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Impact of Competition and Mycorrhizal Fungi on Growth of *Centaurea stoebe*, an Invasive Plant of Sand Dunes

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ABSTRACT.—Soil biota such as arbuscular mycorrhizal fungi (AMF) have been shown to increase invasive plant species success in a wide variety of systems by providing both direct and indirect benefits to the invader. For example, *Centaurea stoebe* invasion in the western US is at least partially due to AMF networks allowing *Centaurea* to parasitize some native plant species. *Centaurea* also invades sand dune systems of the northern Great Lakes region, which often have reduced or altered soil communities compared to other grasslands. In these habitats, AMF may play a different role in invasion success of this species. We conducted a greenhouse experiment to compare effects of soil biota and AMF on competitive interactions between *Centaurea* and two varieties of *Ammophila breviligulata*, a dominant native grass of Great Lakes sand dunes. We found that *Centaurea* growth was slowed by the presence of *Ammophila* competitors, while AMF had no direct or indirect effect on growth. Both *Ammophila* varieties were uninhibited by the presence of *Centaurea*. The commercially available Cape variety of *Ammophila* had more than twice the inhibitory effect of a native Michigan variety on *Centaurea* growth. It does not appear that *Centaurea* takes advantage of AMF networks in this dune system. Indeed, since *Centaurea* growth is actually reduced in direct competition with *Ammophila*, we suspect that invasion of dunes by this species is a result of disturbance. For land managers, planting *Ammophila* in open areas as part of a restoration plan may slow spread of *Centaurea* in this system.

INTRODUCTION

Soil biota such as arbuscular mycorrhizal fungi (AMF) have been shown to increase invasive plant species success in a wide variety of systems (Richardson *et al.*, 2000; Bray *et al.*, 2003; Fumanal *et al.*, 2006). AMF can provide direct benefits to invasive plants by increasing nutrient and water uptake (Smith and Read, 1997) and can also provide indirect benefits to plants by altering competitive hierarchies with native species, or even directly transferring

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resources or carbon between plants (Chiariello *et al.*, 1982; Meding and Zasoski, 2008). However, the generality of these benefits, even for a given plant species, is unknown.

AMF have been shown to have a potential role in the invasion success of *Centaurea stoebe* L. (formerly *C. maculosa* or *C. biebersteinii*; referred to throughout this paper as *Centaurea*) in the western United States. *Centaurea* is one of the most problematic invasive species in North America, infesting nearly 7 million ha of rangeland in the western United States (Sheley *et al.*, 1998), as well as invading lower productivity prairie, savanna grasslands, and sand dunes in the mid-western US (Emery and Gross, 2005; Marshall and Storer, 2008). In the western US, *Centaurea* has been known to form near-monocultures in previously grass-dominated rangeland, leading to altered nutrient cycling, desertification, and erosion problems (Rice *et al.*, 1997; Herron *et al.*, 2001) as well as loss of economically important grazing areas. While a more recent invasion, and so less studied, in Great Lakes sand dunes *Centaurea* appears to overstabilize dune habitat, reducing native plant biodiversity (Marshall and Storer, 2008). For these reasons, *Centaurea* is actively managed as an invasive species in several state and national parks in the region and is listed as a prohibited noxious weed in Michigan (Michigan Department of Agriculture, 1990). Several greenhouse and field studies have shown that *Centaurea* gets little or no direct benefit from AMF but may use AMF networks to parasitize some native plant species in western US grasslands (Marler *et al.*, 1999; Callaway *et al.*, 2004; Carey *et al.*, 2004). However, nothing is known about whether similar interactions occur in Great Lakes sand dunes.

As primary successional ecosystems, sand dunes are one of the few habitats where AMF are not ubiquitous. AMF are virtually absent from young or unvegetated dunes (Sylvia, 1986), with AMF diversity and abundance generally increasing with successional age (Koske and Gemma, 1997) and buildup of soil organic matter (Olsson and Wilhelmsson, 2000). *Centaurea* generally invades early successional areas of dunes dominated by the native grass, *Ammophila breviligulata* (Marshall and Storer, 2008), where AMF are generally present but in lower abundances than more mature soils (Douds and Millner, 1999). In a previous survey of sand dune habitat around the Great Lakes region (Emery and Rudgers, 2010), we found *Centaurea* in seven out of 18 *Ammophila*-dominated sand dune sites, all located in northern Michigan, USA (unpub. data). *Ammophila* itself is facultatively mycorrhizal, and at least one study has shown tiller growth, leaf growth, and flowering to increase when plants were inoculated with AMF (Gemma and Koske, 1989).

Land managers have become concerned about the presence of *Centaurea* in Great Lakes sand dunes and are actively managing habitat to slow the spread of *Centaurea* through control and restoration efforts (N.P.S. 2008). AMF presence in dune soils becomes an important issue for land managers interested in habitat restoration, as some dune restoration sites have reported extremely low mycorrhizal presence (Kurtboke *et al.*, 2007). On the other hand, restoration activities can increase abundance or shift composition of mycorrhizal fungi unintentionally through contaminated nursery soil and plant stock (Koske and Gemma, 1997; Schwartz *et al.*, 2006). Since other studies have shown that AMF can alter competitive interactions among plants (*e.g.*, Hartnett *et al.*, 1993; Scheublin *et al.*, 2007), it is to be expected that soil conditions in dune restorations may alter the performance of plants in those sites.

We conducted a greenhouse experiment to compare effects of soil AMF on competitive interactions between *Centaurea* and two varieties of *Ammophila breviligulata*. Specifically, we asked whether AMF from sand dunes increased performance of *Centaurea* directly and whether AMF served as an indirect route for *Centaurea* to out-compete this dominant native grass. Based on the findings from some studies in the western US, we expected that AMF

would have no direct benefit to *Centaurea* (Marler *et al.*, 1999) but would indirectly facilitate *Centaurea* growth in the presence of other plants.

METHODS

In May 2007, we conducted a greenhouse experiment to examine whether mycorrhizal fungi could alter competitive interactions between *Centaurea* and *Ammophila breviligulata*. Five plant combinations (*Centaurea* and two varieties of *Ammophila* each grown alone, and *Centaurea* grown in competition with each of the two varieties of *Ammophila*) were crossed with three soil treatments. Each treatment combination was replicated seven times. We filled 105 3 L pots with screened and washed play sand (Quikrete Inc., Atlanta, GA) within 5 cm of the top of the pots. This commercial play sand is similar in texture to sand along the Lake Michigan shore and had no AMF spores present (unpub. data). In 35 pots we added 50 ml of live sand inoculum (containing the whole soil community) collected from Sleeping Bear Dunes National Lakeshore in Michigan (44°48'N, 86°4'W). This inoculum was a composite of seven different locations within the park, all dominated by *Ammophila*. The inoculum was collected in Oct. 2006, air dried and stored at -20 C until the start of the experiment. These conditions allowed fungal spores to remain viable. In another 35 pots we added 30 ml of a microbial wash created by mixing 2 L of live inoculum with 2 L of distilled water in a blender. We filtered the solution through a 38 um sieve and 25 um filter paper to remove all fungal spores and hyphae from the wash while retaining bacteria and other small microbes. This allowed us to separate treatment effects due to fungi from the rest of the soil community, though other factors such as nematode presence could be confounded with fungal treatments. Finally, another 35 pots received 50 ml of sand inoculum which had been autoclave sterilized for 1 h to eliminate soil organisms. We added a thin layer of play sand to the top of each pot to prevent contamination.

In 28 pots we planted small tillers (on average, 60 cm from base to longest leaf tip) of the commercially available "Cape" variety of *Ammophila breviligulata* (Church's Greenhouse and Nursery, Cape May, NJ). These tillers were collected from individual plants that had been growing in the greenhouse in initially sterile growing medium (Metromix) for 9 mo before the experiment started. Young tillers were gently broken off of a main plant, and roots were washed to remove planting medium before transplanting tillers to the experiments. As a strongly clonal plant, *Ammophila* rarely produces seeds, especially in the Cape variety, so clonal propagation and planting of tillers was the best option to mimic natural growing patterns. In another 28 pots we planted small tillers of *A. breviligulata* collected from natural populations within Sleeping Bear Dunes. Like the Cape variety, these plants had been growing in sterile growing medium for 9 mo prior to the experiment and tillers were harvested as described above.

After transplanting, the height and total number of leaves were measured on each tiller to serve as a baseline for plant growth. Because *Ammophila* plants were transplanted into the experiment rather than grown from seed, we estimated plant mass at the beginning of the experiment. For 20 extra plants of each variety, we measured height and leaf number, then dried and weighed these plants (average initial aboveground biomass of Cape plants was approximately 1.0 g, while average initial aboveground biomass of Michigan plants was approximately 0.66 g). We then calculated regression coefficients for plant height and mass in order to estimate initial plant mass of the transplanted plants. Total plant growth over the entire experiment could then be calculated by subtracting estimated initial plant mass from the actual final plant biomass.

To set up competition treatments, we added ten *Centaurea* seeds to half of the pots for each variety \times inoculum combination. Seeds were collected from Sleeping Bear Dunes

National Lakeshore in Oct. of 2006 and stored at 4 C until planting. Additionally, *Centaurea* seeds were planted alone in seven pots of each inoculum treatment (21 pots total). After seeds had germinated, we thinned each pot to include only a single *Centaurea* seedling. This experimental set-up mimics competitive interactions found in mature *Ammophila*-dominated communities where *Centaurea* is invading as seedlings.

Plants were grown at 24 C in the greenhouse for 6 mo with no supplemental lighting. After 3 mo, we started applying weekly fertilization with 50 ml of one-eighth strength hydroponic fertilizer (Ionic Grow 3-1-5 N-P-K; Hydrodynamics International, Inc., Lansing MI). Similar fertilization levels were used in previous AMF studies and were most likely not high enough to reduce plant-fungi interactions (Marler *et al.*, 1999). In Dec. 2007, we harvested above- and belowground biomass of all plants in the experiment. We also measured final height and leaf number on all *Ammophila* plants. For the biomass harvest, we gently washed and separated roots of all plants in the pots using a 500 μm mesh sieve, clipping roots off of each plant once they were clean. Roots and aboveground biomass were dried separately at 60 C for 48 h and then weighed.

A small 5 g sample of roots was collected from each plant before drying, boiled in 10% KOH for 30 min and stained using the ink (Shaeffer black) and vinegar method (Vierheilig *et al.*, 1998). Ten 1 cm root sections from each plant were mounted on microscope slides and visually scored for AMF colonization. Each root section was categorized as either 0%, 5%, 25%, 50%, 75%, or 100% colonized based on total root area occupied by AMF hyphae, and root section scores were averaged for a given plant.

One and two factor ANOVAs were used to examine effects of competitors and AMF treatments on plant aboveground and belowground growth. For *Centaurea* we used final biomass in analyses, while we used the change in biomass for the two *Ammophila* varieties in order to account for differences in initial sizes of tillers. Growth values that were negative for *Ammophila* (*i.e.*, final biomass - estimated original biomass < 0 g) were changed to 0 g for all analyses. The different measures of species size reflect initial differences in morphology (mature tillers vs. germinating seedlings) found in field situations. All analyses were performed in SYSTAT v.12 (SYSTAT Software Inc, 2007).

RESULTS

Our soil amendment treatments significantly altered AMF root colonization on all plants, regardless of plant identity (Fig. 1). The live soil treatment resulted in *Centaurea* and *Ammophila* roots all having approximately 30% of roots colonized by AMF (variation between 20 and 40%). Plants in the wash and sterile treatments had very low ($< 10\%$) root colonization by AMF.

Centaurea showed no growth benefit from enhanced AMF colonization when grown by itself or in competition with *Ammophila* (Fig. 2). Even when examining data from the live whole soil inoculum treatment only, AMF percent root colonization as a covariate in the ANOVA was not a significant predictor of *Centaurea* growth (Aboveground: Competitor ID $F_{2,12} = 7.02$, $P = 0.01$; %AMF: $F_{1,12} = 1.85$, $P = 0.20$; Belowground: Competitor ID $F_{2,12} = 18.13$, $P = 0.01$; %AMF: $F_{1,12} = 0.57$, $P = 0.47$; data not shown).

The competitor identity did significantly affect *Centaurea* growth. Competition with the Michigan *Ammophila* reduced aboveground growth of *Centaurea* by approximately 50%, while competition with the Cape *Ammophila* reduced growth by approximately 80% relative to *Centaurea* plants grown alone (Fig. 2A). Michigan *Ammophila* reduced belowground biomass of *Centaurea* by 60%, while Cape *Ammophila* almost completely eliminated belowground growth by *Centaurea* (Fig. 2B). Similarly, competitor identity, but not soil treatment, altered root/shoot ratios for *Centaurea*. Michigan *Ammophila* reduced *Centaurea* root/shoot ratios by half

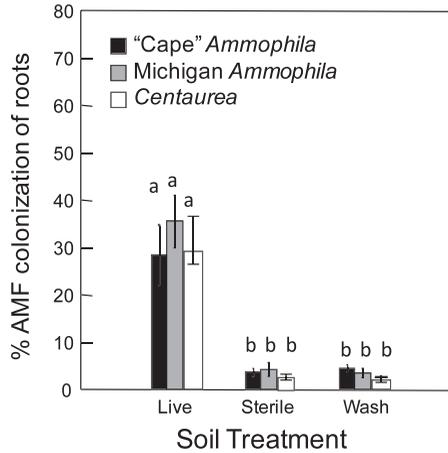


FIG. 1.—Root colonization by AMF for all plants in the experiment. For all plants, the Live treatment had significantly higher AMF colonization than the other two AMF treatments. (Soil: $F_{2,101} = 62.5$, $P < 0.001$; Plant ID: $F_{2,101} = 0.76$, $P = 0.47$; Soil \times Plant ID: $F_{4,101} = 0.34$, $P = 0.85$). Letters indicate significant differences in post-hoc Tukey pairwise comparisons, and error bars indicate one SE.

(3.3 vs. 1.71), while Cape *Ammophila* reduced root/shoot ratios by approximately 90% (3.3 vs. 0.36) (ANOVA results: Soil: $F_{2,44} = 2.29$, $P = 0.12$; Competitor ID: $F_{2,44} = 17.4$, $P < 0.001$; Soil \times Competitor ID: $F_{4,44} = 2.33$, $P = 0.08$; data not shown).

While most *Ammophila* plants actively grew in this experiment (many plants had multiple tillers at the end of the experiment), competition with *Centaurea* had no significant effects on *Ammophila* aboveground or belowground growth, nor root/shoot ratios (both varieties), regardless of the soil treatment (Fig. 3; data for root/shoot ratios not given). Soil treatments also had no significant effects on any measure of *Ammophila* growth. Michigan plants in competition with *Centaurea* on sterile soils had no increase in aboveground biomass during the experiment, though the Soil \times Competitor interaction was not significant in the ANOVA.

DISCUSSION

Our results indicate that *Centaurea* growth is slowed by the presence of *Ammophila* competitors, independent of soil biota. The Cape variety had more than twice the inhibitory effect of the Michigan variety on *Centaurea* growth, while both *Ammophila* varieties were uninhibited by the presence of *Centaurea*. The superior competitive ability of the Cape variety is not surprising, as this variety is an improved cultivar developed by the US Department of Agriculture (Soil Conservation Service, 1977). While the average initial sizes of the two varieties were quite similar (Michigan = 1.005 g, Cape = 1.14 g), Cape had much more growth during the experiment. While this larger size of the Cape variety may partially explain the improved growth suppression of *Centaurea*, the presence of a systemic endophyte in this variety may also be a factor (Halisky and White, 1991; Emery *et al.*, 2010).

It is perhaps surprising that *Centaurea* had no negative effects on *Ammophila* growth, given that *Centaurea* has been shown to be competitively dominant in several other studies (Lesica and Shelly, 1996; LeJeune and Seastedt, 2001; Mangold and Sheley, 2008; Maron and

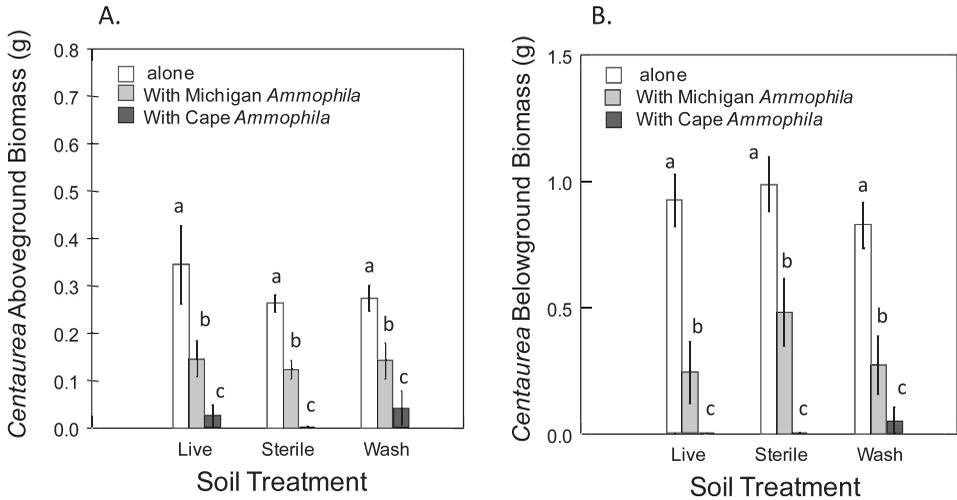


FIG. 2.—*Centaurea* aboveground (A) and belowground (B) biomass in the different treatments. ANOVA results for aboveground growth: Soil: $F_{2,44} = 0.90$, $P = 0.42$; Competitor ID: $F_{2,44} = 42.2$, $P < 0.001$; Soil \times Competitor ID: $F_{4,44} = 0.42$, $P = 0.78$. ANOVA results for belowground growth: Soil: $F_{2,44} = 1.12$, $P = 0.34$; Competitor ID: $F_{2,44} = 78.8$, $P < 0.001$; Soil \times Competitor ID: $F_{4,44} = 0.68$, $P = 0.61$. Letters indicate significant differences in post-hoc Tukey pairwise comparisons, and error bars represent one SE.

Marler, 2008). However, early successional sand dune systems have very low nutrient availability (2–5 ppm, unpub. data; also *see* Lichter, 1998) and native grasses are often more competitive than *Centaurea* in such environments (Herron *et al.*, 2001). There is also some evidence that *Centaurea* success in the western US is due to allelopathic root exudates (Ridenour and Callaway, 2001; Perry *et al.*, 2005). However, soil texture can affect the inhibition strength of allelopathic chemicals, and sandy soils tend to wash out much faster than soils with more clay or organic matter (Inderjit and Dakshini, 1994; Jennings and Nelson, 1998). Under the low nutrient, droughty conditions of sand dunes, it is less surprising that *Centaurea* does not immediately out-compete native grasses. Additionally, a recent study by Reinhart and Rinella (2011) showed that eastern North American species may be more tolerant of competition with *Centaurea* than western species and that *Centaurea* populations may differ in their allelopathic capabilities. Instead, *Centaurea* may successfully invade these dune habitats by either taking advantage of disturbed open habitat (Knoche *et al.*, 2010) or by having a demographic advantage over native plants such as *Ammophila*. While our study only examined competition between mature *Ammophila* tillers and *Centaurea* seedlings, representing the initial stages of competitive interactions leading to invasion, a study by Emery and Gross (2005) showed that reproduction and adult survival were more important than juvenile growth for overall population growth rates of *Centaurea* in a Michigan sand prairie. Our study was unable to address competitive interactions at these adult life stages.

While all plants in our experiment showed increased AMF root colonization with the addition of AMF soil inoculum, this had no effect on growth of any of the plants. While other studies have supported this result for *Centaurea* (Marler *et al.*, 1999; though *see* Harner *et al.*, 2010 for an example of direct positive AMF effects) this lack of direct benefit of AMF on *Ammophila* plant growth is puzzling. While not obligately mycorrhizal, *Ammophila* from

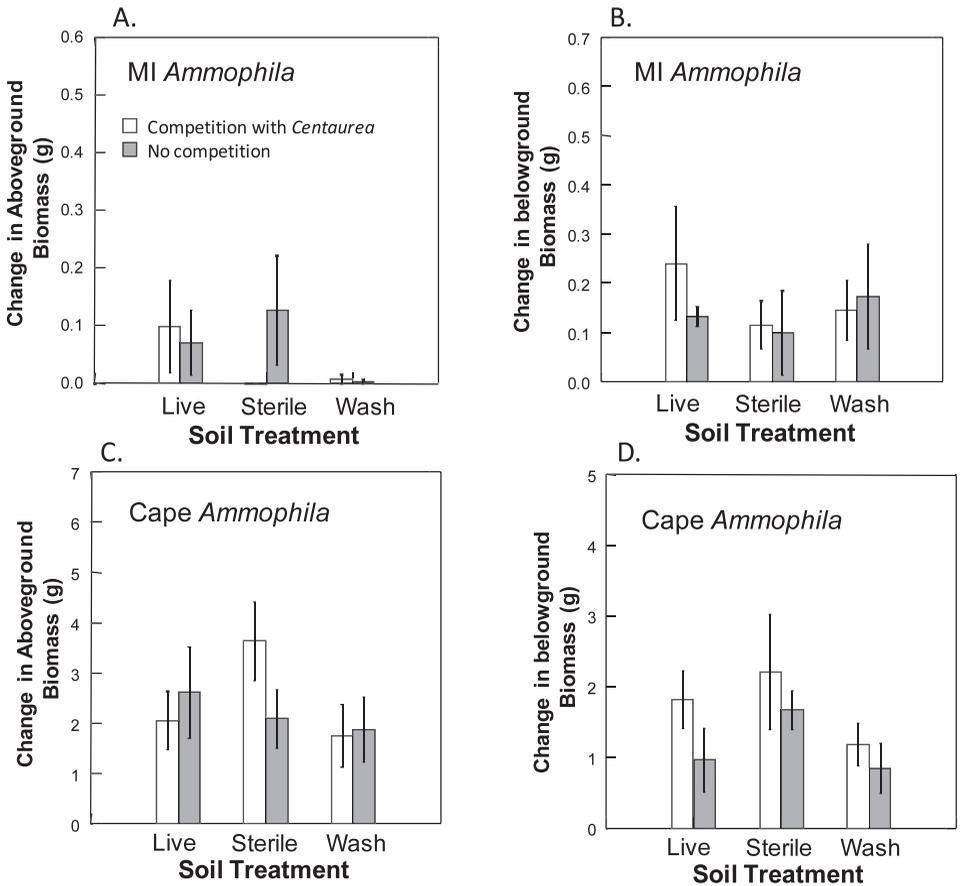


FIG. 3.—Above and below-ground growth of the two varieties of *Ammophila* with and without competition from *Centaurea*. (A–B) aboveground and belowground growth of Michigan *Ammophila*, (C–D) above and belowground growth of Cape *Ammophila*. Note different axis scales. ANOVA results: Michigan *Ammophila* aboveground growth: Soil: $F_{2,25} = 1.21$, $P = 0.32$; Competition: $F_{1,25} = 0.45$, $P = 0.51$; Soil \times Competition: $F_{2,25} = 0.92$, $P = 0.41$; Michigan *Ammophila* belowground growth: Soil: $F_{2,25} = 0.45$, $P = 0.64$; Competition: $F_{1,25} = 0.24$, $P = 0.63$; Soil \times Competition: $F_{2,25} = 0.43$, $P = 0.82$; Cape *Ammophila* aboveground growth: Soil: $F_{2,25} = 1.59$, $P = 0.23$; Competition: $F_{1,25} = 0.36$, $P = 0.56$; Soil \times Competition: $F_{2,25} = 1.73$, $P = 0.20$; Cape *Ammophila* belowground growth: Soil: $F_{2,25} = 2.53$, $P = 0.10$; Competition: $F_{1,25} = 2.88$, $P = 0.10$; Soil \times Competition: $F_{2,25} = 0.20$, $P = 0.82$). Error bars indicate one SE.

the Atlantic coast of the US have been shown to benefit from AMF colonization under field and greenhouse conditions (Gemma and Koske, 1997; Koske and Gemma, 1997). Endophyte presence in some grasses can eliminate benefits of AMF by reducing AMF colonization in roots (Omacini *et al.*, 2006; Mack and Rudgers, 2008). However, our study showed that AMF colonization rates were high in the AMF treatment for all plants, not just those without endophytes (*i.e.*, Michigan plants), and there were no significant differences in colonization rates between the different *Ammophila* varieties. It may be that our experiment was not long enough to detect a benefit from AMF, though it was run over a

6 mo period, which is twice as long as similar studies which have demonstrated positive AMF effects (e.g., Marler *et al.*, 1999). Additionally, our measure of AMF hyphae may not be the best measure of the functioning of the mycorrhizal relationship. Arbuscles may be a more informative measure of AMF functioning, and we were unable to definitively identify arbuscules in root samples.

More likely, since AMF effects on plants can depend on resource availability, size of plants, and AMF community composition (Mummey and Rillig, 2007), in our particular system the native AMF community may simply provide very little benefit to plants during early life stages. The specificity of the mycorrhizal relationship might also have been lost due to the use of commercially-available plants. However, in a field study with the same *Ammophila* varieties, a whole-soil inoculum increased growth and survival of the Michigan variety, but not the Cape, indicating that soil microbial communities can be beneficial under field conditions (Emery and Rudgers, 2011). Results from some other studies indicate AMF may increase plant reproduction and tillering, rather than individual tiller growth *per se* (Gemma and Koske, 1989; Hartnett *et al.*, 1993; Boudreau and Houle, 2001), though seedlings have benefited from AMF in other systems (e.g., van der Heijden, 2004). Alternatively, other organisms, such as nematodes or parasitic fungi, in the whole-soil inoculum may have counteracted any benefit provided by AMF (e.g., Rodriguez-Echeverria *et al.*, 2009). Further work comparing soil communities across dune systems is needed to provide additional insight.

While *Centaurea* is very widespread in Great Lakes sand dunes, it does not appear that this species takes advantage of AMF networks to gain a competitive advantage in this system. Indeed, since *Centaurea* growth is actually reduced in direct competition with the dominant dune grass *Ammophila*, we suspect that invasion of dunes by this species is a result of disturbance, with *Centaurea* taking advantage of open habitat on dunes, rather than directly out-competing native plants. Of course, long term demographic studies would be needed to confirm this. For land managers, planting *Ammophila* in open areas as part of a restoration plan may slow spread of *Centaurea* in this system. While the Cape variety appears to be most capable of slowing growth of *Centaurea*, local genotypes may be a better option due to recent concerns about planting improved cultivars for management purposes (Lesica and Allendorf, 1999).

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