



Plant phenotypic functional composition effects on soil processes in a semiarid grassland



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ABSTRACT

Our knowledge of plant functional group effects on ecosystem processes is relatively well established, but we know much less on how changes in plant phenotypic composition affect ecosystem functioning (i.e., phenotypic functional composition). Understanding phenotypic functional composition (PFC) is relevant in plant communities strongly dominated by a few keystone species, since alteration of phenotypic composition of these species might be a mechanisms by which land management practices such as grazing impact on ecosystem functioning. Here, we report results from a field experiment where we manipulated PFC of *Bouteloua gracilis* (Kunth) Lag. ex Griffiths, a keystone species in the semiarid shortgrass steppe. *B. gracilis*' PFC was altered by using plant genetic lines which expressed consistently either high or low leaf tissue lignin content (LC), a plant trait known to affect soil biogeochemical processes. High-LC lines came from an area subjected to low grazing intensities, whereas low-LC lines came from an area historically overgrazed. Additionally, those plant genetic lines expressing high LC also expressed high dry matter content and vice versa. We established experimental plots with *High* (only high-LC plants), *Low* (only low-LC plants), and mixed (both high- and low- LC plants, *BHL*) LC genetic lines; and measured selected soil processes after the application of a small water pulse. We hypothesised that those soil processes related to microbial activity and nitrogen cycling would be higher in *Low* plots in comparison with *High* and *BHL* plots. Phenotypic functional composition did not affect most of our soil processes including ammonium and nitrate concentrations (inorganic N), microbial activity, potential ammonium mineralization, and microbial profiles of substrate utilization). Nonetheless, we observed a general response to the water pulse so that soil inorganic N increased, but soil water content and soil microbial activity decreased 48 h after the pulse application. This general response suggests that fractions of the soil microbial community with different soil moisture optima mineralise N-rich substrates. Overall, lack of response to plant phenotypic functional composition suggests that grazing effects on soil biogeochemical processes in the shortgrass steppe are not directly mediated through how grazing affects the phenotypic functional composition of *B. gracilis*.

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1. Introduction

Plant functional traits can exert overwhelming effects on ecosystem processes (Hooper and Vitousek, 1997; Diaz and Cabido, 2001). For instance, a number of biodiversity-functioning and vegetation management experiments have shown that ecosystem

functioning (e.g., plant productivity, soil carbon sequestration, nitrogen mineralization) can be strongly affected by the presence of plant species with particular functional traits (named functional types, i.e., nitrogen-fixing legumes, C₄ grasses) (Balvanera et al., 2006; Fornara and Tilman, 2008; De Deyn et al., 2009). While ecosystem processes are dependent on the presence of several plant functional types, many plant communities exhibit intrinsic low species diversity with species abundance distribution dominated by a few keystone species (Preston, 1948; Walker et al., 1999). Some of these keystone species may show high diversity at the genotypic level, such as in the case of *Bouteloua gracilis* (Kunth) Lag. ex Griffiths in the shortgrass steppe (Aguado-Santacruz et al.,

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2004). The shortgrass steppe is a semiarid ecosystem dominated by *B. gracilis*, a C₄ bunchgrass which accounts for up to 85% of the aboveground biomass in the plant community and exerts main control on ecosystem processes (Coffin and Lauenroth, 1988; Burke et al., 1998; Medina-Roldán et al., 2007). Other studies have attested *B. gracilis*' large genetic variability at the local level (Aguado-Santacruz et al., 2004; Arredondo et al., 2005; Smith et al., 2009), but no clear implications of such genetic variability for ecosystem functioning have been examined so far.

Functional consequences of plant diversity have been scaled down to the genotypic (genetic variation usually based on molecular markers data) and phenotypic (when genetic information is not available, but plant traits are expressed consistently among homogenous and distinctive plant genetic lines, e.g., common garden experiments) levels of diversity (Bolnick et al., 2011; Violle et al., 2012). For instance, litter decomposition rates (Madritch et al., 2006), nutrient cycling (Madritch and Hunter, 2002, 2003, 2004; Classen et al., 2007), primary productivity (Crutsinger et al., 2006), and ecosystem stability and resistance to disturbance (Hughes and Stachowicz, 2004) have all been shown to respond to plant genotypic and/or phenotypic diversity. Unlike diversity, less is known on plant phenotypic/genotypic composition effects on ecosystem functioning. Just as environmental conditions shape the genotypic/phenotypic composition of plant populations (Smith et al., 2009; Arredondo et al., 2005; Matlaga and Karoly, 2004), land management regime might affect plant genotypic/phenotypic composition as well. Grazing has been shown to alter genetic structure (Smith et al., 2009; Kloss et al., 2011), genetic diversity (Aguado-Santacruz et al., 2004), and expression of phenotypic traits in grass populations, including *B. gracilis*. For instance, grazing altered phenotypic plasticity in grazing resistance traits of *Bouteloua curtipendula* populations (Smith, 1998). Additionally, differences in leaf tissue lignin content (LC), leaf dry matter content (LDMC, a component of specific leaf area, SLA) and other morphological traits among *B. gracilis* genotypic lines from populations exposed to contrasting grazing regimes have been reported (Arredondo et al., 2005). Since variation in these traits is linked to plant effects on ecosystem functioning, a mechanism by which grazing and other management practices may impact on ecosystem processes is through their selection of plant genotypic/phenotypic composition. However, our knowledge on plant functional trait composition at the intra-specific level on ecosystem processes is not well established.

At the species level, one of the main mechanisms by which different functional types affect soil microbial processes is related to plant traits that determine litter quality. High lignin and condensed tannin contents in plant tissues are known to negatively affect plant litter decomposition and soil nutrient mineralization rates (Schweitzer et al., 2008). For the shortgrass steppe, preliminary work by Arredondo et al. (2005) showed that *B. gracilis* populations exposed to contrasting grazing regimes differed in LDMC and LC, both traits related to litter quality. The question that remains unexplored is whether this grazing-driven differentiation in plant phenotypic composition (referred to as phenotypic functional composition here) affects ecosystem functioning including soil nutrient dynamics, soil microbial activity and community level physiological profiles of soil microbial communities. Here, we explore effects of the phenotypic functional composition of *B. gracilis* on soil microbial activity and selected soil processes. With *B. gracilis* genotypic lines differing in LC and LDMC (Arredondo et al., 2005); we assembled *B. gracilis* synthetic populations that differ in litter quantity and quality, and applied a small water pulse to them to trigger microbial activity. We hypothesise that soil microbial activity and soil nutrient dynamics should be higher in *B. gracilis* phenotypes exhibiting low LC and low DMC (i.e., have high SLA) in contrast to phenotypes with high LC and high DMC (i.e., have low SLA).

2. Material and methods

2.1. Study area

The study area comprises the Vaquerias experimental station (managed by the Research Institute of the Ministry of Agriculture in Mexico), located in the geographic subprovince Los Llanos de Ojuelos, Jalisco, Mexico (21° 46' 50"N; 101° 36' 39" W). Main vegetation in the study area corresponds to the southernmost distribution of the shortgrass steppe biome in North America. Topography corresponds to plains and gentle rolling hills (COTECOCA, 1979). Soils are Xerosols with pH values between 5.5 and 6.5 and low content of organic matter and cation exchange capacity (Aguado-Santacruz and Garcia-Moya, 1998). Climate is semiarid with an average of 380 mm annual rainfall in the last 30 years concentrated between July and September, and an average annual temperature of 18 °C (COTECOCA, 1979). Further details on topography, climate and plant species composition can be found in Aguado-Santacruz and Garcia-Moya (1998) and Medina-Roldán et al. (2007).

2.2. Experimental design

2.2.1. Phenotypic functional composition

In summer 2003, we established *B. gracilis* field synthetic populations with different phenotypic functional composition in a number of 1 × 1 m plots. Phenotypic functional composition of synthetic populations on each plot was determined using the criteria of LC content (litter quality) previously determined in 36 *B. gracilis* genetic lines (Fig. 1, Arredondo et al., 2005). We classified these genetic lines as low-LC plant phenotypes (i.e., LL, between 3.1 and 3.8% of dry matter, DM) coming from a heavily-overgrazed *B. gracilis* population, and high-LC plant phenotypes (i.e., HL, between 4.5 and 5.3% DM) coming from a moderately-grazed population (for more details, see Arredondo et al., 2005). Synthetic populations were assembled by planting nine individuals per plot equidistantly in a 3 × 3 matrix array. Phenotypic functional composition was manipulated by varying the proportion of HL and LL individuals in plots. In this way, we used a high lignin treatment (High) consisting of plots where 3 thirds of individuals were HL, a

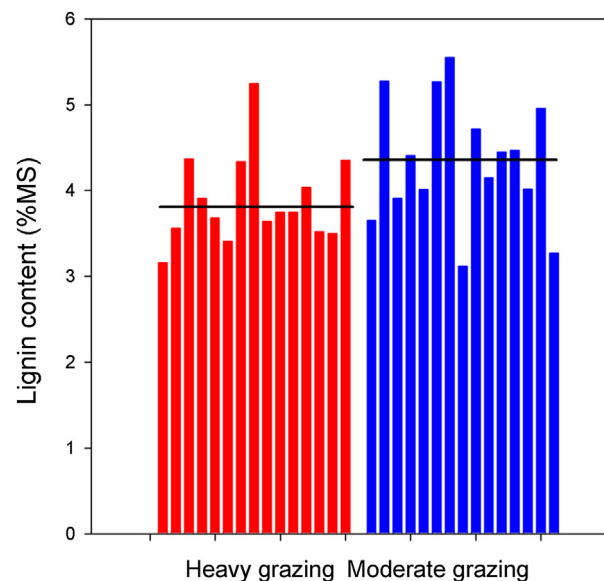


Fig. 1. Lignin content observed on *B. gracilis* individuals collected from two populations subjected to historical heavy vs moderate grazing. Horizontal line depicts the lignin content average for each population.

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