

Effect of drought on morphological and functional traits of *Poa ligularis* and *Pappostipa speciosa*, native perennial grasses with wide distribution in Patagonian rangelands, Argentina

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Abstract. *Poa ligularis* Nees. Ap. Steudel and *Pappostipa speciosa* (Trin. et Rupr.) Romaschenko are dominant perennial grasses in the arid Patagonian rangelands of Argentina. Both species are exposed to periods of water shortage during spring-summer and are grazed by domestic and native herbivores. *Pappostipa speciosa* displays xeromorphic adaptations and is less preferred by herbivores than *P. ligularis*. The knowledge of how drought affects morphological/functional traits in coexisting perennial grass species is useful to understanding the function of desert perennial grasses, and for the use and conservation of Patagonian arid rangelands. The hypothesis of this study was that co-existing perennial grasses contrasting in drought resistance mechanisms display different degrees of phenotypic plasticity in underlying and/or functional traits. Plants of both species were exposed to two levels of gravimetric soil moisture: 16% (~field capacity) and 4%. Plant vegetative and reproductive traits were measured weekly in individual plants and these were harvested at the end of the experiment. Aboveground and root biomass were separated in the harvested plants and the concentration of photosynthetic pigments was assessed in green leaves. The trait response range was also calculated through the plasticity index. In both species, drought stress led to significant reductions in plant height, total plant dry weight, number of total leaves, dry weight of green and senescent leaf, percentage of flowering plants, length of inflorescences, and number, length and dry weight of roots. The concentration of photosynthetic pigments increased under drought in both species. In conclusion, drought strongly affected reproductive and vegetative traits in both species and the greatest negative effect of drought was found in *P. speciosa*, the most conservative species. However, our findings might indicate that both species are able to maintain photosynthetic activity through the increase of photosynthetic pigments under drought conditions in Patagonian rangelands.

Additional keywords: biomass, carotenoid, chlorophyll, growth traits, Patagonian grasses, plasticity.

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Introduction

In semiarid-arid ecosystems, water inputs are scarce, erratic and discontinuous (Noy-Meir 1973). Water shortage affects physiological and biochemical processes in plants, leading to reduced growth and crop (Reynolds *et al.* 2004; Epstein *et al.* 2006; Guo *et al.* 2010), thus exerting a strong selective pressure on dominant plant traits and ecological strategies (Bertiller *et al.* 2005, 2006). In this context, some plant functional traits are strongly related to the fitness and success of individuals in a given environment and provide good indicators about species ecology (Nicoltra *et al.* 2010).

Plant species have evolved different adaptive mechanisms or strategies of drought resistance (Levitt 1980). Drought-avoiding plant species may complete a short life cycle before the drought

period (e.g. annuals) or may have a short growing season (e.g. drought deciduous; Sherrard and Maherali 2006). Drought-avoiding perennials usually have high relative growth rates and high potential for resource capture and may be defined as acquisitive plants (*sensu* Díaz *et al.* 2004). These species often have deciduous leaves with a low concentration of defensive secondary compounds such as soluble phenolics and lignin and they are highly prone to herbivore damage. In contrast, drought-tolerant plants may have the capacity to sustain or conserve plant functions under prolonged periods of water shortage (Lilley *et al.* 1996; Reddy *et al.* 2004; Blum 2005). Drought-tolerant plants are usually evergreens and have low relative growth rates and high potential for resource conservation in the plant (conservative plants *sensu* Díaz *et al.* 2004). These species have

evergreen dense leaves with a high concentration of secondary compounds such as soluble phenolics and lignin (Westoby *et al.* 2002). These secondary compounds increase leaf resistance against water shortage and herbivores as well as the costs of leaf construction, which is compensated with longer leaf lifespan (Coughenour 1985; Adler *et al.* 2004).

Both plant strategies may also be associated with differences in the concentration and composition of photosynthetic pigments, because these are related to growth rates and incorporate a large proportion of nitrogen in their molecular structures (Filella *et al.* 1995). Chlorophylls are important in relation to light absorption and transfer of energy and are indicators of photosynthetic activity of plant tissues. Carotenoids collect light and dissipate the excess of energy, thus avoiding damage to the photosynthetic system (Wright *et al.* 1994; Demmig-Adams *et al.* 1996). Thus, dissipation of excess energy under stress conditions is a major physiological process in plant photo-protection (Chaves *et al.* 2003). In this sense, studies on native shrubs have showed that drought stress decreases pigments content, but increases the ratio of carotenoids to total chlorophylls (Liu *et al.* 2011). In contrast, other studies have reported a higher chlorophyll content in drought-stressed than in well watered plants (El-Sharkawi and Salama 1977; Maroco *et al.* 2000; Arunyanark *et al.* 2008). Accordingly, the effect of water shortage on the concentration and composition of photosynthetic pigments could provide important information about the nutritional and physiological status of plants (Yang *et al.* 2010).

The range of trait responses to environmental changes may differ between species with different resistance mechanisms to drought. Drought-avoiding perennial plants may have a higher response range of underlying and/or functional traits than do drought-tolerant perennial plants, resulting in differences in phenotypic plasticity in the sense of the ability of a genotype to express different phenotypes in different environments (Sultan 2000; Nicotra *et al.* 2010).

Poa ligularis and *Pappostipa speciosa* are two dominant perennial grasses in rangelands of the arid Patagonia (Pazos *et al.* 2007; Moreno and Bertiller 2012). *Poa ligularis* is a deciduous grass with acquisitive and/or mesophytic traits (*sensu* Díaz *et al.* 2004) related to high relative growth rate and potential for resource capture (N-rich green tissues, high leaf production and low lignin concentration in leaves). This species is highly preferred by native and domestic herbivores. Moreno and Bertiller (2012) found that *P. ligularis* could largely vary in the range of trait responses across aridity gradients in Patagonia. These authors observed enhanced mesophytism (e.g. low accumulation of chemical defences) correlated with escape from water shortage and/or herbivores. In contrast, *P. speciosa* is an evergreen grass with conservative and/or xerophytic traits associated with low relative growth rate, high potential for resource conservation, high investment in structural compounds, and is less preferred by herbivores. Moreover, *P. speciosa* has a deeper root system and a longer growing period than does *P. ligularis* (Bertiller *et al.* 1991; Pelliza Sbriller *et al.* 1997; Baldi *et al.* 2004; Pazos *et al.* 2007). Couso and Fernández (2012) found that xerophytism and drought tolerance were negatively related to the range of trait variation and phenotypic plasticity of Patagonian perennial grasses.

Differences in traits and responses of coexisting perennial grass species are consistent with the hypothesis of Chesson *et al.* (2004) that a wide range of variation in traits of coexisting species facilitating survival and growth in water-limited ecosystems might reduce species competition and promote diversity. Better understanding on responses of coexisting species of the same life form to water shortage might improve the knowledge on arid plant functioning and contribute to address issues related to the mitigation of environmental stresses resulting from land use and global climate change (Chesson *et al.* 2004). This knowledge is also useful in the conservation of arid rangelands.

The aim of the present study was to evaluate morphological and functional responses to drought of two coexisting perennial grasses (*P. ligularis* and *P. speciosa*) in the Patagonian Monte, with contrasting drought-resistance and life-history strategies. The hypothesis of the present study was that coexisting perennial grasses contrasting in drought-resistance mechanisms (deciduous versus evergreen) display different degrees of phenotypic plasticity in underlying and/or functional traits. We predicted that *P. ligularis* (deciduous), with higher expression of mesophytic traits, would display higher phenotypic plasticity in most traits under conditions of water shortage than would *P. speciosa* (evergreen).

Materials and methods

Study site

The study was conducted in the southern portion of the Monte Phytogeographic Province Patagonian Monte (north-eastern of Chubut Province, Argentina; Soriano 1950). Mean annual temperature is 13.7°C and mean annual precipitation is 235.9 mm (22-year average, CENPAT–CONICET 2009). Within this area, the drought experiment was performed at the experimental site of the Centro Nacional Patagónico (CENPAT; 42°47'11.68"S, 65°00'28.56"W) under a rain-out shelter.

Study species and plant collection

Two perennial grasses, namely *Poa ligularis* Nees. Ap. Steudel and *Pappostipa speciosa* (Trin. et Rupr.) Romaschenko, were selected for the study.

Plant harvesting for transplanting collection was performed in the Estancia San Luis (42°40'49.3"S 65°21'33.6"W) in a floristically homogeneous stand of ~4 ha, characterised by the *Larrea divaricata* shrubland and perennial grasses (Soriano 1950; Cabrera 1976). Sixty bunches of each species were randomly collected in autumn 2009. Also topsoil (0–20 cm) was extracted neighbouring the collected bunches. After collection, topsoil samples were pooled and sieved with a 2-mm mesh sieve. Individual rooted tillers of each species were separated from each bunch (5–10 tillers per bunch). Tillers were pooled per species and 200 tillers of each species were transplanted in pots (one rooted tiller per pot) filled with 1400 g of the topsoil collected. The pots (8-cm diameter × 15-cm depth) were maintained in a greenhouse for 1 month, up to the beginning of the experiment.

Experimental design

Each species was submitted to two levels of gravimetric soil moisture (GSM), namely, 16% (control) and 4% GSM (drought).

These levels of soil moisture correspond to the highest mean values near field capacity during autumn–winter, and the lowest values during summer drought, respectively, registered under natural field conditions in the Patagonian Monte (Coronato and Bertiller 1997). The pots were placed under a rain-out shelter in the experimental site of CENPAT. The soil moisture of each pot was controlled weekly during spring–summer and fortnightly during autumn–winter, by weighing the pots and applying water to the target weight.

Measurement of plant traits

The experiment was conducted during the period from August 2009 (Day 42) to December 2010 (Day 526). Twenty plants from each soil-moisture level and species were randomly selected at the beginning of the experiment. Plant height (top of the plant), number of fully expanded green leaves, number of senescent leaves, number of flowering tillers, and inflorescence length were assessed monthly in the bunches from August 2009 to December 2010. Three sets of 20 plants from each watering level and species were randomly selected for harvesting at three dates (November 2009, Day 133; August 2010, Day 414; and December 2010, Day 526). Roots were separated from soil by washing them with tap water, using a 1000- μm -mesh sieve. The length of the longest root from the base of tillers was measured and the number of green and senescent (dead) leaves, flowering tillers and roots were recorded. Roots were then separated from the aboveground parts and the dry weight of each part (leaves, crowns and roots) was obtained after 72-h lyophilisation. Both green and senescent leaves included only leaf blades because they were cut at the intersection of the blade and the sheath. Accordingly, crowns included sheaths and the rest of non-photosynthetic tissues of tiller bases. The dry weight of the total plant (the sum of the dry weights of green and senescent leaves, crowns, roots and inflorescences) and the fraction of total plant dry weight represented by leaves, crowns, roots and inflorescences were calculated (Poorter *et al.* 2012). Further, the number of green and senescent leaves as a percentage of the total leaf number was also determined.

Measurement of photosynthetic pigment concentration

Photosynthetic pigments were measured in three plants of each species of each level of soil moisture at the end of the experiment. Plants were harvested and lyophilised in December 2010. Concentrations of Chlorophyll *a* (Chl *a*), Chlorophyll *b* (Chl *b*), total chlorophylls (Chl) and carotenoid (Car) in green leaves were assessed according to the method proposed by Vernon (1960) and McKinney (1941).

Plasticity index

The index of plasticity (IP) was calculated for each plant trait of each species at the end of the experiment, using a modification of the equation proposed by Valladares *et al.* (2000), and depended on the negative or positive effect of water shortage on plant traits with respect to the control (16% GSM treatment).

If drought (4% GSM) negatively affected the values of a trait with respect to the control (16% GSM), then

$$IP = (M_{\max} - M_{\min})/M_{\max},$$

where M_{\max} is the average of the highest value of the control and M_{\min} is the average of the lowest values under drought at the end of the experiment.

If drought positively affected the values of a trait with respect to the control, then

$$IP = (M_{\min} - M_{\max})/M_{\max},$$

where M_{\min} is the average of the lowest value of the control (16% GSM) and M_{\max} is the average of the highest values of the level of drought (4% GSM). Accordingly, IP varied between -1 and 1 .

Statistical analysis

The significance of the differences in means of non-normally distributed response variables (plant height, total leaf and root numbers, root length, number of flowering tillers, inflorescence length, dry weight of total plant, fraction of total plant dry weight represented by leaves, crowns, roots and inflorescences, and number of green and senescent leaves as percentage of total leaf number) between levels of soil moisture (16% and 4% GSM) of each species were analysed by Kruskal–Wallis test.

Two-way ANOVA was used to evaluate the significance of the differences in the concentration of photosynthetic pigments between the two levels of soil moisture (16% and 4% GSM). Bonferroni test was used for multiple comparisons. Data were tested for normality by Shapiro–Wilk test and for homogeneity of variance by Levene's test. Data were square-root transformed to meet the assumptions of ANOVA. Plant traits were grouped according to the IP by using cluster analysis. In this analysis, the square root of Euclidean distance and complete linkage were used.

Results

Effect of drought on vegetative traits and leaf pigments

Drought (4% GSM) led to a significant reduction of plant height in *P. ligularis* and *P. speciosa*, but the species did not differ from each other in plant height at any watering level (Fig. 1a). Drought induced a significant reduction in the number of total leaves in *P. ligularis* and *P. speciosa*. The species did not differ in the number of total leaves under drought conditions. However, *P. ligularis* plants had a larger number of leaves than did *P. speciosa* plants under 16% GSM (Fig. 1b). Overall, drought did not induce changes in the percentage of green and senescent leaves across the experiment (Fig. 1c, d), except for the largest proportion of green leaves and the smallest proportion of senescent leaves in *P. ligularis* in August 2010. Drought negatively affected the dry weight of green leaves in *P. speciosa*, whereas it had no effect on that in *P. ligularis* (Fig. 1e). The dry weight of senescent leaves of both species was reduced under drought conditions (Fig. 1f).

Green leaves of both species had similar concentrations of all pigments at the end of the experiment. The concentrations of all pigments were significantly higher under drought conditions than in the control for both species (Fig. 2).

The number, length and biomass of roots of both species were significantly reduced under drought conditions during the experiment (Fig. 3a–c). *Poa ligularis* had a larger number of roots than did *P. speciosa* under both watering levels (Fig. 3a),

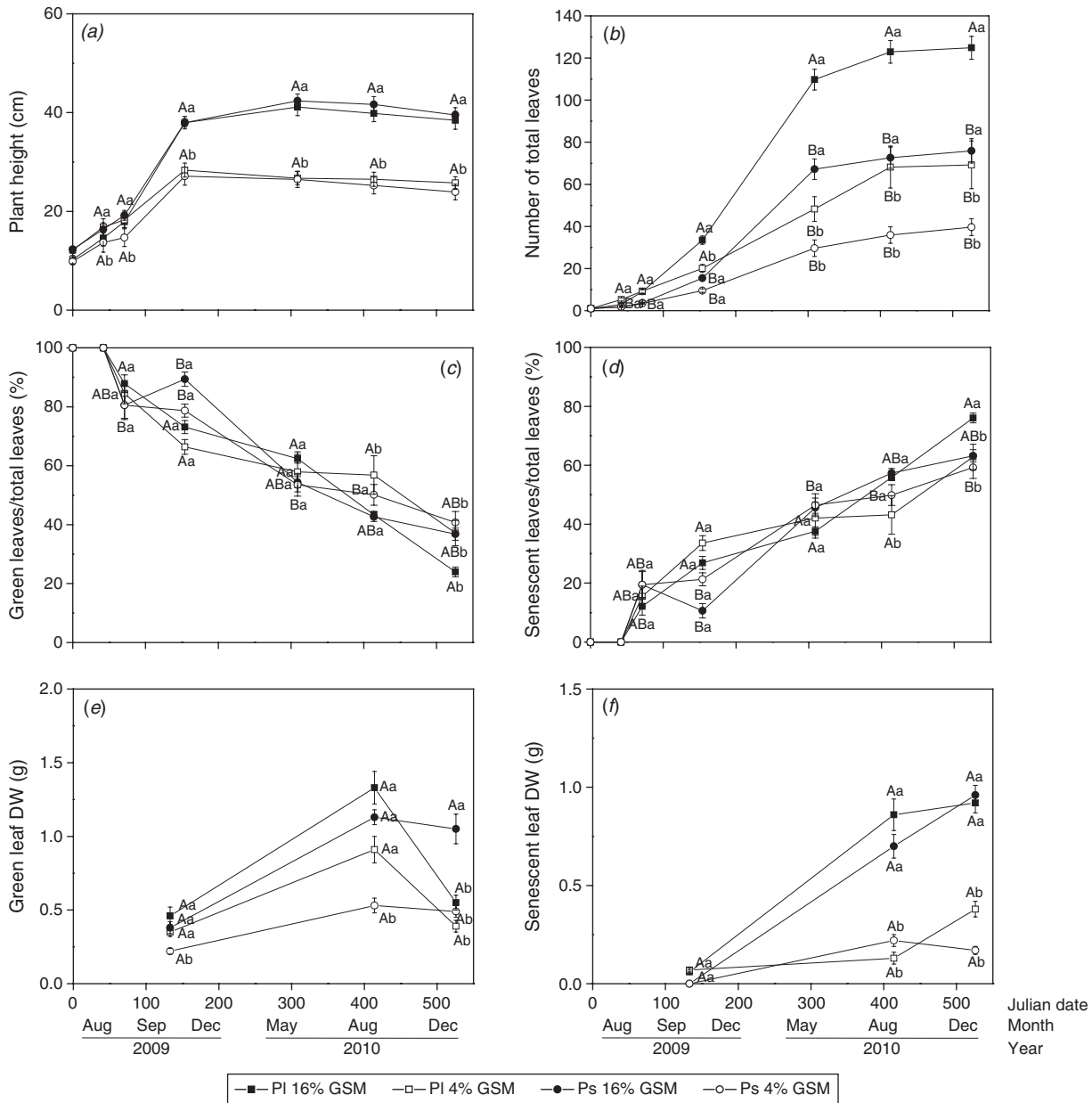


Fig. 1. Means \pm s.e. ($n=20$) of (a) plant height and (b) number of total leaves, (c) number of green leaves and (d) number of senescent leaves (dead) as percentages of the number of total leaves, (e) green-leaf dry weight and (f) senescent-leaf dry weight of *Poa ligularis* (squares) and *Pappostipa speciosa* (circles) at the two gravimetric soil-moisture levels (16% GSM, solid symbols and 4% GSM, open symbols). Different upper-case letters indicate significant differences between species at each watering level and different lower-case letters indicate significant differences between gravimetric soil moisture levels for each species (at $P=0.05$).

whereas root length did not differ between the species at either watering level (Fig. 3b). At the beginning of the experiment (November 2009), *P. speciosa* had a higher root dry weight than did *P. ligularis*, and drought reduced root dry weight in *P. speciosa*. In August 2010, drought reduced root dry weight in both species and the species did not differ in this trait. At the end of the experiment (December 2010), *P. speciosa* at the 16% GSM watering level had higher root dry weight than did *P. ligularis* and drought reduced root dry weight in both species (Fig. 3c).

Effect of drought on reproductive traits

Drought (4% GSM) induced the reduction in the percentage of flowering plants (Fig. 4a) and the number of flowering tillers per bunch in *P. ligularis* (Fig. 4b). The inflorescence length was affected only in *P. speciosa* in 2010 (Fig. 4c).

In December 2009, both the percentage of flowering plants (Fig. 4a) and the number of flowering tillers per bunch (Fig. 4b) were higher in *P. ligularis* than in *P. speciosa* plants under 16% GSM (control plants). The inflorescence length (Fig. 4c) was higher in control plants of *P. speciosa* than in those of *P. ligularis*

in 2010. Inflorescence dry weight was reduced by drought in both species in 2010 (Fig. 4d).

Biomass allocation

The total plant dry weight was negatively affected by drought in both species (Fig. 5a). The belowground:aboveground dry-weight ratio was higher in *P. speciosa* than in *P. ligularis* plants (Fig. 5b) and it was affected by drought in both species only in August 2010. Drought increased the biomass allocation to leaves (Fig. 5c) in both species in August 2010 when the peak of green-leaf biomass occurred. Drought reduced the biomass allocation to roots (Fig. 5d) in both species in August 2010. *Pappostipa speciosa* allocated more biomass to roots than did *P. ligularis* (Fig. 5d). Drought increased the biomass allocation to green leaves (Fig. 5e) in both species in August 2010. Drought

reduced the biomass allocation to senescent leaves in *P. ligularis* in August 2010. *Poa ligularis* allocated more biomass to senescent leaves than did *P. speciosa* (Fig. 1f). Drought did not affect biomass allocation to crowns in either species, although *P. ligularis* allocated more biomass to crowns than did *P. speciosa* (Fig. 5g). Drought did not affect biomass allocation to inflorescences in either species in November 2009. In December 2010, drought reduced biomass allocation to inflorescences in *P. ligularis*. This species allocated more biomass to inflorescences than did *P. speciosa* in 2009 (Fig. 5f).

Plasticity in traits

According to the values of the PI, plant traits were clustered in five groups (Fig. 6, Table 1). Group 1 (PI ranging from 0.65 to 0.87) clustered the species traits with the highest negative response to drought. Among them, the percentage of flowering plants of both species showed the highest PI values. Other reproductive traits (inflorescence length and number of flowering tillers) as well as vegetative traits (total, root and senescent-leaf dry weight) of *P. speciosa* displayed also high PI values. Group 2 (PI ranging from 0.42 to 0.53) clustered the traits with an intermediate negative response to drought, mostly in *P. ligularis*, comprising total, root, senescent-leaf and inflorescence dry weights, as well as root length and some reproductive traits (number of flowering tillers and inflorescence allocation). Green-leaf dry weight and the number of roots in *P. speciosa* showed also intermediate negative responses to drought. Group 3 (PI ranging from 0.12 to 0.29) clustered the traits with a low negative response to drought, including plant height, total number of leaves, belowground:aboveground ratio and root allocation of both species, green-leaf dry weight, inflorescence length and root number of *P. ligularis*, and inflorescence dry weight and root length of *P. speciosa*. Group 4 (PI ranging from -0.15 to 0) clustered the traits that did not change, or showed an extremely low response to drought, such as the fractions of biomass allocation mostly to vegetative organs, and Group 5 (PI ranging from -0.30 to -0.45) clustered the traits the values of which increased in drought-stressed plants. These traits included leaf pigments (Chl a, Chl b, Chl and Car).

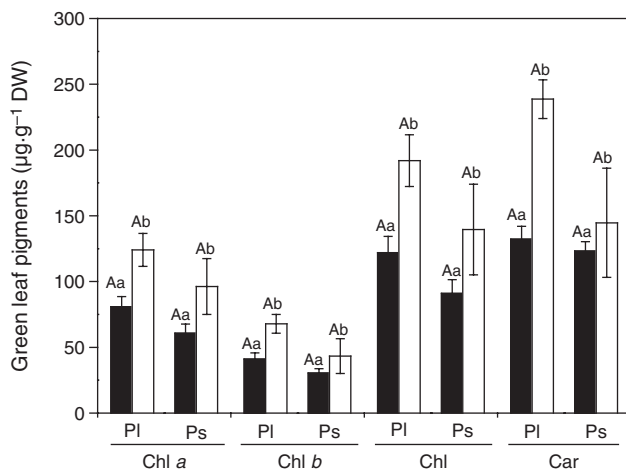


Fig. 2. Photosynthetic pigment concentration of Chlorophyll a (Chl a), Chlorophyll b (Chl b), total chlorophylls (Chl) and carotenoids (Car), in green leaves of *Poa ligularis* (Pl) and *Pappostipa speciosa* (Ps). Values are means \pm s.e. ($n=3$). Different upper-case letters indicate significant differences between species at each watering level and different lower-case letters indicate significant differences between gravimetric soil-moisture levels for each species (at $P=0.05$).

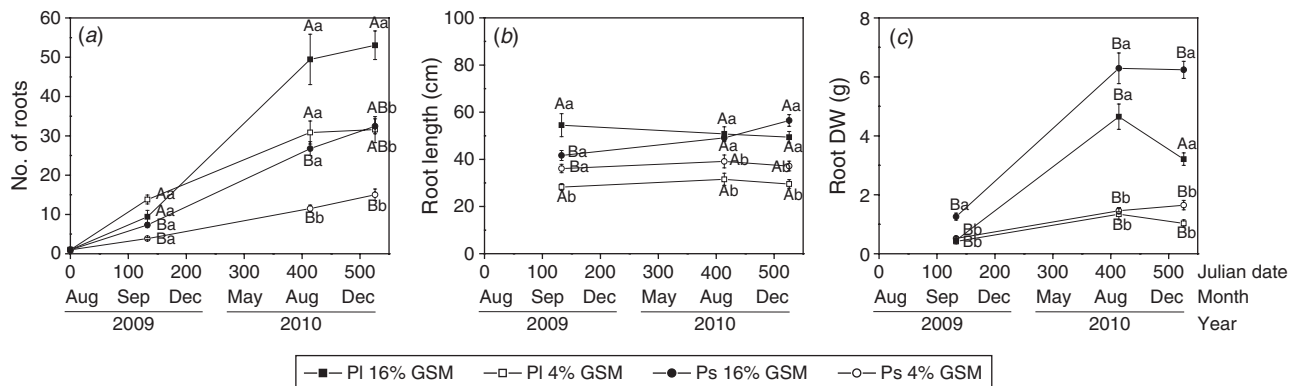


Fig. 3. Means \pm s.e. ($n=20$) of (a) number of roots, (b) root length and (c) root dry weight of *Poa ligularis* (squares) and *Pappostipa speciosa* (circles) at the two gravimetric soil-moisture levels (16% GSM, solid symbols and 4% GSM, open symbols). Different upper-case letters indicate significant differences between species at each watering level and different lower-case letters indicate significant differences between gravimetric soil moisture levels for each species (at $P=0.05$).

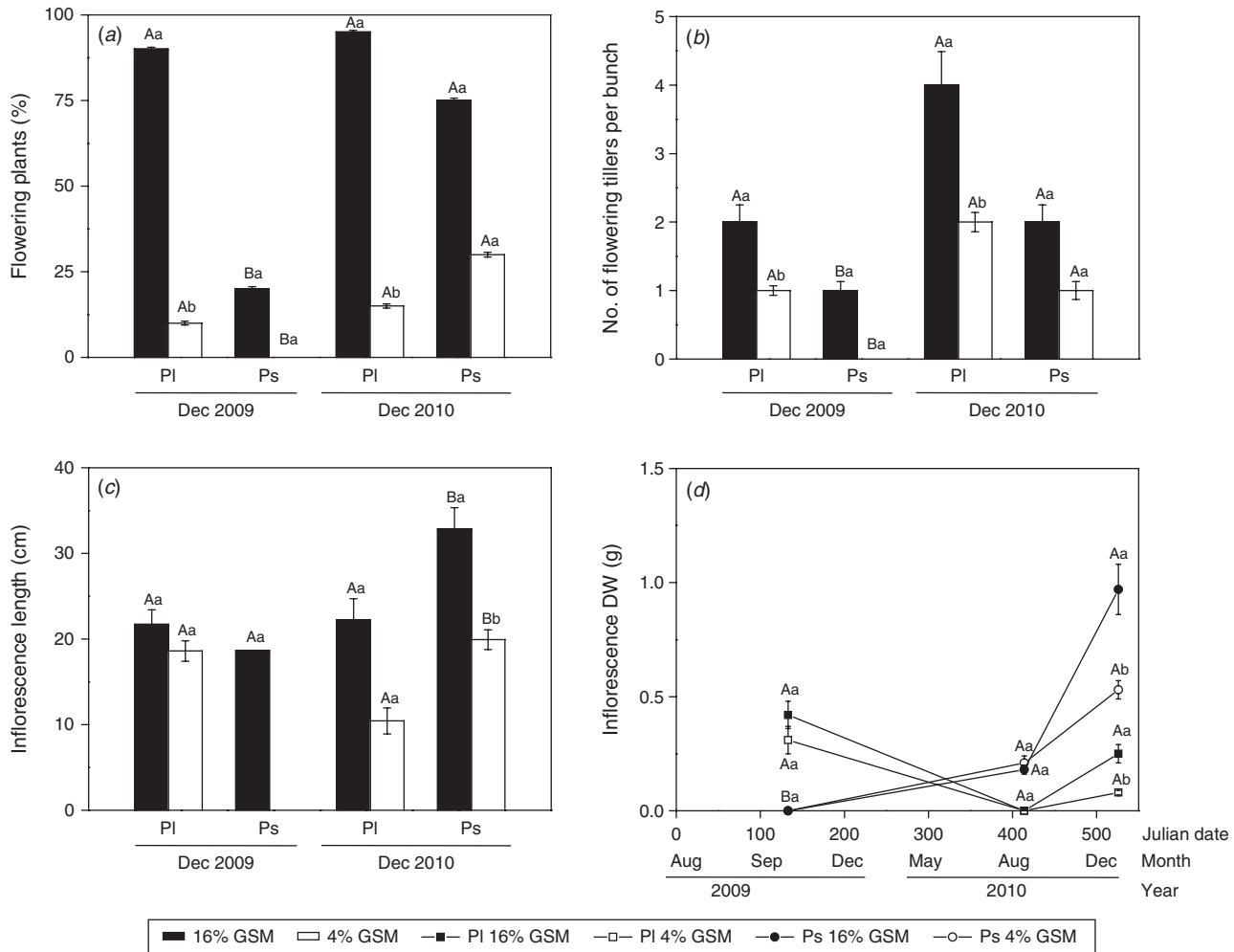


Fig. 4. Means \pm s.e. ($n=20$) of (a) percentage of flowering plants, (b) number of flowering tillers, (c) inflorescence length and (d) inflorescence dry weight of *Poa ligularis* (Pl) and *Pappostipa speciosa* (Ps) at the two gravimetric soil-moisture levels (16% GSM and 4% GSM). Different upper-case letters indicate significant differences between species at each watering level and different lower-case letters indicate significant differences between gravimetric soil-moisture levels for each species (at $P=0.05$).

Discussion

Desert plants are characterised by a suite of morpho-functional traits related to drought tolerance or drought avoidance (Chapin et al. 1993). In general, desert perennial grasses complete their lifecycle at the end of rainy season and before the onset of the dry summer (Bertiller et al. 1991; Neumann 2008). The findings of the present study indicated that drought led to a significant decrease in all traits related to biomass accumulation and growth (plant height, total plant dry weight, number of total leaves, green- and senescent-leaf dry weight, number, length and dry weight of roots), and reproductive output (percentage of flowering plants, number of flowering tillers, inflorescence length and inflorescence dry weight) in both *P. ligularis* and *P. speciosa*.

Biomass reduction under drought has also been observed in several desert species (Gutierrez and Whitford 1987; James et al. 2005). We found that drought also decreased belowground: aboveground dry-weight ratio in both species, as also reported by Frank (2007) in other grasslands. Drought

affected negatively root traits (dry weight, number and length of roots) in both species, but the effect of drought on the dry weight and number of roots was more pronounced in *P. speciosa* than in *P. ligularis*, whereas the effect of drought on root length was more pronounced in *P. ligularis*.

The increase in pigment concentrations in green leaves of both grasses grown under drought, found in our study, is consistent with the results of other studies reporting a higher chlorophyll content in drought-stressed than in well watered plants (El-Sharkawi and Salama 1977; Maroco et al. 2000) as a way to increase drought tolerance (Arunyanark et al. 2008). Further, increased concentrations of carotenoids under drought are consistent with the function of carotenoids as photo-protectors against active oxygen species, thus preventing the oxidative disruption of the photosynthetic process (Smirnoff 1993; Demmig-Adams et al. 1996; Munné-Bosch and Alegre 2000; Farrant et al. 2003; Liu et al. 2011).

Both species showed the strongest negative effect of drought on reproductive traits. Some plants growing under drought

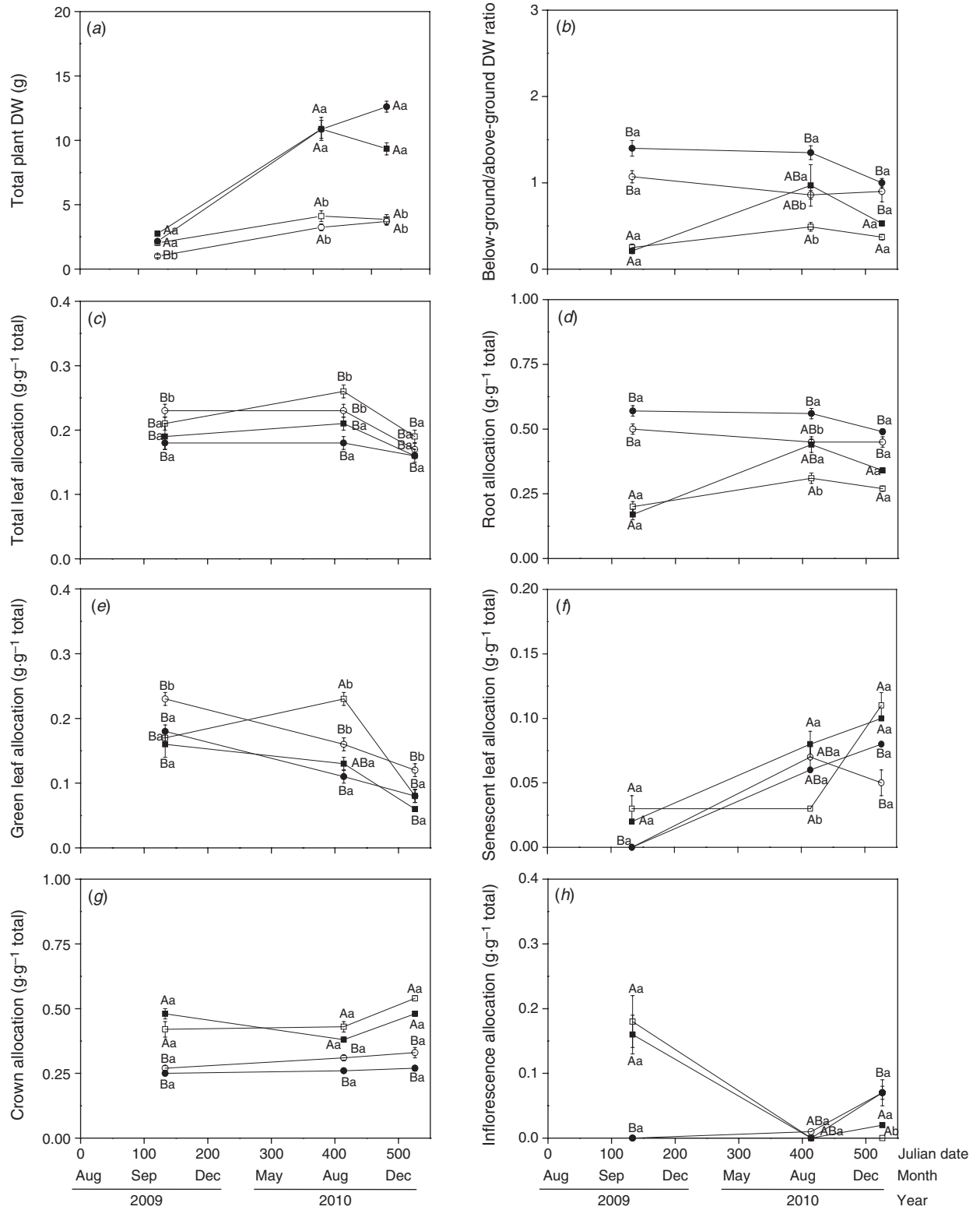


Fig. 5. Means \pm s.e. ($n=20$) of (a) total plant dry weight, (b) below-ground : above ground dry-weight ratio, (c) total leaf allocation, (d) root allocation, (e) green-leaf allocation, (f) senescent-leaf allocation, (g) crown allocation, and (h) inflorescence allocation of *Poa ligularis* and *Pappostipa speciosa* at the two gravimetric soil-moisture levels (16% GSM, solid symbols, and 4% GSM, open symbols). Different upper-case letters indicate significant differences between species at each watering level and different lower-case letters indicate significant differences between gravimetric soil-moisture levels for each species (at $P=0.05$).

Table 1. Summary of the effect of drought on the direction of changes in trait values compared with the control

G1–G3 correspond to decreases in trait values in drought-stressed plants; G4 corresponds to no change or low response in traits values in drought-stressed plants and G5 corresponds to increases in traits values in drought-stressed plants. Traits in bold indicate similar changes in both species

Group	Direction of the response	Plant part	<i>Poa ligularis</i>	<i>Pappostipa speciosa</i>
G1	Decrease	Inflorescence	Percentage of flowering plants	Percentage of flowering plants Inflorescence length Number of flowering tillers Senescent-leaf dry weight Root dry weight Dry weight
		Leaves and crowns		
		Roots		
		Total plant		
G2	Decrease	Inflorescence	Inflorescence allocation Number of flowering tillers Inflorescence dry weight	
		Leaves and crowns	Senescent-leaf dry weight	Green-leaf dry weight
		Roots	Root length Root dry weight	Number of roots
		Total plant	Dry weight	
G3	Decrease	Inflorescence	Inflorescence length	Inflorescence dry weight
		Leaves and crowns	Total leaves (number) Green-leaf dry weight	Total leaves (number)
		Roots	Number of roots Root allocation	Root length Root allocation
		Total plant	Plant height Belowground : aboveground ratio	Plant height Belowground : aboveground ratio
G4	No change or low response	Inflorescence		Inflorescence allocation
		Leaves and crowns	Leaf allocation Percentage of green leaves Percentage of senescent leaves Crown allocation	Leaf allocation Percentage of green leaves Percentage of senescent leaves Crown allocation
		Pigments		Carotenoids
G5	Increase	Pigments	Chlorophylls (a, b, total) Carotenoids	Chlorophylls (a, b, total)

conditions may increase allocation to reproduction, thus contributing to maintain ecological breadth of plant species in poor environments (Sultan 2001); however, this did not occur in the present study.

Higher aboveground vegetative and reproductive allocation (e.g. leaves and inflorescences) and lower belowground allocation (e.g. roots and belowground:aboveground dry-weight ratio) in *P. ligularis* than in *P. speciosa* are in agreement with Poorter and Remkes (1990), who reported that fast-growing species maximise shoot functioning, whereas slow-growing species maximise root allocation. A high investment in leaf biomass is a prerequisite for a high relative growth rates (Lambers *et al.* 1990) and a high investment in root biomass is necessary for drought resistance (Lambers *et al.* 1998).

Phenotypic plasticity is a mechanism used by plants to optimise the acquisition and use of the resources (Bradshaw 1965). In agreement with the stress-resistance syndrome (Grime 1977) and a conservative resource-use strategy (Valladares *et al.* 2000), a low phenotypic plasticity has been linked to enhanced performance under drought (Sánchez-Gómez *et al.* 2008). Drought-avoiding perennial plants may

display higher growth rates and have a higher response range of underlying and/or functional traits than do drought-tolerant perennial plants, resulting in differences in phenotypic plasticity in the sense of the ability of a genotype to express different phenotypes in different environments (Sultan 2000; Nicotra *et al.* 2010). However, in contrast to our prediction, *P. ligularis* (deciduous), with higher expression of mesophytic traits, did not display higher phenotypic plasticity in most of the traits under conditions of water shortage than did *P. speciosa* (evergreen; Carrera *et al.* 2000; Bertiller *et al.* 2005; Campanella and Bertiller 2008).

In conclusion, the findings of the present study showed that drought strongly affected reproductive and vegetative traits in both species and that the greatest negative effect of drought was found in *P. speciosa*, the more conservative of the two species. However, drought increased allocation of biomass to green leaves. Increasing biomass allocation to leaves along with increasing concentration of photosynthetic pigments under drought conditions might indicate that both species display mechanisms to maintain photosynthetic activity under drought conditions; however, this strategy might affect the investment in

root biomass. The differences observed in the plasticity of underlying and/or functional traits between the two grasses in response to drought may partly explain coexistence of *P. ligularis* and *P. speciosa* in the arid Patagonian rangelands.

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