plant species diversity.

Key words: Anthoxanthum; *community dynamics;* Danthonia; *diversity; feedback; host specificity; old field;* Panicum; Plantago; Pythium; *pathogen; soil community.*

INTRODUCTION

It has traditionally been assumed that the maintenance of plant community diversity results from the partitioning of abiotic resources (reviewed by Grace and Tilman 1990, Tilman and Pacala 1993). Models of competition reveal that competing species will coexist when intraspecific competition exceeds interspecific competition, a situation that has generally been presumed to result from abiotic niche differentiation. However, the generality of this view has recently been challenged (e.g., Silvertown and Law 1987, Aarssen 1989) and a potential role of pathogens in mediating species interactions, and particularly plant–plant coexistence, has been suggested (Holt and Pickering 1985, Burdon 1987, Alexander 1990). The importance of pathogens is supported by their ubiquitous occurrence and major impacts on agricultural plant populations. Moreover, recent work in natural communities has found substantial impacts of pathogens on plant demography (Weste 1974, Augspurger 1984, 1988, 1990, Burdon 1987, Alexander et al. 1996) and even suggests a role of pathogens in the course of dune succession (Van der Putten et al. 1993). Nevertheless, the overall role of pathogens in the maintenance of diversity in natural plant communities is not known. This is particularly true for soil pathogens, a group known to be important in agricultural systems (Bruehl 1987, Agrios 1988) but which are unusually difficult to study because of the confounding effects of, and complexity of interactions with, other components of the soil community (e.g., Larkin et al. 1993, Newsham et al. 1995, De Rooij-van der Goes 1995, Bever et al. 1997).

We have found evidence that the soil community, as a whole, can contribute to the maintenance of diversity within plant communities. Using a phenomenological experimental approach, we have found strong negative feedbacks on plant growth through changes in the composition of the soil community (Bever 1994, Bever et al. 1997). Negative feedback occurs when the presence of a plant changes the soil community in a manner that decreases the growth of that particular plant species relative to other species. Models of this process have shown that negative feedback can maintain diversity of a plant community provided that the sign of an interaction coefficient is negative (Bever et al. 1997). This interaction coefficient can be estimated in experimental studies where plants of a particular species are transplanted into soil communities that have previously been ''cultured'' by plants of the same (''home'') or a different (''away'') species; thus, the coefficient can be estimated using a ''home vs. away'' contrast (Bever 1994). In previous studies we found evidence for the existence of negative feedback between *Anthoxanthum*

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odoratum and *Danthonia spicata* and between *A. odoratum* and *Panicum sphaerocarpon* in an old-field community in Durham, North Carolina (Bever 1994). Specifically, Bever (1994) found that growth of *D. spicata* and *P. sphaerocarpon* was significantly reduced with soil communities that had been previously ''cultured'' by plants of the same species, while *A. odoratum* did well in these soils but exhibited reduced growth with soil communities that had previously supported plants of its own species. In independent experiments, we also found evidence of negative feedback between the pairs *Anthoxanthum* and *Plantago,* and *Panicum* and *Plantago* (Bever et al. 1997).

The agents of negative feedbacks in these studies have not been identified, but initial observations indicated that accumulation of species-specific soil pathogens may be responsible. *D. spicata* and *P. sphaerocarpon* both had low root : shoot ratios, likely the result of observed root necrosis (Bever 1994). Several species of soil pathogens, including species of the genus *Pythium,* were subsequently isolated from their roots. It is possible that the observed accumulation of *Pythium* on these two plant species causes more severe effects on *D. spicata* and *P. sphaerocarpon* than on other plant species, suggesting that soil pathogens contribute to the observed negative feedback and thereby play an important role in the maintenance of diversity within this plant community.

In this study, we used these isolates of *Pythium* spp. to test whether the accumulation of species-specific soil pathogens may contribute to the negative feedback observed between certain plant species. Although *Pythium* spp. are known to have substantial impacts on plant survival and growth (reviewed in Hendrix and Campbell 1973, Abad et al. 1994, Larkin et al. 1995), the impact of *Pythium* on unmanaged plant communities has rarely been investigated (but see Augspurger 1990). To investigate the role of soil pathogens in affecting plant community diversity, we tested the effect of *Pythium* spp. on the growth of the plant species in which negative feedback through the soil community had previously been observed (Bever 1994). We then discuss these results in light of the observations of whole-soil community feedback to provide insight into the potential impacts of soil pathogens on plant community diversity.

Methods

In order to investigate the role of *Pythium* in feedback processes within the soil community, we focused on two questions: (1) Do different species of plants exhibit differential responses to the presence of *Pythium* and (2) Do *Pythium* spp. accumulate differentially under these plant species? These objectives were evaluated in two experiments. A full factorial experiment in which four plant species were grown in six treatments consisting of five isolates of *Pythium* and a sterile control allowed us to test differential responses of each plant species to the presence of *Pythium* and to specific *Pythium* isolates. Host-specific differences in rates of accumulation of *Pythium* were assessed using a series of serial dilutions of soil from *A. odoratum* and *P. sphaerocarpon.*

Study system

The plants, pathogens, and soil used for this experiment were obtained from a well-studied old field in Durham, North Carolina. The plant community in this field is diverse and lacks any distinctly dominant species (Fowler and Antonovics 1981). Four common, short-lived perennial plant species were used in this study—three grasses, *Anthoxanthum odoratum* L., *Danthonia spicata* (L.) Beauv., and *Panicum sphaerocarpon* Ell., and a herbaceous species, *Plantago lanceolata* L. Hereafter, all plant species will be referred to by generic name only. Negative feedback on plant growth through changes in the soil community had previously been observed between four of the six pairs of plant species: *Anthoxanthum* and *Danthonia, Anthoxanthum* and *Panicum, Anthoxanthum* and *Plantago,* and *Panicum* and *Plantago* (Bever 1994, Bever et al. 1997). However, in three separate test experiments, no feedback was observed between *Danthonia* and *Panicum* (Bever 1994).

The isolates of *Pythium* (a genus popularly regarded as fungal but accurately classified as an *oomycete* in the Kingdom *Chromista*) used in this experiment were cultured from roots of *Danthonia* and *Panicum* remaining from a previous experiment that demonstrated negative feedback between these species and *Anthoxanthum* (Bever 1994). We were not able to obtain isolates of *Pythium* from *Anthoxanthum* roots. Five isolates identified as four different *Pythium* species were cultured in a manner described below—*Pythium aristosporum, P. arrhenomanes,* and *P. macrosporum* from *Danthonia* and *P. arrhenomanes* and *P. volutum* from *Panicum* (G. Abad, *personal communication*). The species of *Pythium* isolates used in this study infect a wide variety of hosts (Abad et al. 1994, Deep and Lipps 1996, Magarey 1996). In addition, *P. aristosporum, P. arrhenomanes,* and *P. volutum* have all been classified as ''highly aggressive'' species due to their severe impacts on growth and survival of grasses (Abad et al. 1994).

Experiment 1: Plant response to Pythium

Isolation of Pythium.—Isolates of *Pythium* were obtained from root tissues of *Danthonia* and *Panicum* using techniques similar to those described by Martin (1992). Samples of roots from these grasses were rinsed thoroughly with water, surface sterilized with 50% ethyl alcohol, and then dried with sterile paper towels before being placed onto selective media (PARP—pentachloronitrobenzene ampicillin rifampicin pimaricin medium) (Jeffers and Martin 1986). Following incubation at room temperature for 48 h, isolates were trans-

ferred to fresh plates of PARP, and isolate purity was confirmed by growing on corn-meal agar (CMA) (Difco Laboratories, Detroit, Michigan). Species identity of the isolates was determined using sterile grass blade cultures with assistance from M. Cubeta and G. Abad, and stock cultures were stored as agar plugs in test tubes containing sterile deionized water at room temperature.

Preparation of Pythium *inoculum.*—*Pythium* inoculum containing active mycelia and oospores that could survive in and infest the soil of treatment plants was prepared by growing the five *Pythium* isolates in sterile grass blade cultures (Martin 1992). For each of the *Pythium* isolates, two plugs (each 0.5 cm^3) of CMA with mycelium were placed in separate sterile tissue culture dishes (Falcon 3025, 150 × 25 mm style). Sterile deionized water was added to the dishes to a level where the layer of water just covered the agar plugs, and 50 pieces (each 1.0–1.5 cm long) of autoclaved tall fescue grass leaves were placed into each dish. Five replicate dishes containing the grass blade cultures of each isolate were incubated at room temperature under continuous light for 4 d (Abad et al. 1994). Infection of the grass blades by the *Pythium* mycelia was monitored under the dissecting scope, and the experiment was planted 4 d after the grass blade cultures were started, at which time most blades of grass had been infected by the mycelia.

Planting and harvesting processes.—Seedlings of *Anthoxanthum, Panicum,* and *Plantago* were started from seeds of greenhouse-grown plants that were previously collected from the field. *Danthonia* seeds were collected from plants in our study field. All seeds were planted in sterile seedling mix and were allowed to grow until small seedlings of each species were available. In April 1996, between seven and ten replicates of each of the six treatments were planted with each plant species. All plants for this experiment were grown in 385-mL pots filled with sterile background soil. To prepare the background soil, field soil was first crumbled until it passed through a 1-cm mesh. Equal amounts of the sieved field soil and sand were then thoroughly mixed and autoclaved for 1.5 h.

Each *Pythium* treatment was inoculated with one of the isolates of *Pythium* by placing four colonized grass blades from the sterile grass blade culture beneath the top 70 mL of soil in each pot. Control treatments were planted in the same manner with sterile uninoculated grass blades being used in place of the *Pythium* inoculum. Two seedlings of one of the plant species were planted in each pot. The entire experiment was then arranged into two randomized blocks within a greenhouse (10.0°–32.2°C) and pots were spaced sufficiently to prevent cross-contamination by water splash during the course of the experiment. All pots were kept well watered during the first few days of the study to allow initial establishment of the seedlings and *Pythium.* After the 1st wk, the pots were watered as needed.

The first block of the experiment was harvested 5 wk after planting, while the second block grew for 7 wk. During the harvesting process, whole plants were removed from the soil and washed. Roots and leaves were cut apart to be dried and weighed separately. Small root samples were also taken from select pots of the first block and from all pots in the second block to confirm the presence of *Pythium* using the same process described previously.

Data analysis.—Masses of the leaves and roots from both plants in each pot were summed, and the effect of the *Pythium* treatments and plant species on total plant mass and root : shoot ratios was analyzed with an analysis of variance using the general linear models procedure of SAS (SAS 1986). The treatment and interaction sums of squares were decomposed into orthogonal tests (1) of the control treatment against the average effects of the *Pythium* isolates and (2) among the *Pythium* isolates. This technique allows us to separate effects caused by the presence of *Pythium* in general from specific effects of individual isolates. We were particularly concerned with whether differences in susceptibility could explain the previous observation of negative feedback through the soil community between these plant species (Bever 1994). In the earlier studies, the feedbacks were tested using pairwise home vs. away contrasts (Bever 1994, Bever et al. 1997). Feedbacks between the plant species could result from the accumulation of *Pythium* in association with one of these plant species, followed by that plant species being more susceptible to the presence of *Pythium* than other plant species in the community. Therefore, in this experiment, we were specifically interested in evaluating pairwise differences between the four plant species in susceptibility to the *Pythium* isolates. These differences were tested as the single degree of freedom interaction between two plant species and the presence of *Pythium.* Because the pairwise contrasts were not orthogonal, their significance was adjusted by the Dunn-Sidák method to control for multiple tests (Sokal and Rohlf 1981). In testing for interspecific differences in response to specific isolates of *Pythium,* we were also interested in the a priori hypothesis of local adaptation of the *Pythium* isolates from *Panicum* and *Danthonia* to their hosts. This hypothesis was tested by contrasting the average response of *Danthonia* to isolates cultured from *Danthonia,* and *Panicum* to isolates cultured from *Panicum,* against the average response of these two grass species to isolates from the other species.

Experiment 2: Pythium *infection of various plant species*

Differential growth rates of *Pythium* on two of the plant species, *Anthoxanthum* and *Panicum,* were tested in this experiment. Field soil was collected from beneath the two plant species, diced, and homogenized to create soil communities that were initially similar

(as in Bever 1994). This fresh soil mixture was distributed into replicate pots into which were planted six soil-microbe-free tillers (as in Bever 1994) of either *Anthoxanthum* or *Panicum.* The plants were watered as needed but were not fertilized while growing in a Duke University Phytotron controlled environment chamber under 12 h light and at 25°C during the day and 10°C at night. After 7 mo, three cores (1 cm diameter) were taken from each of the nine replicate culture pots, and the soil from the cores of each pot was homogenized to obtain one pooled sample per culture pot. For each homogenized sample, two replicates of three serial dilutions were evenly spread onto selective media (PARP). *Pythium* colonies were counted after 48 h. Colony-forming units per gram soil were estimated based on plate counts. The average inoculum density for each pot was analyzed in an ANOVA using the general linear models procedure of SAS (SAS 1986).

RESULTS

Experiment 1: plant response to Pythium

The presence of *Pythium* reduced plant mass and root : shoot ratios. Plants grown with four of the five *Pythium* isolates had plant masses (Fig. 1a) and root : shoot ratios (Fig. 1b) that were significantly lower than the control treatment. Further, plant species varied in their susceptibility to the presence of *Pythium* in general (as tested by the Plant spp. × *Pythium* interaction, Table 1). Specifically, *Danthonia* and *Panicum* were more susceptible to *Pythium* than *Anthoxanthum* and *Plantago* (pairwise contrasts in Table 1, Fig. 2). This was demonstrated by the fact that masses (Fig. 2a) and root : shoot ratios (Fig. 2b) of *Danthonia* and *Panicum* infected by *Pythium* were less than those species under control conditions, while the masses of *Anthoxanthum* and *Plantago* did not seem affected by *Pythium* infection.

Although the plants differed in their response to the presence of *Pythium* in general, they did not differ in their response to specific isolates of *Pythium* (as tested by the Plant spp. × *Pythium* spp. interaction, Table 1). Of particular interest, we did not find a difference in susceptiblilty between *Danthonia* and *Panicum* to their own or each other's isolates. Thus, there is no evidence of differential adaptation of the isolates from *Danthonia* and *Panicum* on their respective hosts (*Danthonia* vs. *Panicum,* Table 1).

Experiment 2: Pythium *infection of various plant species*

Results of colony formation assays for serial dilutions of *Anthoxanthum* and *Panicum* soil confirmed that *Pythium* populations reached higher densities in the soil of *Panicum* than *Anthoxanthum* ($F_{1,16} = 41.11$, $P < 0.0001$). The mean number of colony-forming units of *Pythium* from *Anthoxanthum* pots was 161.1, while the mean colony-forming units from the *Panicum* pots was 2411.1.

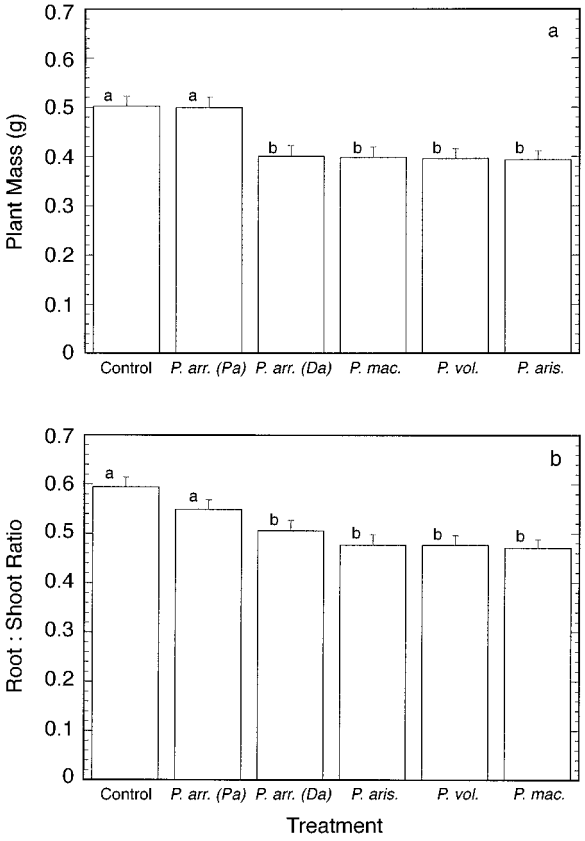

FIG. 1. Average effect of *Pythium* isolates on plant growth. The average response of the four plant species to the *Pythium* isolates and the control are presented for plant mass (a) and root : shoot ratios (b). The least square means and 1 SE are presented. Different letters indicate significant differences in means among the treatments as tested using Tukey's test for multiple comparisons. For these graphs, isolates of *Pythium* are abbreviated as follows: ''*P. arr.*'' for *P. arrhenomanes,* ''*P. aris.*'' for *P. aristosporum,* ''*P. mac.*'' for *P. macrosporum,* and ''*P. vol.*'' for *P. volutum.* ''*P. arr.* (*Pa*)'' indicates that this isolate of *P. arrhenomanes* obtained from roots of *Panicum,* and ''*P. arr.* (*Da*)'' indicates that this isolate was obtained from roots of *Danthonia.*

DISCUSSION

This study indicates that soil pathogens may play a role in maintaining plant community diversity by preferentially infecting and subsequently inhibiting the growth of certain species. Some plant species were more susceptible to harmful effects of *Pythium* infection than others, with *Danthonia* and *Panicum* being more negatively impacted than *Anthoxanthum* and *Plantago.* These host-specific effects may explain the previous observations of negative feedback through the soil community between these plant species (Bever 1994, Bever et al. 1997). For example, the negative feedback observed between *Panicum* and *Anthoxanthum* (Bever 1994, Bever et al. 1997) may result from the increase in density of *Pythium* in response to culturing with *Panicum* as evidenced by root necrosis,

TABLE 1. Analyses of covariance of plant masses and root : shoot ratios for the comparison of *Pythium* treatments.

Source of variation†	df	Plant mass		Root : shoot ratios	
		SS	*P*	SS	*P*
Block	1	6.002	0.0001	0.032	NS
Plant spp.	3	4.257	0.0001	7.918	0.0001
Treatment	5	0.390	0.0001	0.396	0.0001
Control vs. *Pythium*	1	0.147	0.0010	0.254	0.0001
Among *Pythium* spp.	4	0.237	0.0016	0.136	0.0321
Plant spp. × Treatment	15	0.325	0.0618	0.391	0.0134
Plant spp. × *Pythium*	3	0.230	0.0007	0.260	0.0002
An–Da × *Pythium*	1	0.019	NS	0.101	0.0052
An–Pa × *Pythium*	1	0.145	0.0020	0.155	0.0012
An–Pl × *Pythium*	1	0.004	NS	0.000	NS
Da–Pa × *Pythium*	1	0.060	NS	0.006	NS
Da–Pl × *Pythium*	1	0.039	NS	0.102	0.0100
Pa–Pl × *Pythium*	1	0.195	0.0004	0.157	0.0010
Plant spp. × *Pythium* spp.	12	0.103	NS	0.141	NS
Danthonia vs. *Panicum*	1	0.003	NS	0.000	NS
Error	167	2.169		2.101	

Note: The Plant spp. × Treatment interaction tests for differences in responses of the four plant species to the control treatment or the five *Pythium* treatments. This overall interaction term was decomposed into two orthogonal interaction components: the Plant spp. × *Pythium* interaction and the Plant spp. × *Pythium* spp. interaction. The Plant spp. × *Pythium* interaction specifically tests for differences among the four plant species in their average response to the five *Pythium* isolates compared to the sterile control. This interaction component was itself decomposed into six pairwise tests for differential response to the presence of *Pythium.* The Plant spp. × *Pythium* spp. interaction component tests for differences in host-specific effects among the five *Pythium* isolates.

† Plant species abbreviations are as follows: "*An*" = *Anthoxanthum,* "*Da*" = *Danthonia,* "*Pa*" = *Panicum,* "*Pl*" = *Plantago.*

reduced root : shoot ratios, and isolation of *Pythium* spp. in the whole-soil feedback experiment (Bever 1994), and the empirical comparison of *Pythium* colony-forming units isolated from *Anthoxanthum* and *Panicum* in this experiment. This increased density of *Pythium* may then decrease the growth of *Panicum* in its local *Pythium*-enriched soil relative to the growth of *Anthoxanthum* in the same soil. The first experiment also provides evidence that *Pythium* may be an agent of negative feedback observed previously between *Anthoxanthum* and *Danthonia*, *Anthoxanthum* and *Panicum*, and *Panicum* and *Plantago* (Bever 1994, Bever et al. 1997). Our results further suggest that these strains of *Pythium* do not contribute to the negative feedback on plant growth previously observed between *Anthoxanthum* and *Plantago* (Bever et al. 1997). The host-specific effects of *Pythium* found in our study combined with observations of greater competitive ability of *Danthonia* (Kelley and Clay 1987) and *Panicum* (Westover 1995) may work together to maintain these plant species in the community. In addition, other environmental factors, such as aphid-transmitted viruses in *Anthoxanthum* (Kelley 1994) and the aerially transmitted fungal pathogen *Fusarium monofiliforme* in *Plantago* (Alexander 1984) may limit plant population densities in this community. As negative feedback leads to the maintenance of diversity within a community and this study identifies soil pathogens as potentially important agents of this feedback, we suggest that soil pathogens may contribute to the maintenance of diversity within a plant community.

The differential response of the four plant species to *Pythium* was not isolate specific. This, in part, may reflect a generalized resistance or tolerance of *Anthoxanthum* and *Plantago* to these root pathogens. However, even *Danthonia* and *Panicum,* the more susceptible plant species, did not differ in their responses to individual isolates of *Pythium.* In fact, there was no evidence that the pathogens isolated from *Danthonia* exerted a greater effect on that species than the pathogens isolated from *Panicum* or vice versa (as tested by the *Danthonia* vs. *Panicum* contrast, Table 1). This lack of difference among the isolates is consistent with the absence of a differential response of *Danthonia* and *Panicum* to each other's soil communities in three separate measurement attempts (Bever 1994).

While the consistency of results between this experiment and previous observations of feedback through the whole-soil community provides strong evidence that *Pythium* contribute to the observed feedback, we cannot rule out important roles for other components of the soil community. Other potential pathogens (e.g., a *Fusarium* species was also isolated from *Panicum*; J. D. Bever and S. P. Bentivenga, *personal observations*) may be important. Moreover, the communities of rhizosphere bacteria (Westover 1995) and the arbuscular mycorrhizal fungi (Bever et al. 1996) also exhibited striking host-specific differentiation on these plant species, and the differentiation of these communities may contribute to the whole-soil feedback on the plant growth. It is also possible that mycorrhizal fungi and rhizosphere bacteria, which were excluded

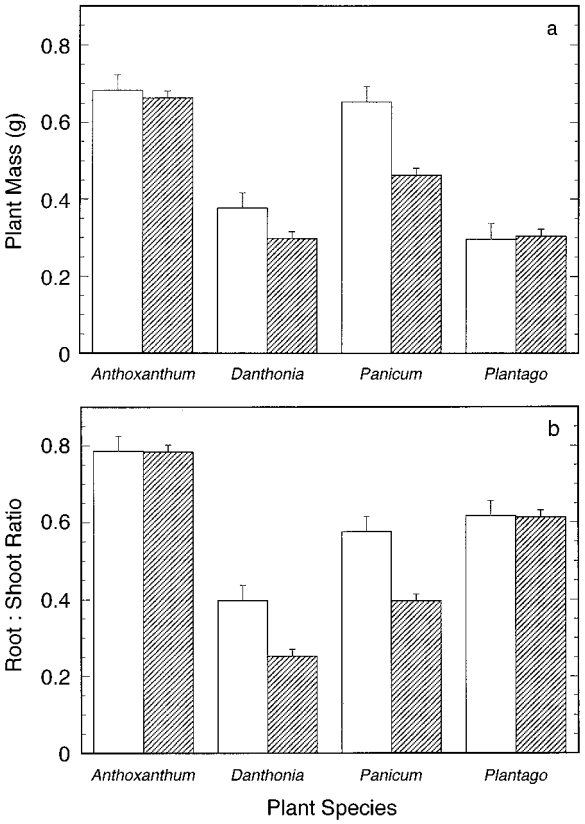

FIG. 2. The response of four plant species to the presence of *Pythium*. The average responses to the five *Pythium* isolates [hatched bars], and to the sterile control [open bars], are presented for each of the four plant species. The least square mean plant mass (a) and root : shoot ratios (b) and 1 SE are presented.

from the present study, could modify the effects of the soil pathogens (Newsham et al. 1995), though this possibility is not supported by the consistency of the results of the present study and the whole-soil tests of feedback.

This experiment provides evidence that *Pythium* can be detrimental to the growth of certain species within a diverse plant community. Previous studies have largely focused on disease and mortality effects of *Pythium* on agronomically important plants (reviewed in Hendrix and Campbell 1973, Larkin et al. 1995, Pankhurst et al. 1995, Deep and Lipps 1996, Magarey 1996, Rizvi and Yang 1996). Only five plants died during the period of this study, and those deaths cannot be conclusively related to the presence of *Pythium*. In fact, as observed previously by Larkin and others (1995), most of the plants inoculated with *Pythium* in this experiment remained asymptomatic throughout the course of the study. Although no disease was obvious, the pathogen decreased plant productivity and inhibited root system development in two of the four plant species. Newsham and others (1994) also suggested that asymptomatic levels of root pathogen infection can alter plant fecundity in the field. Furthermore, four of the five isolates of *Pythium* used in our experiment were identified as species of *Pythium* (G. Abad, *personal communication*) that have been classified as ''highly aggressive'' (Abad et al. 1994) due to their disease-causing potential on other plant species. However, in this seminatural grassland the two isolates of the ''aggressive'' *Pythium arrhenomanes* differed in their aggressiveness, with one isolate not producing significant reductions in growth (Fig. 1). The other isolates did not differ in their effects on plant size.

This study indicates that while *Pythium* reduces the growth and root development of plants overall, certain plant species proved more susceptible to *Pythium* infection, and this differential susceptibility to the pathogens studied suggests that soil pathogens may be agents of negative feedback. These results further support observations of negative feedback between these same plant species. Previous work indicates that this feedback is mediated through changes in their whole-soil communities and, in combination with the present study, indicates that the host-specific effects of these pathogens may not be substantially modified by other components of the soil community. Together these studies suggest that soil pathogens may strongly influence plant community composition and contribute to the maintenance of plant diversity.

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