

Differential water-use strategies and drought resistance in *Trichloris crinita* plants from contrasting aridity origins

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Abstract In arid environments, water availability is the main limiting factor for primary production, and it is expected that not only drought-resistance, but also plant strategies for soil water use will be under natural selection. Our aim was to investigate the strategies of soil water use and the responses to water shortage that lead to variability in drought resistance in *Trichloris crinita* plants (a native forage grass of northwestern Argentina) from sites with contrasting aridity. We established a common-garden experiment with plants from relatively “arid” and “humid” sites (326 and 625 mm mean annual precipitation, respectively).

During 6 weeks, plants were subjected to two contrasting watering levels: control and drought. We found different water use strategies and drought resistance between plants from arid and humid sites: the former used water more conservatively and grew more under drought. During the first 2 weeks of the drought treatment, plants from arid sites dried out the soil slower than those from humid sites. Plants from arid sites subjected to drought showed less leaf senescence and a greater leaf elongation rate and biomass of green leaves than those from humid sites. This variability in adaptation to drought in *T. crinita* plants could be used to select plant materials for arid land revegetation or to be incorporated into breeding programs for forage purposes.

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Introduction

More than half of the land surface of the world is arid or semiarid, with water availability being the main limiting factor for primary production (Nemani et al. 2003). As plants need water to thrive, water shortage acts as an important selective force (Stebbins 1981). Plants can respond to environmental variations at different time scales. While rapid changes can be

achieved through phenotypic plasticity, expressed during the life of an individual, changes over longer-time scales can occur through natural selection of genetically based adaptive traits across generations (Alpert and Simms 2002).

Plant plastic responses to water stress (e.g. changes in soil water absorption, specific leaf area, senescence and stomatal regulation) contribute to regulate the water content of soil and plant tissues. They also affect carbon capture, and hence influence plant survival, growth and reproduction (Orians and Solbrig 1977; Ackerly et al. 2000; Maseda and Fernández 2006). Thus, soil water content both affects and is affected by plants (Goldberg 1990), a key interaction in arid and semiarid ecosystems.

Not only drought-resistance, but also plant strategies for soil water depletion will be under natural selection in arid environments (Heschel et al. 2002; Sperry et al. 2002). However, there are few studies designed to investigate plant strategies for exploiting soil water. Some authors have found that under drought stress, “conservative” water use (slow extraction from the soil) was related to greater growth or fitness than “extractive” water use (Qian and Fry 1997; Heschel et al. 2002; Zhang et al. 2004). A conservative water use could be an advantageous strategy for plants under drought because it can save soil moisture, reduce drought severity and plant tissue desiccation or mortality (Zhang et al. 2004). However, Cohen (1970) points out that there are conditions under which a faster water use will provide advantages: when plants have shallow roots, and therefore compete with direct soil evaporation, or when plant root systems overlap. Advances in this topic could be achieved by intraspecific comparisons, i.e. on populations from contrasting aridity origins where natural selection may have shaped different adaptive plant water use strategies (Mauricio et al. 1997; Via 2002).

The perennial grass *Trichloris crinita* is one of the most important native forage species in northwestern Argentina (Anderson 1983; Blanco and Oriente 2003). It plays an important role in soil protection against erosion (Dalmaso 1994), and has been planted to restore plant cover and forage productivity in overgrazed rangelands of the region (Passera et al. 1992; Quiroga et al. 2009). Investigating responses to drought of populations of this species is a crucial prerequisite to guide the search for plant materials for

revegetation purposes and the design of sustainable management practices.

Our aim was to investigate, in a common garden experiment, the strategies of soil–water use and linked processes that explain differences in drought response of *T. crinita* plants from contrasting aridity origins. We hypothesized that aridity, as a selective force, favors plants that are not only more drought resistant, but that also use soil water more conservatively under drought.

Materials and methods

Experimental approach

Trichloris crinita seeds were collected from sites with contrasting aridity conditions. Plant material was grown in pots in a common garden and once established subjected to two levels of water availability (high = control; low = drought). Data in this paper come from the same experiment reported in a previous paper that analyzed the existence of convergence between aridity and grazing as selective forces (Quiroga et al. 2010). Here, we focused on plant water use strategies in response to drought and their effects on plant growth.

As the experiment was conducted during the plant vegetative phase (over a period of 6 weeks, ending ca. 2 week before flowering), drought resistance was estimated by evaluating the effect of drought on growth variables (leaf elongation rate, leaf biomass) (Tilman and Downing 1994; Engelbrecht and Kursar 2003). We also assessed soil water content dynamics to estimate both its availability and its use by plants, and leaf senescence and specific leaf area to account for plant changes in transpiring and photosynthesizing surface.

Study region

Both seed collection and the experiment were conducted within the arid Chaco phytogeographic region, in northwestern Argentina (between 28°15' S and 33°30' S, and 64°01' W and 67°31' W). Climate is subtropical with hot summers and mild winters (Prohaska 1959). Annual mean temperature varies between 17 and 20 °C (Morello et al. 1985). There is an east–west rainfall gradient ranging from 600 to

300 mm (Cabido et al. 1993; Blanco et al. 2008) with 80 % of the annual rainfall occurring in the southern-hemisphere warm growing season, between November and March. Soils are coarse textured, with low organic matter content (<1.5 % of soil mass) and have a neutral to basic pH (Gómez et al. 1993). Typical vegetation is a xerophytic shrubland (dominated by *Larrea*, *Mimozyanthus*, *Senna* and *Capparis* genera), with scattered trees (mainly *Aspidosperma quebracho-blanco* and *Prosopis* spp.) and an herbaceous layer dominated by C4 perennials grasses (*Trichloris*, *Pappophorum*, *Aristida* and *Setaria* genera) (Ragonese and Castiglioni 1970; Morello et al. 1985).

Study species

Trichloris crinita is a C4 perennial bunchgrass with a summer growth season. Plants are 30–80 cm high, they reproduce by seeds and multiply vegetatively by tillering (Nicora and Rúgolo de Agrasar 1987). According to Peterson et al. (2007), the species presents an amphitropical disjunct distribution, i.e. it is found in two broad regions centered in arid and semiarid rangelands of South and North America.

Plant material collection

In March 2005 (southern hemisphere autumn), we collected seeds at two extremes of the regional precipitation gradient: arid (326 mm/year, Blanco et al. 2008) located at 31°24–32'S–66°46–49'W and humid (625 mm/year) at 29°49–59'S–64°27–29'W. At each location we collected seeds from 20 mother plants, which were sufficiently distant from each other (at least 100 m) to ensure they did not belong to the same vegetatively propagated genotype. Seed collection was stratified according to previous grazing history, as this can affect plant adaptations to drought (Coughenour 1985; Milchunas et al. 1988): half of the sampled mother plants had been under high grazing pressure (near a watering point) and the other half under low grazing pressure (far away from the watering point). We found no differences between plants with different grazing history in variables reported here (but see Quiroga et al. 2010), thus our analysis focuses only on adaptations that are the result of aridity as a selective force.

Plant culture

During the southern hemisphere spring following seed collection, we established a common garden at the Instituto Nacional de Tecnología Agropecuaria (INTA) Chemical experimental station, La Rioja province, Argentina (30°22'S and 66°17'W). In September 2005, we planted seeds in 30-cm diameter × 30-cm high cylindrical pots (large enough to prevent negative effects on plant growth, Passioura 2006), filled with a 2:1 mixture of loamy soil and sand [wilting point at 8 % volumetric water content, according to Saxton and Rawls (2006)]. During the months of plant establishment (September–November) pots were watered to maintain optimal soil water conditions. From the seeds of each mother plant we obtained two experimental units. Each experimental unit consisting of two “daughter” plants (one per pot) from the same mother plant (1 experimental unit = 2 pots = 2 daughter plants). The total number of experimental units was 80 (resulting from 20 replicates × 2 aridity origins × 2 watering treatments).

Watering treatments

Watering treatments were applied for 6 weeks, starting November 30, 2005 when plants had an average of 25 tillers, and finishing on January 9, 2006. Precipitation water input to the pots was avoided by covering them with a 7 × 13 m tarp placed 1.5 m above the plants during each rainfall event. We applied two contrasting watering treatments: control (without water stress, high watering level, W+) and drought (low watering level, W–). Each treatment was applied to half the plants from each origin (i.e. two of the four daughters of each mother plant). W+ plants were watered with 1 L per pot three times a week (3 L/pot/week). W– plants were watered during the first 2 weeks with 1 L per pot once a week (1 L/pot/week), and from the third week onwards twice a week, once with 1 L and once with 0.5 L (1.5 L/pot/week). This procedure served to avoid extreme desiccation and possible plant death, and was implemented because at the end of the second week (day 14 from the beginning of the watering treatment) a significant pulse of leaf senescence was observed in drought stressed plants - mainly those from humid sites- (see Results, Figs. 1a, 2). While this water addition during the second half of the drought treatment caused a temporary increase in

soil water content, it mimicked natural wet–dry cycles in field *T. crinita* plots. During a low-precipitation growing season, a series of rainfall events are followed by periods of gradual drying of the soil (at a rate of $\sim 1\%$ v/v per day) that can last 5–20 days (data not shown).

Measurements

Leaf elongation rate was assessed during the 40 days of the experiment. We marked a tiller per plant, and every one or 2 weeks we measured the growth of its youngest leaf, following the technique described by Golluscio et al. (1998). *Leaf elongation rate* (cm/d) was estimated dividing the leaf length increment by

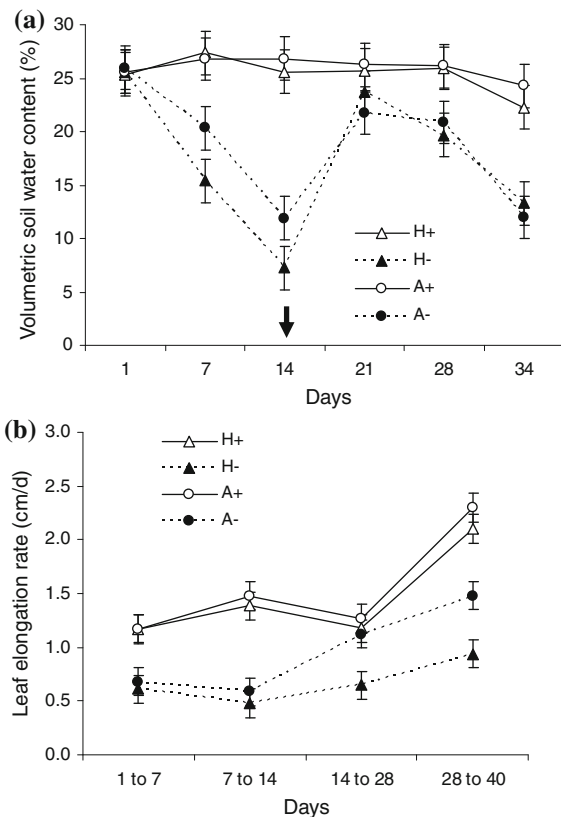


Fig. 1 Aridity origin (humid, H; arid, A) and watering level (high, +; low, -) effect on temporal variation of volumetric soil water content (a) and leaf elongation rate (b). Means \pm standard errors of untransformed variables are shown. Arrow in (a) marks the occurrence of the pulse of senescence and the timing of the increase in water supply in the drought treatment (see Materials and methods)

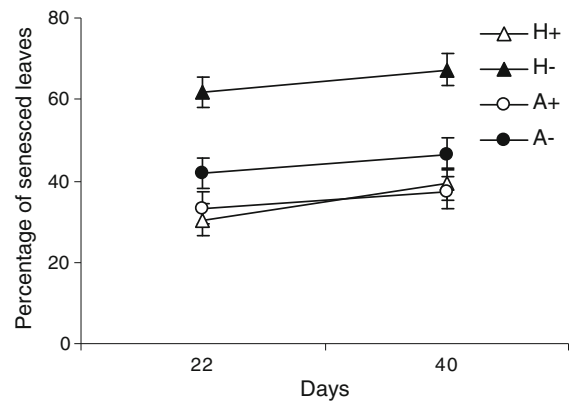


Fig. 2 Aridity origin (humid, H; arid, A) and watering level (high, +; low, -) effect on the percentage of senesced leaves at days 22 and 40 from the beginning of the experiment. Means \pm standard errors are shown

the number of days, for each of the following periods: days 1–7, days 7–14, days 14–28 and days 28–40.

Volumetric soil water content (%) was assessed every week in six pots for each aridity origin \times watering level combination, using “EC10 Sensors” (Decagon Devices, Pullman, Washington, USA). Since all pots had the same soil volume and no drainage from them was observed, differences between pots *volumetric soil water content* could be attributed to differences in plant water absorption (Qian and Fry 1997). Two reasons support the assumption that losses by direct evaporation from the soil were negligible: (1) substrate texture was coarse, i.e. sandy loam (cf. Noy-Meir 1973) and (2) plant foliage covered most of the soil surface.

At the end of the experiment, we harvested the middle portion (3 cm length) of the blade from the last fully expanded leaf of two tillers per plant. The area of each leaf blade portion (length \times width) was calculated, the samples oven-dried (60 °C for 72 h) and weighed to estimate the *specific leaf area* (cm²/g). In the same plants we harvested all leaf blades, which were separated into green and senesced categories, and then oven-dried and weighed. We quantified *green leaf biomass* (including removed leaf blade portions), *total leaf biomass* (green + senesced leaf blades) and *percentage of senesced leaves* [= (biomass of senesced leaves/total leaf biomass) \times 100]. After the pulse of senescence at around day 14, a further measurement of this last variable was also taken. On day 22 we counted, on one tiller per plant, the number of green

and senesced leaves, and used the above equation [$=(\text{senesced}/\text{total}) \times 100$], but using leaf counts instead of leaf biomass.

Some of the mentioned variables were measured in the two plants of each experimental unit (*leaf elongation rate*, *percentage of senesced leaves* at day 22), while the other variables were measured in only one of these two plants (*volumetric soil water content*, *specific leaf area*, *green and total leaf biomass*, *percentage of senesced leaves* at day 40). When both plants of the experimental unit were measured, their values were averaged, i.e. treated as subsamples.

As the response to drought can vary with plant size (Fernández et al. 2002; Poorter et al. 2012), we assessed whether plants from different origins differed in *aboveground biomass* at the beginning of the experiment. We took a digital photograph (at a distance of 50 cm, and an angle of 30° to the horizontal; Sony Cybershot camera) from each “experimental” plant plus from another 20 “extra” plants (ten from arid sites, ten from humid sites). The aboveground biomass (leaf blades + leaf sheaths) of the “extra” plants was then harvested, oven-dried (60 °C for 72 h) and weighed. We estimated the number of pixels corresponding to aboveground biomass in each digital photograph by supervised classification (using ERDAS Imagine 9.1 software). Linear regression functions were fitted to the aboveground biomass (y) versus pixel number (x) relationship (SAS Institute 2011). We obtained two equations of different slope (parallelism test, $P = 0.048$), one for plants from arid sites (relatively more erect and taller plants, Quiroga et al. 2010; $y = 0.000087 x - 1.18$; $R^2 = 0.92$) and another for plants from humid sites ($y = 0.000056 x + 1.04$; $R^2 = 0.76$). When these functions were used to estimate aboveground biomass of “experimental” plants from their pixel values, we found that at the beginning of the experiment plants from arid and humid origins had similar *aboveground biomass* (mean \pm s.e.: 7.3 ± 0.3 g/plant).

Statistical analysis

The experiment had a generalized complete block design (ten blocks, 20 replicates), with a factorial structure of treatments (aridity origin \times watering level) applied to split plots, such that aridity origin

was the main-plot factor and watering levels the subplot factor. Each combination of aridity origin \times watering level was applied to two experimental units (replicates) per block. Grazing history had no effect on any of the variables studied here (but see Quiroga et al. 2010), so it was excluded from the analysis.

Data were analyzed using mixed models by means of the PROC MIXED routine in SAS software (SAS Institute 2011). We considered aridity origin and watering level as fixed effects, blocks and mother plant as random effects, and the resulting interactions as fixed or random effects (according to Littell et al. 1996). For those variables measured two or more times during the experiment, we performed a repeated measure analysis, which in addition to the mentioned factors included time as a fixed effect and experimental unit (nested within the interaction of aridity origin \times watering treatment \times mother plant) as a random effect (Littell et al. 1996). In particular, the aridity origin \times watering level interaction (alone, or included in a three-way interaction with time) is of interest in our study, as it indicates if plants from different aridity origin differ in drought response. Simple effect test (LSMEANS/SLICE; SAS Institute 2011) were used to examine significant two- and three-way interactions. This procedure tests the significance of one factor at each level of another factor, generating the appropriate F test (Westfall et al. 1999). To improve normality data for *leaf elongation rate* [$\ln(x + 1)$] and *volumetric soil water content* (square root) were transformed prior to analysis.

We used regression analysis to describe the relationship between the percentage of senesced leaves and the volumetric soil water content in plants from different aridity origins. For plants of each origin we fitted a regression function considering both watering levels. Values of soil moisture were from day 14, when the soil reached maximum desiccation. Those of senesced leaves corresponded to day 22 (for the same plants, six pots per each aridity origin \times watering treatment combination), when the first “post-pulse” estimation of leaf senescence was made.

Results

Plants from distinct provenances affected *volumetric soil water content* differently and exhibited different

leaf elongation rates in response to drought (aridity origin \times watering level \times time; $P < 0.05$ for both variables; Table 1). At the beginning of the experiment, the soil of all pots had similar water content (Fig. 1a). In the well-watered control level, there were no differences in *volumetric soil water content* (Fig. 1a) or in *leaf elongation rate* (Fig. 1b) over time between plants of humid and arid sites. In contrast, in the low watering level, plants from humid sites desiccated the soil more than plants from arid ones did during the first 2 weeks (day 7, $P = 0.072$; day 14, $P = 0.020$). Moreover, by day 14, the soil of the plants from humid origin reached the wilting point level (8 % volumetric soil water content). At that moment, as explained in “Materials and methods”, a pulse of senescence was observed and the water supply at the low watering level was increased from 1 to 1.5 L/week. From then on, soil water content was similar in pots containing plants from both humid and arid sites (Fig. 1a). During the first 2 weeks *leaf elongation rate* in the low watering treatment was the same for plants from humid and arid origins. From the third week onwards, plants from arid sites showed higher *leaf elongation rate* than plants from humid ones (days 14–28, $P = 0.0002$; days 28–40, $P = 0.0003$; Fig. 1b).

The *percentage of senesced leaves* increased, on average, 6 % between days 22 and 40 ($P = 0.022$). The only significant effect among the two- and three-way interactions was aridity origin \times watering level ($P < 0.0001$; Table 1). Under drought, plants from humid sites showed on both dates higher *percentage of senesced leaves* ($P < 0.0001$ for both dates) than

plants from arid sites (~ 65 vs. ~ 45 %, respectively). However, there were no differences in leaf senescence (~ 35 %) between plants from both origins in the control watering level ($P > 0.5$ for both dates; Fig. 2).

Total leaf biomass (green + senesced) at the end of the experiment was only affected by watering level ($P = 0.011$; Table 1). Plants subjected to drought had 15 % less *total leaf biomass* than control plants (Fig. 3a). Aridity origin and its interaction with watering level had no significant effect on this variable (Table 1). In contrast, *green leaf biomass* was affected by both watering level ($P < 0.0001$) and its interaction with aridity origin ($P = 0.025$; Table 1). Control plants from humid and arid origins had similar *green leaf biomass* ($P = 0.430$). By contrast, under drought plants from arid sites had a *green leaf biomass* 47 % higher than plants from humid sites ($P = 0.032$; Fig. 3b). *Specific leaf area* of plants from both humid and arid sites was also affected differentially by drought (aridity origin \times watering level; $P = 0.002$; Table 1). Control plants from both origins produced leaves with similar *specific leaf area*. But under drought, humid site plants had leaves with a 16 % higher *specific area* than the ones from arid sites ($P = 0.0001$; Fig. 3c).

Discussion

When subjected to drought, plants from both aridity origins showed different patterns of soil water use and differed in variables associated with energy acquisition and growth. Plants from arid sites showed a more

Table 1 Probability values for type 3 tests of fixed effects, obtained from the mixed model analysis

Fixed effect factors and interactions	Volumetric soil water content	Leaf elongation rate	Percentage of senesced leaves	Total leaf biomass	Green leaf biomass	Specific leaf area
Aridity origin, A	0.514	0.013*	0.001**	0.128	0.361	0.010*
Watering level, W	0.044*	<0.0001***	<0.0001***	0.011*	<0.0001***	0.002**
A \times W	0.723	0.066	<0.0001***	0.780	0.025*	0.002**
Time, T	<0.0001***	<0.0001***	0.022*			
A \times T	0.124	0.101	0.546			
W \times T	<0.0001***	<0.0001***	0.743			
A \times W \times T	0.036*	0.018*	0.583			

The first three variables (columns 2–4) were analyzed using repeated measure analysis

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$

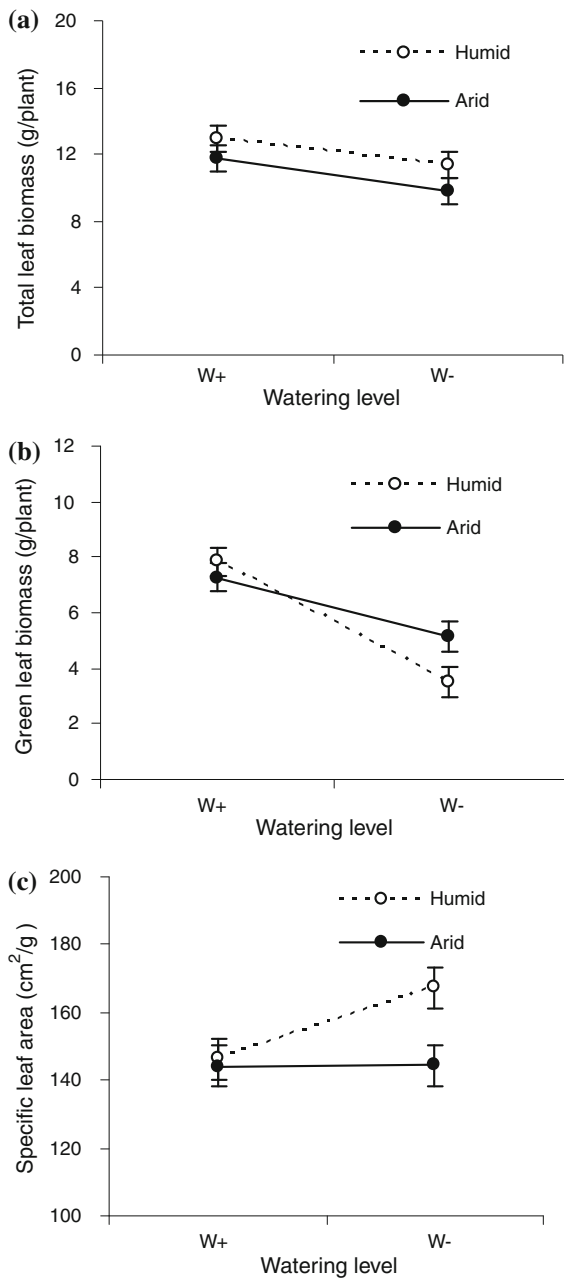


Fig. 3 Aridity origin (Humid; Arid) and watering level (W+; W-) effect on total leaf biomass (a), green leaf biomass (b) and specific leaf area (c) measured at the end of the experiment (day 40 from experiment beginning). Means ± standard errors are shown

“conservative” water use strategy under drought than plants from humid sites. Several authors have suggested that such strategy could favour plant survival in environments where water is the limiting factor (Orians and Solbrig 1977; Fernández and Reynolds

2000; Grime and Mackey 2002; Sperry et al. 2002). Indeed, when subjected to drought, plants from humid sites, besides lowering soil water content to values closer to the wilting point (Fig. 1a), showed higher leaf senescence (Fig. 2), and from the third week onwards suffered a greater reduction in leaf elongation rate than plants from arid sites (Fig. 1b). These differences in leaf senescence between plants from different origins in the low watering level can be explained not only because individuals from the humid sites dried the soil faster than those from arid ones (two first weeks), but also because they showed higher sensitivity to soil moisture decrease (Fig. 4).

Plants from humid sites increased their specific leaf area under drought (ca. 15 %), something that did not happen with plants from arid sites (Fig. 3c). This unexpected result could be explained as a compensation for the lower capacity for carbon capture caused by leaf senescence (Fig. 2). Although we measured specific leaf area in young leaves and values may be lower for older leaves, data from Fig. 3b and 3c suggest that such compensation was only partial: at the end of the experiment under drought conditions, total green leaf surface would have been of approximately 585 cm²/plant (3.50 g/plant of green leaf biomass × 167 cm²/g of specific leaf area) for individuals of humid origin versus 740 cm²/plant (5.14 g/plant × 144 cm²/g) for individuals of arid origin.

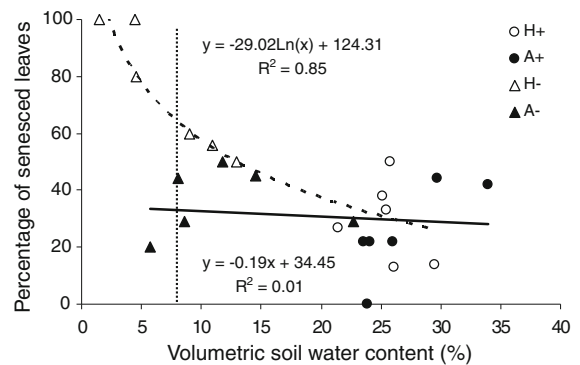


Fig. 4 Effect of soil moisture on leaf senescence for plants from different aridity origins (humid, H; arid, A). For plants of each origin we fitted a regression function considering both watering levels (high, +; low, -); equations and coefficients of determination (R^2) are shown for each origin. Soil moisture values are for day 14, leaf senescence values are for day 22 and the same plants (six pots per each aridity origin × watering treatment combination). Vertical dotted line shows the wilting point (8 %, Saxton and Rawls 2006)

We argue that the sequence of differences in response to drought observed between the two materials suffice to claim that they represent different strategies regarding water use: (i) there was a different rate of soil water extraction between plants from both origins; (ii) plants from humid sites, besides drying the soil quicker, had higher leaf senescence; (iii) these plants that showed more senescence also diminished their leaf growth rate and produced leaf area with lower carbon investment. Particularly in relation to 'ii', plants from arid origin (maintaining transpiring biomass) versus humid origin (strongly reducing transpiring biomass) would fit the proposed "isohydric" and "anisohydric" plant types (Tardieu and Simonneau 1998; Maseda and Fernández 2006). Under drought conditions, isohydric plants maintain their leaf water status at the level of unstressed plants by reducing their leaf transpiration rate (presumably through stomatal regulation, Sperry et al. 2002), thus likely minimizing changes in their transpiring leaf surface. In contrast, anisohydric plants reduce their leaf water status by maintaining the transpiration rate per unit of leaf area at a similar level of that of unstressed plants, and this would likely require a reduction in their transpiring leaf surface (Maseda and Fernández 2006). Our results are also consistent with predictions by Grime and Mackey (2002) who noted that plants from "rich" environments (with high resource availability; in our study: humid origin) tend to show an extractive strategy of resource capture based mainly on morphological plasticity (in our study: leaf senescence, specific leaf area), while plants from "poor" environments (e.g. arid origin) tend to show a conservative resource use strategy based on physiological adjustments (e.g. regulation of soil water extraction).

Soil water extraction by plants is a size-dependent process (Coleman et al. 1994; Poorter et al. 2012). Thus, plants of different size subjected to the same water supply can extract soil water at different rates: larger plants using water faster than smaller plants. We found that even with a similar initial biomass, at the low watering level the plants from humid sites dried soil faster than the ones from arid sites. Only after day 14, when the pulse of leaf senescence occurred and differences in leaf elongation rate arose (Fig. 1b), did plants from arid sites have a greater green leaf biomass than plants from humid sites, showing a size effect. However, consistent with the abovementioned

differences in water extraction during the first 14 days, plants from arid sites with 47 % more *green leaf biomass* (Fig. 3b) did not dry the soil faster than the ones from humid sites during the last weeks at the low watering level (Fig. 1a).

From a practical point of view, our study highlights the importance of aridity as a natural selection force that affects plant strategies to withstand water shortage. Knowledge of the environmental factors that select adaptations to stress is a crucial guide for the collection of plant materials. Water use strategies and differences in drought resistance shown here could be taken into account to obtain varieties adapted to environments with different aridity conditions (Lee 1998; Zhang et al. 2004). As in northwestern Argentina *T. crinita* is an important forage grass, the higher green leaf biomass under low water availability shown by plants from arid sites could be useful to provide forage of higher quality in dry rangelands (Annese et al. 2006).

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