Evidence of Qualitative Differences between Soil-Occupancy Effects of Invasive vs. Native Grassland Plant Species

Authors: Jordan, Nicholas R., Larson, Diane L., and Huerd, Sheri C.

Source: Invasive Plant Science and Management, 4(1) : 11-21

Published By: Weed Science Society of America

URL: https://doi.org/10.1614/IPSM-D-10-00004.1

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Invasive-Plant-Science-and-Management on 27 Jun 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Invasive Plant Science and Management 2011 4:11–21

Evidence of Qualitative Differences between Soil-Occupancy Effects of Invasive vs. Native Grassland Plant Species

Nicholas R. Jordan, Diane L. Larson, and Sheri C. Huerd*

Diversified grasslands that contain native plant species are being recognized as important elements of agricultural landscapes and for production of biofuel feedstocks as well as a variety of other ecosystem services. Unfortunately, establishment of such grasslands is often difficult, unpredictable, and highly vulnerable to interference and invasion by weeds. Evidence suggests that soil-microbial ''legacies'' of invasive perennial species can inhibit growth of native grassland species. However, previous assessments of legacy effects of soil occupancy by invasive species that invade grasslands have focused on single invasive species and on responses to invasive soil occupancy in only a few species. In this study, we tested the hypothesis that legacy effects of invasive species differ qualitatively from those of native grassland species. In a glasshouse, three invasive and three native grassland perennials and a native perennial mixture were grown separately through three cycles of growth and soil conditioning in soils with and without arbuscular mycorrhizal fungi (AMF), after which we assessed seedling growth in these soils. Native species differed categorically from invasives in their response to soil conditioning by native or invasive species, but these differences depended on the presence of AMF. When AMF were present, native species largely had facilitative effects on invasive species, relative to effects of invasives on other invasives. Invasive species did not facilitate native growth; neutral effects were predominant, but strong soil-mediated inhibitory effects on certain native species occurred. Our results support the hypothesis that successful plant invaders create biological legacies in soil that inhibit native growth, but suggest also this mechanism of invasion will have nuanced effects on community dynamics, as some natives may be unaffected by such legacies. Such native species may be valuable as nurse plants that provide cost-effective restoration of soil conditions needed for efficient establishment of diversified grasslands.

Key words: Plant–soil feedback, biofuel, nurse plants, arbuscular mycorrhizal fungi, invasion ecology, soil legacy, invasive plants.

In grassland agroecosystems, perennial weed invasions may be strongly affected by plant–soil biota interactions (Hallett 2006; Raizada et al. 2008; Reinhart and Callaway 2006; Wolfe and Klironomos 2005). In particular, site occupancy by invasive plant species may have strong soil-mediated ''legacy'' effects that influence subsequent plant invasion dynamics. Recent comparative studies have revealed that invasive species appear to experience, on average, less-negative effects from root-zone soil microbe communities than do natives (Kulmatiski et al. 2008), which may experience intense negative feedback from these microbes (Petermann et al. 2008). This evident difference in plant–soil interactions between invasive and native species implies that invasives may be capable of particularly strong soil-legacy effects, as the result of prolonged site occupancy by invasives resulting in changes to multiple attributes of soils.

Documented modifications of the biotic composition of soil on invaded sites include effects on soil food webs (Duda et al. 2003), total soil microbial communities (Kourtev et al. 2002), and mutualistic fungi (Allen et al. 2003; Hawkes et al 2006). Effects on physical or chemical attributes of soil include modification of inputs and cycling of nitrogen (N) and other elements (Ehrenfeld 2003; Haubensak et al. 2004; Hawkes et al. 2005; Sperry et al. 2006), soil organic matter and aggregation (Saggar et al. 1999), and pH (Kourtev et al. 2002), as well as release of allelopathic substances (Thorpe et al. 2009).

DOI: 10.1614/IPSM-D-10-00004.1

* First and third authors: Professor and Research Scientist, Agronomy and Plant Genetics Department, University of Minnesota, 1991 Buford Circle, St. Paul MN 55108; second author: Research Wildlife Biologist, U.S. Geological Survey, Northern Prairie Wildlife Research Center, 1561 Lindig St., St. Paul, MN 55108. Corresponding author's E-mail: jorda020@umn.edu

Interpretive Summary

In the Midwestern United States, regulatory, market, and policy pressures could convert large areas from annual agriculture to seminatural grassland agroecosystems, e.g., as part of a national effort to produce energy crops. Native grassland perennials could be used in these grasslands to reduce production costs, conserve soil quality, conserve native biodiversity, and enhance carbon sequestration in grassland agroecosystems. However, producer interest in seminatural grassland systems is reduced by current difficulties in reliable and cost-effective establishment of these species, and weed management during establishment is a major concern. Many lines of evidence suggest that weedy exotic species can alter soils physically, microbially, or both, creating a “legacy: that persists after control or removal of these species. This legacy effect may contribute significantly to the risk of additional weed invasion and poor performance of desirable species during grassland establishment. We examined such legacy effects of smooth brome, crested wheatgrass, and leafy spurge, three exotic perennials that are highly invasive in grasslands. These species had strong inhibitory legacy effects on certain native species, but other native species were unaffected. We found that native species did not have inhibitory legacy effects, suggesting that managers should expect that successful plant invaders may leave soil legacies that will inhibit native growth in the establishment phase. We found that some natives were unaffected by such legacies, and these particular species may be valuable as “nurse plants” or cover crops that provide cost-effective conditioning of soils, thereby restoring soil conditions needed for efficient establishment of desirable native species.

These effects of invasive species on soils will be significant to plant invasion if they confer a specific advantage to invasive relative to native species. Such advantages have been observed (Corbin and D’Antonio 2004; Ehrenfeld 2003; Jordan et al. 2008; Ortega and Pearson 2005; Richardson et al. 2000). For example, the invasive forb leafy spurge (*Euphorbia esula* L.) transforms the biotic composition of soil to its own advantage (Klironomos 2002), causing growth reduction in several prairie forbs at the seedling stage (Jordan et al. 2008). Similar effects have been observed in other invasive species (Allen et al. 2003; Bray et al. 2003; Callaway et al. 2003; Hawkes et al 2006; Stinson et al. 2006). Invasive species may also have soil-mediated facilitative effects on other invasive species (Jordan et al. 2008).

Additionally, invasive plant species may be less dependent than native species on mutualistic interactions with soil microbiota. For example, invasives may become less dependent on AMF mutualism than conspecifics in the native range (Seifert et al. 2009). AMF are “keystone” root symbionts with a wide range of effects on plant physiology and ecology (Smith and Read 1997) and many North American tallgrass prairie species are highly dependent on AMF (Wilson and Hartnett 1998) for growth and reproduction.

Based on emerging evidence of qualitative functional differences between invasives and natives in plant–soil biota interactions, we propose that there are qualitative differences between soil-legacy effects of invasive and native grassland species, such that soil-mediated effects of invasives on natives differ from the reciprocal effects. Specifically, we hypothesize that (1) soils conditioned by invasives have neutral or facilitative effects on conspecifics and other invasives while exerting negative effects on natives and (2) soils conditioned by natives have negative effects on conspecifics and positive or neutral effects on nonconspecific natives and invasives.

To address these hypotheses, we compared soil-legacy effects of previous soil occupancy by multiple invasive and native species in a single experimental study. Most previous assessments of legacy effects of soil occupancy by invasive species have focused on effects of a single invasive species and have examined responses to soil modifications by only a few native species, exotic species, or both. We conducted an extensive experimental comparison of interspecific effects on growth, mediated by soil occupancy, among a group of co-occurring native and invasive species from the mixed-grass prairie grassland communities of North America. We focused on legacy effects mediated by AMF, given the importance of these fungi in grassland plant communities (Hartnett and Wilson 2002). All native and invasive species examined are mycorrhizal (Wilson and Hartnett 1998, Carey et al. 2004). We estimated effects of soil occupancy by three exotic invasive species: smooth brome (*Bromus inermis* Leyss.; hereafter all species will be referred to by genus), crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.], and leafy spurge (*E. esula*). All are “strong invaders” (Ortega and Pearson 2005), able to become community dominants and to form nearly monospecific stands in invaded grasslands. We derived species-specific profiles of growth response to soil occupancy by other species, which allowed us to evaluate our hypothesis that exotic species differed categorically from natives in soil-mediated legacy effects on other species (Jordan et al. 2008).

Materials and Methods

Study Species and Field Sites. Soils were gathered from each of three nature reserves. In each reserve, a particular invasive species was especially problematic, although all reserves are located within the North American range of all three invasive species. Thus, *Bromus* dominated at Lostwood National Wildlife Refuge (NWR) in North Dakota (48°34′N, 102°26′W); *Agropyron* dominated at Medicine Lake NWR, Montana, (48°59′N, 104°26′W); and *Euphorbia* dominated at Theodore Roosevelt National Park (TRNP), North Dakota (46°59′N, 103°33′W).

Three areas of native vegetation at each reserve were selected and roughly 90 L (24 gal) of soil from the top 15 cm (5.9 in) was harvested per area, gathering equal quantities from six separate sampling points chosen haphazardly in each area. Soil was placed in large containers and plant material and stones were removed. Sampled soils from each reserve were stored in cool (< 25 C [77 F]) conditions and covered to prevent drying during the 4-d sampling period. Soils harvested from Lostwood NWR and Medicine Lake NWR were typic Argiustolls, mainly loam/sandy loam in texture (assessed via hydrometer method outlined in Day 1965). Soils from TRNP were Aridic Ustorhents, mainly loam, clay loam, or sandy loam.

Glasshouse Experiments. Experiments were conducted in a glasshouse on the University of Minnesota campus, St. Paul, MN, from July 2003 to November 2004. At the inception of the experiment, two soil-biotic treatments were imposed, pasteurized (−AMF) and not pasteurized (+AMF). Half of the field soil from each reserve was steam-pasteurized to kill all field soil biota by steaming twice (24 h apart) for 40 min at 80 C, followed by a 20-min aeration to mitigate nitrogen accumulation (modified from Burrows and Pfleger 2002). Soils were mixed 1 : 1 soil : pasteurized sand and placed in 2.5-L pots, keeping soils from each reserve separate. To create the −AMF treatment, we added a ''microbial wash'' to each pot (using methods of Koide and Li 1989); this was an aqueous suspension created by shaking. The inoculum wash was prepared by shaking 20 g (0.7 oz) of each soil ''inoculum'' from each reserve in 1 L distilled water for 10 min. The suspension was passed through an 11-µm filter to exclude spores and other AMF propagules. Pots were inoculated with 20 ml of the filtered suspension (Burrows and Pfleger 2002). This suspension serves to inoculate pasteurized soils with soil microbes smaller than AMF, including fungal pathogens. It reliably reduces differences in non-AMF soil microbial communities between pasteurized and non-pasteurized treatments, so that these treatments can be interpreted as −AMF and +AMF treatments, respectively.

Effects of soil occupancy by plant species and mixtures were estimated by creating soil ''conditioning'' treatments in three separate soils, collected from nature reserves as above. Each soil was conditioned by natives alone and in mixture, as well as by the invasive plant species that was dominant at the respective soil collection site (e.g., *Bromus* was used in soils from Lostwood NWR). In each soil, five soil conditioning treatments were established in 16 replicates: (1) monoculture invasive (species specific to soil collection site), (2) monoculture *Stipa viridula* Trin, (3) monoculture *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths, (4) monoculture *Linum perenne* L. var. *lewisii* (Pursh) Eat. & Wright, and (5) mix of six native species (*Stipa*, *Bouteloua*, *Linum*, *Aster ericoides* L., *Koeleria macrantha* (Ledeb.) Schult., and *Ratibida columnifera* (Nutt.) Woot. & Standl. (nomenclature according to Great Plains Flora Association 1986). Seeds of *Bromus, Agropyron,* and *Euphorbia* were collected at sites of soil collection; seeds of native species were purchased[1]; all native seed was sourced from within the ecoregion of the three soil collection sites and occurred at sites where we sampled.

Soil conditioning treatments were repeated through three 3-mo growth cycles (I: July 28, 2003, to November 10, 2003; II: February 25, 2004, to May 17, 2004; III: June 21, 2004, to August 20, 2004) with cold treatments (∼ 4 C) in between. All conditioning treatments began with 15 to 20 established seedlings per pot and produced abundant aboveground biomass (with the sole exception of *Linum* in the −AMF treatment, as noted below). Aboveground biomass produced in each growth cycle was harvested by pot at the end of each cycle, as was any litter. Pots that lacked regrowth of the conditioning species were reseeded after each of the first two cycles. The conditioning treatments were imposed in a glasshouse with 400-watt high-pressure sodium lamps used for supplemental lighting (14- to 16-h day length) from September to May. Average summer glasshouse temperatures were 27/23 C (day/night); spring and fall temperatures were 21/19 C. Pots were watered as needed. Osmocote 14–14–14[2], a slow-release fertilizer, was added at the start of the second growth cycle (1.25 g pot^{-1}). Pots containing soils from a given collection site were held on adjacent glasshouse benches with no intermingling during the first two growth cycles. In the third cycle, all pots were combined in a randomized complete-block design. A final growth cycle (September 15, 2004, to November 19, 2004) was used to assess effects of treatments on seedling growth. Prior to this cycle, all pots were frozen at ∼ 4 C to eliminate regrowth; crowns that did regrow were pinched back.

In the final cycle, half of each pot was planted with six native and half with six invasive species in a fixed pattern (Figure 1); consequently, the experimental unit for growth responses is a sowing position within a pot conditioned by a given species. Seedlings were thinned to one plant per species per pot. Invasives were *Bromus, Agropyron, Euphorbia, Cirsium arvense* (L.) Scop., *Centaurea maculosa* Lam., and *Poa pratensis* L.; natives were *Stipa, Bouteloua, Linum, Aster, Koeleria,* and *Ratibida. Centaurea* seed was obtained from R. Callaway, University of Montana; *Cirsium* seeds were collected in Ramsey County, MN; and *Poa* was obtained from the University of Minnesota. Pots were monitored for regrowth from perennating structures remaining in the soil. Little regrowth occurred; it was clearly distinguishable from emerged seedlings and was immediately removed by pinching upon observation. After 12 wk, shoot biomass was harvested; at this time,

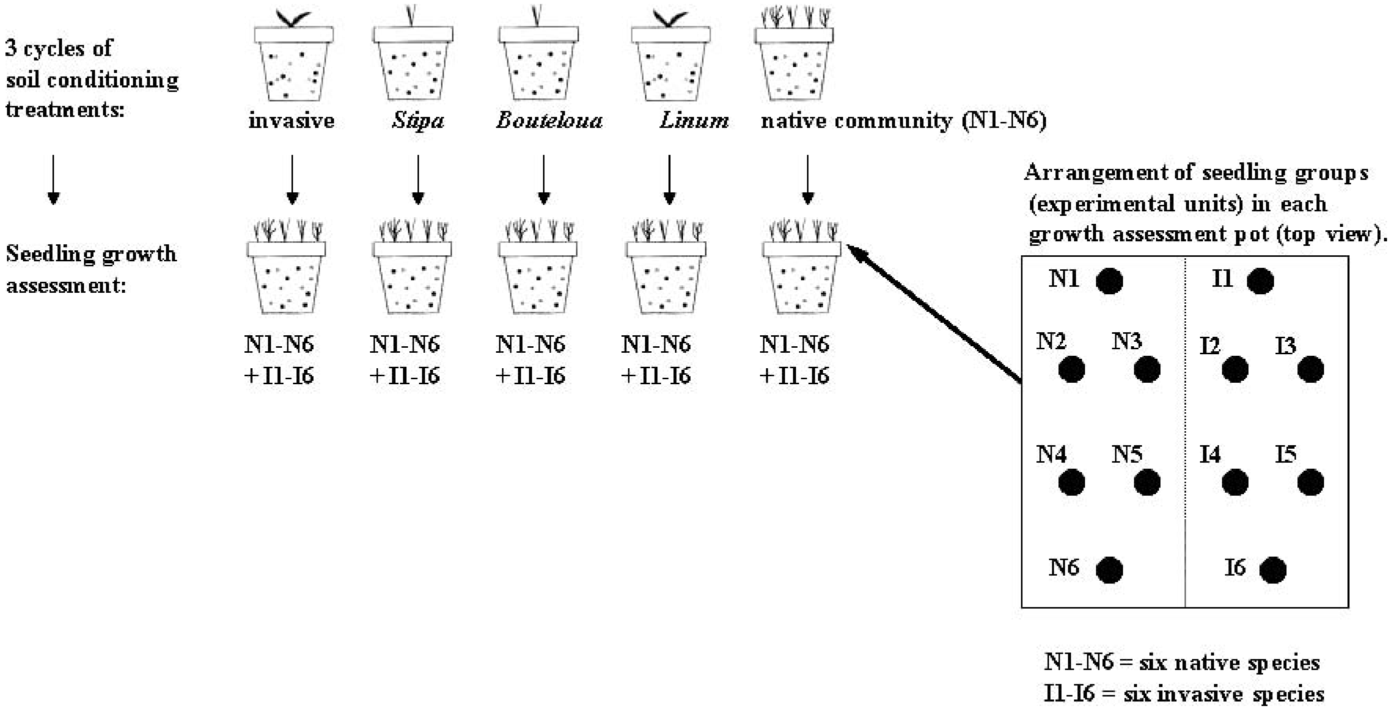

Figure 1. Protocol for estimating effects of soil conditioning by individual invasive species (*Agropyron* [I1], *Bromus* [I2], and *Euphorbia* [I3]), individual native species (*Stipa* [N1], *Linum* [N2], and *Bouteloua* [N3]), and native mixture (*Stipa*, *Bouteloua*, *Linum*, *Aster ericoides* [N4], *Koeleria macrantha* [N5], and *Ratibida columnifera* [N6]). Seedling growth was assessed on six native species (N1 to N6) and six invasive species (I1 to I3 and *Cirsium arvense* [I4], *Centaurea maculosa* [I4], and *Poa pratensis* [I6]; NB, *Aster* (N4) and *Koeleria* (N5) were removed from final analysis. Soil conditioning treatments were applied to each of three soils collected from separate prairie nature reserves as noted in text; each soil was conditioned by natives alone and in mixture, and by the single invasive species that was most dominant at the respective soil collection site. Diagram depicts conditioning treatments applied to one of the three soils.

seedlings of each species were small and well separated from other species in each pot; seedlings were assumed to not interact with other seedlings. For four replicates, soil samples were taken for N and pH, and for these four and one additional replicate, total plant biomass (root and shoot) was harvested for all seedlings. Plants were dried at 60 C for 3 to 7 d and weighed. N (nitrate and ammonium) was determined by a 2-M KCl extraction of 5 g of soil (Robertson et al. 1999). Extracts were analyzed on an OI Corporation SF3000 autoanalyzer.[3] Soil pH was measured electrometrically. Equal amounts of soil and neutralized nanopure water were mixed 1 : 1 and allowed to equilibrate for 30 min. The supernatant was decanted and allowed to resettle for 30 min, the pH of the supernatant was then measured once with an electrode (Robertson et al. 1999).

By comparing seedling biomass production in experimental units originally containing pasteurized or unpasteurized soil and non-AMF soil microbes introduced by a filtrate, we sought to assess species-specific effects of soil conditioning in the presence of AMF indigenous to reserves where each species had invaded, and in the absence of AMF in the control soils. During the three glasshouse growth/vernalization cycles, various soil organisms undoubtedly colonized our experimental soils. However, there was likely little AMF colonization of control soils during the experiment, as we observed no AMF colonization in plants grown in a separate validation experiment (below, and Table 1).

Statistical Methods. We examined effects on each response species of three covariates that could be expected to confound the results of our analysis: soil nitrate (μg N g^{-1} soil), ammonium (μg N g^{-1} soil), and pH. Beginning with the most complete model (one that included all covariates in combination with each explanatory variable), we sequentially removed the highest-level interaction if it was not significant.

For the most part, soil covariates did not influence the results of our experiment; only growth of *Bromus, Koeleria*, and *Aster* had significant interactions with soil variables. Of these, *Bromus* seedling biomass was influenced by both pH and nitrate, but there were no significant interactions between these variables and our measures of plant performance of interest, so the means we report below simply take into account the effects of the covariates.

Table 1. Arbuscular mycorrhizal colonization from greenhouse experiments for soils with arbuscular mycorrhizal fungi (+AMF) from three prairie nature reserves. Estimated colonization rates are mean percentages of observed root samples that contained AMF ± 1 SE. No colonization was observed in pots not receiving AMF inoculum (−AMF). Colonization of invasive species (*Bromus*, *Agropyron*, and *Euphorbia*) was assessed only in soil from nature reserve where that species was particularly abundant.

	Site[a]		
Species	Lostwood NWR	Medicine Lake NWR	TRNP
Bromus inermis	7.8 ± 5.34	—	—
Agropyron cristatum	—	4.7 ± 2.34	—
Euphorbia esula	—	—	47.3 ± 7.05
Aster ericoides	27.1 ± 2.83	24.3 ± 6.14	27.9 ± 4.09
Bouteloua gracilis	9.7 ± 3.02	7.9 ± 2.09	10.0 ± 2.65
Koeleria macrantha	10.6 ± 4.80	6.6 ± 2.32	7.3 ± 2.67
Linum perenne	28.7 ± 4.67	21.0 ± 4.63	35.2 ± 7.44
Ratibida columnifera	36.8 ± 6.06	28.6 ± 1.31	53.1 ± 6.64
Stipa viridula	6.8 ± 1.98	11.2 ± 4.82	7.5 ± 2.55

[a] Abbreviations: NWR, National Wildlife Refuge; TRNP, Theodore Roosevelt National Park.

Koeleria had a significant pH by treatment interaction. Seedling biomass was unrelated to pH if AMF were present ($r = 0.19$, $P = 0.15$), but biomass had a weak positive relationship with pH ($r = 0.31$, $P = 0.02$) when AMF were absent. All three covariates influenced the response of *Aster* in a variety of two- and three-way interactions that are not possible to interpret without further experiments aimed directly at soil characters. Because of these interactions with covariates, we removed *Koeleria* and *Aster* from further analysis.

Species for which covariates were interpretable were then analyzed using the Mixed procedure in SAS 9.2[4] to examine effects of the conditioning species and soil treatment (+AMF or −AMF) on seedling biomass of each tested species. Both plant species and soil were fixed effects, whereas the bench within the greenhouse was a random effect. Conditioning species varied depending on identity (native or invasive) of the response species. For native species, conditioning species included native (mean of individual native species conditioning in separate treatments), *Bromus, Euphorbia*, *Agropyron*, and the native mixture (in which six native species were planted together in a single pot for conditioning). For invasive species, conditioning species included invasive (mean of individual invasive species conditioning in separate treatments), *Linum, Bouteloua, Stipa*, and the native mixture. Our analysis contrasted the responses of individual native and exotic plant species to these soil conditioning treatments. We were particularly interested in the effects of conditioning by invasive species on native species and vice versa. Accordingly, for each native species, we compared biomass production in three soils (each originally collected from the three nature reserves and each conditioned by one of the three invasive conditioning species) to the mean biomass production across the same three soils, each conditioned by three native species and by the native species mixture, after examining plots of individual conditioning effects to insure that no individual-species effects were dominating the native-species means. Similarly, for exotic species, we compared biomass performance in soil conditioned by each of three native species to the mean performance in soil conditioned by three invasive species and by the native species mixture. These comparisons allowed us to test the hypothesis that exotic invasives have effects on natives that differ from the average effect of natives on natives, and the converse hypothesis. Thereby, we addressed the key knowledge gap motivating our study: comparing legacy effects of previous soil occupancy by multiple invasive and native species in a single experimental study. These comparisons produced species-specific profiles of response to soil conditioning by other species. These profiles allowed us to evaluate our hypothesis that these native and exotic species differed categorically in their response to soil conditioning by native or invasive species. Means were compared using Fisher's Protected LSD test. All significance tests were conducted at $\alpha = 0.05$.

Assessment of AMF Colonization. Sampled soils used for the main experiment (above) from each reserve (Lostwood, Medicine Lake, and TRNP) and soil treatment (+AMF or −AMF) were used to assess AMF colonization of selected species. Soils were mixed 1 : 4 soil : pasteurized sand and placed in 656-ml pots. Seeds of *Agropyron, Bromus*, and *Euphorbia* were planted into soils from Lostwood, Medicine Lake, and TRNP sites, respectively (as in the main experiment), and natives used in the main experiment (*Stipa, Bouteloua, Linum, Aster, Koeleria,* and *Ratibida*) were planted in all three soils; all species were thinned to one seedling per pot, with four replicates. Pots were blocked by replicate and grown in the same greenhouse as the first cycle of the main experiment above (July 28, 2003, to October 1, 2003). A microbial wash was applied at the same time as for the larger experiment above. After 10 wk, whole plants were harvested, dried at 60 C for 3 to 7 d, and stored for weighing and AMF assessment. Dried roots were subsampled and stained with aniline blue (modified from Grace and Stribley 1991). To assess mycorrhizal infection and the status of the control pots, the presence or absence of AMF was visually determined by looking for hyphae, arbuscules, and vesicles using a light microscope at ×200 magnification and an adaptation of the magnified intersections method (McGonigle et al. 1990). These assessments verified that pasteurization of inocula prevented AMF colonization, establishing a major difference in microbial composition between these soil treatments: substantial AMF colonization levels were observed across soil collection sites for native plants grown in +AMF soils, whereas we invariably observed no colonization in plants grown in −AMF soils (Table 1).

Results and Discussion

Consistent qualitative differences were evident between exotic and native species in response to repeated rounds of soil conditioning, but these differences depended on whether AMF were present (conditioning treatment by species type by AMF interaction, $F = 4.95$; df = 1, 60; $P = 0.030$). Thus, the effects of AMF were contingent on the identity of the responding species and the main effect of AMF was marginally nonsignificant ($F = 3.46$; df = 1, 45; $P = 0.069$). In soil with AMF, the biomass of all invasive species was greatest in soils conditioned by the three individual native species or by the native mixture, whereas biomass production by invasives was lower in soils conditioned by invasives. Seedling growth of exotic species was generally facilitated by soils conditioned by natives: five of the six exotic species had greater biomass ($P < 0.05$, preplanned comparisons in single-species ANOVA) in soils conditioned by at least two of the three individual native species used for soil conditioning (Figure 2). Native species frequently facilitated invasive species growth by more than 100%, relative to mean performance in soils conditioned by exotics (Figure 2). In contrast, for four of the six exotic species, the native species mixture did not have a facilitative effect on seedling growth. In pasteurized (−AMF) soils, facilitative effects of native species on exotic species were converted to neutral effects relative to invasive effects on these invasive species, and thus the general level of native facilitation on invasive biomass production was much weakened (Figure 2). In −AMF experimental units, maximum biomass production by all exotic species occurred in response to conditioning by *Linum*, which itself produced very little biomass in the absence of AMF. We note that N levels in these units were not anomalously high relative to other treatments (Table 2), suggesting that the observed exotic growth responses do not simply reflect high N levels in these units.

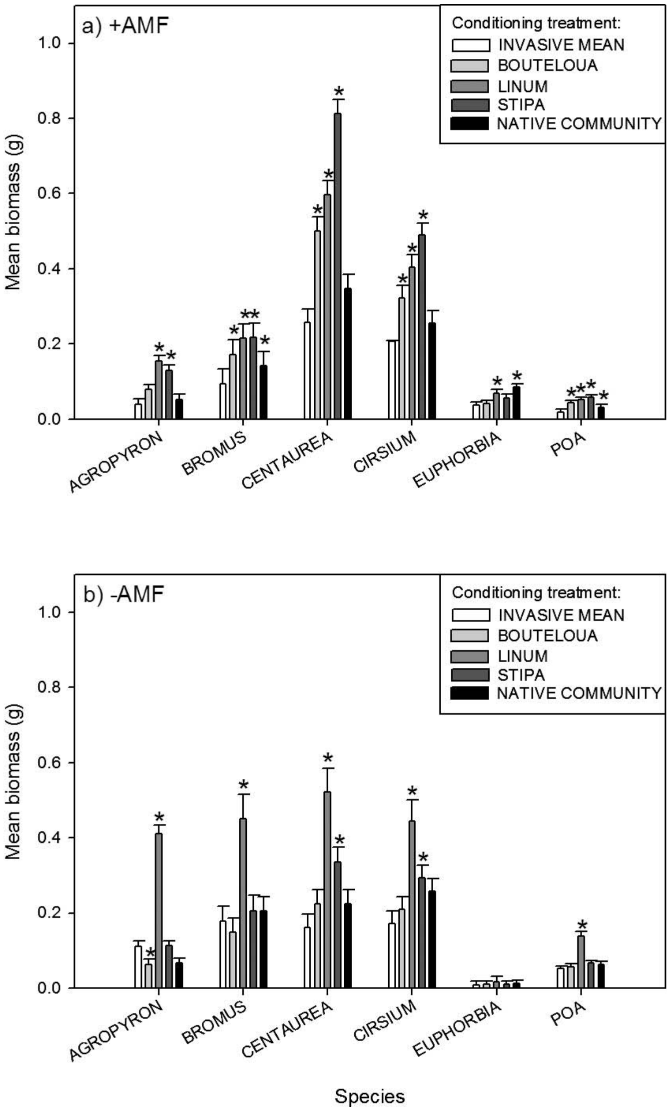

Figure 2. Mean aboveground biomass production by invasive species in soils conditioned by invasive and native species and by a native species mixture, in soils with AMF (+AMF; field soil + microbial wash) or without AMF (−AMF soil; pasteurized soil + microbial wash). All means are based on growth in three soils collected from separate prairie nature reserves as noted in text. Asterisks denote significant differences ($P < 0.05$, preplanned comparisons in single-species ANOVA) between a native-species conditioning treatment and mean biomass production in soil conditioned by three invasive species.

Although native species generally facilitated the growth of exotics in the presence of AMF, the reciprocal effect—facilitation of aboveground biomass production of native species by invasive species, relative to mean performance in soils conditioned by natives—was not observed (with a

Table 2. Nitrate, ammonium, and pH (mean ± SE, $n = 4$) soil measurements for each collection site/conditioning species and mycorrhizal treatment combination used in this study. Soils conditioned by invasive species are labeled by collection site, i.e., Lostwood soils were conditioned by *Bromus*, Medicine Lake soils by *Agropyron*, and TRNP by *Euphorbia*.[a]

			Site		
Soil measurement	Conditioning species	AMF treatment	Lostwood NWR	Medicine Lake NWR	TRNP
Nitrate (μg N g^{-1} soil)	Invasive	+AMF	4.6 ± 1.39	4.1 ± 0.66	3.1 ± 0.30
	Invasive	−AMF	3.5 ± 0.67	3.1 ± 0.32	3.6 ± 0.18
	Stipa	+AMF	4.2 ± 0.64	4.9 ± 1.65	3.8 ± 0.40
	Stipa	−AMF	5.8 ± 1.92	3.1 ± 0.27	4.4 ± 0.63
	Bouteloua	+AMF	3.7 ± 0.58	3.1 ± 0.34	3.7 ± 0.20
	Bouteloua	−AMF	3.7 ± 0.33	4.4 ± 1.07	3.9 ± 0.06
	Linum	+AMF	3.1 ± 0.20	3.3 ± 0.11	4.0 ± 0.31
	Linum	−AMF	4.6 ± 1.61	4.6 ± 2.11	3.5 ± 0.25
	Native community	+AMF	3.6 ± 0.47	3.4 ± 0.24	3.3 ± 0.26
	Native community	−AMF	3.8 ± 0.21	3.0 ± 0.31	3.5 ± 0.30
Ammonium (μg N g^{-1} soil)	Invasive	+AMF	3.0 ± 0.66	2.4 ± 0.19	2.7 ± 0.13
	Invasive	−AMF	2.1 ± 0.05	1.9 ± 0.42	1.8 ± 0.07
	Stipa	+AMF	2.4 ± 0.10	3.9 ± 1.55	2.1 ± 0.05
	Stipa	−AMF	2.1 ± 0.10	1.9 ± 0.11	1.9 ± 0.02
	Bouteloua	+AMF	2.5 ± 0.24	2.2 ± 0.09	2.7 ± 0.32
	Bouteloua	−AMF	2.7 ± 0.63	1.7 ± 0.08	1.1 ± 0.17
	Linum	+AMF	2.5 ± 0.23	2.1 ± 0.09	2.5 ± 0.09
	Linum	−AMF	1.7 ± 0.12	1.4 ± 0.02	1.6 ± 0.08
	Native community	+AMF	2.8 ± 0.16	2.6 ± 0.21	2.6 ± 0.41
	Native community	−AMF	2.3 ± 0.06	2.0 ± 0.10	2.0 ± 0.23
pH	Invasive	+AMF	7.8 ± 0.07	7.9 ± 0.22	8.1 ± 0.07
	Invasive	−AMF	7.7 ± 0.11	7.9 ± 0.09	8.5 ± 0.03
	Stipa	+AMF	8.1 ± 0.15	7.9 ± 0.10	8.1 ± 0.07
	Stipa	−AMF	7.8 ± 0.07	7.9 ± 0.05	8.5 ± 0.10
	Bouteloua	+AMF	8.0 ± 0.08	7.9 ± 0.12	8.1 ± 0.11
	Bouteloua	−AMF	7.9 ± 0.07	8.0 ± 0.05	8.6 ± 0.05
	Linum	+AMF	7.9 ± 0.09	7.9 ± 0.08	8.3 ± 0.03
	Linum	−AMF	7.9 ± 0.08	7.9 ± 0.09	8.6 ± 0.08
	Native community	+AMF	8.0 ± 0.05	7.9 ± 0.10	8.4 ± 0.06
	Native community	−AMF	7.9 ± 0.10	8.0 ± 0.13	8.6 ± 0.04

[a] Abbreviations: AMF, arbuscular mycorrhizal fungi; NWR, National Wildlife Refuge; TRNP, Theodore Roosevelt National Park.

single exception, Figure 3). Typically, conditioning by exotic species did not significantly reduce native biomass production, but such antagonistic effects ($P < 0.05$, preplanned comparisons in single-species ANOVA) were evident in *Bouteloua*, *Linum*, and *Stipa* (Figure 3). As was true for the invasive species, the effect of invasive conditioning on natives was affected in some cases by the microbial composition of conditioned soils. In particular, the invasive forb *Euphorbia* had an antagonistic effect on all native species in +AMF soils; in −AMF soils these effects were converted to neutral or facilitative effects for five of the six native species. We note that our experiment does not enable the various direct and indirect effects of AMF colonization (e.g., on physical structure and nutrient availability of soils) to be resolved, although our use of soil chemistry covariates indicates that the observed effects of AMF are not mediated by effects of soil nitrate, ammonium, and pH.

Our results underscore the importance of AMF in the functional ecology of grassland perennials (Wilson and Hartnett 1998) and raise the possibility that restoration of AMF in soils may be important to efficient establishment of the diversified biofuel grasslands that are now attracting much interest (Tilman et al. 2006a, b). The effects of soil conditioning were strongly affected by the presence of AMF, suggesting that observed legacy effects were mediated by changes in the composition of AMF communities in experimental soils. The facilitative effects of natives on

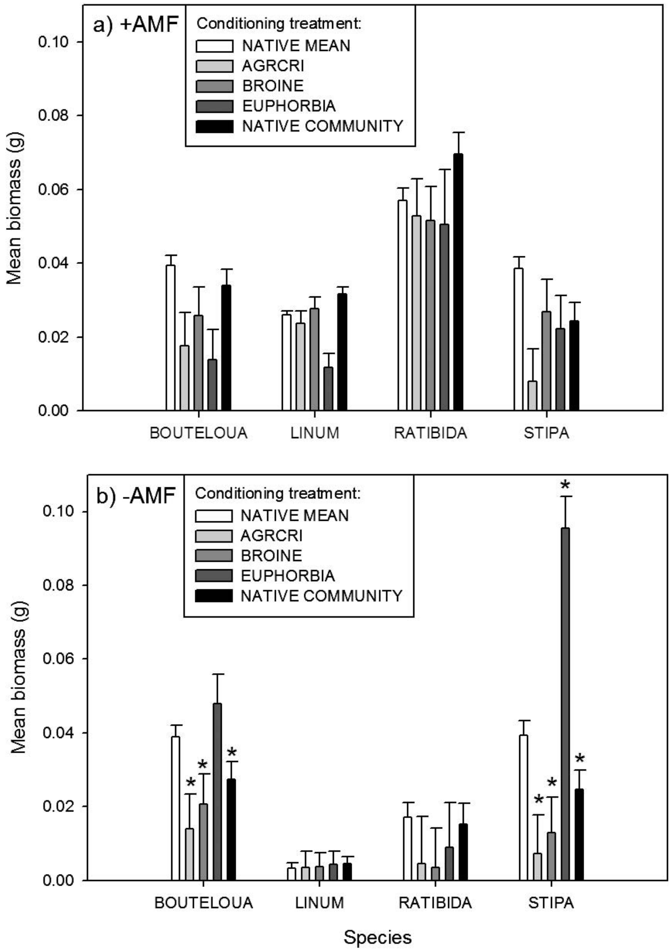

Figure 3. Mean aboveground biomass production by native species in soils conditioned by invasive and native species and by a native species mixture, in soils with AMF (+AMF; field soil + microbial wash) or without AMF (−AMF soil; pasteurized soil + microbial wash). Note difference in scale on y-axis for Figures 2 and 3. Means in soils conditioned by invasive species are based on growth in a single soil (collected in different nature reserves as noted in text); means in soils conditioned by native species are based on growth in all three of the collected soils. Asterisks denote significant differences ($P < 0.05$, preplanned comparisons in single-species ANOVA) between an invasive-species conditioning treatment and mean biomass production in soil conditioned by three native species.

invasives observed in +AMF treatments might reflect some growth-inhibiting artifact of pasteurization, but the multiple rounds of conditioning used in our protocol reduce the likelihood of such an effect. Moreover, our group has applied recently developed methods for identifying AMF taxa in plant roots via molecular methods (Aldrich-Wolfe 2007) to exotic and native species grown in this experiment. Preliminary results (N. R. Jordan, unpublished data) indicate that invasive perennials of grassland agroecosystems do not host AMF taxa that occur in desirable native perennials, suggesting that repeated rounds of conditioning may create substantially differentiated AMF communities in experimental soils. These same exotic species have been shown to create soil microbial legacies that sharply limit growth of a number of these same native perennials (Jordan et al. 2008).

There is growing recognition of the significance of aboveground–belowground interactions in plant community dynamics (van der Putten et al. 2009); meta-analyses (Kulmatiski et al. 2008) suggest that plant interactions with soil biota can be comparable in magnitude to factors such as herbivory and competition. A variety of evidence on soil-mediated interspecific effects of exotic perennial invasive species (Mangla et al. 2008; Vogelsang and Bever 2009) suggests a conceptual model of an exotic weed invasion process in grassland agroecosystems. In this model, certain exotic species, upon invasion, occupy soils long enough to affect some biotic or abiotic modification that reduces fitness of natives relative to exotics, facilitating further invasion and impeding restoration of native perennial communities. Such differential soil-mediated effects on native vs. invasive species could support self-reinforcing invasion processes, i.e., an "invasional meltdown," driven by cofacilitation by multiple invasive species (Best and Arcese 2009; Jordan et al. 2008) or by reducing the ability of native species to establish and persist in modified soils (Standish et al. 2008) even when management actions are taken to aid establishment (Lombardo et al. 2007). Such processes may establish a "stable degraded state" in a grassland agroecosystem (Kulmatiski 2006; Suding et al. 2004;), enforced by a legacy of extensive invasive modification of soil (Peltzer et al. 2009; Rout and Callaway 2009) that facilitates reinvasion even after effective control or removal of invasives.

This conceptual model hinges on a key functional difference between soil-mediated effects of invasive and native species on plant community dynamics. Specifically, the premise of the model is that exotics have neutral or facilitative effects on conspecifics and other exotics (Kulmatiski et al. 2008), and exert negative effects on natives (Batten et al. 2008; Jordan et al. 2008; Vogelsang and Bever 2009). Natives are presumed to have negative effects on conspecifics (Kulmatiski et al. 2008) and nonnegative effects on nonconspecific natives and on exotics. Thus, soil-mediated effects of invasives on natives are hypothesized to differ from such effects of natives on invasives. Evidence regarding such qualitative differences in interspecific effects of invasives and natives is limited, despite the potential importance of these effects to community dynamics. In particular, soil-mediated interspecific effects of native species on exotics are poorly known and theoretical expectations are not clear (Reynolds and Haubensak 2009).

Most previous comparisons of interspecific effects of soil occupancy by invasive and native exotic species have focused on effects of a single invasive species and have examined responses to invasive soil occupancy in only a few native or invasive species, or both. Damaging effects of invasive species on natives were observed in some cases (Batten et al. 2008; Mangla et al. 2008; Niu et al. 2007; Reinhart and Callaway 2006), but not others (Batten et al. 2008; Rowe and Brown 2008; van Grunsven et al. 2007). Most previous work has compared the effects of invasive soil occupancy to that of a mixture of natives or used field-collected soil from a native plant community (Allen et al. 2003; Niu et al. 2007; Stinson et al. 2006; Vogelsang and Bever 2009; Yu et al. 2005) as the basis of comparison for interspecific soil-mediated effects of exotic species. Only a few studies (Batten et al. 2008; Rowe and Brown 2008; van Grunsven et al 2007) have taken the important step of comparing individual interspecific legacy effects of invasive and native species in a single experimental study, and none has examined multiple invasive and native species in a single study. Our results provide a more comprehensive assessment of the effects and responses to soil occupancy of individual co-occurring exotic and native species.

In accord with the key premise of the conceptual model outlined above, we observed a consistent qualitative difference in soil-mediated interspecific effects of the co-occurring invasive and native species used in this experiment: natives facilitated invasives, but invasives did not facilitate natives. Among the range of observed soil occupancy effects of three invasives on natives, a few were strongly antagonistic, relative to the corresponding effect of natives. However, many of these invasive effects were not significantly more antagonistic than the corresponding effect of natives. Our results thus provide the first indication of the variability of soil-mediated interspecific effects of invasives on natives, among a group of co-occurring exotic and invasive plant species. We note that no native species was affected negatively by all three invasive species, and the variability in responses among native species suggests that soil occupancy by invasives will have complex effects on native community dynamics.

We observed a marked functional difference between soil-mediated interspecific effects of natives and invasives that was not anticipated from previous research: the extensive facilitation of exotic species growth by native species, when evaluated relative to the corresponding effect of invasives on natives. As was the case for native responses to invasives, variability in observed responses among these invasives suggests that soil occupancy by natives will create a complex pattern of facilitation among invasive species that enter a plant community. Four of the six invasive species examined in this experiment experienced significant facilitation by all three native species; the other two invasives were significantly facilitated by at least one native species. Estimated facilitative effects of individual natives differed in magnitude for some invasives (e.g., *Centaurea*), whereas other invasives had more uniform responses to native soil occupancy (*Poa*). Soil conditioning by the native mixture was less facilitative to invasives than individual native species effects; Vogelsang and Bever (2009) observed a similar negative effect of a mixture. The mechanistic basis of a difference between soil-conditioning effects of mixtures vs. individual species is not clear, but additional experimental comparisons of such effects are warranted to better understand soil-mediated invasion in plant communities.

If invasive perennials create legacy effects that damage native species of interest in grassland restoration, then a cost-effective method for remediating these soil effects will be needed to reduce the risk of further weed invasion and other problems (e.g., lack of diversity, reduced stands and yields) that would result from poor establishment of these species in grassland restoration efforts. Certain native species show potential for cost-effective remediation, via the microorganisms with which they associate (Azcon-Aguilar et al. 2003; Barni and Siniscalco 2000; Smith et al. 2003), potentially countering effects of invasive species on soil microbial communities and soil attributes. The term ‘‘nurse species’’ has been applied to native plant species that first reoccupy a site after disturbance, and that have a facilitative effect on other native species (Lockwood and Samuels 2004). Many kinds of facilitative effects by such species have been demonstrated, including protection from physical stresses or herbivory, increasing nutrient supply, and enabling effective pollination and dispersal (Bertness and Callaway 1994; Callaway 1997; Larson and Siemann 1998; Lortie et al. 2004; Padilla and Pugnaire 2006), but soil-mediated facilitative effects have not been evaluated experimentally. For example, Canada wildrye (*Elymus canadensis* L.)—a native species widely regarded as a nurse species by grassland managers—is able to establish and produce substantial aboveground biomass in situations where large seedbanks of annual weeds are present (N. R. Jordan, unpublished data); such aboveground growth presumably creates potential for substantial effects on soil microbial communities. Canada wildrye has been shown (Noyd et al. 1995) to develop high levels of AMF colonization in soils where other native perennial grasses were poorly colonized. Therefore, it is plausible that such species can ameliorate damaging soil-mediated legacy effects of invasive species, and may restore populations of mutualistic soil biota (e.g., AMF) that may not be supported during soil occupancy by invasive species. Such facilitative plant species may serve, in effect, to couple plant and microbe dispersal processes on highly disturbed lands, such that other plant species and microbial symbionts co-occur and can form effective mutualisms (Enkhtuya et al. 2005; Oba et al. 2004; Smith et al. 2003). Hence, nurse plants may be crucial to the establishment of grassland agroecosystems that benefit from an ''environmental filter'' (Belyea 2004) that appears to result from successful restoration, in which plant community development increasingly limits invasion (Bezemer et al. 2004, Blumenthal et al. 2005).

Sources of Materials

[1] Native seeds, Prairie Mountain Roots, Arcola, Saskatchewan, Canada.

[2] Osmocote 14–14–14, The Scotts Company LLC, Marysville, OH.

[3] SF3000 autoanalyzer, OI Corporation, College Station, TX.

[4] SAS Version 9.2, SAS Institute, Inc., Cary, NC.

Acknowledgments

We thank our field and laboratory assistants, D. Buhl and W. Newton, for statistical advice; several colleagues for manuscript review; and the Minnesota Agricultural Experiment Station for its support. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. government.

Literature Cited

Aldrich-Wolfe, L. 2007. Distinct mycorrhizal communities on new and established hosts in a transitional tropical plant community. Ecology 88:559–566.

Allen, E. B., M. E. Allen, L. Egerton-Warburton, L. Corkidi, and A. Gomez-Pompa. 2003. Impacts of early- and late-seral mycorrhizae during restoration in seasonal tropical forest, Mexico. Ecol. Appl. 13: 1701–1717.

Azcon-Aguilar, C., J. Palenzuela, A. Roldan, S. Bautista, R. Vallejo, and J. M. Barea. 2003. Analysis of the mycorrhizal potential in the rhizosphere of representative plant species from desertification-threatened mediterranean shrublands. Appl. Soil Ecol. 22:29–37.

Barni, E. and C. Siniscalco. 2000. Vegetation dynamics and arbuscular mycorrhiza in old-field successions of the western Italian Alps. Mycorrhiza 10:63–72.

Batten, K. M., K. M. Scow, and E. K. Espeland. 2008. Soil microbial community associated with an invasive grass differentially impacts native plant performance. Microb. Ecol. 55:220–228.

Belyea, L. 2004. Beyond ecological filters: feedback networks in the assembly and restoration of community structure. Pages 115–132 *in* V. Temperton, R. Hobbs, S. Halle, and T. Nuttle, eds. Assembly Rules and Restoration Ecology: Bridging the Gap between Theory and Practice. Washington, DC: Island Press.

Bertness, M. D. and R. Callaway. 1994. Positive interactions in communities. Trends Ecol. Evol. 9:191–193.

Best, R. J. and P. Arcese. 2009. Exotic herbivores directly facilitate the exotic grasses they graze: mechanisms for an unexpected positive feedback between invaders. Oecologia 159:139–150.

Bezemer, T. M., O. Graca, P. Rousseau, and W. H. van der Putten. 2004. Above- and belowground trophic interactions on creeping thistle (*Cirsium arvense*) in high- and low-diversity plant communities: potential for biotic resistance? Plant Biol. 6:231–238.

Blumenthal, D. M., N. R. Jordan, and E. L. Svenson. 2005. Effects of prairie restoration on weed invasions. Agric. Ecosyst. Environ. 107: 221–230.

Bray, S. R., K. Kitajima, and D. M. Sylvia. 2003. Mycorrhizae differentially alter growth, physiology, and competitive ability of an invasive shrub. Ecol. Appl. 13:565–574.

Burrows, R. L. and F. L. Pfleger. 2002. Arbuscular mycorrhizal fungi respond to increasing plant diversity. Can. J. Bot. 80:120–130.

Callaway, R. 1997. Positive interactions in plant communities and the individualistic-continuum concept. Oecologia 112:143–149.

Callaway, R. M., B. E. Mahall, C. Wicks, J. Pankey, and C. Zabinski. 2003. Soil fungi and the effects of an invasive forb on grasses: neighbor identity matters. Ecology 84:129–135.

Carey, E. V., M. J. Marler, and R. M. Callaway. 2004. Mycorrhizae transfer carbon from a native grass to an invasive weed: evidence from stable isotopes and physiology. Plant Ecol. 172:133–141.

Corbin, J. D. and C. M. D'Antonio. 2004. Effects of exotic species on soil nitrogen cycling: implications for restoration. Weed Technol. 18: 1464–1467.

Day, P. R. 1965. Particle fractionation and particle size analysis. Pages 545–567 *in* C. Black, ed. Methods of Soil Analysis. Part 1. Madison, WI: American Society of Agronomy and Soil Science Society of America.

Duda, J. J., D. C. Freeman, J. M. Emlen, J. Belnap, S. G. Kitchen, J. C. Zak, E. Sobek, M. Tracy, and J. Montante. 2003. Differences in native soil ecology associated with invasion of the exotic annual chenopod, *Halogeton glomeratus*. Biol. Fertil. Soils 38:72–77.

Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6:503–523.

Enkhtuya, B., M. Poschl, and M. Vosatka. 2005. Native grass facilitates mycorrhizal colonisation and P uptake of tree seedlings in two anthropogenic substrates. Water Air Soil Pollut. 166:217–236.

Grace, C. and D. Stribley. 1999. A safer procedure for routine staining of vesicular-arbuscular mycorrhizal fungi. Mycol. Res. 95:1160–1162.

Great Plains Flora Association. 1986. Flora of the Great Plains., 1400 p.

Hallett, S. G. 2006. Dislocation from coevolved relationships: a unifying theory for plant invasion and naturalization? Weed Sci. 54:282–290.

Hartnett, D. C. and G.W.T. Wilson. 2002. The role of mycorrhizas in plant community structure and dynamics: lessons from grasslands. Plant Soil 244:319–331.

Haubensak, K. A., C. M. D'Antonio, and J. Alexander. 2004. Effects of nitrogen-fixing shrubs in Washington and coastal California. Weed Technol. 18:1475–1479.

Hawkes, C. V., J. Belnap, C. D'Antonio, and M. K. Firestone. 2006. Arbuscular mycorrhizal assemblages in native plant roots change in the presence of invasive exotic grasses. Plant Soil 281:2369.

Hawkes, C. V., I. F. Wren, J. D. Herman, and M. K. Firestone. 2005. Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. Ecol. Lett. 8:976–985.

Jordan, N., D. Larson, and S. Huerd. 2008. Soil modification by invasive plants: effects on native and invasive species of mixed-grass prairies. Biol. Invasions 10:177–190.

Jordan, N. R., J. Zhang, and S. Huerd. 2000. Arbuscular-mycorrhizal fungi: potential roles in weed management. Weed Res. 40:397–410.

Klironomos, J. N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature 417:67–70.

Koide, R. T. and M. G. Li. 1989. Appropriate controls for vesicular arbuscular mycorrhiza research. New Phytol. 111:35–44.

Kourtev, P. S., J. G. Ehrenfeld, and M. Haggblom. 2002. Exotic plant species alter the microbial community structure and function in the soil. Ecology 83:3152–3166.

Kulmatiski, A. 2006. Exotic plants establish persistent communities. Plant Ecol. 187(2):261–275.

Kulmatiski, A., K. H. Beard, J. R. Stevens, and S. M. Cobbold. 2008. Plant–soil feedbacks: a meta-analytical review. Ecol. Lett. 9:980–992.

Larson, J. L. and E. Siemann. 1998. Legumes may be symbiot limited during old field succession. Am. Midl. Nat. 140:90–95.

Lockwood, J. L. and C. L. Samuels. 2004. Assembly models and restoration practice. Pages 55–70 *in* V. Temperton, R. Hobbs, S. Halle, and T. Nuttle, eds. Assembly Rules and Restoration Ecology: Bridging the Gap between Theory and Practice. Washington DC: Island Press.

Lombardo, K., J. S. Fehmi, K. J. Rice, and E. Laca. 2007. *Nassella pulchra* survival and water relations depend more on site productivity than on small-scale disturbance. Restor. Ecol. 15:177–178.

Lortie, C. J., R. W. Brooker, P. Choler, Z. Kikvidze, R. Michalet, F. I. Pugnaire, and R. M. Callaway. 2004. Rethinking plant community theory. Oikos 107:433–438.

Mangla, S., Inderjit, and R. M. Callaway. 2008. Exotic invasive plant accumulates native soil pathogens which inhibit native plants. J. Ecol. 96:58–67.

McGonigle, T. P., M. H. Miller, D. G. Evans, G. L. Fairchild, and J. A. Swan. 1990. A new method which gives an objective measure of colonization of roots by vesicular- arbuscular mycorrhizal fungi. New Phytol. 115:494–501.

Niu, H.-B., W.-X. Liu, F.-H. Wan, and B. L. Wan. 2007. An invasive aster (*Ageratina adenophora*) invades and dominates forest understories in China: altered soil microbial communities facilitate the invader and inhibit natives. Plant Soil 294:73–85.

Noyd, R. K., F. L. Pfleger, and M. P. Russelle. 1995. Interactions between native prairie grasses and indigenous arbuscular mycorrhizal fungi—implications for reclamation of taconite iron-ore tailing. New Phytol. 129:651–660.

Oba, H., N. Shinozaki, H. Oyaizu, K. Tawaraya, T. Wagatsuma, W. L. Barraquio, and M. Saito. 2004. Arbuscular mycorrhizal fungal communities associated with some pioneer plants in the lahar area of Mt. Pinatubo, Philippines. Soil Sci. Plant Nutr. 50:1195–1203.

Ortega, Y. K. and D. E. Pearson. 2005. Weak vs. strong invaders of natural plant communities: assessing invasibility and impact. Ecol. Appl. 15:651–661.

Padilla, F. M. and F. I. Pugnaire. 2006. The role of nurse plants in the restoration of degraded environments. Front. Ecol. Environ. 4: 196–202.

Peltzer, D. A., P. J. Bellingham, H. Kurokawa, L. R. Walker, D. A. Wardle, and G. W. Yeates. 2009. Punching above their weight: low-biomass non-native plant species alter soil properties during primary sucession. Oikos 118:1001–1014.

Petermann, J. S., A.J.F. Fergus, L. A. Turnbull, and B. Schmid. 2008. Janzen–Connell effects are widespread and strong enough to maintain diversity in grasslands. Ecology 89:2399–2406.

Raizada, P., A. S. Raghubanshi, and J. S. Singh. 2008. Impact of invasive alien plant species on soil processes: a review. Proc. Natl. Acad. Sci. India Sect. B (Biol. Sci.) 78:288–298.

Reinhart, K. O. and R. M. Callaway. 2006. Soil biota and invasive plants. New Phytol. 170:445–457.

Reynolds, H. L. and K. A. Haubensak. 2009. Soil fertility, heterogeneity, and microbes: towards an integrated understanding of grassland structure and dynamics. Appl. Veg. Sci. 12:33–44.

Richardson, D. M., N. Allsop, C. M. D'Antonio, S. J. Milton, and M. Rejmanek. 2000. Plant invasions—the role of mutualisms. Biol. Rev. 75:65–93.

Robertson, G. P., D. C. Coleman, C. S. Bledsoe, and P. Sollins, eds. 1999. Standard Soil Methods for Long-Term Ecological Research. Long-Term Ecological Research Network Series. New York, NY: Oxford University Press.

Rout, M. E. and R. M. Callaway. 2009. An invasive plant paradox. Science 324:734–735.

Rowe, H. I. and C. S. Brown. 2008. Native plant growth and seedling establishment in soils influenced by *Bromus tectorum*. Rangeland Ecol. Manag. 61:630–639.

Saggar, S., P. McIntosh, C. Hedley, and H. Knicker. 1999. Changes in soil microbial biomass, metabolic quotient and organic matter turnover under *Hieracium pilosella* L. Biol. Fertil. Soils 30:232–238.

Seifert, E. K., J. D. Bever, and J. L. Maron. 2009. Evidence for the evolution of reduced mycorrhizal dependence during plant invasion. Ecology 90:1055–1062.

Smith, R. S., R. S. Shiel, R. D. Bardgett, D. Millward, P. Corkhill, G. Rolph, P. J. Hobbs, and S. Peacock. 2003. Soil microbial community, fertility, vegetation and diversity as targets in the restoration management of a meadow grassland. J. Appl. Ecol. 40:51–64.

Smith, W. E. and D. J. Read. 1997. Mycorrhizal Symbiosis. 2nd ed. Pp. ix+ 605. San Diego, CA: Academic.

Sperry, L. J., J. Belnap, and R. D. Evans. 2006. *Bromus tectorum* invasion alters nitrogen dynamics in an undisturbed arid grassland ecosystem. Ecology 87:603–615.

Standish, R. J., V. A. Cramer, and R. J. Hobbs. 2008. Land-use legacy and the persistence of invasive *Avena barbata* on abandoned farmland. J. Appl. Ecol. 45:1576–1583.

Stinson, K. A., S. A. Campbell, J. R. Powell, B. E. Wolfe, R. M. Callaway, G. C. Thelen, S. G. Hallett, D. Prati, and J. N. Klironomos. 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. PLoS Biol. 4: 727–731.

Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. Trends Ecol. Evol. 19:46–53.

Thorpe, A. S., G. C. Thelen, A. Diaconu, and R. M. Callaway. 2009. Root exudate is allelopathic in invaded community but not in native community: field evidence for the novel weapons hypothesis. J. Ecol. 97:641–645.

Tilman, D., J. Hill, and C. Lehman. 2006a. Carbon-negative biofuels from low-input high-diversity grassland biomass. Science 314: 1598–1600.

Tilman, D., P. B. Reich, and J.M.H. Knops. 2006b. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441:629–632.

van der Putten, W. H., R. D. Bardgett, P. C. de Ruiter, W.H.G. Hol, K. M. Meyer, T. M. Bezemer, M. A. Bradford, S. Christensen, M. B. Eppinga, T. Fukami, L. Hemerik, J. Molofsky, M. Schadler, C. Scherber, S. Y. Strauss, M. Vos, and D. A. Wardle. 2009. Empirical and theoretical challenges in aboveground–belowground ecology. Oecologia 161:1–14.

Van Grunsven, R.H.A., W. H. van der Putten, T. M. Bezemer, W.L.M. Tamis, F. Berendse, and E. M. Veenendaal. 2007. Reduced plant–soil feedback of plant species expanding their range as compared to natives. J. Ecol. 95:1050–1057.

Vogelsang, K. M. and J. D. Bever. 2009. Mycorrhizal densities decline in association with nonnative plants and contribute to plant invasion. Ecology 90:399–407.

Wilson, G.W.T. and D. C. Hartnett. 1998. Interspecific variation in plant responses to mycorrhizal colonization in tallgrass prairie. Am. J. Bot. 85:1732–1738.

Wolfe, B. E. and J. N. Klironomos. 2005. Breaking new ground: soil communities and exotic plant invasion. Bioscience 55:477–487.

Yu, X. J., D. Yu, Z. J. Lu, and K. P. Ma. 2005. A new mechanism of invader success: exotic plant inhibits natural vegetation restoration by changing soil microbe community. Chin. Sci. Bull. 50:1105–1112.

Received January 4, 2010, and approved July 30, 2010.