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Grazing effects on fungal root symbionts and carbon and nitrogen storage in a shortgrass steppe in Central Mexico

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Abstract

Livestock grazing is the principal driver of land use change in semiarid grasslands of Mexico. Despite the vast expansion of grasslands and the alarming extent of land degradation associated with overgrazing, our understanding of the effects of heavy grazing on root fungal symbiosis and the sizes of soil carbon (C) and nitrogen (N) stocks is still limited. This research was conducted in the shortgrass steppe in Los Llanos de Ojuelos, Jalisco, Mexico, where *Bouteloua gracilis* is a keystone species. We examined soil C and N storage and root colonization of *B. gracilis* by fungal symbionts (arbuscular mycorrhizal fungi (AMF) and dark septate endophytes (DSE)) along a grazing gradient. Roots of *B. gracilis* were examined for root colonization of AMF and DSE. Soil samples were analyzed for total C and N content. Under moderate grazing, soil C and N were 20% higher than under no-grazing and extremely heavy grazing. Grazing intensity did not differently affect root fungal colonization. However, while the two fungal symbionts coexisted on *Bouteloua* plant roots, a four times higher root colonization by DSE than by AMF suggests that competition for resources may control symbiont abundance. Considering total root fungal colonization by both symbionts (for DSE 37% and for AMF 10%), and a slightly higher colonization in the less fertile sites, we suggest this fungal symbiosis may play an important role linking the aboveground and belowground C cycle in these semiarid grasslands in Central Mexico.

Keywords: Arbuscular mycorrhiza; Dark septate endophytes; Overgrazing; Semiarid grassland; Soil carbon and nitrogen stock

1. Introduction

In arid and semiarid grasslands, storage of soil organic carbon (C) and total nitrogen (N) (Asner and Martin, 2004) and root fungal symbioses (Barrow et al., 1997) are key biogeochemical processes and biotic interactions, respectively, that may be highly susceptible to heavy livestock grazing. Previous studies

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examining the effects of grazing by large herbivores on soil C and N have reported both positive and negative balances. Grazing may alter the C balance at the plant and ecosystem level; e.g. it may induce a switch in plant C partitioning preferentially to shoots as a physiological adjustment to recover the leaf area, or it may change the C balance by a shift in plant community composition. At the ecosystem level, grazing-induced changes in soil physical, chemical and hydraulic properties and microenvironmental conditions influence the C balance by altering litter input (quality and quantity), decomposition and mineralization rates (Gill, 2007; Medina et al., 2007). Large herbivores affect N cycling in grasslands by two related mechanisms (Frank and Groffman, 1998). Firstly, through N addition via excreta deposition and, secondly by lowering the C/N ratios of plant litter, root tissue and the quantity of soil organic matter (Frank and Groffman, 1998).

Grazing may also influence colonization frequency and composition of root fungal symbionts both directly as a consequence of temporary C limitation in individual plants and indirectly through grazing-induced changes in soil nutrient availability (Smith and Read, 1997). Since grazing may temporarily reduce root growth and divert most assimilated C to new leaf area (Briske and Richards, 1995; Caldwell et al., 1981), root colonization of arbuscular mycorrhizal fungi (AMF) is expected to decline in C-limited grasses and this may be more pronounced in low-soil resource conditions (Gehring and Whitham, 2002). Until now no consistent pattern of root colonization in response to grazing has emerged (Grigera and Oesterheld, 2004; Reece and Bonham, 1978). Root colonization by dark septate endophytes (DSE) is another rather common plant–fungal interaction in grass species of semiarid ecosystems; yet, the functional role of DSE from a plant and/or ecosystem perspective is still unknown (Barrow, 2003; Jumpponen, 2001) and less though its response to livestock grazing.

The shortgrass steppe in Central Mexico covers 9–10% of its territory and is dominated by the grazing tolerant caespitose grass *Bouteloua gracilis* H.B.K Lag. Ex Steud. *B. gracilis* controls the structure and function of this ecosystem type (Burke et al., 1999); however, large areas are affected by different degrees of deterioration. This is primarily caused by uncontrolled grazing in vast communal land triggering shifts in plant community composition, structure and function (Aguado-Santacruz and García-Moya, 1998; Medina et al., 2007) and an overall decline in *B. gracilis* (Medina et al., 2007) accompanied by the expansion of vegetation-free interspaces and/or by an increase in the abundance of subordinate grasses, forbs and/or shrubs.

Research addressing the regulatory effects of grazing on ecosystems has recognized their important influence on energy and nutrient flows in grasslands (Ritchie et al., 1998), however until now no consistent relationship has been identified between grazing and soil C and N (Bardgett and Wardle, 2003; Milchunas and Lauenroth, 1993) and plant responses at the level of root symbiosis, likely because of the wide range of interacting factors controlling ecosystem responses. Bardgett and Wardle (2003) outlined three key mechanisms by which herbivores potentially influence soil processes: (1) alterations in the quantity of resource input into soil, (2) alterations in the quality of resource input into soil, and (3) long-term alterations in plant community composition.

Since *B. gracilis* is the dominant species in the shortgrass steppe of Mexico, independent of grazing history, alterations in the quantity of shoot and root litter inputs may be a key influence of livestock grazing on soil processes in these ecosystems. Hence, the objective of this study was to examine how differences in productivity of *B. gracilis* affect organic C and total N pools in grassland soils (mechanism 1 see above) in sites with contrasting grazing histories. We sampled along a gradient of known plant productivity of *B. gracilis* in the shortgrass steppe of Central Mexico, where vegetation composition and ecosystem processes are controlled by *B. gracilis*. We hypothesized that sites with long-term heavy grazing and substantial loss in productivity of *B. gracilis* would exhibit lower soil C and N pools compared with similar grassland sites with long-term moderate grazing. We further hypothesized that total soil C and N pools would be more depleted beneath extended vegetation-free interspaces than underneath *B. gracilis* plants as a consequence of reduced lateral root growth and enhanced wind and water erosion. Finally, we expected that this spatial pattern would be more pronounced in sites with heavy than with moderate grazing.

Differences in grazing history may influence the composition and abundance of AMF and DSE of the dominant grass species as a consequence of changes in plant growth and C allocation strategies (Barrow, 2003; Reece and Bonham, 1978). Hence, we hypothesized that under heavy grazing *B. gracilis* roots will be less colonized by symbionts. Given the lack of information on fungal associations in shortgrass steppe ecosystems in Mexico, we addressed this hypothesis by posing some basic questions: (1) do both fungal symbionts decline