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THE RESPONSE OF ARBUSCULAR MYCORRHIZAE TO FERTILIZATION, MOWING, AND REMOVAL OF DOMINANT SPECIES IN A DIVERSE OLIGOTROPHIC WET MEADOW[1]

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In a wet oligotrophic meadow located in the Czech Republic, a factorial experiment with treatments consisting of fertilization, mowing, and removal of the dominant species (*Molinia caerulea*) was established in 1994. In 1997 *Holcus lanatus, Molinia caerulea, Potentilla erecta, Prunella vulgaris,* and *Ranunculus auricomus* were examined for arbuscular mycorrhizal (AM) hyphae, arbuscles, and vesicles three times over the season. Time had a significant effect on AM in all five species. Except for *Molinia* arbuscles, a modal effect occurred, with the second sampling having a greater level of AM structures than the first and the third. Fertilization had the greatest effect on AM levels by decreasing the level of *Holcus* hyphae and vesicles, *Potentilla* vesicles, *Prunella* hyphae, and *Ranunculus* hyphae and vesicles. Mowing significantly increased the number of *Potentilla* vesicles, and the removal of dominant species had no significant effects. Interactions between time and treatments were common. Significant effects to the arbuscle:vesicle ratio were infrequent, and those that occurred were related to changes over the season. Seasonal effects appear to have a more powerful effect on AM structures and the arbuscle:vesicle ratio than do treatment effects. In a second experiment, *Ranunculus auricomus, R. acris,* and *R. nemorosus,* sampled four times over the season, showed significant changes in AM colonization. Overall, AM structures either declined over the season or increased from April to May and then declined. There was no AM colonization response to a spring fertilization in the three species. It is postulated that the patterns observed are due to phosphorus availability and seasonal changes in soil moisture and rates of root growth and turnover.

Key words: arbuscular mycorrhizae; Czech Republic; fertilization; meadows; mowing; oligotrophic; removal of dominant.

In Central Europe, meadows at lower elevations are anthropogenic in origin, having been used for hay production and require traditional management practices, i.e., mowing and no or limited fertilization to maintain their diverse species assemblage (Bakker, 1989; Oostermeijer, van't Veer, and den Nijs, 1994). Recently, due to economic pressures, management practices of these meadows have changed dramatically, with either intensified fertilization or abandonment of meadows. Both processes produce changes in species composition that are accompanied by extirpation of some species and an overall loss of species diversity (Bakker, 1989). When traditionally managed these meadows are quite diverse, often containing >50 species/m^2, many of which are endangered (Klimeš, Jongepier, and Jongepierová, 1995; Krenova and Lepš, 1996). Thus, these meadows are a focus of research efforts, an important aspect of which is the response of meadow species to treatments based upon traditional and modern management practices. Mycorrhizae may be important in the maintenance of species diversity in these meadows (Grime et al., 1987; Gange, Brown, and Farmer, 1990; Francis and Read, 1995; Zobel, Moora, and Haukioja, 1997; Wilson and Hartnett, 1997).

Arbuscular mycorrhizae (AM) are important components of virtually all terrestrial ecosystems (Brundrett, 1991; Smith and Read, 1997). It is estimated that >90% of all higher plants are mycorrhizal and >80% of these form AM relationships (Smith and Read, 1997). Plants colonized by AM fungi usually exhibit improved growth due to enhanced nutrient uptake, principally phosphorus (e.g., Koide, 1991; Boerner, 1992; Mullen and Schmidt, 1993), although many cases of antagonistic relationships between plants and AM fungi exist (e.g., Francis and Read, 1995). In high-phosphorus environments, i.e., with fertilization, AM may not be beneficial to the plant because the plant continues to export carbon to the fungi while receiving in return phosphorus that could be extracted from the soil without AM (Chambers, Smith, and Smith, 1980; Graham, Leonard, and Menge, 1981; Schwab, Menge, and Leonard, 1983; Braunberger, Miller, and Peterson, 1991). However, reports also exist of high AM colonization and enhanced plant growth at high available phosphorus concentrations (Davis, Young, and Rose, 1984; Smith et al., 1986). Other edaphic factors such as excess nitrogen (Hall, 1978; Chambers, Smith, and Smith, 1980) and pH (Wang et al., 1993; Porter, Robson, and Abbott, 1987; Al-Agely and Reeves, 1995) may also create conditions for little or no benefit to the host plant from AM. In addition to affecting plant perfor-

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TABLE 1. Characteristics of each target species and their responses to treatments such that a ''+'' corresponds to species increase under a given treatment, ''−'' species decrease, and ''0'' to no response. Species responses are described in detail in Lepš (1999).

Species	Species characteristics			Species response		
	Growth form	Height (cm)	Flowering period	Fertilization	Mowing	Dominant removal
Holcus lanatus	perennial broadleaved tussock grass	60	May–June	−	+	+
Molinia caerulea	perennial broadleaved tussock grass	>100	August–September	0	−	
Potentilla erecta	clonal creeping plant from rhizomes	<20	late May–August	−	−	+
Prunella vulgaris	low erect herb with rooting nodes at the base	<15	June–September	−	+	+
Ranunculus acris	erect herb	50	May–September	+	+	+
Ranunculus auricomus	erect herb	30	late April–May	+	+	+
Ranunculus nemorosus	erect herb	50	May–June	−	+	+

mance, these factors also influence host plant dependency on AM symbiosis and the level of root colonization (Menge et al., 1982; Kitt, Hetrick, and Wilson, 1988).

Grazing has been found to dramatically reduce AM colonization and spore densities. This may be due to a decrease in leaf area and an increase in root:shoot ratio that result in a decreased source capacity insufficient to satisfy root and AM fungi sink demands (Bethlenfalvay and Dakessian, 1984; Bethlenfalvay, Evans, and Lesperance, 1985). Many studies have found that seasonal factors, which are directly related to host plant development stage or physiological state, play a major role in AM colonization levels (Read, Koucheki, and Hodgson, 1976; Rabatin, 1979; Gay, Grubb, and Hudson, 1982; Allen, 1983; Allen, Allen, and West, 1987; Brundrett and Kendrick, 1988; Sanders, 1990, 1993; Sanders and Fitter, 1992a; Mullen and Schmidt, 1993). For example, AM fungal colonization is often lowest in early summer due to rapid root growth outstripping the spread of AM colonization (Douds and Chaney, 1982; Warner and Mosse, 1982; Dickman, Liberta, and Anderson, 1984; Ebbers, Anderson, and Liberta, 1987).

The aim of this study was to assess the influence over time of management techniques that maintain meadow diversity on AM colonization levels through measurements of three AM structures, hyphae, arbuscles, and vesicles, in two field experiments. In the first experiment, using five vascular plant species we assessed the effects of different treatments (fertilization, mowing, and removal of the dominant species) upon AM levels over time. In the second experiment we assessed AM levels over time in three *Ranunculus* species with a fertilization treatment.

MATERIALS AND METHODS

Study area—Ohrazeni is a ~1-ha wet oligotrophic meadow located in southwestern Czech Republic, 10 km southeast of Ceské Budejovice, (48°57′ N, 14°36′ E), at an elevation of 510 m a.s.l. Mean annual temperature is 7.8°C, and mean annual precipitation is 620 mm (Ceské Budejovice meteorological station; Vesecký, 1960). July is the wettest and warmest month with 102 mm of precipitation and temperatures range from a minima of 11.6°C to a maxima of 24.1°C. Mean January (the coldest month) temperatures range from a mean daily minima of −6.2°C to a mean maxima of 0.6°C. Soil nutrient levels are low (total nitrogen 6–8 g/kg dry soil mass, total phosphorus 400–500 mg/kg dry mass, C/N ratio 16–20 (Lepš, unpublished data). See Lepš (1999) for description of the vegetation. Nomenclature follows Rothmaler (1976).

Experiment 1—Treatments were established in a 24 4-m^2 quadrat factorial design in three complete blocks in 1994 (Lepš, 1999). The treatments were fertilization, mowing, and removal of the dominant species (*Molinia caerulea*). The fertilization treatment was an annual application of 65 g/m^2 of commercial NPK fertilizer [12% N (nitrate and ammonium), 19% P (as P_2O_5), and 19% K (as K_2O)], applied in two dosages, 50 g/m^2 in autumn and 15 g/m^2 in spring (starting in 1997 the total dosage was applied in spring). The mowing treatment was annual scything of the quadrats in late June or early July. *Molinia caerulea* was manually removed by screwdriver in April 1995, and new individuals are removed annually. The community is nutrient limited; fertilization increased aboveground biomass from 350 to nearly 600 g/m^2 [dry mass] (Lepš, 1999).

The roots of two individuals of *Holcus lanatus*, *Molinia caerulea*, *Potentilla erecta*, *Prunella vulgaris*, and *Ranunculus auricomus* were excavated in each of the 24 quadrats on 20 May, 10 June, and 5 July 1997. *Molinia caerulea* was only present in half of the plots because it had been removed from the ''removal of dominant species'' treatment quadrats. Mowing occurred after the second sampling period and before the third. Plants were frozen until 24 August 1997. Roots were separated, washed, cleared, and stained with chlorazone black (Brundrett, Melville, and Peterson, 1994). Percentage AM colonization of fine roots (<1 mm in diameter) was estimated by placing a grid of 1-cm squares below a petri plate that contained the root sample under a dissecting microscope. One hundred locations in which a root crossed a line on the grid were scored for hyphae, arbuscles, and vesicles. Many samples were examined under higher power to ascertain that the structures were indeed AM. The number of mycorrhizal ''hits'' is used as an estimate of percentage root colonized by the three AM structures (Brundrett, Melville, and Peterson, 1994).

For the two specimens of a species in a quadrat, percentage hypha, arbuscle, and vesicle values were averaged. These pooled quadrat values were used in statistical analysis. Due to the difficulty of isolating fine roots from meadow samples, the number of viable root samples in 17% of the quadrats was one. In these cases the AM colonization values from this one sample were used as the quadrat value. For each quadrat the number of arbuscles was divided by the number of vesicles to achieve an arbuscle:vesicle ratio.

Quadrat values were arcsine transformed to improve normality and homoscedasticity assumptions and analyzed by univariate repeated-measures ANOVA at $\alpha = 0.05$ (Zar, 1984; Wilkinson, 1997). Repeated-measures analysis is used when the same quadrat is measured repeatedly

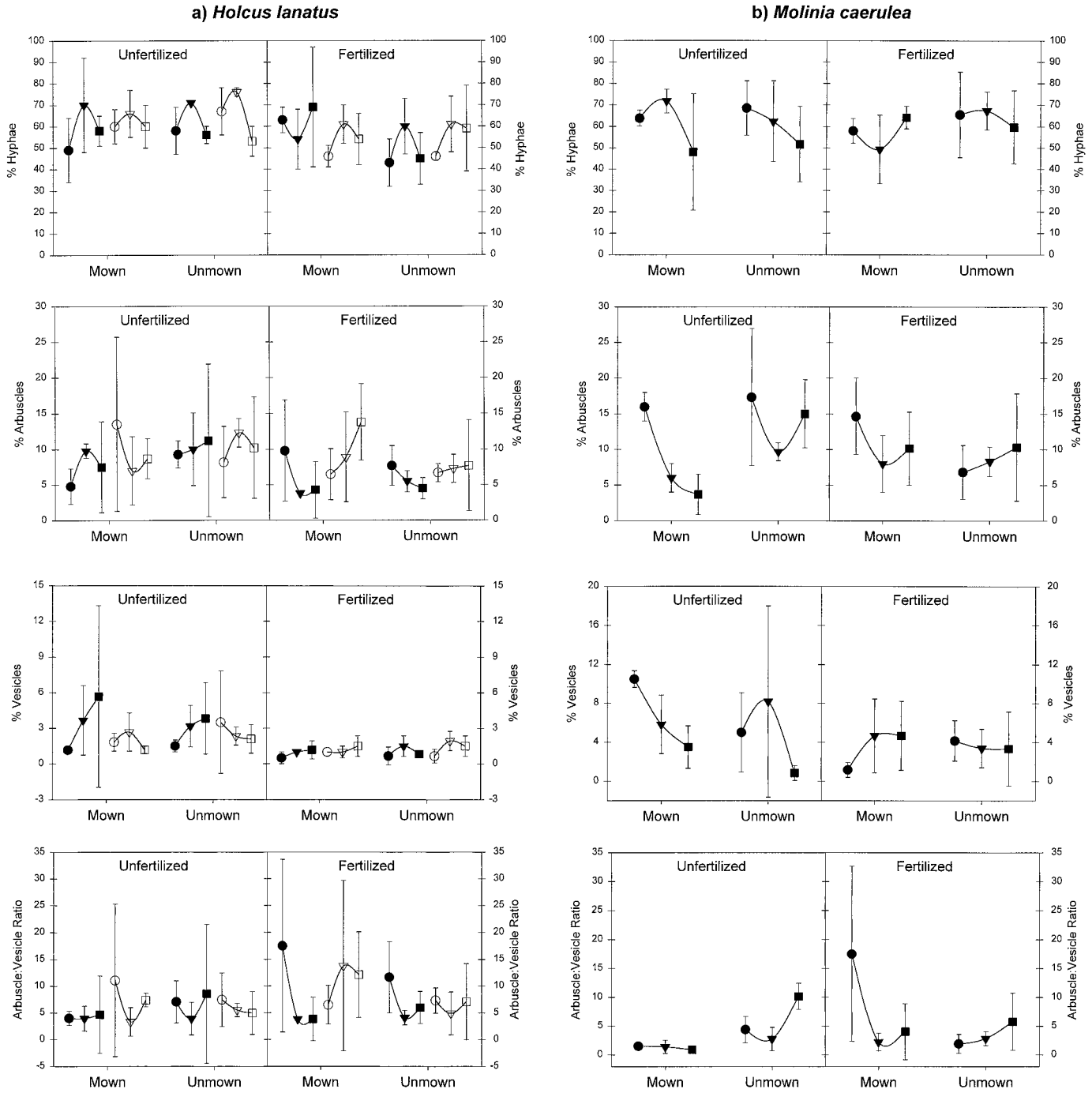

Fig. 1. Percentage hypha, vesicle, and arbuscle colonization and arbuscle:vesicle ratio for five species in a three-treatment factorial design sampled three times over the 1997 growing season. Treatments were fertilization, mowing, and removal of the dominant species (*Molinia caerulea*). The solid symbols represent nonremoval of the dominant species and the open symbols represent removal. Because *Molinia* is the dominant species there is no dominant-removed treatment for that species. Collection dates are represented by the symbols as follows: "○" = 20 May, "▽" = 10 June, and "□" = 5 July (mean ± 1 SD, $N = 3$). See Table 2 for ANOVA results. (a) *Holcus lanatus.* (b) *Molinia caerulea.*

over time. Repeated-measures ANOVAs were conducted for each species for each AM structure to determine whether treatments influenced AM colonization levels, whether there were differences over time in AM colonization, and whether there were any interactions between treatments and between treatments and time. Initially, ANOVAs were conducted with all block interaction effects. For each ANOVA the block effect was tested to determine whether blocks were poolable, i.e., whether or not there are significant differences between blocks. Blocks with no significant differences can be pooled. This was done by dividing the largest mean square error for a block interaction treatment, in the section of the ANOVA table that does not include time, by the smallest mean square error. The resulting $F_{2,2}$ values were tested for significance at $\alpha = 0.10$. This was repeated for the section of the ANOVA table with $F_{4,4}$ values, i.e., the part of the ANOVA table that includes time.

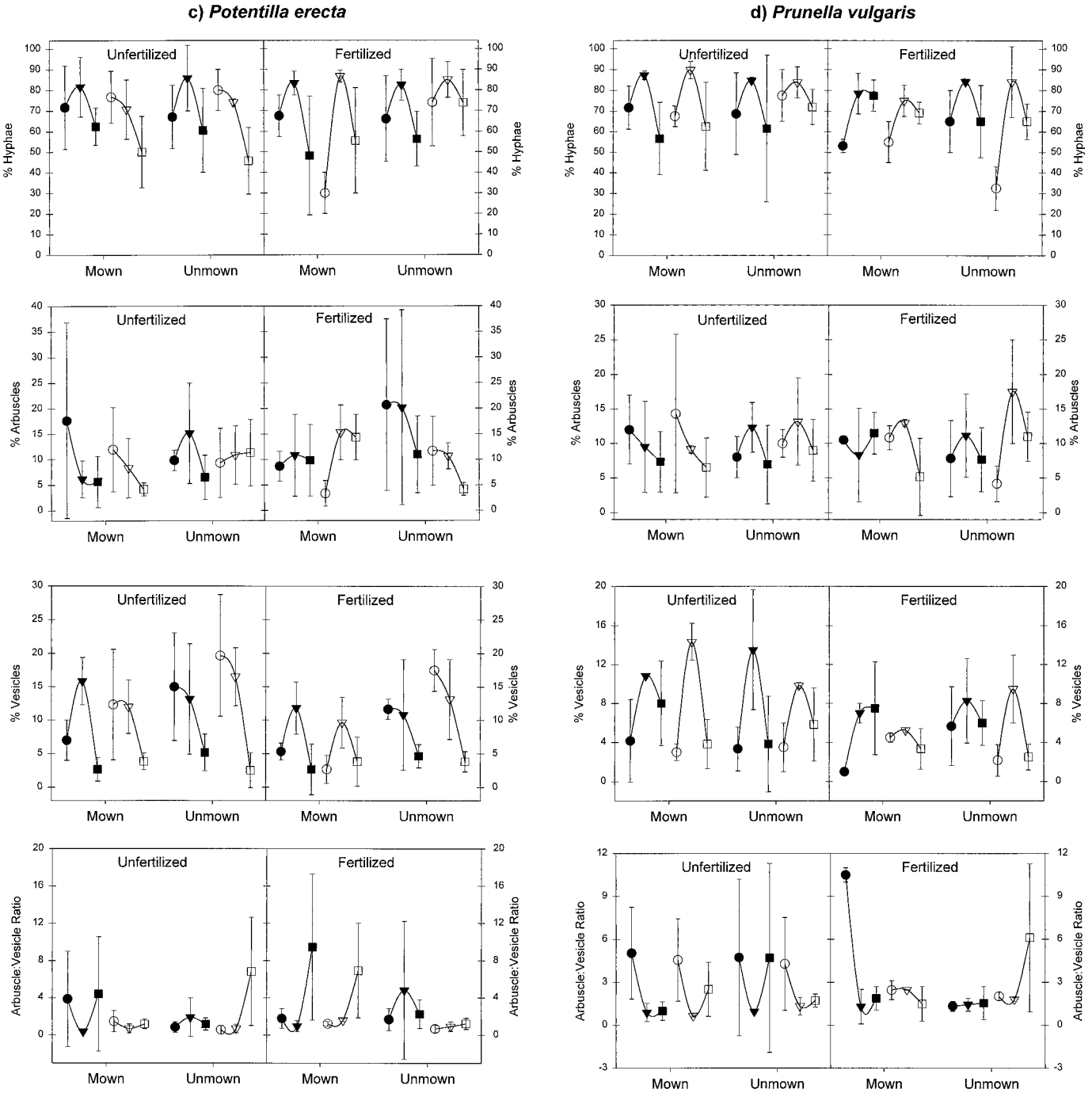

Fig. 1. Continued. (c) *Potentilla erecta.* (d) *Prunella vulgaris*.

If either section of the ANOVA was significant, blocks were not pooled because of the existence of a significant block effect. The ANOVAs with pooled blocks were recalculated.

Experiment 2—Three *Ranunculus* species, *R. acris, R. auricomus,* and *R. nemorosus,* are common in these wet oligotrophic meadows. In order to assess temporal changes in AM colonization of these species, nine individuals of each species were harvested on 28 April, 22 May, 24 June, and 16 July. In addition, on 22 May nine plants of each species were fertilized with 65 g of NPK fertilizer in a 16-cm^2 area around the base of the plant. Fertilized plants were harvested on 16 July. Samples were prepared as above.

Percentage values of each AM structure for each species were arcsine transformed and analyzed by ANOVA at $\alpha = 0.05$ with Tukey's posthoc test (Zar, 1984; Wilkinson, 1997). For each species arcsine-transformed AM levels were compared between unfertilized (using the 16 July samples) and fertilized plants by a two-sample t test at $\alpha = 0.05$.

The species—Cover of all species in all plots was regularly recorded, and species responses are described in detail in Lepš (1999). In Table

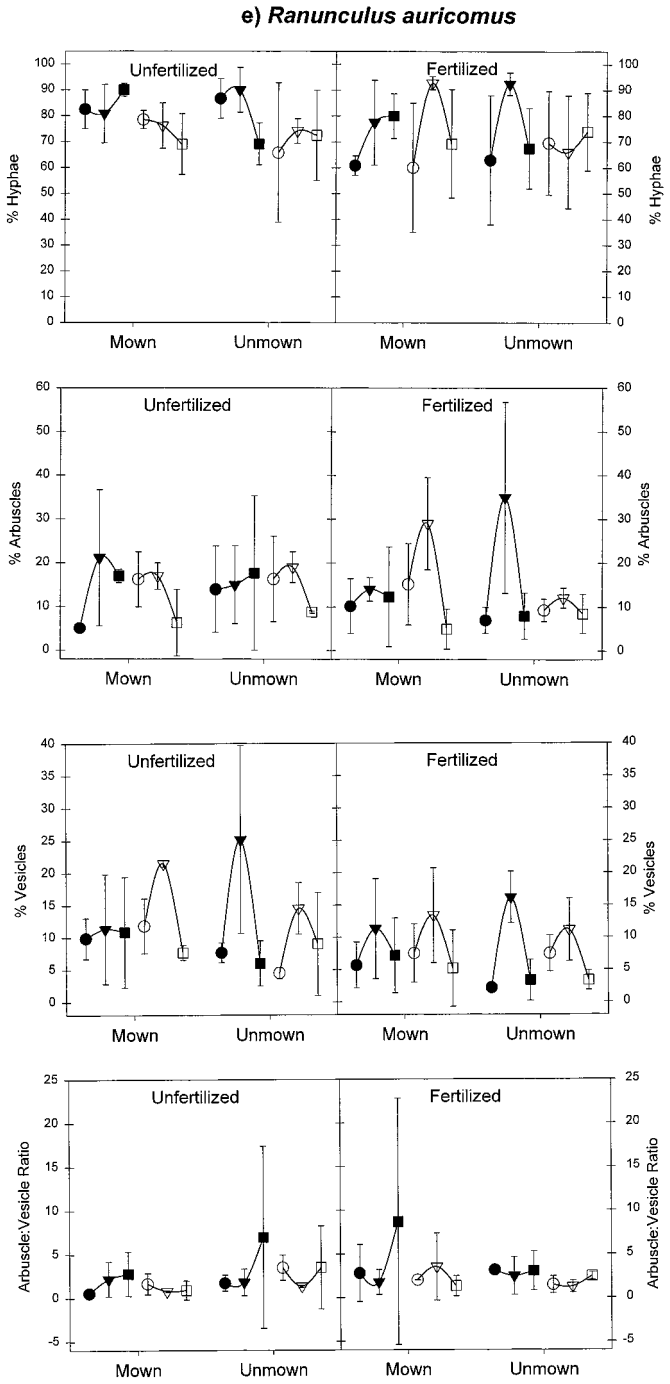

Fig. 1. Continued. (e) *Ranunculus auricomus.*

1 we briefly present characteristics of each target species and their responses to treatments such that a "+" corresponds to species increase under a given treatment, "−" species decrease, and "0" to no response.

RESULTS

Experiment 1—*Ranunculus* species cover increased in all three treatments (Table 1). *Molinia* and *Potentilla* decreased in both fertilization and mowing treatments. *Holcus* and *Prunella* decreased with fertilization and increased with mowing. Species increased in cover with the removal of the dominant species (see Lepš, 1999).

All plants were mycorrhizal in all treatments. Hyphal levels ranged from trace to a high of 95%. Infrequently, plant roots did not contain arbuscles or vesicles, but at least one of the individual plants in every treatment quadrat had arbuscles and vesicles. For all the species there were occasionally significant differences in AM colonization across treatments, and species showed significant trends in AM colonization across the growing season (Fig. 1a–f; Table 2). Blocks were pooled for the AM structures in several species (Table 2).

Fertilization caused a decrease in *Holcus* hyphae and vesicles, *Potentilla* vesicles, and *Ranunculus* vesicles (Fig. 1a–f; Table 2). *Prunella* hyphae decreased at $P = 0.066$. Mowing significantly increased the number of *Potentilla* vesicles. Removal of dominant had no significant effects. Significant interactions between treatments were only observed for *Holcus* hyphae (mown × fertilization $P = 0.054$) and mown × removal of dominant) and *Ranunculus* hyphae (fertilization × removal of dominant).

Time had a significant effect on hyphae for all species except *Molinia* and *Ranunculus.* Arbuscles showed a significant time effect only in *Molinia* and *Ranunculus.* Vesicles showed a significant time effect in *Potentilla, Prunella,* and *Ranunculus.* In all of these cases, except for *Molinia* arbuscles, a modal effect occurred with the second sampling period having a greater level of AM than the other sampling periods. In *Molinia* arbuscles the opposite effect was seen, with the second sampling period having the lowest value.

Significant interactions between time and treatments were seen in *Potentilla* hyphae (time × fertilization × removal of dominant), arbuscles (time × mown × fertilization), and vesicles (time × mown), in *Prunella* hyphae (time × mown × fertilization), arbuscles (time × mown), and vesicles (time × fertilization), and in *Ranunculus* vesicles (time × mown × removal of dominant). For the *Potentilla* vesicles time × mown interaction *Potentilla* in unmown quadrats had more than twice the number of vesicles at the first sampling period than in mown quadrats, but the number of vesicles were similar between the mown and unmown treatments in the second and third sampling periods. For the *Prunella* arbuscles the time × mown interaction *Prunella* in mown quadrats had many more arbuscles than in unmown quadrats in the first sampling period, by the second sampling period *Prunella* in unmown quadrats had more arbuscles, and arbuscle levels declined to a similar value in both treatments by the third sampling period. The *Prunella* vesicles time × fertilization interaction was as follows: both fertilized and unfertilized plants had the fewest vesicles in the first sampling period and both increased for the second sampling period and declined for the third. The difference between the two treatments is that there were many more vesicles in the second sampling period for the fertilized plants than the unfertilized plants. The other values were similar.

Significant effects in the arbuscle:vesicle ratio occurred infrequently. When they did occur, they were primarily related to changes over the season. The ratio changed across the season for *Potentilla* and *Prunella* as shown by a significant time effect. The ratio in *Potentilla* was similar in the first two sampling periods and increased on

TABLE 2. *P* values for a factorial design with three replications sampled three times over the 1997 growing season. Data are presented in Fig. 1a–f. Arbuscular mycorrhizal structures were ''hyph'' = hyphae, ''arb'' = arbuscles, ''ves'' = vesicles, and ''ratio'' = arbuscle:vesicle ratio. Treatments were ''fert'' = fertilization, ''mown'' = mowing, and ''dom'' = removal of the dominant species (*Molinia caerulea*). Due the removal of *Molinia* there is no ''dom'' treatment for that species. Comparisons were by repeated-measures ANOVA. Degrees of freedom for all comparisons that do not involve ''Time'' are 1 and for all comparisons that involve ''Time'' are 2. *P* values < 0.10 are in boldface.

	Holcus lanatus								*Molinia caerulea*			
	hyph*		arb*		ves*		ratio*		hyph		arb*	
Source	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Fert	**11.278**	**0.005**	2.481	0.138	**12.336**	**0.003**	1.680	0.213	1.395	0.281	0.713	0.423
Mown	0.714	0.412	0.013	0.912	0.048	0.829	0.417	0.528	0.998	0.348	0.658	0.441
Dom	0.125	0.729	1.816	0.197	0.397	0.538	0.360	0.557	—	—	—	—
Fert × Mown	**4.263**	**0.054**	1.139	0.302	0.015	0.903	0.902	0.356	0.328	0.633	**4.401**	**0.074**
Fert × Dom	1.657	0.217	0.233	0.636	1.770	0.202	0.019	0.892	—	—	—	—
Mown × Dom	**4.698**	**0.047**	0.729	0.406	0.696	0.418	0.976	0.338	—	—	—	—
Fert × Mown × Dom	2.877	0.111	0.000	0.987	0.535	0.476	0.002	0.961	—	—	—	—
Time	**4.239**	**0.023**	0.040	0.9061	1.255	0.299	1.583	0.221	1.350	0.288	**4.481**	**0.036**
Time × Fert	1.671	0.204	0.298	0.744	0.144	0.866	0.187	0.830	1.143	0.346	1.808	0.196
Time × Mown	0.973	0.389	0.307	0.737	0.202	0.819	0.052	0.949	0.011	0.927	2.512	0.113
Time × Dom	0.066	0.936	0.371	0.693	1.474	0.244	0.808	0.455	—	—	—	—
Time × Fert × Mown	0.536	0.591	0.405	0.671	0.419	0.660	0.100	0.905	2.609	0.105	0.541	0.597
Time × Fert × Dom	0.869	0.428	**2.577**	**0.092**	1.843	0.175	**2.596**	**0.090**	—	—	—	—
Time × Mown × Dom	0.229	0.788	0.521	0.599	0.162	0.851	0.720	0.663	—	—	—	—
T × F × M × D	1.581	0.221	1.845	0.175	0.171	0.843	1.122	0.338	—	—	—	—

* Blocks were pooled.

the third. The ratio in *Prunella* decreased from the first to the second sampling period and increased for the third. Time × mown was a significant interaction in *Molinia* and *Prunella.* Both species showed a modal effect with the second sampling period having a lower ratio than the first and third periods. However, the ratio in *Molinia* was much larger in the first sampling period in the mown plots than in subsequent sampling periods and in the unmown quadrats the ratio was much larger in the third sampling period than in the earlier sampling periods. A similar pattern occurred in *Prunella* but less dramatically. The mown × fertilization interaction was significant at $P = 0.54$ in *Molinia.* A higher level interaction was significant in *Potentilla* (time × mown × fertilization).

Experiment 2—The three *Ranunculus* species showed significant changes in AM colonization across the season (Table 3). Overall, AM structures either declined over the season, or increased from April to May and then declined. Hyphae decreased significantly over the season only for *R. acer.* Arbuscles declined over the season for all three species, although for *R. auricomus* the highest level occurred at the second sampling. Vesicles increased from April to May and then declined over the remainder of the season for *R. acer* and *R. nemorosa.* There was no AM response to fertilization in the three species.

DISCUSSION

For every species studied, in both experiments, time had a significant effect on levels of at least one AM structure, showing that levels of AM fungal structures, hyphae, arbuscles, and vesicles in the root, change over the season. This is not surprising because phosphorus demands of the plant and moisture levels in the soil change over the season, and rates of root growth and turnover vary. In addition, temporal factors play a major role in host benefit from AM colonization, such that AM may only benefit plants during the brief periods when phosphorus demand is high (Fitter, 1989; Sanders and Fitter, 1992b). Arbuscles, because they are the site of the exchange of materials between plant and fungus, are the best indicators of the quantity of material flow and therefore the intensity of the mutualism.

In Experiment 1, at the time of the first sampling, roots are probably growing rapidly and outstripping the spread of AM colonization, i.e., hyphal and arbuscle growth (Douds and Chaney, 1982; Warner and Mosse, 1982; Dickman, Liberta, and Anderson, 1984; Ebbers, Anderson, and Liberta, 1987). In the second sampling period phosphorus demands were high because the plants were flowering and/or fruiting and root growth had slowed, and thus AM colonization levels were high. AM levels decrease by the third sampling period, most likely due to a reduction in plant phosphorus demand. In 1997, the third sampling period was after peak flowering and fruiting for all of the species, except *Molinia caerulea,* so phosphorus demand was low by this time. In Experiment 2, where a significant time effect occurred, 22 May had the highest AM levels in four of the cases, and 28 April had the highest in the other two cases. In all of these cases there was a decline in AM levels after the second sampling period.

Of the three treatments in Experiment 1, fertilization had the most dramatic effect and caused a decrease in hyphae in one species and in vesicles in three species. The dependence of a plant species on the AM mutualism decreases in the presence of high levels of available phosphorus (Fitter, 1977; Graham, Leonard, and Menge, 1981; Schwab, Menge, and Leonard, 1983) and may be reflected by a reduction in hyphae or arbuscles. Vesicles indicate carbon storage and their reduction with fertilization may indicate a reduced reliance by the plant on the fungus and hence a reduction in carbon translocation to the fungus. A fertilization effect was observed in Experiment 1 and not in Experiment 2. This was most likely due to the several years of fertilization plants were sub-

TABLE 2. Extended.

	Molinia caerulea				*Potentilla erecta*							
	ves*		ratio*		hyph*		arb*		ves*		ratio*	
Source	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Fert	2.274	0.188	1.244	0.297	0.063	0.804	0.446	0.514	**4.872**	**0.042**	0.734	0.404
Mown	0.451	0.543	0.001	0.980	0.512	0.484	0.507	0.487	**11.264**	**0.005**	0.858	0.368
Dom	—	—	—	—	0.058	0.813	0.594	0.452	1.301	0.270	0.724	0.404
Fert × Mown	0.524	0.489	**5.076**	**0.054**	0.468	0.504	0.049	0.828	0.116	0.738	0.869	0.365
Fert × Dom	—	—	—	—	2.138	0.163	0.230	0.639	0.063	0.804	0.427	0.523
Mown × Dom	—	—	—	—	1.664	0.215	0.462	0.506	0.407	0.530	0.289	0.598
Fert × Mown × Dom	—	—	—	—	1.573	0.228	0.958	0.344	1.406	0.253	1.370	0.259
Time	1.187	0.332	2.594	0.106	**6.357**	**0.005**	**2.583**	**0.091**	**6.144**	**0.006**	**7.074**	**0.003**
Time × Fert	2.080	0.158	2.387	0.124	**3.201**	**0.055**	1.134	0.334	0.546	0.584	0.753	0.479
Time × Mown	0.294	0.751	**5.365**	**0.016**	0.232	0.795	0.736	0.488	**3.895**	**0.031**	**2.722**	**0.081**
Time × Dom	—	—	—	—	0.293	0.747	1.146	0.331	1.328	0.279	0.142	0.868
Time × Fert × Mown	1.571	0.242	**2.992**	**0.079**	2.337	0.113	**5.781**	**0.007**	0.059	0.942	**4.887**	**0.014**
Time × Fert × Dom	—	—	—	—	**6.912**	**0.003**	0.056	0.945	0.626	0.541	0.583	0.563
Time × Mown × Dom	—	—	—	—	1.229	0.306	1.211	0.311	2.147	0.134	**3.120**	**0.058**
T × F × M × D	—	—	—	—	0.235	0.793	0.261	0.772	0.590	0.560	0.330	0.722

jected to in Experiment 1 as opposed to the single fertilization event in Experiment 2. Fertilization changes the competitive environment of the plant, and tall erect herbs, such as *Ranunculus auricomus,* increase in cover by overtopping the other species (Lepš, 1999).

The interactions between time and fertilization show that fertilization influences the effect that time has on AM levels. The cases where an interaction occurred did not necessarily have a significant fertilization effect. The interactions may be due to differences in root growth and turnover and the dynamics of phosphorus demand. Higher level interactions become increasingly difficult to interpret, as species-specific and season-specific dynamics of the AM mutualism interact with all the factors.

All three of the treatments alter the competitive environment of the plant. AM have been found to influence competitive outcomes in both the greenhouse (Fitter, 1977; Grime et al., 1987; Hetrick, Wilson, and Hartnett, 1989; Hartnett et al., 1993; Moora and Zobel, 1996; Titus and del Moral, 1998) and the field (Allen and Allen, 1984, 1990; Johnson et al., 1991). Competition has been found to have a significant effect on AM levels in the greenhouse (Titus and del Moral, 1998), but the effect on AM levels in the field is unclear. Although both mowing and removal of dominant had powerful effects on community composition and structure, as did fertilization (Lepš, 1999), their influence on variables directly related to AM levels may be less dramatic because they do not directly change phosphorus levels; rather they change plant-plant interactions. Phosphorus and protection from pathogens (Newsham, Fitter, and Watkinson, 1995) are generally thought to be the primary benefits the plant receives from the mutualism. The significant effects that were found from mown and mown × time may be due to differences in root growth and turnover with the reduction in leaf area that accompanies mowing and the resulting changed competitive environment. Likewise, *Molinia* and *Prunella* saw a significant change in the arbuscle:vesicle ratio with a time × mown interaction. Aboveground *Molinia* cover decreased with mowing and *Prunella* increased (Table 1). It appears that for these two species mowing causes the ratio to peak early in the season, with many arbuscles and little carbon storage by the fungus, whereas for unmown plants there are many more vesicles at the end of the season when plant growth has slowed and carbon has accumulated in the vesicles. If the plant is mowed during the season, the removal of leaf area may prevent the accumulation of carbon by the fungus in the mown plots. Removal of dominant species had little influence on AM levels. Higher level interactions involving mowing and removal of dominant species did occur.

The ratio between mycorrhizal arbuscles and vesicles may give an indication of the relative cost/benefit of the fungus to the plant (Abbott, Robson, and de Boer, 1984; Braunberger, Miller, and Peterson, 1991). If roots experience high nutrient conditions and the plant is less dependent upon AM for phosphorus, the plant may cause a reduction in the number of arbuscles (Duke, Jackson, and Caldwell, 1994). Under lower nutrient conditions the plant causes an increase in arbuscle formation in order to increase phosphorus transfer from the fungus to the plant, thereby increasing the ratio of arbuscles to vesicles. A treatment that changes carbon flow to the fungus would be expected to influence the arbuscle:vesicle ratio. In addition, the plant and fungal species involved in the mutualism may influence the ratio (Yawney and Schultz, 1990; Streitwolf-Engel et al., 1997; van der Heijden et al., 1998), plant stress may cause an increase in the number of vesicles (Reece and Bonham, 1978; Cooke, Widden, and O'Halloran, 1993; Duckmanton and Widden, 1994), and root age has been found to alter the ratio with arbuscles forming first in young roots and vesicles increasing in frequency as the roots age (Cooke, Widden, and O'Halloran, 1993).

Changes in the arbuscle:vesicle ratio were primarily related to changes in arbuscle and vesicle numbers across the season rather than to treatment effects. For example, in *Potentilla* and *Prunella,* this could be related to an increased need for phosphorus during fruit production because both species show an increase in the ratio during the third sampling period when fruits are being produced. For both of these species the number of arbuscles and vesicles decreased from the second to the third sampling period, however, the number of vesicles decreased more than the number of arbuscles, which led to an increase

TABLE 2. Extended.

Prunella vulgaris								*Ranunculus auricomus*							
hyph		arb*		ves*		ratio*		hyph*		arb*		ves*		ratio*	
F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
3.889	**0.066**	0.001	0.970	0.834	0.376	0.058	0.812	**3.630**	**0.077**	0.191	0.668	**7.302**	**0.016**	0.460	0.507
0.233	0.636	0.001	0.975	0.039	0.845	0.107	0.747	0.181	0.677	0.004	0.951	0.155	0.699	0.082	0.778
0.039	0.845	0.843	0.373	1.703	0.211	0.220	0.646	1.393	0.256	0.273	0.609	0.000	0.999	1.702	0.211
0.022	0.884	0.020	0.891	2.885	0.109	1.156	0.298	0.013	0.910	1.891	0.188	0.343	0.566	2.200	0.157
2.581	0.128	0.023	0.883	0.259	0.618	0.006	0.940	**4.499**	**0.050**	0.040	0.844	0.069	0.799	0.345	0.565
0.000	0.983	1.403	0.253	0.239	0.631	1.180	0.294	0.141	0.713	0.653	0.430	**3.842**	**0.069**	0.116	0.737
0.202	0.659	0.053	0.820	1.320	0.268	**4.054**	**0.061**	0.291	0.597	1.924	0.185	0.403	0.535	0.047	0.831
4.588	**0.017**	2.229	0.126	**7.631**	**0.002**	**12.289**	0.000	1.915	0.164	**5.598**	**0.008**	**5.579**	**0.008**	1.422	0.256
2.231	0.123	2.206	0.128	**3.747**	**0.035**	0.649	0.529	1.079	0.352	0.504	0.609	0.154	0.858	0.027	0.974
0.048	0.953	**4.194**	**0.024**	0.482	0.622	**6.445**	**0.004**	0.652	0.528	0.020	0.981	0.932	0.404	0.151	0.860
1.934	0.161	0.479	0.624	0.998	0.418	**3.093**	**0.059**	0.339	0.715	**2.537**	**0.095**	0.238	0.788	1.235	0.304
3.380	**0.047**	0.005	0.995	0.499	0.612	2.437	0.103	1.176	0.322	**2.498**	**0.098**	0.514	0.603	0.614	0.547
0.229	0.797	1.161	0.326	0.808	0.455	**3.143**	**0.057**	0.809	0.455	0.275	0.762	0.343	0.712	0.276	0.761
0.440	0.648	0.537	0.590	2.066	0.143	2.105	0.138	**3.039**	**0.062**	1.402	0.263	**19.172**	**0.000**	0.268	0.767
1.581	0.221	0.209	0.813	1.533	0.231	**3.096**	**0.059**	1.088	0.349	**2.686**	**0.084**	**3.239**	**0.053**	0.970	0.390

in the ratio. The significant time × mown interaction in *Molinia* and *Prunella* is more complex, but a similar seasonal pattern to that described above occurs in the unmown plots where the ratio increases for the third sampling period. In mown plots this did not occur, perhaps due to the removal of leaf area. However, changes to the ratio could be due to other stress-related factors or to the aging of roots across the season.

The relationship between species cover response to treatments (Table 1) and effects of treatments on AM levels (Fig. 1a–f; Table 2) is unclear. In most cases a species cover response to a treatment was observed, but significant effects of those treatments on AM levels were not found. For example, *Prunella* shows the greatest response of any of the species to fertilization and mowing (Lepš, 1999), however, the effects of these treatments on AM levels were not significant. When *Holcus* and *Potentilla* cover decreased in response to fertilization, the number of vesicles also decreased. This would imply that fertilization led to a decrease in carbon flow to the fungus because these species were outcompeted by other species in a high nutrient environment and were reduced in cover (Lepš, 1999). However, when *Potentilla* cover decreased in response to mowing, the number of vesicles increased. The only instance where an increase in species cover led to a significant change in an AM structure is the increase in *R. auricomus* that occurred with fertilization, which caused a decrease in number of vesicles. The cover increases that all of the species experienced with the removal of the dominant did not cause any significant change in AM levels. As to the arbuscle:vesicle ratio, it appears that changes in the ratio were primarily related to changes in arbuscle and vesicle numbers across the season rather than to treatment effects. These results underscore the idea that the relationships between AM and plant response are complex and a large number of variables is involved. One of the most important of these is that changes in AM structures across the season are much stronger than the effects of any of the treatments on the AM structures.

Numerous factors influence results obtained in surveys of AM distribution and abundance. Therefore, when AM colonization levels in plants are assessed, the results may not reveal the actual extent or the importance of the symbiosis (McGonigle, 1988). Likewise, the variable nature of the symbiosis must be considered when growth effects on plants from AM colonization are measured. Due to this variability the role of AM is complex and will fluctuate because of a host of interacting biotic, abiotic, temporal, and spatial factors.

TABLE 3. Percentage AM colonization values for three *Ranunculus* species over the 1997 growing season and with a fertilization treatment. Comparisons were by ANOVA. Different superscripts show mycorrhizal levels that differ at $\alpha = 0.05$ based on Tukey's posthoc test (mean ± 1 SD, $N = 9$).

Species	Structure	28 April	22 May	24 June	16 July	Fertilized*	*F*	*P*
Ranunculus	hyphae	83 ± 13^{a}	84 ± 12^{a}	72 ± 22^{ab}	50 ± 38^{b}	40 ± 23	3.14	0.288
acris	arbuscles	17 ± 11^{a}	15 ± 11^{ab}	5 ± 6^{bc}	3 ± 3^{c}	1 ± 1	5.66	0.003
	vesicles	13 ± 4^{a}	15 ± 8^{a}	10 ± 5^{ab}	3 ± 2^{b}	4 ± 3	8.12	0.000
Ranunculus	hyphae	64 ± 19	74 ± 17	64 ± 10	58 ± 26	51 ± 14	1.30	0.293
auricomus	arbuscles	13 ± 13^{ab}	18 ± 14^{a}	8 ± 4^{ab}	2 ± 2^{b}	3 ± 2	4.50	0.010
	vesicles	16 ± 13	15 ± 5	14 ± 3	8 ± 5	11 ± 8	2.16	0.113
Ranunculus	hyphae	77 ± 15	82 ± 12	69 ± 26	68 ± 29	79 ± 26	0.61	0.615
nemorosus	arbuscles	21 ± 12^{a}	13 ± 8^{ab}	9 ± 8^{bc}	5 ± 6^{c}	10 ± 11	5.04	0.006
	vesicles	12 + 7^{ab}	24 + 16^{a}	9 + 6^{b}	7 + 4^{b}	9 + 6	5.80	0.003

* Fertilized was not included in the ANOVA. Fertilized percentage AM colonization values were compared by *t* test against the percentage AM colonization values of 16 July. No significant differences were found.

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