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ORIGINAL PAPER

Arbuscular mycorrhizal fungi enhance spotted knapweed growth across a riparian chronosequence

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Abstract Arbuscular mycorrhizal fungi (AMF) mediate nutrient uptake that accelerates plant growth and reproduction. Thus, AMF may promote plant invasions often observed along rivers. We assessed the importance of AMF in improving growth of the invasive species, spotted knapweed (*Centaurea stoebe*), during succession of riparian vegetation along a flood plain in Montana, USA. We grew spotted knapweed with and without AMF in soils collected from riparian sites ranging from 1 to 72 years old and measured the plant's growth response to AMF. We observed variability in relative effects of AMF, with greatest growth benefits in recently deposited alluvial sediments. We then separated effects of soil and inoculum source by growing spotted knapweed with soils and inocula collected from young or old sites and found that growth responses were greatest in young soils regardless of inoculum source. Our results demonstrate that AMF directly benefit growth of spotted knapweed, especially in soils that typify early successional sites on this alluvial flood plain.

Keywords Arbuscular mycorrhizal fungi · *Centaurea* · Floodplain · Mycorrhizal responsiveness · Riparian · Spotted knapweed

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Introduction

Arbuscular mycorrhizal fungi (AMF) are ubiquitous components of terrestrial ecosystems across the world with multiple functions from the level of individual plants to the ecosystem (Rillig 2004; Smith and Read 2008). Distribution and functions of AMF at transitional zones between aquatic and terrestrial ecosystems, such as flood plains, remain less studied. Riparian zones and vegetation chronosequences on flood plains host a much more diverse flora than surrounding upland communities (Naiman and Décamps 1997; Nilsson and Svedmark 2002; Mouw and Alaback 2003). Vascular plant diversity is determined, in part, by floods and ground water that maintain heterogeneity in habitats and variation in microsites on alluvial surfaces (Pollock et al. 1998; Tabacchi et al. 1998; Stanford et al. 2005; Jansson et al. 2007; Mouw et al. 2009). Non-native plants also occur in the diverse plant assemblages along rivers

(Planty-Tabacchi et al. 1996; Hood and Naiman 2000; Richardson et al. 2007), and riparian areas serve as corridors for spread of exotics (Stohlgren et al. 1998; Tickner et al. 2001). However, soil-based mechanisms underlying success of non-native species remain poorly understood in riparian zones, as well as in other ecosystems (Beauchamp et al. 2005; Wolfe and Klironomos 2005).

Flood plains along rivers with natural or near-natural flow regimes are model systems for testing hypotheses about interactions among non-native plants, soil, and mycorrhizal fungi because of the diversity of habitats and disturbance regimes in close proximity to one another. Riparian plant communities exhibit pronounced successional stages due to movements of river channels that erode vegetated patches and deposit sediment for establishment of seedlings (Latterell et al. 2006; Whited et al. 2007). Concurrent with vegetation development are changes in soil properties, such as increased concentrations of silt relative to sand and increased organic matter content, which influence availability of nutrients to support plant growth (Van Cleve et al. 1993). Mycorrhizal fungi occur in riparian areas (e.g., Helm et al. 1996; Harner et al. 2004; Jacobson 2004; Beauchamp et al. 2006; Piotrowski et al. 2008a; Harner et al. 2009), but their functions in promoting plant growth, especially growth of non-native species, are unknown across floodplain chronosequences.

We determined how an invasive plant responds to AMF as riparian soils and vegetation develop by studying a soil chronosequence spanning nearly 75 years on a flood plain of the Middle Fork of the Flathead River, Montana. We selected the non-native herbaceous plant, spotted knapweed (*Centaurea stoebe* L. subsp. *micranthos* (Gugler) Hayek, following Ochsmann (2001); also known as *C. maculosa* in North American literature), as a mycorrhizal host because it grows in sites of all ages on this flood plain (M. Harner, personal observation). Spotted knapweed is of concern for conservation due to its widespread invasion across western North America (LeJeune and Seastedt 2001). In contrast to its native range in Europe where it is primarily a grassland species, in North America, spotted knapweed thrives on fluvial bars, even along rivers with natural flow regimes, and reaches heights >1.5 m (M. Harner, personal observation). Spotted knapweed associates with AMF. However, most research suggests the plant is not dependent on AMF or highly responsive to colonization except in the presence of specific neighboring plants (Marler et al. 1999; Zabinski et al. 2002; Callaway et al. 2004a), but there is evidence that AMF may enhance growth of spotted knapweed directly (Carey et al. 2004).

Plant responses to AMF depend on environmental conditions, and relationships between spotted knapweed and AMF have not been examined in a riparian context. In this study, we determined mycorrhizal responsiveness across a floodplain chronosequence by growing spotted knapweed with and without AMF in soils collected from sites of eight different ages, ranging from recently deposited alluvia with pioneer herbaceous vegetation (1-year-old) to soil from cottonwood-conifer forests (72-year-old). We predicted that AMF-facilitated benefits to plant growth decline with site age, due to increasing availability of nutrients in organic forms, changes in availability of host plants, and concurrent declines in relative abundances of AMF to serve as inocula (Piotrowski et al. 2008a). In a second experiment, we separated effects of soil from source of inocula by growing spotted knapweed in soils from young and old sites with inocula collected from young (<5-year-old) or old (>40-year-old) sites. Collectively, these experiments contribute to knowledge of how belowground interactions influence growth of an exotic species in the context of a large, dynamic floodplain ecosystem.

Materials and methods

Study site

We collected soils and roots from the Nyack Flood Plain (48°26′30″N, 113°48′12″W) located 20 km upstream from West Glacier, Flathead County, Montana, on the southern boundary of Glacier National Park. The Middle Fork of the Flathead River is a freely flowing river with mean annual flow of 82 $m^3 s^{-1}$, an average peak annual discharge of 541 $m^3 s^{-1}$ associated with spring snowmelt, and an average base flow of 17 $m^3 s^{-1}$ that usually is reached in fall or early winter (Whited et al. 2007). The flood plain is 10-km long by 3-km wide and is a site of long-term research focusing on ecosystem

dynamics of a large floodplain system (Stanford et al. 2005). Nyack hosts a diverse flora with over 200 species of vascular plants, twice as many species as in some adjacent, upslope areas (Mouw and Alaback 2003). Actively scoured areas of the flood plain consist of gravel bars and patches of regenerating vegetation, and infrequently inundated areas contain mature forests of cottonwoods and conifers (Mouw and Alaback 2003). Spotted knapweed has established across the flood plain but is most invasive in recently scoured regions (Mouw et al. 2009) and grows as single-species patches or near neighboring plants, especially pioneer species like cottonwoods (M. Harner, personal observation).

We focused sampling on a 2-km reach of the upstream portion of the flood plain, a losing reach where surface water enters the alluvial aquifer (Poole et al. 2002; Harner and Stanford 2003). Here we delineated a chronosequence of vegetation and soil development based on previous tree ring analyses (Harner and Stanford 2003) and aerial photographs (Whited et al. 2007). The chronosequence is comprised of terrestrial habitat patches established by depositional processes associated with floods. Plant communities develop from pioneer assemblages of trees and shrubs (*Populus* and *Salix* spp.) intermixed with AMF-hosting herbaceous plants, to mature forests of ectomycorrhizal fungi (EMF)-hosting trees with an understory of AMF-hosting plants (Mouw and Alaback 2003, Piotrowski et al. 2008a, Mouw et al. 2009).

Physical and chemical properties of soil and abundances of mycorrhizal fungi were described initially across this chronosequence by Piotrowski et al. (2008a). Concentrations of soil nutrients were low, with organic matter <4% (by mass), and NO_3^-–N and Olsen P ranging from 0.8–5.0 μg g^{-1} to 1.7–4.0 μg g^{-1}, respectively (Piotrowski et al. 2008a). Abundance of AMF increased rapidly early in succession and peaked within 13 years following initial plant establishment, whereas EMF increased linearly through time (Piotrowski et al. 2008a). This change corresponded to development of an organic soil horizon (Piotrowski et al. 2008a), and possibly to inhibition of AMF by phenolics in leaf litter (Piotrowski et al. 2008b). Subsequent surveys identified AMF propagules in sediments deposited by a flood, indicating that inocula are available in early-successional sites (Harner et al. 2009).

Experiment 1

In the first experiment spotted knapweed (*Centaurea stoebe* L. ssp. *micranthos*) was grown in field soil (+AMF) or sterile soil with an added microbial wash (−AMF) from sites of eight different ages to compare the plant's growth response to AMF as soils develop. We collected soils at sites that were 1, 5, 14, 22, 34, 46, 56, and 72 years old in October 2006. We collected soil (2 l; 0–15 cm depth), including roots, from five random locations per site and homogenized all subsamples. In the laboratory, half of the homogenized soil from each site was steam-sterilized at 90°C for a minimum of 4 h using a Pro-Grow Electric Soil Sterilizer (Model SS-5, Pro-Grow Supply Corp, Brookfield, Wisconsin, USA) to eliminate AMF and to reduce other microbes. Subsamples of field and sterilized soil were air-dried and analyzed for pH, soluble PO_4^{3-}–P, and extractable NH_4^+–N and NO_3^-–N to determine if steaming affected nutrient concentrations. Soil pH was measured in deionized H_2O (1:1, wt/vol). Inorganic N and soluble P were analyzed after extraction with KCl (Mulvaney 1996) and CaCl (Kuo 1996), respectively, using an Auto-Analyzer 3 (Bran Luebbe, Chicago, Illinois, USA). We created a microbial wash to return a portion of the non-mycorrhizal microbial community to the sterile soil following the process described by Koide and Li (1989). Microbial washes were made for each site by combining 1:10 soil:water (vol:vol), mixing in a blender, allowing the mixture to settle 20–30 min, and decanting through Whatman No. 1 filter paper (11 μm).

Experiment 1 had a factorial design of 2 AMF treatments × 8 soil ages. The AMF factor was either field soil (+AMF) or sterile soil with an added microbial wash (−AMF). The soil factor consisted of soil collected from the eight sites. Each treatment combination was replicated five times for a total of 80 experimental units. Each experimental unit consisted of a pot (6 cm diam. × 25 cm depth plastic Conetainers (Ray Leach Conetainer Nursery, Canby, Oregon, USA)) with a 1:1 soil/sterile sand (600–1,000 μm diam.) mix and a plant. We mixed soil and sand because we anticipated this would facilitate harvesting root systems. Three spotted knapweed seeds were planted in each pot. Pots containing sterile soil received 50 ml of microbial wash, and pots with field soil received 50 ml of water when seeds were

planted. Plants were grown in a growth chamber (18 h photoperiod, 21°C day/21°C night temperature, 350 μmol m^{-2} s^{-1} PAR), positioned randomly, and watered every other day with tap water. After 10 days, seedlings were thinned to 1 per pot. Plants were harvested at 54 days, before becoming root-bound or flowering.

Experiment 2

In Experiment 2, we grew spotted knapweed in soils from young and old sites with mycorrhizal inocula collected from young and old sites to separate effects of soil and inoculum sources on plant growth. We obtained soil from six early successional sites (<10-year-old) and six mid-late successional sites (>40-year-old) in October 2006. Soil was collected (10 l; 0–15 cm depth) from five random locations per site. We homogenized soil from the six sites within a successional stage and steam-sterilized (90°C; 8 h). We collected fragments of roots and adhering soil from herbaceous understory plants in the same early and mid-late successional sites to serve as mycorrhizal inocula. We homogenized root fragments from the six sites within a successional stage. Roots were placed in plastic bags, transported on ice and stored at 4°C for 6 days before use in experiments.

Experiment 2 had a factorial design with three sources of inocula × two sources of soil. The inoculum factor consisted of a control (no inocula), young inocula (homogenized inocula from six sites <10 years), or old inocula (homogenized inocula from six sites >40 years). The soil factor consisted of young soil (homogenized soil from six early successional sites <10 years) or old soil (homogenized soil from six late successional sites >40 years). Each treatment combination was replicated 10 times for a total of 60 experimental units. Each experimental unit consisted of a pot (same dimensions as above), sterile field soil, microbial inocula, and a plant. Inoculated treatments received 20 ml of root fragments (cut into 2 cm lengths) and adhering soil from either young or old sites. To introduce all possible forms of inocula, we added a mix of roots and soil because AMF propagules come in the form of spores, hyphae, and colonized roots. Pots contained a bottom layer of sterile sand (100 ml), a layer of sterile soil (200 ml), a layer of soil with microbial inocula (220 ml), and a top layer (75–100 ml) of sterile soil. Two spotted knapweed seeds were added to each pot. After 10 days, seedlings were thinned to 1 per pot. Plants were watered daily with tap water, grown as described in Experiment 1, and harvested at 38 days.

Plant and mycorrhizal measurements

We collected plant shoots and roots at the end of experiments. Roots were washed gently in tap water. Plant material was dried at 60°C for 48 h and weighed to determine biomass. For mycorrhizal analysis, dried roots were cleared in 10% KOH at 80°C for 30 min, acidified in 1% HCl for 10 min, stained with trypan blue in lactoglycerol (0.05%) at 80°C for 15 min, and placed in lactoglycerol overnight. We mounted root segments on slides and scored for mycorrhizal colonization at magnification of 200× using a modification of the magnified intersections method (McGonigle et al. 1990) on a Nikon Eclipse E600 microscope. We scored 50–100 root intersections from each sample. Data are reported as percent of intersections with AMF structures (AM hyphae, vesicles, or arbuscles).

Data analysis

To meet assumptions for statistical tests, percent AMF root colonization data were arcsine transformed, and soil N, soil P, and plant biomass data were $\log_{10}$ transformed. In Experiment 1, soil characteristics were compared between field and sterile soils with multivariate analysis of variance (MANOVA). Effects of site age, treatment (+AMF/−AMF), and their interactions on percent AMF root colonization and plant biomass also were tested with MANOVA, with Tukey's post-hoc comparisons among sites. In Experiment 2, the effect of soil type (young soil or old soil) on percent AMF root colonization and biomass were compared within treatments (young inocula, old inocula, or no inocula) with MANOVAs. We limited our inference to within each inoculum source because inocula from young and old sites may have differed in densities of propagules (i.e., old sites may have had lower densities of AMF spores or less AMF hyphae), for which we did not control. In both experiments, mycorrhizal responsiveness (MR) was calculated as the difference in plant size (total dry weight of above and belowground biomass) between mycorrhizal

plants (W_m) and non-colonized plants (W_{nc}) and expressed relative to growth of plants without mycorrhizae [$100 \times (W_m - W_{nc})/W_{nc}$] to represent percent growth improvement attributable to mycorrhizae (Janos 2007). In Experiment 2, we randomly selected samples of each of the two treatments to be compared, calculated MR, and repeated this 100 times to determine means and 95% confidence intervals for MR. Spearman correlation analyses were used to describe associations between mycorrhizal responsiveness and soil characteristics in Experiment 1 and percent AMF root colonization and plant biomass in Experiment 2. Statistical analyses were performed using SPSS version 12.0 for Windows (Chicago, IL, USA). Differences were considered significant at $P \leq 0.05$.

Results

Mycorrhizal responsiveness of spotted knapweed across the chronosequence (Experiment 1)

In field soils from across the chronosequence, soil pH averaged 7.9 ± 0.07 (± SE), soluble PO_4^{3-} averaged 0.31 ± 0.05 μg g^{-1}, and extractable inorganic N ($NH_4^+ + NO_3^-$) averaged 4.2 ± 0.63 μg g^{-1} (Fig. 1). Mass ratios of inorganic N to soluble P declined logarithmically across the chronosequence, peaking at 49:1 in the youngest soils and remaining below 21:1 at other sites. While steam sterilization did not affect soil pH or PO_4^{3-} ($P > 0.05$), it increased total inorganic N ($F_{1,14} = 8.32$, $P = 0.01$; Fig. 1).

At time of harvest (54 days), no AMF structures were observed in any plants grown in the sterile soil with an added microbial wash (−AMF). All plants grown in field soil (+AMF) were colonized by AMF. Mean percent of root length colonized ranged from 63% to 87% in field soils and varied among sites (Tables 1), with the 34-year site having lower colonization than all but the 5-year site ($P < 0.05$). Site age and treatment also affected plant biomass (Table 1). Plants were smaller in the 34-year site compared to all but the 22-year site ($P < 0.05$). Within treatments, spotted knapweed plants grown in sterile soil (−AMF) were small and of similar size among soils of different ages (Fig. 2). In contrast, plants grown in field soil (+AMF) consistently were larger than plants grown in sterile soil, except from the oldest site (Fig. 2). Mycorrhizal responsiveness was greatest in youngest soil (475%), lowest in oldest soil (34%), and variable in other soils (range: 118–245%). Mycorrhizal responsiveness correlated positively with N:P ratios (Spearman's $r = 0.762$, $P = 0.03$, $n = 9$), but not with pH, soluble P, or extractable inorganic N in field soils.

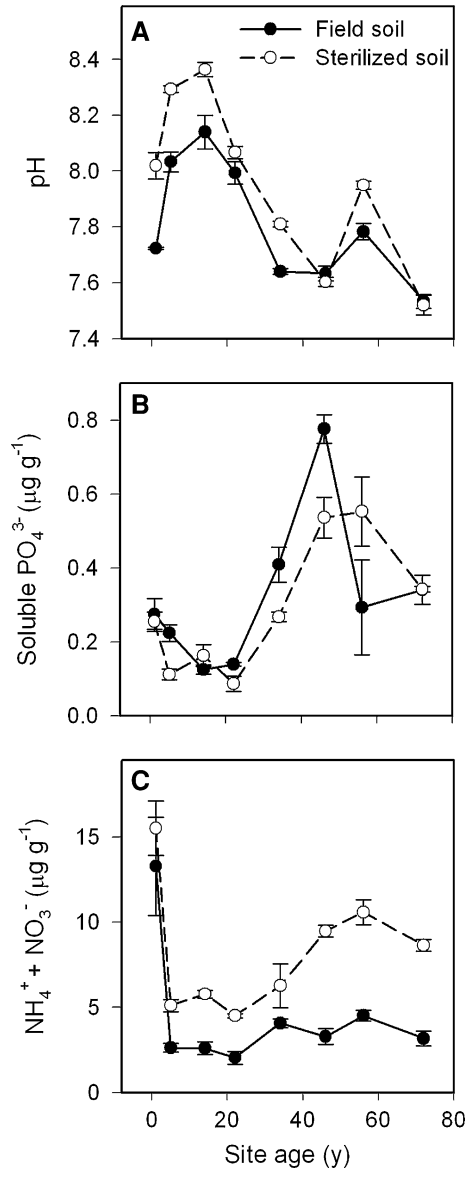

Fig. 1 Soil chemistry across the riparian chronosequence: **A** pH, **B** soluble PO_4^{3-}, and **C** extractable $NH_4^+ + NO_3^-$ in field soil (*filled circle*) and sterile soil (*unfilled circle*). Values are means ± SE; $n = 3$

Table 1 Multivariate ANOVA results summarizing effects of site age and treatment (+AMF/−AMF) on percent AMF colonization and biomass of *Centaurea* in Experiment 1

Source	AMF colonization			*Centaurea* biomass		
	df	*F*	*P*	df	*F*	*P*
Site age	7	2.2	0.05	7	8.6	<0.01
Treatment	1	6433.0	<0.01	1	154.8	<0.01
Site age × Treatment	7	2.2	0.05	7	3.0	0.01

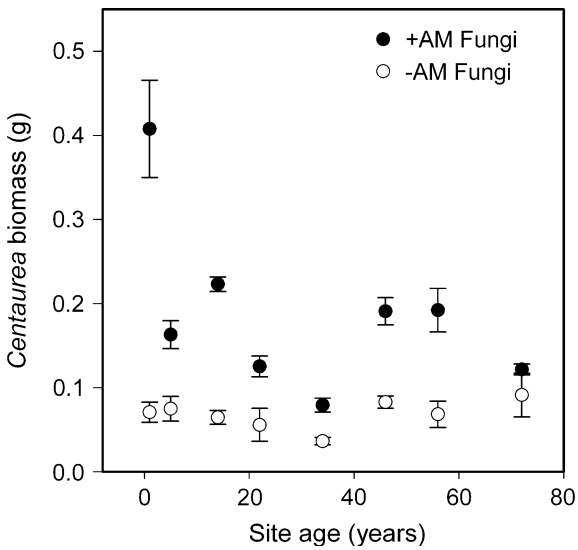

Fig. 2 Biomass of spotted knapweed (*C. stoebe*) grown in field soil containing AMF (*filled circle*) or in sterile soil without AMF (*unfilled circle*). Points represent means ± SE; $n = 5$. There were significant effects of site age and treatment on plant biomass (Table 1)

Table 2 Multivariate ANOVA results summarizing effect of soil source (young or old site) on percent AMF colonization and biomass of *Centaurea* for each source of inocula in Experiment 2

Inoculum source	AMF colonization			*Centaurea* biomass		
	df	*F*	*P*	df	*F*	*P*
Young site	1	2.9	0.11	1	12.8	0.00
Old site	1	0.1	0.73	1	7.2	0.01
No inocula	1	1.0	0.33	1	64.4	<0.01

Effect of AMF in young versus old soils (Experiment 2)

At time of harvest (38 days), plants grown in sterile soils were not colonized by AMF. All plants grown in soil that received mycorrhizal inocula were colonized. Across the two soils tested (young and old soil), mean percent root length colonized ranged from 68% to 72% and 44% to 47% for plants that received inocula from young and old sites, respectively, but colonization did not differ significantly across soils given the same inocula ($P < 0.05$; Fig. 3A; Table 2). Spotted knapweed plants obtained varying biomass across treatments (Fig. 3B; Table 2). Plants were smallest when grown in young soil without inocula, and were ten times larger in old soil with inocula from young sites. Spotted knapweed consistently obtained greater biomass in old soils than in young soils for each source of inocula (Fig. 3B). Mycorrhizal responsiveness, however, was greatest for plants grown in young soils, regardless of inoculum source (Fig. 4). Across sources of inocula, AMF colonization was correlated positively with plant biomass in

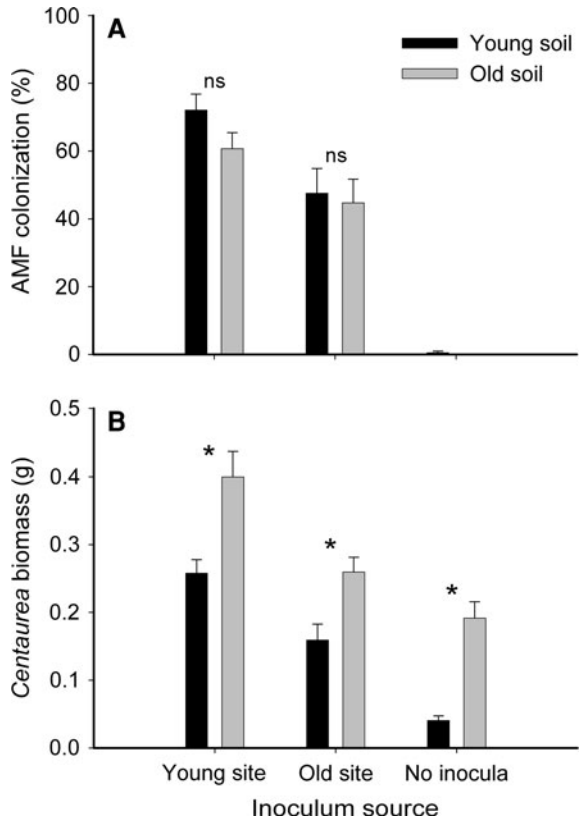

Fig. 3 Percent AMF root colonization (**A**) and biomass of spotted knapweed (*C. stoebe*) (**B**) grown with inocula from young or old sites in soils from young or old sites. *Bars* represent means ± SE; $n = 10$. *Asterisks* indicate significantly different means within an inoculum source ($P \leq 0.05$). *NS* non-significant differences

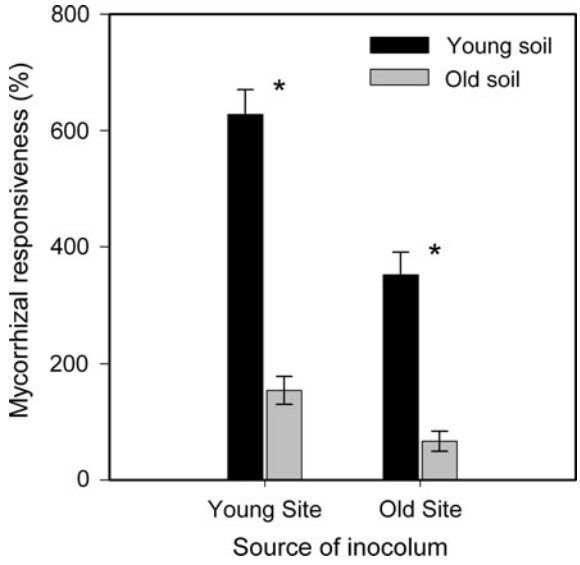

Fig. 4 Mycorrhizal responsiveness of spotted knapweed (*C. stoebe*) to AMF inocula from young or old sites. *Bars* represent the mean difference in biomass between inoculated and control treatments, expressed relative to biomass of controls, with 95% CI. *Asterisks* indicate significantly different means within an inoculum source ($P \leq 0.05$)

early successional soils ($r_s = 0.77$, $P < 0.01$; Fig. 5A), but this association was absent in old soils ($r_s = 0.24$, $P = 0.30$; Fig. 5B).

Discussion

Spotted knapweed exhibited a strong, positive growth response to AMF in most conditions tested. This result differs from many studies that have observed spotted knapweed unresponsive to AMF unless grown with neighboring plants from which it can exploit resources (Marler et al. 1999; Zabinski et al. 2002; Callaway et al. 2004a). In soils collected across the riparian chronosequence, spotted knapweed grew significantly larger with AMF in 7 of 8 soils tested, demonstrating that it responds to mycorrhizae across a wide-range of soils that differ in physical and chemical properties and AMF inoculum potential (Piotrowski et al. 2008a). In Experiment 2, percent AMF root colonization correlated positively with biomass obtained by plants in young soil, lending further support that AMF may directly improve growth of spotted knapweed. We also found evidence

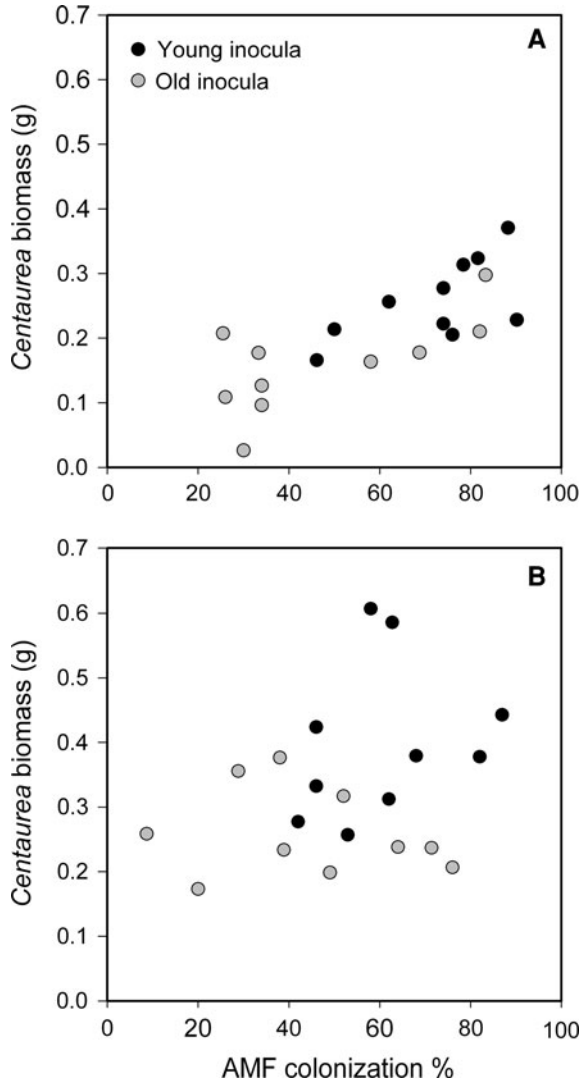

Fig. 5 Correlation between percent AMF root colonization and total biomass when plants grown in soil from **A** young sites or **B** old sites and inoculated with AMF collected from young (*filled circle*) or old (*unfilled circle*) sites. AMF colonization was correlated positively with plant biomass in early successional soils but not in soils from older sites

of variability in MR across the chronosequence, rather than a clear decline with site age, as we had predicted. Variability in MR likely results in sites that are more favorable to growth of some species than others because plant species differ in their growth responses to mycorrhizal fungi, which in some cases can be negative (Klironomos 2003). This heterogeneity may in turn contribute to the overall high plant diversity of both native and non-native species often

observed on flood plains (Mouw and Alaback 2003; Mouw et al. 2009).

Variations in experimental conditions may explain why we detected a growth response of spotted knapweed to AMF, whereas other studies have not. We also observed higher levels of AMF colonization than reported in other papers (Marler et al. 1999; Callaway et al. 2003, 2004a; Zabinski et al. 2002). We did not add supplemental fertilizer because of the short duration of our study and our desire not to increase nutrient supply to levels greater than those available in the field. Studies that document *Centaurea* spp. unresponsive to AMF have added fertilizer, typically a modified Hoagland's solution (Marler et al. 1999; Zabinski et al. 2002; Callaway et al. 2003). These additions may reduce the need for AMF to acquire limiting nutrients from soil and instead lead to direct root uptake, where there may be no advantage to plant growth compared to non-mycorrhizal controls. Nutrient additions may reduce the need for AMF, thereby leading to lower levels of colonization. We also used higher ratios of field soil to sand than most other studies. Variation in soil texture could affect architecture of root systems and AMF, and thus, MR among studies.

Results of both of our experiments indicate that MR of spotted knapweed was greatest in soils from early successional floodplain sites. In the chronosequence experiment, we could not separate whether this MR was due to characteristics of the soil or inocula. From previous work we know the system shifts in dominance from AMF to EMF as riparian vegetation matures (Piotrowski et al. 2008a). Therefore, inocula associated with root fragments may have higher proportions of EMF relative to AMF in older soils, due to increasing growth of EMF-dominated cottonwood and conifer trees. We attempted to minimize this effect by sampling roots and adhering soil from herbaceous, AMF-dominated plants, but some tree roots may have been interconnected with herbaceous roots. In addition, abundance and community composition of AMF may change over the chronosequence, with varying effects on plant growth. Despite potential variation in quality of inocula, the pattern of greater MR in young versus old soil was maintained in Experiment 2, irrespective of inoculum source. Furthermore, the strong positive association between percent AMF root colonization and plant growth that we detected in young soils was absent from old soils in Experiment 2, suggesting that AMF provide the greatest growth benefit in young soil. The recently deposited sand at young sites had low availability of phosphorus relative to nitrogen, as well as low organic matter content (Piotrowski et al. 2008a; this study). In our experiments with spotted knapweed grown without neighbors, AMF may have contributed to direct uptake of phosphorus and other nutrients in the young soils.

In our study, AMF inocula were available in the 1-year-old site in sufficient amounts to result in root colonization of nearly 80% and to increase spotted knapweed growth by 4–5 times relative to soils without inocula (Experiment 1). If the mycorrhizal benefit measured in our greenhouse study extends to the field, then it is possible spotted knapweed grows much faster if it establishes on early-successional sites where AMF inocula are present, potentially permitting this invasive species to gain dominance. Although spotted knapweed was present at sites of all ages, it is especially abundant on gravel bars in the scoured areas along Nyack Flood Plain (Mouw et al. 2009). Widespread establishment of a mycotrophic species, like spotted knapweed, could shift the system toward dominance by plants with mycorrhizal associations, rather than maintaining a period of dominance by non-mycotrophic species in early successional sites. Furthermore, presence of spotted knapweed may affect growth and development of other plants that colonize sites later in succession. Spotted knapweed alters soil microbial communities (Callaway et al. 2004b; Mummey et al. 2005; Mummey and Rillig 2006; Broz et al. 2007), uses AMF hyphal networks to exploit neighboring plants for resources (Marler et al. 1999; Zabinski et al. 2002; Callaway et al. 2004a), and can benefit directly from AMF (Carey et al. 2004; this study). When conditions permit concurrent colonization by spotted knapweed and AMF, their interactions could have cascading effects on the structure of native plant communities that typically colonize these early successional sites.

We found evidence that AMF directly contribute to vigorous growth of spotted knapweed in soils that typify early successional sites on this alluvial flood plain. It is important to understand how such soil-based processes influence invasive species in all types of ecosystems, but especially in riparian ecosystems that often support much of the regional plant diversity

(Mouw and Alaback 2003), which may be altered by introductions of new species. For optimal management of flood plains, knowledge of how interrelationships among plants and soil microbial communities influence and are affected by the introduction of non-native species is needed (Wolfe and Klironomos 2005). We found a wide range of mycorrhizal responsiveness across the flood plain, which indicates that broad environmental conditions need to be studied to understand the role of plant–soil–microbe interactions for the success of invasive species. Future studies should consider the influence of environmental variation when evaluating interactions between non-native vegetation, soil microbial communities, and their feedbacks on native plants in the actively scoured zones of flood plains.

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