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Phenotypic plasticity of morpho-chemical traits of perennial grasses from contrasting environments of arid Patagonia

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ABSTRACT

We hypothesized that the combined effect of aridity and relative shrub cover could lead to differences in phenotypic plasticity among perennial grass populations opposed to those expected by aridity. We selected two populations of *Festuca pallescens* and two of *Poa ligularis* from contrasting environments across a gradient of aridity and relative shrub cover. We collected 10–20 bunches of each population. A half of each was herborized (*in situ* set) and the other was transplanted in pots and maintained at soil field capacity during one year (common growing conditions set). We assessed morpho-chemical traits of bunches of each set and calculated the phenotypic plasticity index of each trait as the change in the trait expression between *in situ* and common growing conditions. Both species showed the largest phenotypic plasticity at sites that represent mid values of aridity and relative shrub cover for Patagonian ecosystems. *P. ligularis* showed larger phenotypic plasticity than *F. pallescens*. According to our hypothesis *F. pallescens* showed higher phenotypic plasticity at the mid than at the wet site while the reverse occurred with *P. ligularis*. We concluded that unpredictable environments could lead to increased phenotypic plasticity of traits. This idea should be further investigated.

1. Introduction

Plant traits vary widely across regional and global climatic gradients (Austin and Sala, 2002; Wright et al., 2004; Bertiller et al., 2006). Several studies identified the main trade-offs characterizing plant performance in a wide range of habitats. Across these gradients, fast growing plants from resource-rich sites are mostly associated with high phenotypic plasticity while low phenotypic plasticity would prevail in slow-growing plants from resource-poor habitats (Garnier, 1998; Cornelissen et al., 1999; Aerts and Chapin, 2000; Fonseca et al., 2000; Wright and Westoby, 2002; Wright et al., 2002, 2004; Reich and Oleksyn, 2004; Roche et al., 2004; Bertiller et al., 2005). However, these relationships are not clearly defined in more constrained gradients such those occurring within arid environments (Moreno and Bertiller, 2012).

Arid ecosystems are characterized by scarce, highly variable, and erratic precipitation (Noy Meir, 1973). Shrubs and perennial grasses are the dominant plants in most arid ecosystems of the world (Noy-Meir, 1973; Aguiar and Sala, 1994; Adler et al., 2004; Armas et al., 2008) and some studies showed that shrub cover is positively correlated to aridity across regional gradients (Bertiller et al., 2005, 2006). Perennial grasses and shrubs have different mechanisms of resistance to water shortage. Perennial grasses are usually drought-avoiding species with more mesophytic traits and higher phenotypic plasticity than shrubs (Coughenour et al., 1984, 1985; Busso and Richards, 1993; Craine et al., 2002; Grassein et al., 2010; Pazos et al., 2010). In contrast, shrubs are drought-tolerant plants having usually xerophytic traits and well-developed chemical and structural defenses against water shortage and herbivores (Bertiller et al., 1991; Ivanov et al., 2008; Campanella and Bertiller, 2009). Due to these characteristics, shrubs may facilitate the establishment and growth of perennial grasses by creating ameliorated microenvironments around them or protecting herbaceous plants from herbivores (Aguiar and Sala, 1994, 1999; Bertiller et al., 2002; Bertiller and Ares, 2008; Lopez et al., 2009).

Perennial grass species display high morphological variability across both regional and local arid-semiarid gradients and there is evidence that this trait variability may result from complex interactions between climatic gradients and local neighborhoods (Correa, 1978; Fernandez et al., 2004; Bertiller et al., 2006; Moreno and Bertiller, 2012). It may be expected higher plasticity in

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perennial grasses from environments with higher and predictable resource levels than in resource-poor environments (Lambers et al., 2000). In this sense, fixed traits could be thought as the most adaptive way to cope with aridity. However, Couso and Fernandez (2012) reported increasing phenotypic plasticity for fitness-related traits (those related to growth, reproduction and survival) of perennial grasses and decreasing capacity to tolerate drought with decreasing aridity. However, these authors also found trait-dependent responses for other traits such as mechanistic traits describing allocation (root biomass and shoot/root biomass). In contrast, Moreno and Bertiller (2012) showed that the variation of traits of perennial grasses related to drought tolerance across aridity gradients may be opposite to that expected by the effect of aridity (i.e. enhanced mesophytism, reduced chemical defenses at the driest sites) reflecting escape from drought and/or herbivores in the mild or protected neighborhoods induced by local shrub arrangements. This might indicate that both aridity and shrubby neighborhoods could affect oppositely perennial grass traits in arid environments and these trait variations may be either attributed to phenotypic plasticity (Grassein et al., 2010; Couso and Fernandez, 2012) or to different genotypes with fixed phenotypes (Oyarzabal et al., 2008). Accordingly to these results, we hypothesized that the combined effect of aridity and relative shrub cover could lead to differences in phenotypic plasticity among perennial grass populations opposed to those expected by aridity. To test this hypothesis, we evaluated changes in morpho-chemical traits between *in situ* and common growing conditions to assess phenotypic plasticity of perennial grass populations of *Poa ligularis* and *Festuca pallescens* from sites with contrasting aridity and relative shrub cover.

2. Materials and methods

2.1. Study species and sites

P. ligularis Nees ap. Steudel and *F. pallescens* (St-Yves) Parodi are two perennial grasses with a wide geographical distribution in Patagonia and high morphological variability across the environments where they grow. *F. pallescens* is characteristic of semiarid ecosystems and the morphology of this species may vary from tall bunches with long leaves to low bunches with short leaves (Correa, 1978). This variation was observed across both regional and local environmental gradients (Fernandez et al., 2004; Moreno and Bertiller, 2012). The phenology of this species varies among sites with different temperature and/or water regime and this variation was maintained when growing in common gardens (Ares et al., 1990). *P. ligularis* is a perennial grass characteristic of arid ecosystems displaying high genetic (Hunziker, 1978) and phenotypic variability (Correa, 1978; Giussani et al., 1996; Giussani, 2000). Moreno and Bertiller (2012) reported changes in leaf traits of *P. ligularis* and *F. pallescens* with increasing aridity as well as local leaf trait changes induced by the vicinity to shrubs.

We selected two populations of each perennial grass species (*P. ligularis* and *F. pallescens*) from sites with contrasting aridity index (AI) and relative shrub cover (RSC). The selected sites were PLdry (AI: 7.2, RSC: 92%), PLmid (AI: 3.9, RSC: 31%) for *P. ligularis* and FPmid (AI: 3.68, RSC: 23%), FPwet (AI: 1.07, RSC: 0.01%) for *F. pallescens* at the dry and wet site, respectively. These sites are near the driest and the wettest extremes of the distribution areas of each species encompassing those of the extra-Andean Patagonian ecosystems (Bertiller et al., 2006). The RSC (shrub cover as percent of total cover) and the AI, calculated from mean annual temperature (MAT) and mean annual precipitation (MAP), of each site were taken from Carrera and Bertiller (2010) and Moreno et al. (2010). High AI-values indicate high aridity conditions. These sites differ in the amount and in the inter-annual variation of annual precipitation. The gamma parameter, characterizing the inter-annual variability of the precipitation (Barros and Rivero, 1982), also varied among *P. ligularis* sites: Sierra Chata: 3.90, Pampa del Castillo: 4.35 and *F. pallescens* sites: Gastre: 4.2, Ea La Pepita: 10. A large gamma parameter indicates low inter-annual variation of precipitation, thus precipitation is more variable, more erratic, and less predictable in the sites with the highest aridity index than in the wettest extreme of the aridity gradient (Table 1).

2.2. Material collection, common growing conditions and morpho-chemical traits

Both species are perennial bunch (caespitose) grasses (Correa, 1978) and each bunch is a compact spatial arrangement of clonal tillers (genet) (Briske and Derner, 1998). We randomly collected between 10 and 20 bunches of each species at each site during the period from end of vegetative growth to early reproductive growth (November–December 2007). A half of the tillers of each bunch were herborized to assess morpho-chemical traits *in situ*, and the other half were transplanted in pots (1.5 l) to assess morpho-chemical traits in a common garden. The pots were filled with a soil mixture in equal proportion of soils of wet sites (high fertility: N: 1.35 ± 0.05 mg g^{-1}, C: 12.42 ± 1.03 mg g^{-1}), and dry sites (low fertility: N: 0.44 ± 0.02 mg g^{-1}, C: 5.59 ± 0.15 mg g^{-1}). Subsequently, the pots were placed in a partially shaded place in an experimental site (CENPAT, Puerto Madryn- Chubut: 42°49′46″ S, 65°04′56″ W) in December 2007. The use of a soil mixture in the pots of the common garden and shading allowed homogenizing the substrate and reducing the atmospheric demand in order to reach “optimal” common growing conditions but could eventually introduce some confounding effect of nutrients and shading on the experiment. All the pots received weekly irrigation to field capacity (20%) during 12 months. Soil moisture was controlled with a TDR IMKO sensor. The mean annual precipitation during the study was 100.1 mm, and the mean annual temperature was 14.3 °C (Laboratory de Climatology of the National Patagonian Center-CENPAT-CONICET, www.cenpat.edu.ar). The common garden conditions represented situations with large periods of continuous and high soil humidity (20% throughout the one-year study period) more favorable than those prevailing *in situ* for the four study perennial grass populations. Although, the yearly water balance in the wet extreme is nearly at equilibrium between precipitation and evapotranspiration, precipitation is concentrated in the cold seasons (autumn and winter) and soils in the rooting depth have water contents lower than 7% during summer (Coronato and Bertiller, 1996). Similarly, soil water content in the rooting depth in the field at the dry extreme of the gradient in summer is lower than 6% (Coronato and Bertiller, 1997) thus achieving contrasting environmental conditions in the field compared to the common garden. Aboveground parts of plants of each pot were harvested in December 2008.

We measured morphological and chemical traits on homogenous tillers (number of leaves, tiller hierarchy) collected from bunches of each species and site grown *in situ* and under common garden conditions. Herborized plants were rehydrated before measurements. Tiller height ($n = 3$ per bunch) was measured in vegetative tillers from the base up to the top of the longest leaf. Length, width, and area of blades were measured on digitized images of the youngest full expanded green leaf of each tiller ($n = 5$ tillers per bunch). After that, blades were dried at 60 °C for 48 h and weighed to estimate the dry mass. The specific blade area (SBA) of the youngest full expanded green leaf of the tiller was calculated as blade area/blade dry mass ($n = 5$ tillers per bunch). We used the blades of the remnant totally full expanded young green leaves