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Original article

Variation of morphological and chemical traits of perennial grasses in arid ecosystems. Are these patterns influenced by the relative abundance of shrubs?

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ABSTRACT

We asked whether morphological and chemical traits of perennial grasses in semiarid-arid ecosystems are influenced by the abundance of coexisting shrubs, in northern-central Patagonia, Chubut Province, Argentina. We selected populations of two perennial grass species, highly preferred by herbivores (4 for *Festuca pallescens* and 8 for *Poa ligularis*) at 10 sites distributed across a wide range of aridity. We assessed the relative shrub cover (shrub cover as percent of total cover) of each site and randomly collected 5 to 10 bunches of each grass species per site in December 2007 (late vegetative-early reproductive growth period). We measured the height of vegetative tillers, and morphological (length, width, area, dry mass, and specific area) and chemical (N, C, soluble phenolics and lignin concentration) attributes of full expanded green blades in the collected bunches. Further, we computed the aridity index of each site using temperature and precipitation data. The aridity index ranged from 1.07 to 3.9 at *F. pallescens* sites and from 3.6 to 7.3 at *P. ligularis* sites. The relative shrub cover increased significantly with aridity varying from 0.01 to 99%. Tiller height, blade length, and blade area of *P. ligularis* increased significantly with increasing relative shrub cover and aridity. Concentration of soluble phenolics in blades of both species decreased with increasing relative shrub cover and aridity. N concentration in blades of *P. ligularis* and specific blade area in *F. pallescens* decreased with increasing relative shrub cover and aridity. We conclude that some traits of perennial grasses (phenolics concentration in green blades in both species, and tiller height and some blade attributes in *P. ligularis*) were influenced by shrub cover itself. The variation in these traits was opposite to that expected by the effect of aridity and could be associated with escape from herbivores and/or drought, enhanced mesophytism, and reduced chemical defenses.

1. Introduction

Perennial grasses and shrubs are the dominant life forms in most semiarid and arid ecosystems of the world (Ares et al., 1990; Armas et al., 2008; Sala et al., 1989). The relative contribution of these life forms to the total plant canopy cover varies with aridity, prevailing shrubs at the driest ecosystems and perennial grasses at the wettest ones (Aguiar et al., 1996; Archer et al., 1988; Bertiller et al., 2006; Moreno et al., 2010; Ni, 2003). This could be partially explained by differences between these life forms related to strategies for plant water conservation and soil water use in space and time, among others (Breshears and Barnes, 1999; Grace, 1998; Reynolds et al., 2004). Shrubs usually have well developed chemical and structural defenses against water shortage and herbivores and may develop dimorphic or deep root systems allowing them to access to stable resources stored in the deep soil (Bertiller et al., 1991; Campanella and Bertiller, 2009; Kursar and Coley, 2003; Sala et al., 1989; Schenk and Jackson, 2002). In contrast, perennial grasses have lower structural and chemical defenses against herbivores and water shortage than shrubs, are generally highly preferred by herbivores (Baldi et al., 2004; Bertiller, 1996; Cingolani et al., 2005; O'connor, 1991), and are mostly limited to use highly variable resources stored in the upper soil due to their shallow root systems. Moreover, perennial grasses have more homogeneous morphology, phenology and foliar traits than shrubs (Bertiller et al., 1991; Carrera et al., 2003, 2005; Lee and Lauenroth, 1994; MacCarron and Knapp, 2001).

Several studies indicated that shrubs may facilitate the establishment and growth of herbaceous plants such as perennial grasses by creating ameliorated microenvironments around them or may protect these herbaceous plants from herbivores due to their strong physical and chemical defenses (Aguiar and Sala, 1994, 1999; Ares et al., 2007; Bertiller et al., 2002; Bertiller and Ares, 2008; Lopez et al., 2009; Soriano et al., 1994). The eventual

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escape from herbivores and drought could exert a strong influence on perennial grass morphological, physiological and life history traits, opposite to those expected by aridity (Abule et al., 2005; Landsberg et al., 1999; Pazos et al., 2007). This, in turn, could be advantageous for perennial grasses growing in the driest ecosystems with high shrub cover by reducing the high costs of production of structural and chemical defenses (Westoby et al., 2002).

Some studies found increasing expression of perennial grass xeromorphic traits such as decreasing leaf N, specific leaf area, and plant stature or increasing concentration of secondary compounds, among other traits, with increasing aridity (Adler et al., 2004; Fernandez and Reynols, 2000; Grace, 1998; Rotundo et al., 2006). However, Oyarzabal et al. (2008) highlighted that some changes in perennial grass traits with aridity are not only determined by climate itself but also could be related to the photosynthetic pathway, being responses higher for C_4 than for C_3 species. Moreover, some studies carried out in Patagonia (Argentina) reported decreasing expression of xeromorphic traits in perennial grasses with increasing aridity (Bertiller et al., 2005, 2006; Mazzarino et al., 1998). These results could be associated with the fact that Patagonian perennial grasses could be benefited by neighboring shrubs with strong physical and chemical defenses providing refuges against herbivores (Moreno et al., 2010) or creating ameliorated microclimatic conditions for perennial grass growth (Aguiar et al., 1992; Aguiar and Sala, 1994; Bertiller et al., 2002; Soriano et al., 1994). Also, shrubs could facilitate perennial grass growth through hydraulic lift (Ludwig et al., 2003; Prieto et al., 2012) but there is no evidence for perennial grasses in Patagonia (Fernandez et al., 2008). The shrub matrix covers c.a. 40–60% of the soil in the driest sites (less than 200 mm annual precipitation) and less than 20% in the wettest sites (200–500 mm annual precipitation) of Patagonia (Bertiller et al., 1995; Bertiller and Ares, 2008; Bisigato and Bertiller, 1997). The relative contribution of shrubs to the total plant cover is over 90% in the driest sites where perennial grasses usually form a ring at the border or periphery of shrub canopies (Aguiar et al., 1992; Bertiller et al., 2002; Pazos et al., 2007). In contrast, shrubs contribute with less than 10% to the total plant cover growing scattered in a matrix of perennial grasses in the wettest sites (Bertiller et al., 1995; León et al., 1998; Soriano, 1956). Accordingly, the aridity gradient in Patagonia is associated with a wide range of variation in absolute and relative shrub cover. In this context, we asked whether the morphological and chemical traits of perennial grasses in semiarid-arid ecosystems are influenced by aridity itself or they are also affected by the relative abundance of coexisting shrubs. We hypothesized that shrubs exert a strong effect on traits of neighboring perennial grasses opposite to those expected by the effect of aridity. We predicted that increasing relative shrub cover would be associated with enhanced expression of mesophytic traits and reduced accumulation of chemical defenses in perennial grasses. To test the hypothesis and prediction, we assessed the variation in morphological (tiller height, green blade dimensions, and specific blade area: SBA) and chemical traits (N, C, phenolics and lignin concentration in green blades) with increasing relative shrub cover/aridity in two perennial grass species with wide geographical distribution. These selected traits are related to grass defenses against herbivores and water shortage (Grace, 1998).

2. Materials and methods

2.1. Species geographical distribution

We selected two cold season C_3 perennial grass species highly preferred by herbivores: *Festuca pallescens* and *Poa ligularis* with a wide geographical distribution in northern-central Patagonia of Argentina (Correa, 1978). *F. pallescens* is characteristic of the Subandean and San Jorge Gulf Districts of the Patagonian Phytogeographic Province and *P. ligularis* is one of the dominant perennial grasses in the Occidental and Central Districts of the Patagonian Phytogeographic Province and the southern Monte Phytogeographical Province (Bertiller et al., 2006). Both species coexist in the Occidental and San Jorge Gulf districts of the Patagonian Phytogeographical Province.

2.2. Sampling

We randomly collected 5–10 bunches (depending on bunch size) per species at 10 sites selected across an aridity gradient encompassing the area of distribution of both species (Table 1) during the vegetative-reproductive growth period (December 2007). *P. ligularis* was collected at 8 sites and *F. pallescens* at 4 sites since the distribution area of the former is wider than that of *F. pallescens* (Correa, 1978). Two of these sites were common to both species. All the study sites have been grazed by low densities of native herbivores (*Lama guanicoe*, *Dolichotis patagonum*, *Lepus europaeous*) and since the early 1900s by sheep (Ares et al., 1990).

We selected a representative vegetation stand of about 1 ha (minimal area *sensu* Mueller-Dombois and Ellenberg, 1974) at each site and we visually estimated the total and shrub species cover using cover categories with increments of 1% within the whole vegetation stand as reported in Bertiller and Ares (2008). Further, we calculated the relative shrub cover as the percent of shrub cover in the total cover per site. Data on mean annual temperature (MAT), mean annual precipitation (MAP) and aridity index (AI) of each site were taken from Carrera and Bertiller (2010) and Moreno et al. (2010). The aridity index (AI) of each site was computed as PET/MAP, being PET (mean annual potential evapotranspiration) = 69.4 × MAT (Le Houérou, 1990; UNESCO, 1979). High AI-values indicate high aridity conditions.

2.3. Perennial grass traits across the gradient

We measured morphological and chemical traits of the perennial grass bunches collected at each site as follows:

1. Height of vegetative tillers ($n = 3$ per bunch) from the base up to the top of the longest leaf.
2. Length, width, area, and dry mass of the blade of the youngest full expanded green leaf of the tiller ($n = 5$ tillers per bunch). The measurements of length, width and area of leaf blades

Table 1
Site location, Phytogeographical Province (P: Patagonian, M: Monte) and District (S: Subandean, O: Occidental, SJG: San Jorge Gulf), aridity index (AI), mean annual temperature (MAT), mean annual precipitation (MAP), and species collected at each site (*Festuca pallescens*: Fp, *Poa ligularis*: Pl). Aridity index (AI) = PET/MAP, where PET (mean annual potential evapotranspiration) = 69.4*MAT (Le Houérou, 1990; UNESCO, 1979). High AI-values indicate high aridity. Data on AI, MAT, MAP were taken from Carrera and Bertiller (2010) and Moreno et al. (2010).

Site location	Phytogeographical province-district	AI	MAT	MAP	Species
44°58′47.4″S, 71°17′0.0″W	P-S	1.07	7.68	500.0	Fp
45°36′15.3″S, 71°26′11.3″W	P-S	1.36	7.54	385.0	Fp
42°23′31.0″S, 68°56′41.9″W	P-O	3.68	7.95	150.0	Pl-Fp
45°41′11.6″S, 67°53′26.6″W	P-SJG	3.97	8.58	150.0	Pl-Fp
45°35′19.5″S, 70°20′14.8″W	P-O	4.30	9.29	150.0	Pl
43°13′01.6″S, 65°0.1′29.1″W	P-C	5.04	13.30	183.3	Pl
43°51′30.2″S, 68°13′29.4″W	P-C	5.97	11.29	131.3	Pl
42°33′33.5″S, 66°33′50.4″ W	M	6.44	12.76	137.5	Pl
43°44′40.4″S, 66°20′21.9″W	P-C	6.61	12.38	130.0	Pl
42°45′42.5″S, 66°01′02.5″W	M	7.31	13.16	125.0	Pl