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SOIL FUNGI AND THE EFFECTS OF AN INVASIVE FORB ON GRASSES: NEIGHBOR IDENTITY MATTERS

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Abstract. We studied the effects of soil fungi on interactions between *Centaurea melitensis*, an exotic invasive weed in central California, and two co-occurring grasses, *Nassella pulchra* and *Avena barbata*. The fungicide benomyl reduced the abundance of arbuscular mycorrhizal (AM) fungi in plant roots but did not affect non-AM fungi. *Centaurea* plants grown alone were >50% smaller with the resident microbial community intact than when benomyl was applied. When grown with *Nassella*, the effect of benomyl was reversed. *Centaurea* grew almost five times larger with the resident microbial community intact. Fungicide had no effect on the biomass of *Centaurea* grown with *Avena*, but biomass of *Centaurea* was significantly lower when grown with *Avena* than when grown with *Nassella* or alone. Photosynthetically fixed carbon may have been transferred from *Nassella* via soil fungi to *Centaurea*, constituting a form of soil fungi-mediated parasitism, but such a transfer did not occur from *Avena* to *Centaurea*. Second, *Nassella* may have been more inhibited by soil pathogens in the presence of *Centaurea* than when alone, and the inhibition of *Nassella* may have released *Centaurea* from competition. A third possibility is that *Nassella* has strong positive effects on the growth of soil fungi, but the positive feedback of beneficial soil fungi to *Nassella* is less than the positive feedback to *Centaurea*. Regardless of the mechanism, the difference in soil fungicide treatment effects on competition between *Centaurea* and *Nassella* vs. *Centaurea* and *Avena* has important implications for the invasion of California grasslands.

Key words: Avena, *California grasslands;* Centaurea; *competition; fungi; indirect interactions; invasion; mycorrhizae;* Nassella; *soil fungi.*

INTRODUCTION

Soil fungi may affect plant communities through their roles as decomposers, parasites, and mycorrhizal mutualists. Mycorrhizal fungi can alter interactions among plants through direct effects, e.g., by providing more resources to one species than to another (Hetrick et al. 1989, Hartnett et al. 1993), and potentially through indirect effects, e.g., by the transfer of resources and fixed carbon between individuals (Chiarello et al. 1982, Francis and Read 1984, Grime et al. 1987, Moora and Zobel 1996, Walter et al. 1996, Watkins et al. 1996, Simard et al. 1997, Marler et al. 1999, but see Robinson and Fitter 1999). These effects of mycorrhizal fungi can vary with resource availability (Allen and Allen 1990, Hetrick et al. 1990, 1992, Johnson et al. 1997, Simard et al. 1997), the size of neighboring plants (Marler et al. 1999), and the composition of the fungal community (van der Heijden et al. 1998). The direct effects of soil fungi are dependent on the plant species involved (Hartnett et al. 1993), but we know little about species specificity in these interactions (see Francis and Read 1984, Grime et al. 1987, Simard et al. 1997).

Exotic plants often displace native species, and in doing so they appear to provide clear examples of intense direct competition. However, Marler et al. (1999) demonstrated that the native resident microbial community (i.e., no fungicide treatment) indirectly enhanced the negative effect of the noxious weed *Centaurea maculosa* (spotted knapweed) on *Festuca idahoensis* (Idaho fescue), a bunchgrass native to the northern Rocky Mountains. Soil fungi had no direct effect on either species when they were grown alone. However, when the species were grown together, *Festuca* plants were 170% larger in sterilized soil than in untreated soil. In contrast, *Centaurea* plants were 66% larger in untreated soil than in soil treated with fungicide. There are more than 10 species in the genus *Centaurea* that have become invasive weeds (e.g., see Plate 1) and several of these wreak substantial damage on native communities and agricultural productivity in North America. *Centaurea melitensis* is an annual weed that is rapidly spreading in southern and central California. Native to southwestern Europe, *C. melitensis* is not common in its native habitat and is generally associated with communities of other winter annuals. The winter annual species, *Avena barbata* (wild oats),

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PLATE 1. *Centaurea solstitialis* invasion in central Argentina. Photograph by José Hierro.

was introduced to North America over 200 yr ago and is naturally associated with *C. melitensis* in Europe. The recent invasion of *C. melitensis* has reacquainted these species in California grasslands. Here we have investigated the effects of soil fungi on interactions between an invasive exotic and naturalized exotic, and between the invasive exotic and a grass species native to California grasslands, *Nassella pulchra* (ex *Stipa*). Our fundamental goal is to examine how soil fungi vary in their effects on interactions between different species within plant communities.

METHODS

We conducted an experiment in which we tested the effects of soil fungi on the growth and reproduction of *C. melitensis*, *Nassella pulchra*, and *Avena barbata*, (from here on the latter two will be referred to primarily by genera) and on the interactions between *C. melitensis* and the two grass species. *Nassella pulchra* is a perennial bunchgrass that is native to California. It may have been a dominant species prior to the invasion of exotic Eurasian annual grasses such as *Avena* species (Dyer and Rice 1997, 1999, Hamilton et al. 1999).

Our experiment was conducted in a naturally lit greenhouse at the University of California, Santa Barbara campus. Light intensity was 75–90% of ambient when the sun was overhead. We placed one replicate (initial $n = 20$ replicates for each treatment, final $n =$ 17–20 replicates) of each of the treatments in blocks to insure that no one treatment was located disproportionally in a particular part of the greenhouse.

Nassella, *Avena*, and *C. melitensis* were grown alone and in interspecific pairs, both with and without added fungicide. Four-liter pots were filled with washed blasting grade, 20/30 grit, aolean sand. To each pot we added an inoculum consisting of 200 mL of whole field soil collected at the University of California Natural Reserve System's Sedgwick Ranch located in the Santa Ynez Valley of Santa Barbara County, California. Soil was collected from the upper 15 cm of the profile at several locations in grasslands where all three of the experimental species were common, and soil from all locations was thoroughly mixed before using it as inoculum. The inoculum, containing all components of the soil microbial community, was then mixed thoroughly with sand to produce a 20:1 sand:soil growth medium with a pH of 6.8 ± 0.3, $n = 10$. We used a sand:soil combination because we have not been able to accurately collect fine roots of *C. maculosa* in past experiments with whole soil. Grasses were germinated in the pots and thinned to one individual per pot. Seven weeks after the grasses were planted, pregerminated *C. melitensis* seedlings were planted in the pots with an individual grass or alone, and thinned to one individual per pot. Three weeks after *C. melitensis* seedlings were planted, soil fungi were reduced in half the pots with benomyl applied in 100 mL water per pot at the concentration of 50 mg benomyl/kg soil (Hetrick et al. 1989). Benomyl was added every 3 wk for the duration of the experiment. The use of benomyl is a recommended method for arbuscular mycorrhizal (AM) fungal experiments (Fitter and Nichols 1988, Smith et al. 2000), and has been shown to have minimal direct effects on plants (Paul et al. 1989). However, benomyl kills some other fungi as well as AM fungi and may cause unintended changes in the microbial community (West et al. 1993, Newsham et al. 1994). Past experiments with *C. maculosa* suggest that benomyl has similar effects on plant interactions as whole-soil sterilization (Marler et al. 1999). We watered plants four times per week until water drained from the pots. All treatments received 100 mL of a one-eighth strength Hoagland's solution every 3 wk.

Fourteen weeks after the grasses were started (7 wk after the *Centaurea* were planted) all plants were harvested, separated into roots and shoots, dried for 48 h at 60°C, and weighed for total biomass. A subsample of dry fine roots was prepared (modified methods of Phillips and Hayman 1970) and checked for fungal

TABLE 1. Percentage root colonization by arbuscular mycorrhizal (AM) and non-AM fungi of *Centaurea melitensis, Avena barbata*, and *Nassella pulchra* in benomyl and no-benomyl treatments with all neighbor treatments combined.

Species	AM fungi		Non-AM fungi	
	No benomyl (%)	Benomyl (%)	No benomyl (%)	Benomyl (%)
Centaurea melitensis	22.1 ± 5.0	1.3 ± 0.8	15.2 ± 6.0	8.2 ± 2.1
Avena barbata	6.4 ± 4.7	0.1 ± 0.1	19.6 ± 9.3	6.7 ± 4.5
Nassella pulchra	4.5 ± 1.8	0.1 ± 0.1	25.7 ± 7.0	16.6 ± 7.9

Notes: Means and one standard error are presented. See Table 2 for ANOVA.

colonization under 100× magnification. We examined the roots of 50 plants from subsets of all treatments for AM fungi and non-AM fungi using the "magnified intersections" method described in McGonigle et al. (1990) and Marler et al. (1999) to determine the percentage of colonized root length; AM fungi were distinguished from non-AM fungi by the presence of arbuscules, vesicles, hyphal coils, and nonseptate hyphae. Non-AM fungi included melanized hyphae and spores, septate hyphae, and nonseptate hyphae associated with non-AM fungi structures including oospores. Biomass and flower production of *Centaurea* were analyzed with separate two-way ANOVAs in which the effects of each grass species, with and without fungi, were isolated. Biomass and flower production of *Nassella* and *Avena* were analyzed using separate two-way ANOVAs in which the effects of *C. melitensis* and fungicide were tested.

RESULTS

AM and non-AM fungi were present in the roots of all three plant species, and the overall effect of benomyl significantly reduced AM fungi across all three species ($P = 0.018$) and in the roots of *C. melitensis* and *Avena* specifically (Tables 1 and 2). Non-AM fungi in the roots tended to decrease with benomyl treatments, but were not significantly affected across all species ($P = 0.268$) or for any species individually. Non-AM fungi were especially prevalent where root tissue came into contact with a layer of paper towel that was used at the bottom of pots to eliminate loss of soil through drainage holes, but we estimate that this situation affected <5% of the total root mass of our plants. Where roots grew through fragments of paper towels, aseptate hyphae proliferated in the debris and entered the roots, but did not form other types of fungal structures within the roots. Non-AM fungal sporangia were also present in large concentrations (>20%) in 5 of 50 plants, but across different species and treatments. All of these fungi were included in our non-AM fungi counts.

Untreated soil had negative effects on *C. melitensis* and *Avena*, relative to those species' growth in soil with fungicide applied, but had no direct effects on *Nassella*. When grown without grasses, *C. melitensis* plants were >50% smaller in untreated soils than in the fungicide treatment (Fig. 1, Table 3). There were similar significant effects on flower production (Table 3, data not presented). In the presence of *Nassella* the effect of fungicide treatment on *C. melitensis* was reversed, with *C. melitensis* growing 3.8 times larger (Fig. 1, Table 3) and producing 5.4 times as many flowers when grown in untreated soil with *Nassella* than when grown in untreated soil and no *Nassella* (Table 3). Also, *C. melitensis* was 1.6 times larger and produced almost twice as many flowers when grown with

TABLE 2. ANOVA for the effects of fungicide, species, and neighbors on AM and non-AM fungi in the roots of *Centaurea melitensis, Nassella pulchra*, and *Avena barbata*.

Effect	df	*F*	*P*
AM fungi			
Fungicide	1, 49	6.00	0.018
Species	2, 49	3.68	0.032
Neighbor	1, 49	0.75	0.391
F × S	2, 49	0.83	0.234
F × N	1, 49	1.29	0.284
S × N	2, 49	0.32	0.968
F × S × N	2, 49	0.41	0.960
Non-AM fungi			
Fungicide	1, 49	1.26	0.268
Species	2, 49	2.96	0.200
Neighbor	1, 49	2.50	0.120
F × S	2, 49	0.21	0.815
F × N	1, 49	0.61	0.805
S × N	2, 49	3.40	0.042
F × S × N	2, 49	1.77	0.087

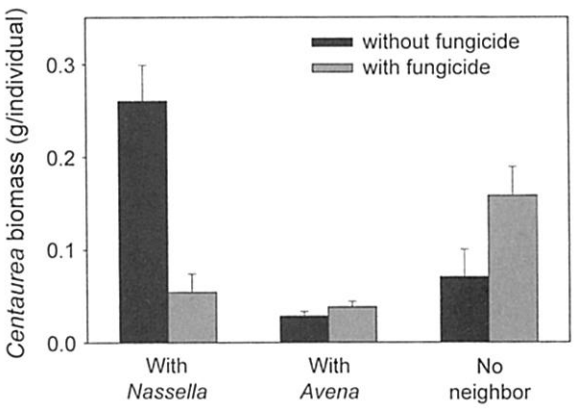

FIG. 1. Biomass of *Centaurea melitensis* when grown alone, with *Nassella pulchra*, or with *Avena barbata*, and either with or without benomyl (fungicide). See Tables 3 and 4 for ANOVA results. Error bars represent one standard error.

TABLE 3. ANOVA for the effects of *Nassella pulchra* and fungicide on *Centaurea melitensis* biomass and flower number.

Effect	df	MS	*F*	*P*
Biomass				
Nassella	1, 77	0.033	1.72	0.193
Fungicide treatment	1, 77	0.063	3.27	0.075
Nassella × fungicide	1, 77	0.405	21.93	0.001
Flower number				
Nassella	1, 77	7.31	6.56	0.012
Fungicide treatment	1, 77	3.16	2.88	0.094
Nassella × fungicide	1, 77	25.80	23.45	0.001

Note: In this test *Centaurea* grown alone was compared only to *Centaurea* grown with *Nassella*.

Nassella and in untreated soil, than when grown alone in the fungicide treatment. Taking another perspective, when *C. melitensis* was grown with *Nassella* and without fungicide it grew to be 4.9 times larger than when grown with *Nassella* in the fungicide treatment (Fig. 1, Table 3). When benomyl was applied, the presence of either *Nassella* or *Avena* caused large reductions in growth of *C. melitensis* with final biomasses of *C. melitensis* being approximately one-third and one-fourth, respectively, of that of *C. melitensis* when grown alone. The fungicide application did not affect *C. melitensis* biomass when it was grown with *Avena* (Fig. 1, Table 4).

The fungicide application in the presence of *C. melitensis* did not have a significant effect on the final biomass of either *Nassella* (Fig. 2, Table 5) or *Avena* (Fig. 3, Table 6), but when treatments with and without *C. melitensis* were combined, the application of the fungicide had a positive effect on the biomass and the flower production of *Avena*. The fungicide treatment did not change the outcome of the interaction between *C. melitensis* and *Avena* (no significant fungicide treatment by neighbor interactions). When fungicide and no-fungicide treatments were combined, *Avena* produced 30% more biomass and 38% more flowers in the presence of *C. melitensis* than in its absence (Fig. 3, Table 4).

TABLE 4. ANOVA for the effects of *Avena barbata* and fungicide on *Centaurea melitensis* biomass and flower number.

Effect	df	MS	*F*	*P*
Biomass				
Avena	1, 79	0.129	12.58	0.001
Fungicide treatment	1, 79	0.047	4.62	0.035
Avena × fungicide	1, 79	0.030	2.97	0.089
Flower number				
Avena	1, 79	3.43	5.37	0.023
Fungicide treatment	1, 79	3.16	2.88	0.094
Avena × fungicide	1, 79	2.39	1.88	0.217

Note: In this test *Centaurea* grown alone was compared only to *Centaurea* grown with *Avena*.

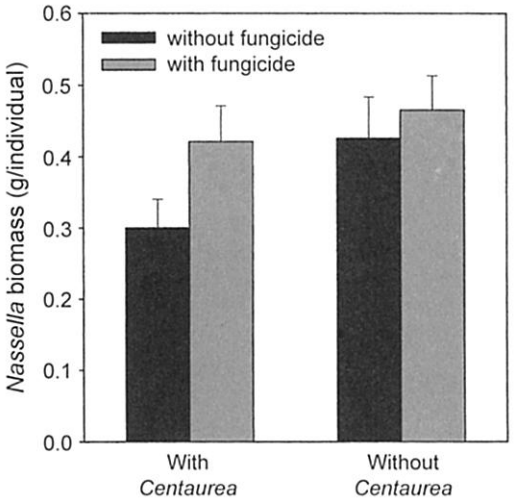

FIG. 2. Biomass of *Nassella pulchra* when grown alone or with *Centaurea melitensis*, and either with or without benomyl (fungicide). See Table 5 for ANOVA results. Error bars represent one standard error.

DISCUSSION

The overwhelming success of invasive plants in natural communities has been attributed to allelopathy and competitive ability (Callaway and Aschehoug 2000) and the absence of their consumers (Van Driesche and Bellows 1996). In our experiments, we found that the competitive dominance of the invasive *Centaurea melitensis* over the native *Nassella pulchra* was sharply reduced when AM fungi in the soil were reduced. Furthermore, when soil fungicide was applied, we found significant, direct, competitive effects of *Nassella* on *C. melitensis*. These plant–plant interactions were substantially different in untreated soil where the resident soil microbial community was intact. In the presence of both untreated soil fungi and *Nassella*, *C. melitensis* greatly increased in growth and flower production. Thus it appears that soil fungi are altering plant–plant interactions, and that indirect plant–fungus–plant interactions may affect dominance hierarchies among these species. These results support other experiments in which the presence of both *Nassella* and an intact resident soil microbial community (no fungicide) allowed *C. melitensis* to fully compensate for the removal of 30–90% of its aboveground biomass (at the time of defoliation) in just seven weeks (Callaway et al. 2001).

TABLE 5. ANOVA for the effects of *Centaurea melitensis* and fungicide on *Nassella pulchra* biomass.

Effect	df	MS	*F*	*P*
Biomass				
Centaurea	1, 72	0.141	3.40	0.069
Fungicide treatment	1, 72	0.102	2.48	0.120
Centaurea × fungicide	1, 72	0.018	0.43	0.515

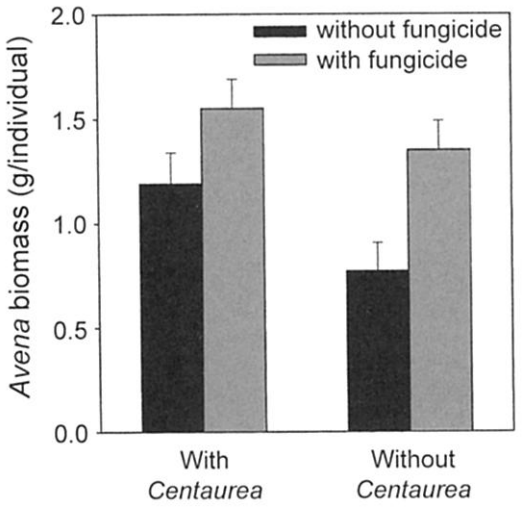

FIG. 3. Biomass of *Avena barbata* when grown alone or with *Centaurea melitensis*, and either with or without benomyl (fungicide). See Table 6 for ANOVA results. Error bars represent one standard error.

Understanding the complex interactions that produced the results of our experiments is limited because we do not know the specific mechanisms by which soil fungi regulated interactions among *Centaurea melitensis* and the grass species and because of the limitations inherent to fungicide application in greenhouse experiments. For example, even though benomyl reduced AM fungi more than non-AM fungi, we do not know how the fungicide altered the composition of the microbial community as a whole. Large compositional changes in either fungal or bacterial species with benomyl treatments could create conditions that are unrealistic in nature. Similarly, microbial communities that develop in soils in greenhouses may differ from those in natural soils.

We do not know the mechanism by which the growth of *C. melitensis* was enhanced in the presence of both soil fungi and *Nassella pulchra*, and at a cost to *Nassella*. We propose three different mechanisms for this result, which may not be mutually exclusive. First, work with other *Centaurea* species (Grime et al. 1987, Marler et al. 1999, E. V. Carey and R. M. Callaway, *unpublished manuscript*) suggests that *Centaurea* may benefit from a form of soil fungi-mediated parasitism in which fixed carbon or other resources are transferred from the grasses to the *Centaurea* via a common network of AM fungi. Our results for *C. melitensis* and *Nassella pulchra* are consistent with this hypothesis. Our results are also consistent with the hypothesis that different combinations of plant species may change the composition of the microbial community, by shifts in the composition of the total fungal community (see Bever 1994, Bever et al. 1997), or by shifts in the composition of AM fungal communities (Johnson et al. 1997, Egerton-Warburton and Allen 2000). Our benomyl treatments greatly increased the relative proportion of non-AM to AM fungi in the roots of all species. This may have been because most basidiomycete fungi are unaffected by benomyl and may have increased after the addition of the fungicide. A third possibility is that *Nassella* may have strong positive effects on the growth of soil fungi, but the benefit of soil fungi to *Nassella* is less than the benefit of soil fungi to *Centaurea*. Regardless of the specific mechanism, our results clearly indicate that the particular pairing of plant species can significantly alter the way soil biota affect plant–plant interactions. Even though the mechanisms for this response are not clear, we found that soil fungi enhanced the negative effect of the invasive forb, *Centaurea melitensis*, on the native bunchgrass, *Nassella pulchra*, but that soil fungi had negative effects on *C. melitensis* when *Nassella* was not present.

Centaurea melitensis' apparent inability to competitively dominate *Avena barbata* in soil with intact resident microbial communities, as *C. melitensis* did with *Nassella*, may be due to *Avena* having a different relationship with soil fungi than *Nassella*, although this is speculative at this point. *Avena*, as many grass species, may be facultative in its mycorrhizal relationships. Hartnett et al. (1993) and Hetrick et al. (1989) have demonstrated shifts in plant species composition in fungicide-treated tallgrass prairies that were attributed to the host plant's differential responses to the presence of AM fungi. It is also possible that *Avena*, which co-occurs with *C. melitensis* in many places in Europe (R. Callaway, *personal observation*), has evolved effective mechanisms to prevent the formation of hyphal linkages or has evolved a low susceptibility to fungal pathogens that thrive in the rooting zone of *Centaurea*.

Marler et al. (1999) found similar, but less pronounced, interactions among *Centaurea maculosa*, *Festuca idahoensis*, and soil fungi from invaded grasslands in the northern Rocky Mountains. In other experiments with stable isotopes, *C. maculosa* leaves appeared to acquire up to 15% of their carbon from neighboring *Festuca*, and in the same experiments *C. maculosa* grew larger in the presence of *Festuca* and soil fungi than with fungi alone (E. V. Carey and R. M.

TABLE 6. ANOVA for the effects of *Centaurea melitensis* and fungicide on biomass and flower number of *Avena barbata*.

Effect	df	MS	*F*	*P*
Biomass				
Centaurea	1, 79	2.00	4.52	0.037
Fungicide treatment	1, 79	4.72	10.64	0.002
Centaurea × fungicide	1, 79	0.05	0.12	0.726
Flower number				
Centaurea	1, 78	305.0	5.08	0.027
Fungicide treatment	1, 78	818.5	13.62	0.001
Centaurea × fungicide	1, 78	29.1	0.48	0.489

Callaway, *unpublished manuscript*). Another experiment, however, found no evidence for the transfer of a ^{13}C label from *F. idahoensis* to *C. maculosa* (Zabinski et al., *in press*). Carbon transfer among plants via soil fungi remains controversial (Robinson and Fitter 1999), but a number of other studies have provided evidence for interspecific carbon transfer (Francis and Read 1984, Grime et al. 1987, Moora and Zobel 1996, Watkins et al. 1996, Simard et al. 1997). However, none of these studies have been able to quantify carbon transfer at the level that would account for such significant differences in biomass as was seen between *Centaurea* growing with *Nassella* with vs. without fungicide. In many of these experiments, as in ours, fungicide treatments may have affected mutualistic, pathogenic, and saprophytic fungi, as well as AM fungi.

We found no effects of soil fungal treatments on the biomass of *Nassella* in the absence of *Centaurea*, but the final biomass of *Nassella* tended to be less in the presence of both soil fungi and *C. melitensis*. Although this tendency was not statistically significant, the trend toward reduction in *Nassella* biomass corresponds quantitatively with the enhancement of *C. melitensis* biomass when it was grown with untreated soil fungi and *Nassella* together, and is consistent with all three of our mechanistic hypotheses. The lack of a statistically significant effect of *C. melitensis* and AM fungi on *Nassella* biomass may have been due to our experimental approach in which the grasses were grown for seven weeks prior to the addition of *C. melitensis* plants.

Avena responded much differently than *Nassella* to the fungicide treatments in the presence of *C. melitensis*. Untreated soil fungi had a negative effect on *Avena* biomass and reproduction independently of *C. melitensis*. However, with or without fungicide, *Avena* plants grew larger and produced more flowers in the presence of *C. melitensis* than in its absence. This positive response of *Avena* to *C. melitensis* is difficult to interpret, but our results clearly indicate that *Avena* is capable of benefiting from the presence of *C. melitensis*, at least under the conditions of our experiment.

Soil fungicide had strong positive effects on the growth and reproduction of *C. melitensis* when this invasive species was grown alone. Negative effects of soil fungi may have been due to pathogenic fungal species being favored over mutualistic species in the absence of a grass, or by increases in the relative strength of the pathogenic effects of mycorrhizal species (Johnson et al. 1997). This result differs from the results of experiments with *Centaurea maculosa*, in which the direct effects of soil fungi on the weed were either insignificant or weak (Marler et al. 1999; E. V. Carey and R. M. Callaway, *unpublished manuscript*).

Whatever the reason for the difference in the effect of *C. melitensis* on *Nassella* vs. that on *Avena*, it has implications for the invasion of California grasslands by *C. melitensis*. Caution is necessary when extrapolating our results from greenhouse conditions and fungicide applications to natural processes in the field, but our results raise the possibility that soil fungi may contribute to the success of *C. melitensis* invading grasslands dominated by *Nassella*, but that invasion of grasslands dominated by *Avena* may be resisted. Further experiments such as the addition of specific AM species, manipulation of AM and non-AM fungi separately, and extension of these experiments to the field are needed to understand the mechanisms behind our results. However, our findings contribute to the rapidly expanding body of literature pointing to the importance of interactions between plants and soil microbes as determinants of plant community structure and diversity.

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