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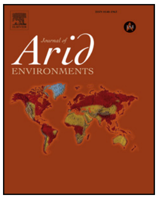

Communities of arbuscular mycorrhizal fungi associated with perennial grasses of different forage quality exposed to defoliation

Mariela Lis Ambrosino[a], Marta Noemí Cabello[b], Carlos Alberto Busso[c,*],
María Silvana Velázquez[d], Yanina Alejandra Torres[e], Daniela Solange Cardillo[f],
Leticia Soledad Ithurrart[c], Oscar Alberto Montenegro[g], Hugo Giorgetti[g], Gustavo Rodriguez[g]

[a] *CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas de la República Argentina), Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, 6300 Santa Rosa, Provincia de La Pampa, Argentina*
[b] *CIC (Comisión de Investigaciones Científicas de la Provincia de Buenos Aires), Instituto de Botánica Spegazzini, Facultad de Ciencias Naturales y Museo, Universidad Nacional de la Plata (UNLP), 1900 La Plata, Buenos Aires, Argentina*
[c] *CERZOS [Centro de Recursos Naturales Renovables de la Zona Semiárida (CONICET)], Departamento de Agronomía-Universidad Nacional del Sur, 8000 Bahía Blanca, Provincia de Buenos Aires, Argentina*
[d] *CONICET, Instituto de Botánica Spegazzini, Facultad de Ciencias Naturales y Museo (UNLP), 1900 La Plata, Buenos Aires, Argentina*
[e] *CIC, Departamento de Agronomía -Universidad Nacional del Sur, 8000 Bahía Blanca, Provincia de Buenos Aires, Argentina*
[f] *CERZOS - CONICET, Provincia de Buenos Aires, Argentina*
[g] *Chacra Experimental de Patagones, Ministerio de Asuntos Agrarios, 8504 Carmen de Patagones, Provincia de Buenos Aires, Argentina*

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ABSTRACT

Vegetation management practices, such as defoliation may alter the composition of plant communities and/or the fungi-forming arbuscular mycorrhiza (AMF). We determined the species identity, density, frequency and diversity of AMF spores from soil under the canopies of three native perennial grass species in rangelands of Argentina: 1) *Poa ligularis* and *Nassella tenuis* (preferred by livestock) and 2) *Amelichloa ambigua* (not preferred). For each species, plants either remained undefoliated or were defoliated twice to a 5 cm stubble height during the growing season. Most active meristems remained on the plants after defoliations. AMF communities were sampled prior to (i.e., 48 soil samples) and following (i.e., 72 soil samples) each defoliation event. Spores were grouped in 15 morphospecies. Density, richness and diversity of AMF spores were not influenced by defoliation, and species richness and diversity of AMF were similar among species. Total spore density was greatest for *P. ligularis* at the sampling prior to defoliation, but this difference did not persist following the defoliation events. The most abundant AMF families were: Acaulosporaceae, Diversisporaceae and Glomeraceae. These results demonstrate that responses of the studied variables were insensitive to the defoliation treatments, and were largely unaffected by the studied grass species.

1. Introduction

Arbuscular mycorrhizal fungi (AMF) affect the structure and dynamics of plant communities, especially in nutrient-poor soils (Van der Heijden et al., 1998). In turn, plant communities are important determinants in the distribution and composition of AMF in the soil (Johnson et al., 1992). Beneficial associations between individual plants or species and AMF are largely dependent on the species of the associated AMF, as AMF species vary in their demand for carbon from shoots and phosphorous translocation from roots to shoots (Pearson and Jakobsen, 1993).

Grazing management practices can alter plant species composition (Distel and Bóo, 1996; Augustine et al., 2017; Porensky et al., 2017), but their effects are largely unknown for fungal diversity in arid and semiarid rangelands. Herbivory affects mycorrhizal colonization by inducing changes in root morphology and soil physicochemical properties in addition to alterations in plant community structure (Su and Guo, 2007). For example, herbivory-induced changes in soil structure can reduce sporulation of AMF due to decrease in soil pore size (Allen and Allen, 1980). Lower infiltration rates from herbivory-induced changes to soil bulk density and plant basal cover (Thurow et al., 1986) can reduce soil moisture, and consequently spore germination (Daniels

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* Corresponding author.
E-mail addresses: marielalisambrosino@yahoo.com.ar (M.L. Ambrosino), mcabello@ymail.com (M.N. Cabello), carlosbusso1@gmail.com, cebusso@criba.edu.ar (C.A. Busso), mariasilvanavelazquez@gmail.com (M.S. Velázquez), yatorres@criba.edu.ar (Y.A. Torres), danicardillo@yahoo.com (D.S. Cardillo), leticia.ithurrart@uns.edu.ar (L.S. Ithurrart), chacraexpp@gmail.com (O.A. Montenegro), chacraexpp@gmail.com (H. Giorgetti), chacraexpp@gmail.com (G. Rodriguez).

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and Trappe, 1980). Thus, reductions in VAM fungi sporulation and spore germination are often associated with drier and more compacted soil.

Rangelands in higher ecological states (i.e., greater abundance of higher seral species), can have a greater quantity and diversity of the AMF community (Mendoza et al., 2002). Thus, grazing mismanagement, which induces replacement of desirable (i.e. preferred) plant species by undesirable ones, and degrades the ecological state of vegetation community, results in reducing litter decomposition rate and nutrient mineralization of plant communities (Milton et al., 1994).

Effects of grazing or defoliation on the colonization by AMF have been inconsistent (Frank et al., 2003; Yang et al., 2013; Saravesi et al., 2014). For example, increased root growth of the C3 perennial grass *Poa pratensis* following defoliation suggests that greater belowground energy allocation also increased investment in mycorrhizal symbiosis which in turn increased spore abundance Frank et al. (2003). In contrast, defoliation of the legume *Medicago sativa* decreased plant biomass and AM colonization; the latter was likely limited by host carbon availability (Saravesi et al., 2014). Furthermore, grazing in an alpine-meadow on the Qinghai-Tibetean Plateau in China did not affect AM root colonization and spore density (Yang et al., 2013). These authors indicated that it is possible that the AM fungus *Rhizofagus intraradices* (= *Glomus intraradices*) shows a wide tolerance to environmental stress or there is functional diversity within this species. However, these three studies differ in the (1) defoliation characteristics (artificial, actual grazing, intensity, duration and frequency); (2) environmental set ups (greenhouse, growth chamber, field conditions); (3) study functional groups (grasses, legumes); (4) abiotic growth conditions (e.g., temperature: from a little more than 1 °C–22 °C), and (5) sampling time scales (from 3 to 9 weeks). Rodríguez Echeverría et al. (2008) reported that the number of AMF spores associated to *Ammophila arenaria*, an important sand dune-fixing species, varied significantly with sampling time at various locations of the European coast. Even more, Yang et al. (2013) pointed out that temperature differences of 1.2 °C during daytime and 1.7 °C at night determined that warming with grazing significantly increased AM fungal operational taxonomic units richness in roots of *A. arenaria*, compared to the grazing only treatment. These authors suggested that AM fungi might demonstrate complex responses under multiple global change factors in ecosystems.

In arid and semiarid rangelands, where nutrient availability is limiting, intensive grazing can negatively affect AMF (Cai et al., 2014). However, moderate grazing can maintain dominance of preferred species (Augustine et al., 2017; Porensky et al., 2017) with a resulting symbiosis with AMF stimulating organic matter decomposition and soil nutrient cycling (Nuccio et al., 2013). The key to the resilience of these higher seral plant communities is that AMF species in the genera *Glomus* and *Rhizophagus,* common in arid and semiarid environments, tolerate lower levels of carbohydrates coming from the host plants, which increase their growth and abundance (Eom et al., 2001; Saito et al., 2004; Su and Guo, 2007; Barto and Rillig, 2010; Yang et al., 2013). Since plants within a community can associate with different AMF species, it is expected that grazing and defoliation will result in a high variability in the various plant developmental morphology states and function of AMF species (Klironomos et al., 2004).

Our objectives were to (1) identify the species of AMF spores rhizospheric soil of three native perennial grasses with contrasting grazing preferences, and (2) to evaluate the effects of defoliation on AMF spore density, richness, frequency and diversity. We hypothesized that (1) soil closest to roots as possible contains a different density of AMF spores on the different studied grass species, and (2) AMF density, richness, frequency and diversity from soils directly beneath perennial grass plants will be non-responsive after three to four weeks from a moderate defoliation, when active (i.e., intercalary, apical) meristems remain on the plants after defoliation.

2. Methods

2.1. Study site

The study was conducted in 2012 within a 1.12 ha exclosure where domestic herbivores were excluded from grazing since 1996 in the Chacra Experimental Patagones, located at the south of the Province of Buenos Aires, Argentina (40° 39′S, 62° 54′W; 40 m.a.s.l.). This area is within the phytogeographical province of the Monte (Cabrera, 1976). The site was cleared of woody vegetation and undergrowth in 1951 and cropped until 1975. Desertification in this region is evident by a loss of plant cover, decreases in soil fertility, and increases in soil compaction and salinization (SAyDS, 2011).

Climate is temperate-semiarid, with 421 mm of mean annual precipitation (1981–2012) with a maximum of 877 mm in 1984 and a minimum of 196 mm in 2009 (Torres et al., 2013). Mean annual temperature is 14.1 °C (1981–2012; Torres et al., 2013).

Soil in the exclosure is a typical Haplocalcid (Giorgetti et al., 1997), with the 0–20 cm depth having pH of 8.26, organic matter content of 2.2%, total nitrogen of 0.12% and extractable phosphorus levels of 9.9 ppm.

2.2. Plant species

The plant community is dominated by perennial grasses with differing quality for grazing livestock and isolated shrub species (Giorgetti et al., 1997). *Poa ligularis* Ness. is a dominant, cool-season, preferred (i.e., desirable) perennial grass species. As grazing intensity increases *Nassella tenuis* (Phil.) Barkworth replaces *P. ligularis* (Distel and Bóo, 1996), and with further increases in grazing intensity a non-preferred species (i.e. undesirable: *Amelichloa ambigua* (Speg.) Arriaga and Barkworth) becomes dominant (Giorgetti et al., 1997). These C_3 perennial grass species not only differ in grazing tolerance but also exhibit differences in forage and litter quality, and root morphology characteristics (Table 1).

2.3. Experimental design and treatments

Using a completely randomized experimental design, 12 individual plants per species and 12 sites approximately 1 m^2 in surface area without vegetation (controls) were randomly selected at the end of the growing season in December 2011. Unvegetated sites among vegetation patches were irregular as the result of topographic characteristics and previous grazing mismanagement. These sites were useful as a control for evaluating species-specific effects of the various perennial grasses.

Soil samples (2.5 cm diameter, 0–10 cm depth) were collected from beneath each individual plant and the control plots at the beginning of the experiment, prior to initiation of defoliation treatments (n = 48 samples). Soils were re-sampled beneath individual plants approximately 35–40 days following each defoliation event.

When plants were at the dormant stage of developmental morphology (January 2012: Giorgetti et al., 2000), they were all defoliated

Table 1
Major characteristics of the native perennial grass species under study (Distel and Bóo, 1996; Giorgetti et al., 1997; Saint Pierre et al., 2004a; Moretto and Distel, 2003).

	Poa ligularis	*Nassella tenuis*	*Amelichloa ambigua*
Successional stage	Late	Intermediate	Early
Forage quality	Highly Preferred	Preferred	Non preferred
Litter quality	High (high N, low C/N and lignin)	High (high N, low C/N and lignin)	Low (low N, high C/N and lignin)
Root morphology	Fine	Fine	Coarse