



Interaction between legume and arbuscular mycorrhizal fungi identity alters the competitive ability of warm-season grass species in a grassland community



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ABSTRACT

Arbuscular mycorrhizal fungi (AMF) and N₂-fixing legumes can alter the community structure of grasses. However, the effect of AMF, N₂-fixing legumes, and their interaction on the dynamics of prairie grass communities remains unclear. The aim of this study was to clarify the influence of two AMF (*Glomus cubense* and *Glomus* sp.) and two legumes (*Medicago sativa* and *Dalea purpurea*) on the competitive relationship between three native cool-season (*Elymus canadensis*, *Elymus trachycaulus* ssp. *subsecundus*, and *Elymus lanceolatus* ssp. *lanceolatus*) and two native warm-season species of grasses (*Schizachyrium scoparium* and *Bouteloua gracilis*). Results show that AMF and legumes altered the community structure of the grasses. *G. cubense* favoured the productivity of warm-season *B. gracilis* when growing with *M. sativa*. This might be related to a negative impact of *G. cubense* on the nitrogen-fixing activity of *M. sativa* and to a lower N-use efficiency of *E. canadensis* and *E. lanceolatus* ssp. *lanceolatus* under competition. This suggested an increased ability of *B. gracilis* to use the available N resource as affected by more competitive species, whereas *Glomus* sp. reduced the competitive ability of this grass when associated with *M. sativa*. The decrease in *B. gracilis* biomass was thus likely caused by enhancement of P uptake by *M. sativa* over this grass. *Glomus* sp. was beneficial to *S. scoparium*, another warm-season species, in the absence of legumes, and this may be attributed to improved P-use efficiency of this grass under competition with cool season-grasses. In contrast, AMF and legumes were not beneficial for the cool season grasses. *G. cubense* depressed the growth of *E. trachycaulus* ssp. *subsecundus*, and *M. sativa* decreased nutrient uptake by cool-season native grasses. This study shows that beneficial effect of the arbuscular mycorrhizal symbiosis on the coexistence of warm-season grasses with more competitive cool-season grasses depends on the identity of the AMF symbiont, the presence of legume species, and nitrogen resource availability that was affected by the most competitive species or P-use efficiency of warm season species.

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1. Introduction

The AMF supply soil nutrients, particularly nitrogen (N) and phosphorus (P) to their host plant, while the plant reciprocates by providing carbon and energy to the fungus (Smith and Read, 2008).

The presence of arbuscular mycorrhizal fungi (AMF) in plant communities can influence plant coexistence (Hart et al., 2003; Stein et al., 2009; Chagnon et al., 2012) by altering their competitive relationship (Scheublin et al., 2007; Wagg et al., 2011). The influence of AMF on plant community structure may result from the different effects of AMF on competing plant species, which can be negative, neutral or positive (Johnson et al., 1997; Hart et al., 2003; Klironomos, 2003; Smith et al., 2011), depending on the degree of physiological compatibility existing between the fungal symbiont and host plant (van der Heijden et al., 1998), nutrient availability (Johnson, 2010), and plant species interactions (Mariotte et al.,

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2012). The variation in the effects of AMF on plant growth can be explained by the variation in the C cost for the nutrient benefit provided in different AMF-plant associations (Smith et al., 2011).

The different responses of plants to the AMF symbiosis in a plant community can promote plant coexistence and hence increase plant community productivity (Wagg et al., 2011; Mariotte et al., 2012). However, Daisog et al. (2012) have shown that AMF may alter the coexistence of crops with agricultural weed species differing in their mycorrhizal status. Previous studies demonstrated that prairie grasses had different responses to AMF and thus that AMF influence plant community structure in the prairie (Wilson and Hartnett, 1998). Research shows that the warm-season grasses are more responsive to AMF than cool-season grasses (Hetrick et al., 1988; Wilson and Hartnett, 1998; Hoeksema et al., 2010) because they have coarser and less branched root systems, relying on AMF for nutrient uptake (Hetrick et al., 1991; Hartnett and Wilson, 2002).

Pastures composed of warm-season and cool-season native grass species provide good quality forage for early and late season grazing (Tilman et al., 2001; Schellenberg et al., 2012). The inclusion of N₂-fixing legumes with native grass mixtures at seeding may result in the establishment of self-sustaining and permanent pastures in the Prairie ecozone. The inclusion of N₂-fixing legumes in forage stands increases plant productivity (Temperton et al., 2007; Nyfeler et al., 2009) particularly through the transfer of fixed N from legumes to grasses (Temperton et al., 2007). This N transfer can take place through legume root exudation (Jalonen et al., 2009) or decomposition and mineralization of legume tissues (Ledgard and Steele, 1992; Sierra and Desfontaines, 2009). Uptake and translocation of N by AMF hyphal networks may facilitate this transfer of N (Bethlenfalvay et al., 1991; Miller and Allen, 1992; He et al., 2003; Smith and Read, 2008).

Several studies have shown that AMF influence the competitive relationship between legumes and neighbouring grasses by favouring the legume component in mixes where the legume is more responsive to AMF than the grass (Scheublin et al., 2007; Wagg et al., 2011), but in other cases, AMF increased the competitive ability of grass rather than of the legume component, favouring grass uptake of the N₂-fixed and released by the legume (Hamel et al., 1991). This suggests that the effect of AMF on the competition between grass and legumes depends on the relative efficiency of the symbiosis formed by the grass and legume component of a plant community (Hamel et al., 1991, 1992; Scheublin et al., 2007). However, the effect of the N₂-fixing legumes and the AMF on plant growth and nutrition of forage mixtures containing warm- and cool-season native grasses is poorly understood.

The aim of this study was to clarify the influence of AMF and legumes on the competitive relationship between native grasses. Specifically, we tested (1) if the interactive effect of N₂-fixing legumes and AMF alters the competitive ability of prairie grasses, and (2) if the identity of the AMF and neighbouring N₂-fixing legumes determines the competitive ability of warm- and cool season prairie grasses in a plant community.

2. Materials and methods

2.1. Experimental design and biological material

The experiment had a randomized 3 × 3 factorial design with five repetitions. The first factor, inoculation, had three levels: plant communities were non-inoculated, inoculated with *Glomus cubense* Rodr. & Dalpé (INCAM-4 = DAOM 2411981) or inoculated with *Glomus* sp. (INCAM-8), a non-described species (Dalpé, personal communication). Both AMF isolates were graciously provided by Dr. Yakelin Rodriguez, Instituto Nacional de Ciencias Agrícolas,

San José de las Lajas, Cuba. The second factor also had three levels, the inclusion of *Medicago sativa* L. (alfalfa), *Dalea purpurea* Vent. (purple prairie clover) or the absence of legume in the plant communities. The treatment combinations were applied on pot-grown stands composed of three cool-season grasses, *Elymus canadensis* L. (Canada wildrye), *Elymus trachycaulus* (Link) Gould & Shin. ssp. *subsecundus* (Link) (awned wheatgrass), and *Elymus lanceolatus* (Scribn. & Sm.) Gould ssp. *lanceolatus* (northern wheatgrass) and two warm-season grasses, *Bouteloua gracilis* (H.B.K.) Lag ex Steud. (blue grama) and *Schizachyrium scoparium* (Michx.) Nash (little blue stem). The grass and legume seeds were provided by Ducks Unlimited Canada Inc, Saskatchewan Provincial office.

2.2. Germination of seeds

Seeds of the native grasses *E. canadensis* and *S. scoparium* needed a cold treatment to relieve dormancy. They were then placed between two wet filter papers in Petri dishes at 5 °C for two weeks in the dark and after that exposed to light at room temperature for one week until germination. The seeds of *E. trachycaulus* ssp. *subsecundus*, *E. lanceolatus* ssp. *lanceolatus*, *B. gracilis*, and of the legumes *M. sativa* and *D. purpurea* were simply placed on wet filter papers in Petri dishes in the dark for two days to allow germination. Germinated seeds were transferred into small pots filled with vermiculite and were watered daily with distilled water for two weeks, after which the seedlings were transferred into the experimental pots as described below.

2.3. Growth conditions

The 10-L pots were filled with 10 kg dry weight of pasteurized soil (90 °C, 1 h). The Brown Chernozemic soil was a loamy sand with pH of 6.5, EC of 0.48 ms cm⁻¹ containing 19.7 µg of NH₄-N, 14.1 µg of NO₃-N, 21.9 µg of PO₄-P and 357 µg of K per g soil after pasteurization. The soil was taken from the Bulin site located near Swift Current, Saskatchewan. Designated pots received 6 g of AMF inoculum consisting of chopped leek roots infected by one of the mycorrhizal isolates, or of autoclaved roots. The AMF inocula were placed 5 cm below the soil surface. *M. sativa* was inoculated with 0.2 g of *Sinorhizobium meliloti* (Nitragin Gold) and *D. purpurea* with 0.2 g of *Rhizobium* sp. isolated from *Onobrychis* sp. (Nitragin type F). The rhizobium strains were used as dry powdered culture. Groups composed of the five grass species, or of the five grass species and a legume species were grown in each pot in a growth chamber with 16 h photoperiod per day, a temperature cycle of 23 °C day/19 °C night, and 60% relative humidity. After 4 weeks, each pot was fertilized twice a week with 500 mL of a modified Long Ashton nutrient solution containing: 750 mg KNO₃, 200 mg NaH₂PO₄ H₂O, 244 mg MgSO₄, 950 mg Ca(NO₃)₂·4H₂O, 1.7 mg MnSO₄, 0.25 mg CuSO₄·5H₂O, 0.30 mg ZnSO₄·7H₂O, 3.0 mg H₃BO₃, 5.0 mg NaCl, 0.09 mg (NH₄)₆Mo₇O₂₄·4H₂O and 32.9 mg NaFe-EDTA per L. Pots were watered as required with distilled water.

2.4. Harvest, sampling and analysis

After five months of growth, plants were cut at ground level, dried separately at 40 °C for 3 days, weighed to determine drymass and the dry plants were ground. A subsample of ground plant material was digested (Varley, 1966) and the concentration of N (Noel and Hambleton, 1976) and P in plant tissues was measured (Milbury et al., 1970) on a segmented flow auto analyser (Technicon, AAI System, Tarrytown, NY). Uptake of P and N by each species was calculated by multiplying plant biomass by the concentration of each individual nutrient. Nitrogen- and phosphorus-use efficiencies were calculated as total aboveground biomass divided by total

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