

Mycorrhizae and Fine Root Dynamics of *Centaurea maculosa* and Native Bunchgrasses in Western Montana

Abstract

Centaurea maculosa is an invasive exotic pest plant of intermountain grasslands of the western United States. We investigated whether there were differences in fine root and mycorrhizal development between the exotic forb *C. maculosa* and two native grasses, since these are factors known to influence competitive ability of plants. We measured colonization by arbuscular mycorrhizal (AM) fungi of the native bunch grasses *Pseudoroegneria spicata* and *Festuca idahoensis*, and *C. maculosa*, and used root periscopes to investigate fine root patterns of *P. spicata* and *C. maculosa*. AM fungal colonization of the exotic was similar to *F. idahoensis* in 1995 (43.6% vs. 44.7%), and was higher than *P. spicata* in 1995 and 1996 (43.6% vs. 26.9%, and 55.4% vs. 15.6%). Colonization of the grasses was not affected by the presence of *C. maculosa*. Fine roots of *C. maculosa* developed earlier, with a higher proportion of deep roots than *P. spicata*. Thirty nine per cent of *C. maculosa* roots, but only 25% of *P. spicata* roots, were deeper than 30 cm. Early and deep root development and extensive mycorrhizal colonization in the field may contribute to competitive dominance of *C. maculosa*.

Introduction

Spotted knapweed (*Centaurea maculosa* Lam.) is one of the most destructive exotic pest plants in North America, and can establish nearly monocultural stands in previously diverse intermountain prairie communities. Invasions are influenced by both the abiotic conditions of the new range and by biological traits of the invading species; insight into biology of invasive plants can contribute to our understanding of invasions. With as much as 50-80% of net productivity in prairie communities being belowground (Caldwell 1979), it is important to understand belowground interactions, and their role in the competitive effects of exotic species (Harris 1967, D'Antonio and Mahall 1991, Goodwin 1992, Holmes and Rice 1996). Spatial and temporal rooting patterns, and mycorrhizal associations are two major factors influencing belowground competition. Occupation of soil space is a primary determinant of below ground competitive ability, and can be quantified as root density, vertical distribution, and phenology (Casper and Jackson 1997, Schenk et al. *in press*). High root density enhances the exploitation of patchy resources (Jackson and Caldwell 1989, Callaway 1990, Caldwell et al. 1991, Jackson et al. 1990, Caldwell et al. 1996),

and can exclude neighbor root systems. This can in turn produce strong competitive effects on neighbors (Callaway et al. 1991, Schenk et al. *in press*). The phenology of root growth may contribute to preemptive occupation of space, and the ability of plants to respond to ephemeral resource availability (Harris 1967, Jackson and Caldwell 1989, Holmes and Rice 1996, Casper and Jackson 1997).

For many species, the performance of fine roots is closely tied to the development of mycorrhizal associations. Arbuscular mycorrhizal (AM) fungi are common root symbionts that can improve plant mineral status (Allen and Allen 1990, Brundrett 1991) and influence the outcome of competitive interactions among host species. Plant response to AM fungi depends on resource availability, species-specific differences in mycorrhizal dependence (Hetrick et al. 1989, Allen et al. 1984, 1988, Grime et al. 1987, Allen and Allen 1990, Hartnett et al. 1993, Zobel and Moora 1995, Moora and Zobel 1996), and the species composition of the AM fungal community (Allen and Allen 1988, Johnson 1993, Francis and Read 1994, Bever et al. 1996). AM fungi have been shown to influence competition between exotic and native species (Goodwin 1992, Marler et al. 1999) but little is known about the impact of invasions on native mycorrhizae (but see Johnson and Wedin 1997).

Fine root dynamics and mycorrhizal colonization are often interrelated in their effects. For

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example, rooting patterns can be more plastic if plants are facultatively mycorrhizal, and plants with more fibrous root systems tend to be less dependent on mycorrhizae (Hetrick 1991, Hetrick et al 1992, Muthukumar et al 1996). Timing of root growth and level of colonization by AM fungi have also been shown to influence the effectiveness of root boring insects used as biological control agents on the noxious weed *Centaurea diffusa* Lam. (diffuse knapweed) (Harris and Clapperton 1997). However, few field studies have addressed the dynamics of AM fungi and rooting patterns for the same species in the same habitat.

We investigated the dynamics of fine roots and mycorrhizae in the field for the noxious weed *Centaurea maculosa* and native bunchgrasses, with the objective of describing patterns in and relationships between their development. We compared fine root density and phenology at four depths between *C. maculosa* and *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass, syn. *Agropyron spicatum*), and compared the extent and phenology of mycorrhizal colonization of *C. maculosa*, *P. spicata* and *Festuca idahoensis* Elmer (Idaho fescue).

Methods

Study Areas

We quantified root distributions and phenologies for *C. maculosa* and *P. spicata*, and mycorrhizal colonization for *C. maculosa*, *P. spicata* and *F. idahoensis* occurring on a southwest slope of Mount Sentinel (elevation 1294m), adjacent to the University of Montana campus in Missoula in 1995. Mycorrhizal colonization of *C. maculosa* and *P. spicata* was also measured at a site 4.2 km east of Hamilton, Montana (elevation 1334 m, approximately 80.5 km south of Missoula) in 1996. Both sites have been invaded by other exotic species, including *Linaria dalmatica* (L.) Mill. (Dalmatian toadflax), *Euphorbia esula* L. (leafy spurge), and *Bromus tectorum* L. (cheatgrass), but retain remnant patches of native prairie in good condition (i.e. very few exotic plants).

Root Density, Depth, and Phenology

In April 1995, we inserted 60-cm-long plexiglass tubes under 10 large *C. maculosa* plants and 10 large *P. spicata* plants as permanent mini-rhizotrons for root viewing. Since *C. maculosa* has been

shown to have allelopathic effects on neighbors (Ridenour 1995), we placed periscope tubes beneath *P. spicata* individuals growing without *C. maculosa* nearby (>5m). The periscope tubes were inserted at a 15-degree angle from vertical to enhance root contact with the transparent walls. Sections were marked at fifteen-cm intervals on the wall of the tube, and weekly or bi-weekly measurements were taken with a root periscope (Richards 1984) beginning on April 13, 1995 and ending on September 28, 1995. On each sampling date, all white tips of fine roots were counted in each of the following depth categories: 0-15 cm, 15-30 cm, 30-45 cm and 45-60 cm along the tube surface. We counted only roots with white growing tips because they were the most likely to be growing and absorbing resources.

Sampling and scoring of roots for mycorrhizal colonization.

We sampled AM fungal colonization of grasses and *C. maculosa* that were isolated and that were intermixed, providing an estimate of plant community effects on mycorrhizal colonization. At the Missoula and Hamilton sites, we identified communities that were 1) "native," i.e. 0-10% *C. maculosa*; 2) "mixed," 10-25% *C. maculosa*; or 3) "exotic," with more than 25% cover by *C. maculosa*. These categories are merely descriptive. We collected roots in the top 15-cm of soil from 15 randomly selected individuals of each grass species from native and mixed communities. While mycorrhizae can be found at depths greater than 15 cm, they often decline sharply with depth (Cooke et al. 1993, Al-Agely and Reeves 1995, Barnola and Montilla 1997, Ingleby et al. 1997), so we sampled in the top 15 cm for consistency. Samples were taken with a trowel, and roots were taken attached to the culms, so root identification would be possible. We collected at least 15 *C. maculosa* individuals from the mixed and exotic communities. Sampling was repeated at six-week intervals (mid-May, early July, and mid-August) over the summers.

Roots were washed in the lab, then cleared in 2.5% KOH for 48 hours, acidified in 5% HCl for 12 hours, and stained in trypan blue for 12 hours. All steps were done at room temperature. Vesicles, arbuscules and hyphae were scored using a magnified intersection method (McGonigle et al. 1990). For each individual we scored four transects

through 36 one-cm root sections for a total of approximately 144 random intersections per individual.

Statistical Analyses.

Repeated measures ANOVA was used to test for differences in root density between the two species and the four depths over the 1995-growing season. Fine root data was normally distributed and was not transformed.

Data for total colonization and vesicle density in 1995 (Missoula site) were transformed with arcsine of square root functions prior to analysis. These data were normal for the 1996 season (Hamilton site) and were not transformed. Arbuscule data in both years were not normal even after transformation, so the non-parametric Mann-Whitney U-test for rank was used for analysis. For *C. maculosa*, a two-way analysis of variance was used to determine the effect of community type (exotic or mixed) and sampling date on total colonization and vesicle density. For *P. spicata* and *F. idahoensis*, a separate three-way analysis of variance was used to test the effect of host species, community (native or mixed) and sampling date on total colonization and vesicle colonization. The three species could not be analyzed in the same ANOVA since the treatments within community type were different for the grasses and *C. maculosa*. Comparisons between total colonization and vesicle density of *C. maculosa* and the grass species were made with t-tests. Comparisons of arbuscule density between species and community types were made with the Mann-Whitney U-test for rank.

Results

Rooting patterns.

Averaged over all depths and sampling dates, *C. maculosa* and *P. spicata* did not differ in fine root density (Table 1, $P=0.519$). However, there was a significant difference in root density at the different depths ($P<0.001$), and the interaction term for species by depth was significant ($P<0.001$), indicating root growth differed with depth for the two species. *Centaurea maculosa* developed fine roots earlier than *P. spicata* at all root depths (Figure 1), and its roots were more abundant at the two lower soil depths than those of the bunchgrass. Over the entire measurement period, *C. maculosa*

TABLE 1. Repeated measures ANOVA for differences in rooting distribution between *C. maculosa* and *P. spicata* over time.

Source	Type 3		Mean Squares	F	Sig.
	Sum of Squares	df			
Intercept	372171	1	372171	310.80	0.00
Species	504.34	1	504.34	0.42	0.52
Depth	60037.10	3	20012.40	16.71	0.00
Species*depth	11839.80	3	3946.604	3.30	0.03
Error	81426.800	68	1197.453		

had 39% of its total roots in the lower 30 cm of soil, while *P. spicata* had 24% at that depth. *Centaurea maculosa* had 4 times as many roots as *P. spicata* in the 45-60 cm layer of soil (Figure 1).

At shallow depths (0-15 cm), phenological fluctuations in root density of the two species were correlated ($r=0.69$), suggesting that fine roots of both species were responding similarly to environmental conditions (e.g. soil moisture or temperature) over the growing season. No significant correlation was observed for roots at the 45-60 cm profile ($r=0.14$) indicating that root dynamics were less affected by seasonal changes, and were largely driven by inherent species-specific morphology and development.

Mycorrhizal colonization

Total mycorrhizal colonization did not differ between *C. maculosa* and *F. idahoensis*, but both of these species had higher total colonization than *P. spicata* (Table 2). At both sites, vesicle density was significantly higher in *C. maculosa* roots than in either grass species (Table 2). At the Missoula site, *F. idahoensis* had the highest arbuscule density, while *C. maculosa* and *P. spicata* did not differ significantly. At the Hamilton site, *C. maculosa* had significantly more arbuscules than *P. spicata* (Table 2).

Timing of sampling had a significant effect on total AM colonization of *C. maculosa* in both years (1995 $P_{\text{date}}=0.001$, 1996 $P_{\text{date}}=0.005$). Total colonization of *C. maculosa* was higher in July and August than in May at the Missoula site, and peaked in July at the Hamilton site (Figure 2). The analysis of variance did not indicate an effect of sampling date on total colonization of the grasses in 1995 ($P_{\text{date}}=0.086$), although post hoc

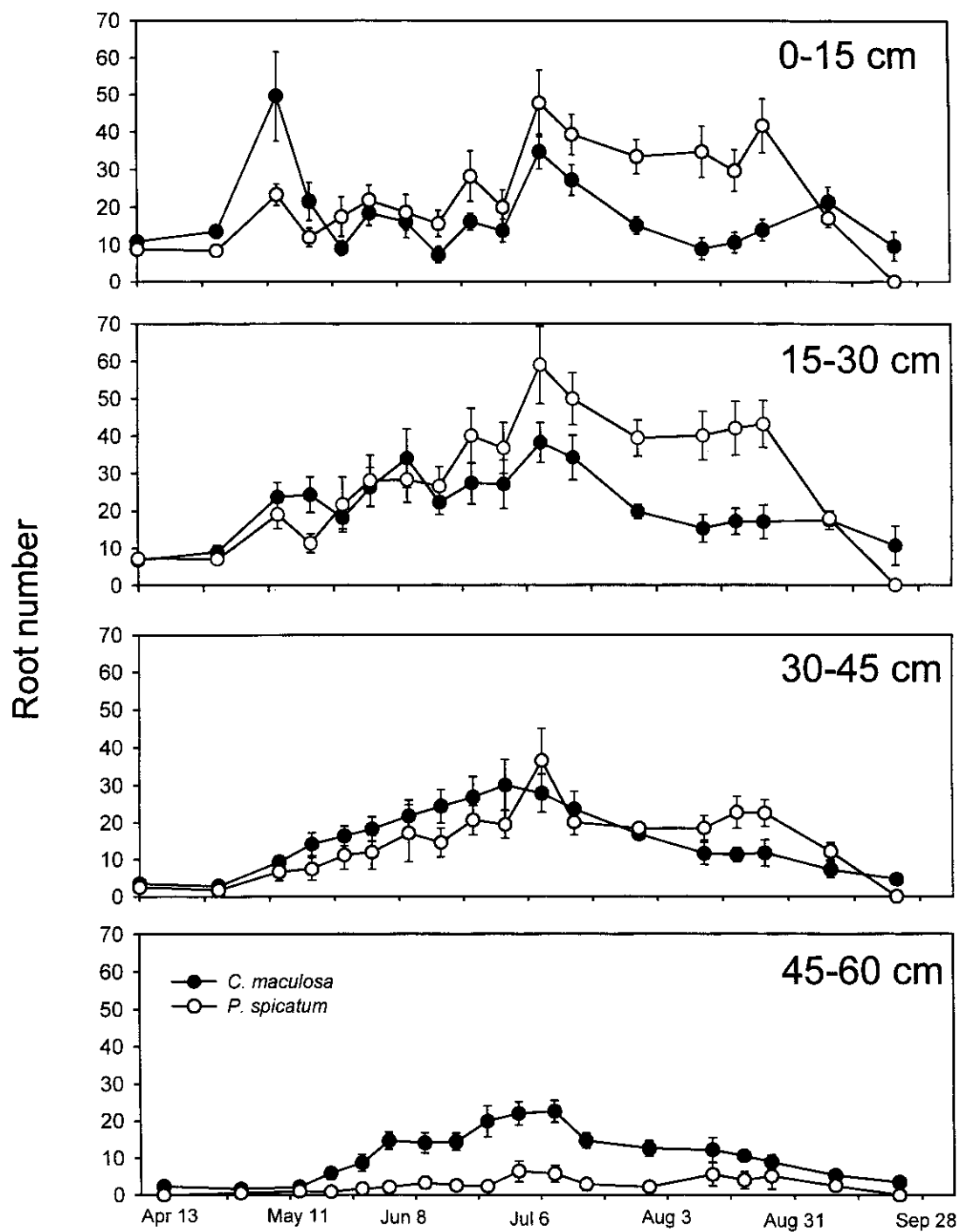


Figure 1. Number of fine roots of *C. maculosa* and *P. spicatum* at each depth in 1995. Error bars represent one standard error of the mean.

TABLE 2. Comparisons of mean AM colonization among species. Transformed values for vesicle density and total colonization were compared with t-tests; actual means are given. Arbuscule density was compared with the Mann-Whitney U test for rank. Values in a column at each site that are followed by different letters are significant at $P < 0.05$. Values in parentheses are the standard error of the mean.

	Total colonization ¹	Vesicle colonization ¹	Arbuscule colonization
Missoula site ¹	mean (s.e.)	Mean (s.e.)	Mean (s.e.)
<i>P. spicata</i>	0.269(0.018)a	0.021(0.004)a	0.008 (.002) a
<i>F. idahoensis</i>	0.447(0.021)b	0.025(0.003)b	0.043 (.009) b
<i>C. maculosa</i>	0.436(0.023)b	0.045(0.006)c	0.004 (.001) a
Hamilton site			
<i>P. spicata</i>	0.156 (0.013) a	0.011 (.002) a	.002 (.001) a
<i>C. maculosa</i>	0.554 (0.021)b	0.038 (.004) b	.006 (.001) b

¹At the Missoula site, total colonization and vesicle density were transformed with arcsine of the square root function. At the Hamilton site, total colonization and vesicle density were normally distributed.

analysis suggests that total colonization of *P. spicata* decreased over the growing season (Figure 2). However, in 1996 sampling date did influence total colonization of *P. spicata* ($P_{\text{date}} < 0.0001$), which increased over the season.

Vesicle colonization of *C. maculosa* roots significantly increased over the season in 1995 ($P_{\text{date}} = 0.036$) but there was no effect of date on vesicle colonization at the Hamilton site ($P_{\text{date}} = 0.148$). There was no significant effect of date on vesicle density in grass roots in either year. Community type did not affect total AMF colonization of any species. However, vesicle colonization of *C. maculosa* differed between community types in both years (1995 $P_{\text{community}} = 0.015$, 1996 $P_{\text{community}} < 0.01$), but in different directions each year: colonization was higher in the mixed community in 1995, but higher in the exotic community in 1996. This is further compounded by the difference in sites each year.

Discussion

Our comparison of root phenology and mycorrhizal colonization suggests several mechanisms that may contribute to competitive dominance of *C. maculosa*. *Centaurea maculosa* developed roots earlier at all depths, and produced more roots throughout the growing season at the 45–60 cm depths, than the native *P. spicata*. Such rapid acquisition of space is important for competitive dominance (Casper and Jackson 1998, Schenk et al. *in press*). Ability to occupy belowground space more rapidly than natives may allow *C. maculosa* to preempt available resources, as has been shown

for other invasive species (Harris 1967, Sheley et al. 1993). Earlier growth and deeper rooting distribution suggests that the invader may have access to a wider range of soil resources than *P. spicata*. The fact that there was no effect of community type on AM fungal colonization indicates that interference with native mycorrhizae is not a likely mechanism of competitive dominance.

Mycorrhizal colonization levels were consistently higher for *C. maculosa* than *P. spicata*. Since we observed AM colonization at two sites in separate years, it is impossible to make strong conclusions about phenological differences between species in vesicles or arbuscules. These are known to vary with differences in soil types (Johnson-Green et al. 1994, Klironomos 1995) and between years for reasons that are not understood (Allen et al. 1989, Sanders and Fitter 1992). Levels of total mycorrhizal colonization were comparable between *C. maculosa* and *F. idahoensis*, and were higher at both sites in *C. maculosa* than *P. spicata*. AM fungi strongly enhance *C. maculosa*'s competitive dominance over *F. idahoensis* in greenhouse experiments (Marler et al. 1999), so the high level of colonization we found allows for the possibility of similar mechanisms functioning in the field. Also, higher levels of mycorrhizal colonization may increase phosphorus and nitrogen uptake (Hoffman and Mitchell 1985, Allen and Allen 1990) over *P. spicata*.

Early in the season, *C. maculosa* generated more fine roots with a lower level of AM colonization, while later in the season, colonization levels increased while fine root production decreased. It

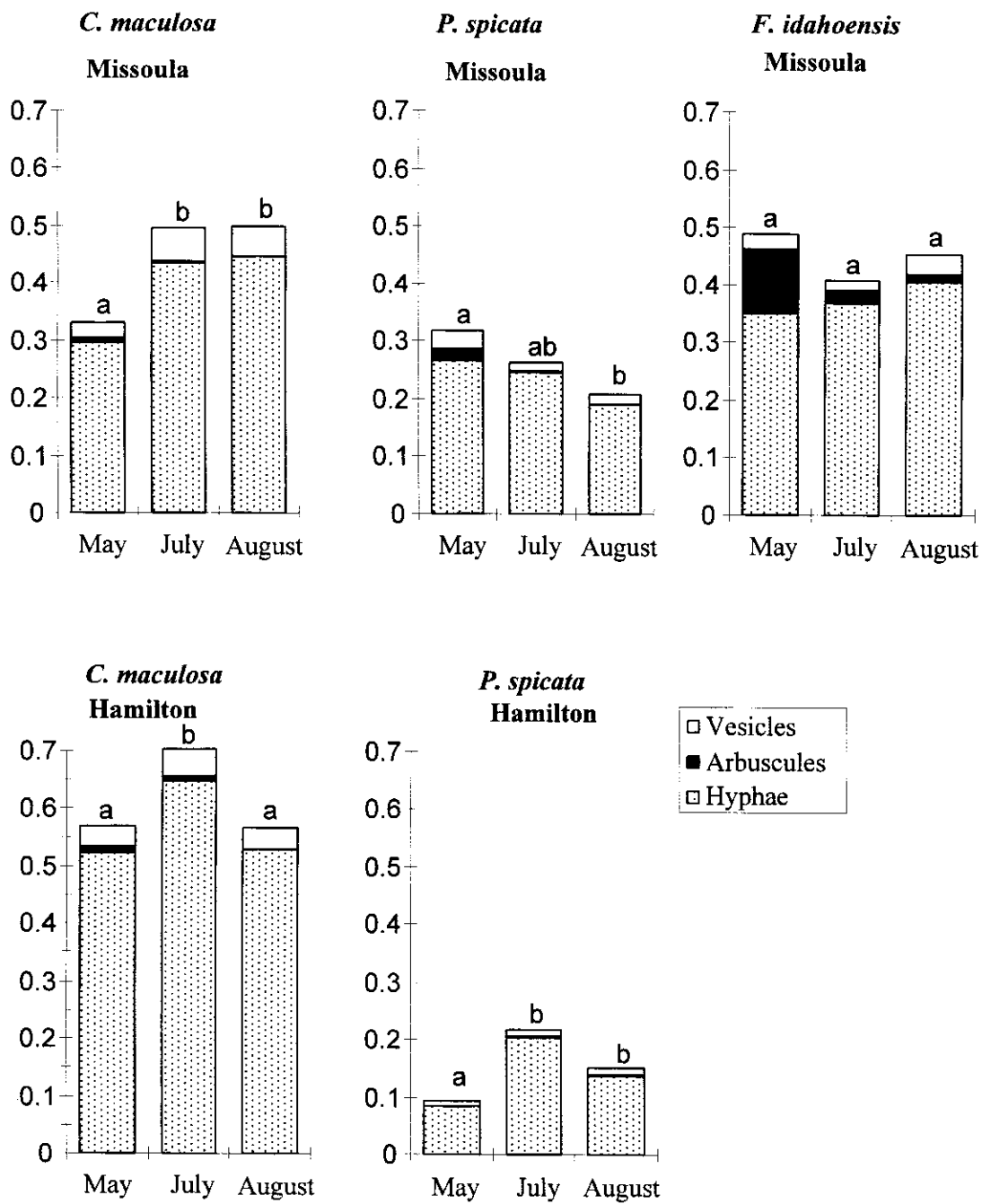


Figure 2. Proportion of roots colonized by arbuscular mycorrhizal fungi in 1995 (Missoula) and 1996 (Hamilton).

is noteworthy that *C. maculosa* allocated more carbon to roots at deeper levels, while maintaining mycorrhizal associations at shallow depths.

Our data support a growing body of work that suggests below ground processes are important to the invasiveness of *Centaurea maculosa*. By developing fine root systems more rapidly and in deeper soil horizons, and by utilizing *in situ* mycorrhizal communities, this exotic invader may gain competitive advantages over native species. This study should be considered preliminary, and more detailed studies encompassing multiple years

are warranted to further investigate these relationships.

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