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Morphological and growth responses to water stress of two sub-populations of *Bromus pictus* from soils with contrasting water availability

Respuestas morfológicas y de crecimiento al estrés hídrico de dos subpoblaciones de *Bromus pictus* provenientes de suelos con contrastante disponibilidad de agua

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ABSTRACT

We studied morphological and growth responses to drought of two sub-populations of *Bromus pictus* from communities with soils with different water availability from the Patagonian steppe. After a process of acclimatization common to both sub-populations, individuals from both sub-populations were subjected to three levels of water availability during 44 days. Independently of the water availability treatment, the sub-population from the community of high soil water availability showed higher aboveground relative growth rate (RGR) and higher leaf size (area and weight) compared to the sub-population from the community of low soil water availability. These results prove the expected evolution of higher growth rates and leaf sizes in resource rich environments. The sub-population from the community with low water availability also showed a higher tillering rate and a more prostrate morph than the sub-population from the community with high water availability. A higher number of small tillers may be a useful strategy for a quick response to water inputs and for distribute the risk of drought-induced mortality. A more prostrate morph may also present advantages like reducing the area exposed to dry air. The results obtained showed that soil heterogeneity may promote genetic variation. We were unable to detect statistically significant interactions between population and water availability treatments. The genetic variation found between the populations may be useful to develop breeding programs of a native species and may also increase the evolutionary potential of a native species to adapt to environmental changes.

Key words: arid lands, drought, ecotypes, genetic variation, soil depth.

RESUMEN

Nosotros estudiamos respuestas morfológicas y de crecimiento a la sequía para dos subpoblaciones de *Bromus pictus* provenientes de comunidades con suelos de distinta disponibilidad de agua en la estepa patagónica. Luego de un proceso de aclimatización común a ambas subpoblaciones, individuos de cada subpoblación fueron sometidos a tres niveles de disponibilidad de agua durante 44 días. Independientemente del nivel de disponibilidad hídrica, la subpoblación proveniente de la comunidad con mayor agua disponible exhibió una mayor tasa de crecimiento relativa aérea (RGR) y mayor tamaño foliar (área y peso) comparado con la subpoblación proveniente de la comunidad con menor agua disponible. Estos resultados prueban la evolución esperada de mayores tasas de crecimiento y tamaños de hoja en aquellos ambientes ricos en recursos. La subpoblación proveniente de la comunidad con menor agua disponible también exhibió una mayor tasa de macollaje y un hábito de crecimiento más postrado que la subpoblación proveniente de la comunidad con mayor agua disponible. Un mayor número de macollos pequeños puede ser una estrategia útil para una rápida respuesta a los pulsos de agua y para distribuir el riesgo la muerte inducida por sequías. Un hábito de crecimiento más postrado puede también presentar ventajas tales como reducir el área expuesta al aire seco. Los resultados obtenidos demuestran que la heterogeneidad del suelo puede promover variación genética, aunque no permitieron detectar interacciones estadísticamente significativas entre los factores vinculados con las poblaciones y la disponibilidad de agua. La variación genética encontrada entre las poblaciones puede ser útil para desarrollar programas de mejoramiento e incrementar el potencial evolutivo de una especie nativa para adaptarse a cambios ambientales.

Palabras clave: ecotipos, profundidad del suelo, sequía, tierras áridas, variación genética.

INTRODUCTION

Genetic variability may represent a key attribute in species ability to adapt to spatial heterogeneity (Endler 1986, Linhart & Grant 1996). Studies of adaptations of sub-populations of native species to local microenvironments in the same regional climate would be especially useful in understanding the role of landscape heterogeneity in the population genetic structure. Different environmental conditions like exposure to sun, height above sea level, and soil heterogeneity, like variation in depth or texture, may generate different selection pressures that lead to genetic differentiation (Linhart & Grant 1996). This kind of studies may also be useful in predicting evolutionary responses of populations to global changes (Bradshaw & McNeilly 1991, Etterson & Shaw 2001). A population with sub-population genetic differentiation due to environmental spatial heterogeneity has a higher evolutionary potential to adapt to new climatic scenarios (Etterson & Shaw 2001). The study of genetic differentiation in native species may also be useful to develop breeding programs of native plants for restoration of degraded lands (Theunissen 1997, M'Seddi et al. 2002). The existence of genetically improved native populations in some trait of interest may accelerate the process of re-vegetation (Jones & Johnson 1994). In the present paper, morphological and growth responses to drought of two sub-populations of a native perennial grass from communities exposed to different water availability have been evaluated.

The occidental district of the Patagonian steppe presents two contrasting communities associated to different soil types ("deep-soil" and "shallow-soil" communities) (Golluscio et al. 1982). The dominant "deep-soil" community corresponds to sandy soil with more than 50 % pebbles. There is a calcareous layer approximately 0.6 m deep (Paruelo et al. 1988). In this community, grass rooting is at least 0.3 m deep (Soriano et al. 1987). The "shallow-soil" community is found in spots of different size in a matrix of "deep-soil" community. Soils of this community have an upper layer of 0.05 m of sandy texture on top of a 0.1 m layer of sandy clay texture that prevents root penetration (Golluscio et al. 1982). This

reduces the availability of water and increases the length of drought periods. Plant populations may respond to drought by phenotypic plasticity or adaptation (Silvertown & Doust 1993). This environmental heterogeneity has the potential to influence the distribution of genetic variation among sub-populations through several evolutionary processes, including natural selection. The hypothesis underlying this paper is that, whether natural selection is the main evolutionary process shaping the distribution of genetic variation in the Patagonian steppe, sub-populations from communities having lower water availability would present traits related to a higher success under drought condition compared with sub-populations from communities having high water availability. Otherwise, sub-populations from high water availability communities would have more growth potential than sub-populations from communities having lower water availability.

The success of plants under drought depends on the growth potential and/or the tolerance to stress (Hochwender et al. 2000, Stowe et al. 2000). These two components can be visualized when plotting some variable related to fitness (e.g. biomass) across a stress gradient (e.g. increasing levels of drought), often called a reaction norm. The biomass attained when stress is zero (visualized as the y-intercept) represents the growth potential (Sultan 2000, Sarkar & Fuller 2003). For example, if one population has a higher y-intercept compared to other it means that the first presents a higher growth potential than the later. Otherwise, the slope of this relation represents the tolerance to stress. For example, a population that reduces growth lesser than other when stress is increasing has higher tolerance compared to the later. Extreme reaction norms are showed in Fig. 1, where success in drought (e.g. biomass attained in the highest stress level) is determined entirely by tolerance (Fig. 1A) or entirely by growth potential (Fig. 1B) (Hochwender et al. 2000). Figure 1C shows a hypothetical situation in which selection by drought may favor the less tolerant sub-population (sub-population 1).

The reaction norm analysis is applied to compare different species, populations, sub-populations or even individual genotypes. In this paper we applied this approach to compare

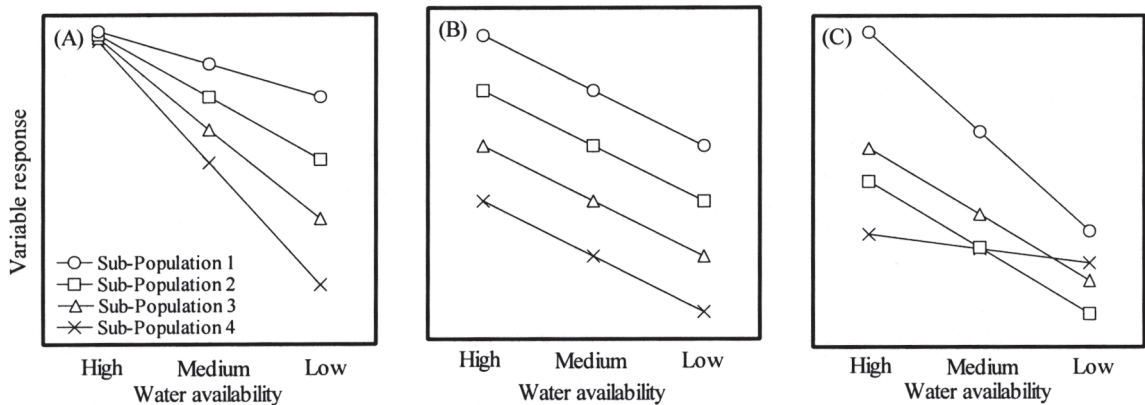


Fig. 1: Fitness components in drought in three hypothetical situations. (A) and (B) correspond to extreme situations. In (A) the subpopulations did not differ in potential growth, and fitness in drought depends entirely on tolerance. In (B) the subpopulations did not differ in tolerance, and fitness in drought depends entirely on potential growth. (C) corresponds to a particular case in which the less tolerant subpopulation (1) had higher fitness in drought than the most tolerant subpopulation (4). Graphs modified from Hochwender et al. (2000).

Componentes del "fitness" (una medida de la aptitud ecológica) en sequía para tres situaciones hipotéticas. (A) y (B) corresponden a situaciones extremas. En (A) las subpoblaciones no difieren en su potencial de crecimiento y el "fitness" en sequía depende solamente de la tolerancia. En (B) las subpoblaciones no difieren en tolerancia y el "fitness" en sequía depende solamente del crecimiento potencial. (C) Corresponde a un caso particular en cual la subpoblación menos tolerante (1) tiene mayor "fitness" en sequía que la subpoblación más tolerante (4). Las figuras fueron redibujadas a partir de Hochwender et al. (2000).

two sub-populations of *Bromus pictus*, a native perennial grass of high palatability which is threatened by sheep overgrazing (Aguiar et al. 1999)¹. Increasing our knowledge of its ecophysiology and genetic variation will contribute to develop breeding programs for revegetation. The main objective of our work was to evaluate the responses to drought of two sub-populations of *Bromus pictus* from "deep-soil" and "shallow-soil" communities. In order to evaluate these responses, a common garden experiment was performed in which water availability was manipulated.

MATERIAL AND METHODS

Description of communities

Individuals of *Bromus pictus* (from now on *Bromus*) were sampled from the Instituto Nacional de Tecnología Agropecuaria (INTA),

Experimental Field Station at Río Mayo, Chubut, Argentina (45°41' S, 70°16' W, 500 m of altitude). Mean annual precipitation for a 37-year record is 152 ± 44 mm, with > 70 % of the precipitation occurring in fall-winter (Jobbágy et al. 1995). Mean annual temperature is 8.1 °C with monthly mean values ranging from 2 °C (July) and 14 °C (January) (Beltrán 1997).

Vegetation corresponds to the occidental district of the Patagonian steppe (Soriano 1983). The typical community ("deep-soil" community) is co-dominated by grasses and shrubs, which cover 25 and 12 %, respectively, and contribute more than 96 % of the total plant biomass (Fernández et al. 1991, Golluscio & Sala 1993, Jobbágy & Sala 2000). The patch structure of the community is characterized by shrubs surrounded by a grass ring (Soriano et al. 1994, Aguiar & Sala 1999). The dominant grass species are *Stipa speciosa* Trin. Et Rupr., *Poa ligularis* Nees ap. Steud., *Stipa humilis* Vahl and *Bromus pictus* Hook. The dominant shrubs species are *Senecio filaginoides* AD., *Mulinum spinosum* (Cav.) Pers. and *Adesmia campestris* (Rendle) Skottsb. Forbs contribute less than 1 % to plant cover; however species

¹ AGUIAR MR, PA CIPRIOTTI, WB BATISTA & AC PREMOLI (1999) Viabilidad de poblaciones de gramíneas patagónicas en peligro de extinción por sobrepastoreo. Abstracts of the IXX Reunión Argentina de Ecología, Tucumán, Argentina, 220 pp.

richness is higher than in shrubs or grasses (Golluscio & Sala 1993). For more than 100 years, sheep have been the main herbivore due to extensive grazing for wool and meat production; stocking rates ranges between 0.2 to 0.4 sheep ha⁻¹ (Soriano 1983, Golluscio et al. 1998, 1999).

There is also a less typical community ("shallow-soil" community) that appears in the form of spots (that vary from 20 to 100 m diameter) immersed in a matrix of "deep-soil" community. The "shallow soil" community is less dominated by the perennial grasses mentioned above and more by the shrubs *Nassauvia glomerulosa* (Lag.) Don, *Chuquiraga aurea* Skottsberg and *Chuquiraga kingii* Ball (Golluscio et al. 1982). This community is dominant in the more arid regions located to the east (central district) (León et al. 1998).

The "shallow-soil" community is considered to be more xeric than the "deep-soil" community. Grass roots reach a depth of at least 0.3 m in the "deep-soil" community (Soriano et al. 1987). Shrub roots in the "shallow-soil" community do not penetrate the clay layer (Golluscio et al. 1982). Soil water storage in the layer explored by grass roots is 19.3 mm in the "deep-soil" community and 3.5 mm in the "shallow-soil" (calculated from Golluscio et al. 1987)². Furthermore, net primary productivity is 57 ± 5.2 g m⁻² yr⁻¹ and 21.5 ± 3.5 g m⁻² yr⁻¹ for "deep-soil" and "shallow-soil" communities respectively (Golluscio et al. 1987).

Experiment description

Bromus genets were collected from two different stands of "deep-soil" (n = 6) and "shallow-soil" (n = 6) sub-populations in April 2001. The diameter of spots of "shallow-soil" community was approximately 100 m. Genets were at least 3 m apart from each other. The genets were clonally multiplied in 1.5 L pots at an open greenhouse at the Instituto de investigaciones Fisiológicas y

Ecológicas Vinculadas a la Agricultura (IFEVA), Universidad de Buenos Aires (34°35' S, 58°29' W). Pots were filled with sand and watered with 25 mL Hoagland solution once a week and with water as needed for plant growth without any water limitation. During the fourth month, the genets were clonally multiplied again and grown for two additional months. Four ramets from each genet were randomly selected. One of these ramets from each genet was harvested as the time zero measure (six ramets from "deep-soil" and six from "shallow-soil"). The other three ramets from each genet were randomly assigned to water availability treatments. At the time of the treatments, the contribution of original tissue of plants was insignificant since most of the tissues of final plants were originated in the common garden. The mean temperature in the open greenhouse during experiment was 21.8 °C, ranging from 10.1 to 34.4 °C. The mean of PAR radiation was 35.1 mol m⁻² day⁻¹, ranging from 2.9 to 55.4 mol m⁻² day⁻¹. The mean relative humidity was 71.4 %, ranging from 48.8 to 91.7 %.

Drought treatments were imposed by watering to get three ranges of gravimetric water availability: 80-90 %, 50-60 % and 20-30 % of field capacity. The amount of water needed to achieve each gravimetric water content was determined by weighting pots at field capacity (W_{FC}) and pots with sand completely dried at 80 °C during 72 h (W_D). The difference W_{FC} - W_D corresponds to the weight of water at field capacity (100 % of water availability). The three ranges were determined by linear extrapolation according to the relationship between gravimetric water and percentage of water capacity. Pots were weighed daily and when pot weight reached the lower value of the target range, water was added to reach the higher level. Hoagland solution was applied instead of water until the doses of 25 mL Hoagland solution per week was reached.

The individuals were harvested at day 44. Morphological variables measured were shoot biomass, root biomass (0-10 cm deep and 11-20 cm deep), number of tillers, tiller insertion angle, leaf area and leaf weight. Tiller insertion angle was measured as degrees from the horizontal with a plastic protractor. Shoot biomass is positively related with seed

² GOLLUSCIO RA, JM PARUELO & MR AGUIAR (1987) Relaciones suelo vegetación en distintos ambientes del sudoeste de Chubut. Abstracts of the la XIII Reunión Argentina de Ecología, Bahía Blanca.

production ($R^2 = 0.91$, $P < 0.01$, Rotundo & Aguiar unpublished data). Leaf area was measured by scanning and counting pixels. As described above, the ramets harvested at time zero of each genet of each sub-population were used to measure the relative growth rate (RGR), as a growth variable calculated: $RGR = (\ln(\text{biomass}_{\text{final}} - \text{biomass}_{\text{initial}}) / \text{duration of experiment (days)})$ (Hunt 1990).

The experimental design was factorial with water availability (high, medium, low), sub-populations ("deep soil" and "shallow soil") and genets (six from "deep soil" and six from "shallow soil") as factors. A general linear model was used with genets nested within sub-populations (Montgomery 1997) as,

$$Y_{ijkl} = \mu + W_i + S_j + G(S)_{k(j)} + WS_{ij} + e_{ijkl}$$

where Y_{ijkl} represents the variable response (aerial biomass, leaf area, and so on) for the l^{th} observation (plant) from the k^{th} genet, j^{th} sub-population and i^{th} water treatment; μ is the general mean; W_i indicates the three different water availability levels (i); S_j represents the two different sub-populations (j); $G(S)_{k(j)}$ represents the different genets nested within each sub-population (k); WS_{ij} represents the interaction term between water availability and sub-populations; and finally e_{ijkl} indicates the error term. Each genet was considered as a true replicate of the factor sub-population, thus the experiment has a total of three treatments x two sub-populations x six genets = 36 pots. Data were checked for ANOVA assumptions and were log transformed when needed.

RESULTS

The reduction in water availability reduced aboveground biomass for both sub-populations in the same way and thus there was no significant water availability x sub-population interaction (Fig. 2A). Belowground biomass was not statistically affected by water availability (Fig. 2B). Thus, total biomass followed the same pattern as above ground biomass (Fig. 2C). None of the three variables were statistically affected either by sub-population main effect or by water availability x sub-population interaction (Fig. 2).

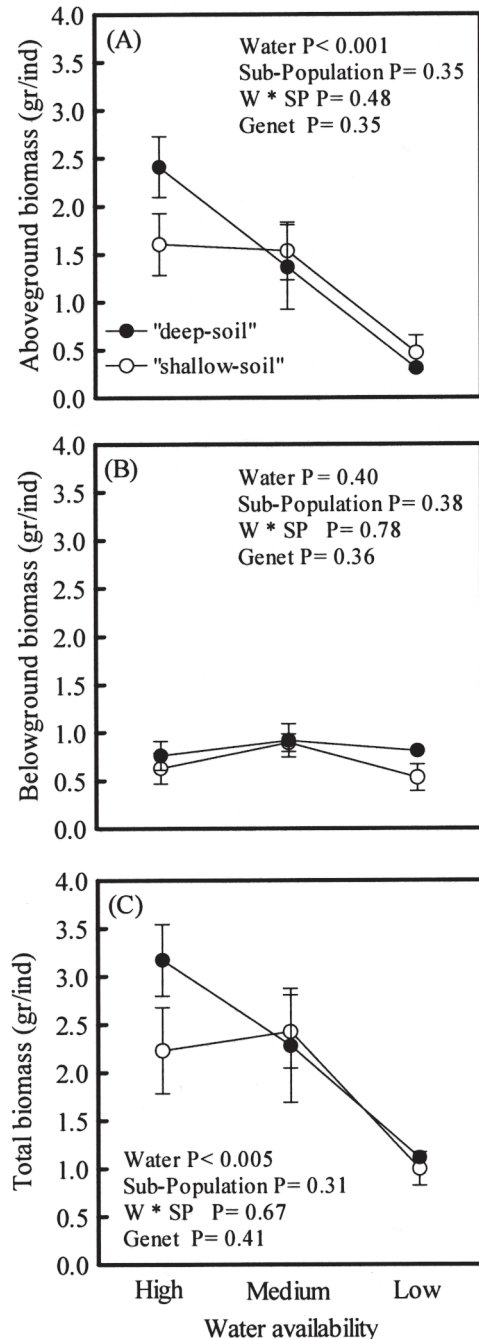


Fig. 2: Effect of drought for two sub-populations of *Bromus* from "deep-soil" and "shallow-soil" communities across a water availability gradient. Variable responses are (A) aboveground biomass, (B) belowground biomass, and (C) total biomass. Data are means \pm SE.

Efecto de la sequía para dos subpoblaciones de *Bromus* provenientes de comunidades de "suelos profundos" y "suelos someros" a través de un gradiente de disponibilidad de agua. Las variables de respuesta son (A) biomasa aérea, (B) biomasa subterránea, y (C) biomasa total. Los datos representan medias \pm EE.

Low water availability also reduced aboveground RGR in both sub-populations (Fig. 3A). Aboveground RGR was, on average, significantly higher in the “deep-soil” than in the “shallow-soil” sub-population (Fig. 3A). Belowground RGR was not significantly affected either by water availability main effect or by sub-population (Fig. 3B). Thus, total RGR followed the same pattern as aboveground RGR, and the effect of sub-population was marginally significant (Fig. 3C). None of these variables were significantly affected by water availability x sub-population interaction.

Individual leaf area ($\text{cm}^2 \text{ leaf}^{-1}$) and weight (mg leaf^{-1}) were significantly reduced by low water availability (Fig. 4A and 4B). This effect was the same for the two sub-populations, as indicated by the lack of sub-population by water availability interaction (Fig. 4A and 4B). On average, leaf size (area and weight) was higher in the “deep-soil” sub-population than in the “shallow-soil” population (Fig. 4A and 4B).

Tiller angle was not significantly affected by water availability (Fig. 4C). The “deep-soil” sub-population showed a significantly higher tiller angle respective to soil surface than the “shallow-soil” sub-population (Fig. 4C). This results in a more erect morph of the “deep-soil” sub-population than the “shallow-soil” sub-population. There was no significant effect of the interaction of water availability by sub-population.

Tillering rate was marginally reduced by the reduction in water availability (Fig. 4D). Tillering rate was, on average, significantly greater in the “shallow-soil” sub-population than in the “deep-soil” sub-population (Fig. 4D). The interaction of water availability by sub-population was not statistically significant.

DISCUSSION

Genetic differentiation mainly occurred in morphological variables and in less degree in growth variables. This was shown by the main effect of sub-population in all the morphological variables measured and in only one of the growth variables (aboveground RGR). Also, the effect on aboveground RGR was marginal. The lack of population by water availability interaction indicates that both populations presented the same tolerance to the drought imposed in this study.

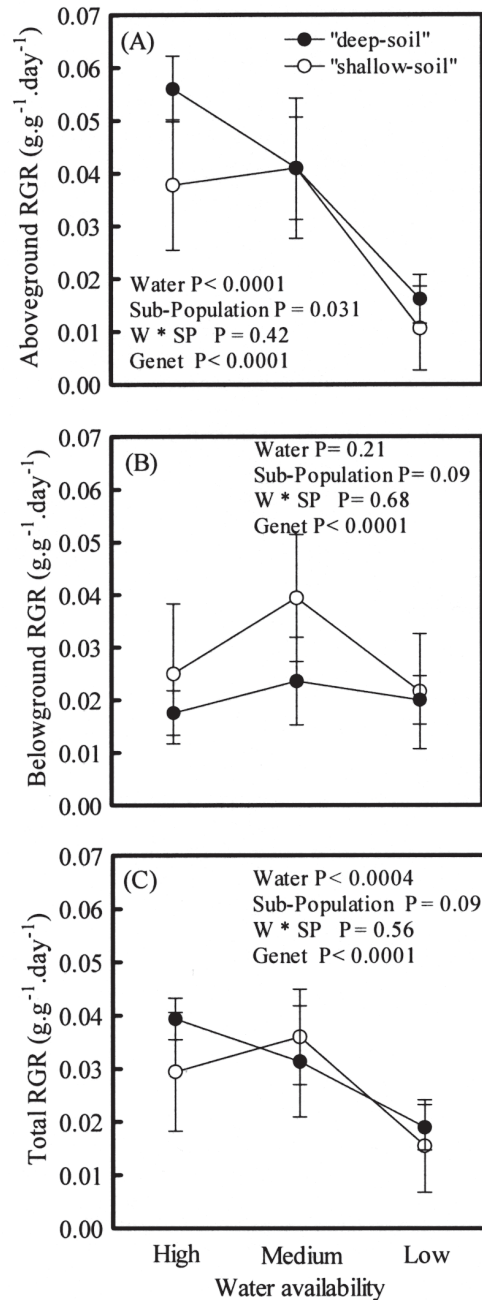


Fig. 3: Effect of drought for two sub-populations of *Bromus* from “deep-soil” and “shallow-soil” communities across a water availability gradient. Variable responses are (A) aboveground relative growth rate, (B) belowground relative growth rate, and (C) total relative growth rate. Data are means \pm SE.

Efecto de la sequía para dos subpoblaciones de *Bromus* provenientes de comunidades de “suelos profundos” y “suelos someros” a través de un gradiente de disponibilidad de agua. Las variables de respuesta son (A) tasa aérea de crecimiento relativa, (B) tasa subterránea de crecimiento relativa, y (C) tasa total de crecimiento relativa. Los datos representan medias \pm EE.

Genetic differentiation can occur when selective pressures overwhelm homogenizing gene flow (Linhart & Grant 1996, Barton & Partridge 2000). According to this, there are no physical barriers for gene flow between the two sub-populations. However, two facts may explain low levels of gene flow in our system. First, *Bromus* is a cleistogamous species (Naranjo et al. 1990) and thus gene flow by pollen between the sub-populations is avoided. Secondly, seed dispersion by wind occurs only at short distances (< 1m) (M.R. Aguiar unpublished results) which also prevents gene flow between the sub-populations.

Higher RGR is expected to be selected in resource rich environments (Chapin et al. 1993). The results obtained confirm this statement since “deep-soil” sub-population had a marginal higher above RGR than the “shallow-soil” sub-

population. Likewise, the “deep-soil” sub-population had a higher leaf size (area and weight) than the “shallow-soil” sub-population. This result agrees to the theoretical model developed by Givish & Vermeij (1976) predicting the evolution of optimal leaf size. They proposed that the optimal leaf size maximizes the difference between the benefits of increased photosynthesis and the cost of increased water loss. This optimal leaf size will be smaller under reduced water availability. This pattern has been observed at the inter-specific level along rainfall gradients (Fonseca et al. 2000) and our results support the model at the intra-specific level and within the same regional climate. Parallel to the variation in leaf size that we found, other physiological and anatomical traits may also change (Dong & Zhang 2001).

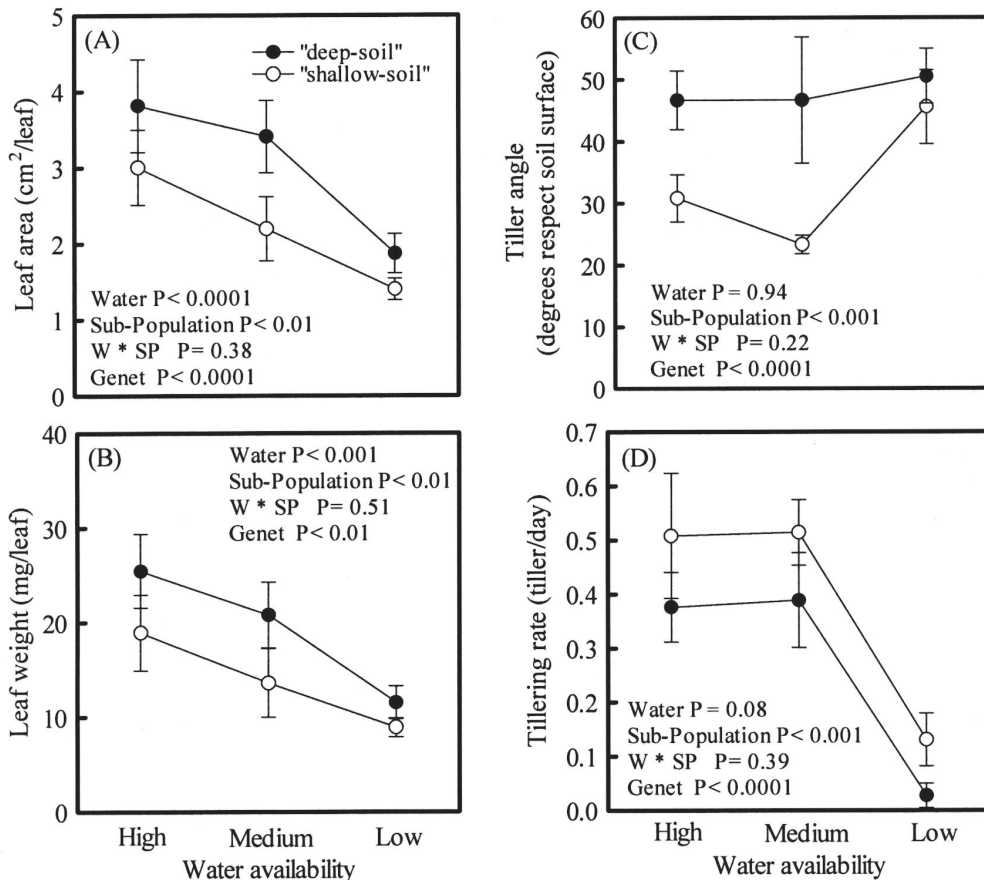


Fig. 4: Effect of drought for two populations of *Bromus* from “deep-soil” and “shallow-soil” communities across a water availability gradient. Variable responses are (A) leaf area, (B) leaf biomass, (C) tiller angle and (D) tillering rate. Data are means \pm SE.

Efecto de la sequía para dos subpoblaciones de *Bromus* provenientes de comunidades de “suelos profundos” y “suelos someros” a través de un gradiente de disponibilidad de agua. Las variables de respuesta son (A) área foliar, (B) biomasa foliar, (C) ángulo de inserción de los macollos, y (D) tasa de macollaje. Los datos representan la medias \pm EE.

The more prostrate morph of the “shallow-soil” sub-population could present advantages in reducing the whole-plant area exposed to dry air. In addition, “shallow-soil” sub-population had higher tillering rate than “deep-soil” population. This negative correlation between tiller number and leaf size was proposed by Gorhan (1979). A higher number of smaller tillers may be a useful strategy to facilitate a quick response to water inputs (Coughenour 1985). This is because there are several growth points that enable the plant to make an efficient use of the short period of water availability. Besides, a high number of small tillers may distribute the risk of drought-induced mortality and may increase the rate of post-defoliation recovery (Coughenour 1985). Most of these attributes present in the “shallow-soil” sub-population, which would be adaptative in arid habitats, may also be beneficial to overcome grazing (Coughenour 1985). Since overgrazing has led to local extinction of *Bromus* in some locations (Aguiar et al. 1999), “shallow-soil” sub-populations may be able to colonize degraded “deep-soil” communities in the long term. This speculation enhanced the importance of knowing the prior differences in the genetic structure in the space to understand the present and future dynamics of these populations.

No statistically significant effect of the interaction of water availability x sub-population was found for either of the variables measured. Thus, results fit better with the model presented in Fig. 1B, where there are average differences between the sub-populations due to differences in the intercept. However, the expected result that would evidence home-site advantage, and thus genetic differentiation, would be the one presented in Fig. 1C [sub-population 2 (“deep-soil”) and sub-population 4 (“shallow-soil”)]. A possible explanation of these findings could be that our treatments only manipulate one component of the water cycle, which is water supply and not water demand. In drier conditions (water demand relative to water supply) present in the shallow-soil community compared to the deep-soil community, where atmospheric demand is by far higher than the experimented in the greenhouse, the more prostrate and small sized “shallow-soil” sub-population would be more successful than the more erect and high sized “deep-soil” sub-population.

Due to the intrinsic limitations of a greenhouse experiment, it is wise to be cautious when extrapolating these results to field situations. The differentiation measured in the present paper was expressed in a set of environmental conditions that may not be exactly the same experienced by the plants in the field. However, since the effect of soil depth is principally due to reduced water availability, we are confident that the drought treatments employed in this experiment capture what happens in the field in a high degree. Taking the above mentioned limitation into account, the result will be discussed in the context of *Bromus* reseeding and in the context of global change.

The reseeding of degraded steppes of Patagonia with *Bromus* would be necessary in order to increase its carrying capacity for sheep production. The availability of improved populations of native plants may foster the revegetation of degraded lands (Jones & Johnson 1994). Even though native grasses used for revegetation are not improved, domestication (e.g., cultivation and seed harvesting) usually involves a mass selection procedure (Poehlman & Sleper 1995). Our results showed that within this site, there is genetic variation in traits related to drought resistance that could be target of selection to obtain improved populations. We also speculate that these traits would be useful to overcome the effects of grazing. Since sheep grazing is the main land use of Patagonia these traits may have economic impact.

Human activities are causing environmental changes in a global scale (Vitousek 1994). There is uncertainty about how plant populations will respond to current global changes. Historically, plants have responded to climate change by adaptation or migration (Davis & Shaw 2001). Some models of evolutionary responses to global climate changes predict that we should expect considerable extinction due to restricted opportunities of migration associated to landscape fragmentation (Bradshaw & McNeilly 1991). Thus, the primary strategy of species survival may be the evolution of appropriate genotypes based on variation among individuals within the same local population (Etterson & Shaw 2001). In the Patagonian steppe, the genetic variation promoted by soil heterogeneity would increase the evolutionary potential of *Bromus* to adapt

to drier conditions predicted for these sites (Sala 2001). This kind of research will become highly necessary if we want to predict the responses of populations to new climatic or land-use scenarios.

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