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Aridity and grazing as convergent selective forces: an experiment with an Arid Chaco bunchgrass

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Abstract. It has been proposed that aridity and grazing are convergent selective forces: each one selects for traits conferring resistance to both. However, this conceptual model has not yet been experimentally validated. The aim of this work was to experimentally evaluate the effect of aridity and grazing, as selective forces, on drought and grazing resistance of populations of *Trichloris crinita*, a native perennial forage grass of the Argentinean Arid Chaco region. We collected seeds in sites with four different combinations of aridity and grazing history (semiarid/subhumid × heavily grazed/lightly grazed), established them in pots in a common garden, and subjected the resulting plants to different combinations of drought and defoliation. Our results agreed with the convergence model. Aridity has selected *T. crinita* genotypes that respond better to drought and defoliation in terms of sexual reproduction and leaf growth, and that can evade grazing due to a lower shoot : root ratio and a higher resource allocation to reserves (starch) in stem bases. Similarly, grazing has selected genotypes that respond better to drought and defoliation in terms of sexual reproduction and that can evade grazing due to a lower digestibility of leaf blades. These results allow us to extend concepts of previous models in plant adaptation to herbivory to models on plant adaptation to drought. The only variable in which we obtained a result opposite to predictions was plant height, as plants from semiarid sites were taller (and with more erect tillers) than plants from subhumid sites; we hypothesize that this result might have been a consequence of the selection exerted by the high solar radiation and soil temperatures of semiarid sites. In addition, our work allows for the prediction of the effects of dry or wet growing seasons on the performance of *T. crinita* plants. Our results suggest that we can rely on dry environments for selecting grazing-resistant genotypes and on high grazing pressure history environments for selecting drought-resistant ones.

Key words: Argentinean Arid Chaco region; avoidance; common garden; convergence; defoliation; drought; evolution; natural selection; resistance; tolerance; Trichloris crinita.

INTRODUCTION

Aridity and grazing are probably the selective forces with the most influential effects on the evolution of grasses, as suggested by paleontological records showing the synchronized advent of the Poaceae family, the first grazers, and increasing aridity conditions (Stebbins 1981, Coughenour 1985, Milchunas et al. 1988). It has been hypothesized that aridity and grazing have been convergent selective pressures on grasses, each one of them selecting at the same time for higher drought and grazing resistances (Coughenour 1985, Milchunas et al. 1988). This convergence would be explained because both aridity and grazing regularly produce partial or total loss of plant tissues (Orians and Solbrig 1977, Mooney and Gulmon 1982). Therefore, traits selected under drought would be useful to cope with grazing, and vice versa. Among these characteristics, the most relevant are low plant height, tissue toughness, resource allocation to reserves, opportunistic activation of growth points, and regrowth ability after damage (Coughenour 1985, Milchunas et al. 1988).

The evolutionary convergence model has been frequently used to explain the response of plant communities, populations, or individuals to grazing or defoliation, and to aridity or water stress (Dyer et al. 1991, Milchunas and Lauenroth 1993, Loreti et al. 2001, Adler et al. 2004, Cingolani et al. 2005). Several studies evaluated separately the effect of each selective force, aridity or grazing, on plant adaptations (Detling and Painter 1983, Jaramillo and Detling 1988, Painter et al. 1989, 1993, Dyer et al. 1991, Loreti et al. 1994, 2001, Clifton-Brown and Lewandowski 2000, Tomás et al. 2000, García et al. 2002, Greco and Cavagnaro 2002).

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Moreover, Milchunas and Lauenroth (1993) and Adler et al. (2004) studied the influence of aridity and grazing history on grazing resistance of plant communities. However, convergence between aridity and grazing as pressures selecting both high drought and grazing resistances apparently has not been experimentally assessed (Adler et al. 2004).

The study of plant adaptive responses to aridity and grazing is important not only for the advancement of ecological theory, but also from an applied perspective. In the Arid Chaco phytogeographic region of northwest Argentina, as in other arid and semiarid regions of the world, this kind of investigation is relevant because raising domestic animals in extensive range is the main agricultural activity (Anderson et al. 1980, Blanco et al. 2005). Knowledge of responses to drought and grazing of native forage species is basic for the design of proper management practices and in the quest of plant materials for restoring rangeland or increasing forage productivity (Rice and Emery 2003, Quiroga et al. 2009). In addition, evaluating the convergence model is relevant to understanding the causes of genetic variation in plant adaptation to drought and grazing and would tell us how much we can rely on semiarid or high grazing pressure provenances to select for drought- and grazing-resistant cultivars.

Selective forces favor genotypes showing greater fitness (differential reproduction) and cause changes in genetic composition at the level of individuals and populations, which scales up to communities or ecosystems (Lewontin 1970, Orians and Solbrig 1977, Stebbins 1981, Endler 1986, Milchunas et al. 1988, Mauricio et al. 1997, Strauss and Agrawal 1999). At the population level, evolution modifies the relative frequency of different genotypes within a species (Detling and Painter 1983, Coughenour 1985, Kotanen and Bergelson 2000, Greco and Cavagnaro 2002). A common method to evaluate plant adaptations to a selective force at the population level is the collection of plant propagules from areas with historically different levels of this selective pressure, and their establishment in a common site to assess relevant plant traits. Hence, differences obtained within a common environment (e.g., greenhouse, garden) between plants of different origin can be interpreted as adaptation to the selective force, suggestive of genetic differences (Wu and Jain 1978).

Plant resistance to any biotic or abiotic stressor is composed of both avoidance and tolerance traits (Coughenour 1985, Briske 1991, Mauricio et al. 1997, Kotanen and Bergelson 2000, Adler et al. 2004). Avoidance traits allow plants to reduce the incidence of the stressor on their tissues (e.g., avoid defoliation), while tolerance traits allow plants to sustain function after a stressor acts on their tissues (e.g., regrowth after defoliation). Regrettably, it is difficult to assess grazing resistance in plants in controlled experiments (greenhouse or common garden) because plants cannot easily be subjected to grazing directly (McNaughton 1979). An alternative way to estimate grazing resistance is to separately assess each of their components, avoidance and tolerance (Stowe et al. 2000, Adler et al. 2004), focusing on defoliation—the most important direct effect of grazing. Studies evaluating tolerance or avoidance to herbivory at the plant or population level are abundant (Simms and Rausher 1989, Mauricio et al. 1997, Fornoni and Nuñez-Farfán 2000, Hochwender et al. 2000, Juenger et al. 2000, Adler et al. 2004).

In this study we evaluated the effect of aridity and grazing selective pressures on drought and grazing resistances of populations of *Trichloris crinita*, a native perennial grass of the Arid Chaco region. We collected seeds on sites with different aridity and grazing history, established them in a common garden, and then applied different levels of drought and defoliation. Our hypothesis was that plant drought and grazing resistances increases with both historical aridity and historical grazing pressure of the collection site. Predictions related to this hypothesis are shown in Table 1.

MATERIALS AND METHODS

Study region

The work was performed in the phytogeographic Arid Chaco region, located in northwest Argentina, between 28°15′ S and 33°30′ S, and between 64°01′ W and 67°31′ W. This region covers ~100 000 km^2, it is at an altitude of 200–700 m, and is surrounded by mountains of ~2000 m (Morello et al. 1985). The climate is subtropical, with mean annual temperatures ranging from 17°C to 20°C (Morello et al. 1985), and an east–west precipitation gradient of 600 mm to 300 mm (Cabido et al. 1993, Blanco et al. 2008). Most annual precipitation (80%) occurs in the southern hemisphere warm season, between November and March. Summers are hot and have 20–25 days with maximum temperatures $>$ 40°C; winters are mild and have only 5–10 days with minimum temperatures $<$ 0°C (Prohaska 1959). Predominant soils are coarse textured, with low organic matter content (<1.5% of soil mass) and neutral to basic pH (Gómez et al. 1993). Typically, vegetation is a subtropical xerophytic shrubland, with scattered trees, mainly *Aspidosperma quebracho-blanco* and *Prosopis* spp. Most common shrubs correspond to the *Larrea*, *Mimozyganthus*, *Senna*, and *Capparis* genera. The herbaceous stratum is composed principally by C4 perennial grasses of the *Trichloris*, *Chloris*, *Pappophorum*, *Aristida*, and *Setaria* genera (Ragonese and Castiglioni 1970, Anderson et al. 1980, Morello et al. 1985). As precipitation increases from 300 to 600 mm, the cover of trees increases from 11% to 26%, that of the herbaceous layer from 20% to 49%, and the cover of shrubs remains almost constant, going from 63% to 59% (Cabido et al. 1993). Although we can refer to sites on the extremes of the precipitation gradient as relatively "mesic" or "xeric" (Cabido et al. 1993), we refer to them as "subhumid" or "semiarid" for consistency with Milchunas et al. (1988).

TABLE 1. Interactions/factors related to our hypothesis, the question that each one responds to, and formulated predictions in relation to drought resistance, and grazing resistance (partioned in defoliation tolerance and grazing avoidance).

Prediction	Interaction/factor	Question of interest related to interaction
Drought resistance		
1.a) Plants from semiarid sites are more drought resistant than plants from subhumid sites.	Aridity history × drought	Are there differences in drought resistance between plants from different sites on the precipitation gradient?
1.b) Plants from heavily grazed sites are more drought resistant than plants from lightly grazed sites.	Grazing history × drought	Are there differences in drought resistance between plants from different sites on the grazing gradients?
Defoliation tolerance		
2.a) Plants from semiarid sites are more defoliation tolerant than plants from subhumid sites.	Aridity history × defoliation	Are there differences in defoliation tolerance between plants from different sites on the precipitation gradient?
2.b) Plants from heavily grazed sites are more defoliation tolerant than plants from lightly grazed sites.	Grazing history × defoliation	Are there differences in defoliation tolerance between plants from different sites on the grazing gradients?
Grazing avoidance		
2.c) Plants from semiarid sites had more grazing avoidance capacity than plants from subhumid sites.	Aridity history	Are there differences in grazing avoidance capacity between plants from different sites on the precipitation gradient?
2.d) Plants from heavily grazed sites had more grazing avoidance capacity than plants from lightly grazed sites.	Grazing history	Are there differences in grazing avoidance capacity between plants from different sites of the grazing gradients?

Study species

Trichloris crinita is one of the most important forage species not only in the Arid Chaco region (Anderson et al. 1980, Anderson 1983, Dalmasso 1994, Blanco and Orionte 2003), but also in the rest of Chaco, and in the adjacent Monte and Caldenal phytogeographic provinces (Sal 1989, Dalmasso 1994, Greco and Cavagnaro 2002). The species is also present in Paraguay, Bolivia (Nicora and Rúgolo de Agrasar 1987), southern United States, and northern Mexico (Sal 1989). Cattle preference for *T. crinita* is associated with its high protein content (Nicora and Rúgolo de Agrasar 1987). In addition, the species protects against soil erosion (Dalmasso 1994). Previous work has found a marked intraspecific variability in plant height, aboveground and root biomass, and tiller and inflorescence production (Sal 1989) associated with the degree of aridity at the site (Greco and Cavagnaro 2002). *Trichloris crinita* is a C4 perennial bunchgrass of summer growth, which reproduces by diaspores (hereafter "seeds") and also vegetatively, by tillering. Plants are 20–40 cm in height in vegetative stages and 50–100 cm when flowering. Seeds are located in dense inflorescences, each inflorescence sitting on one erect, 30–100 cm long boot (Nicora and Rúgolo de Agrasar 1987). The reproductive biology of the species is not well known; some studies suggest that it would be selfing or apomictic (Sal 1989, Greco and Cavagnaro 2002), while others suggest some degree of outcrossing (Pezzani and Montaña 2006). Shoot : root ratio varies from 1.0 to 3.7 among different populations (Greco and Cavagnaro 2002). In sum, three key elements justified our election of *T. crinita* as study species: (1) it is broadly distributed in the region and grows under variable aridity and grazing conditions; (2) it is consumed by cattle and hence it is possible that grazing can act as selective force over it; (3) previous research encountered intraspecific genetic variability.

Study approach

We established a common garden with potted plants of four origins (combination of "semiarid" vs. "subhumid" locality and "heavy" vs. "light" grazing intensity history) and subjected them to the four treatments resulting from the combination of two watering and two defoliation levels. Plants were established during the spring of 2005, subjected to treatments the ensuing summer, and harvested ~6 months after planting.

Resistance to a given stress was studied in genetically related individuals (see Mauricio et al. 1997) obtained from seeds, because vegetative propagation could have introduced residual environmental effects (McCain and Davies 1983, Blanco and Orionte 2003). Thus, each of four plants derived from the same mother plant was subjected to one of the treatments resulting from the combination of watering and defoliation levels.

We subjected plants of the four origins to two contrasting watering levels. In this way, we were able to quantify drought resistance, because plants subjected to a given amount of water supply can simultaneously express strategies of avoidance (e.g., decrease their water uptake rate) and tolerance (e.g., survive despite low plant water potential). In contrast, to estimate grazing resistance we assessed tolerance and avoidance separately. We assessed tolerance to defoliation by defoliating half the plants from each of the four origins with a similar intensity, and leaving the other half non-defoliated. Grazing avoidance was inferred from major morphological and chemical traits (listed in *Measurements: Grazing-avoidance related variables*), known to be related to grazers' impact on grasses, evaluated in well watered and non-defoliated plants (control level of watering and defoliation).

Experimental design was a split-plot in randomized complete blocks ($n = 10$), with a two-way (factorial) structure in both main plots (aridity history × grazing history) and subplots (drought × defoliation). Most response variables were measured at the end of the experiment (a few of them weekly), and were selected to be related to fitness (sexual reproduction, vegetative reproduction, leaf growth, total biomass) and grazing avoidance (green and senesced leaf blade digestibility, starch and soluble carbohydrate storage in stem bases and roots, shoot : root ratio, plant height; Grime 1977, Coughenour 1985, Milchunas et al. 1988, Briske 1991, Adler et al. 2004).

Plant material collection and culture

In March 2005, at the end the growing season, we collected seeds at two extreme points of the precipitation regional gradient (326 and 625 mm/yr; Blanco et al. 2008). At each extreme of the precipitation gradient, we collected *T. crinita* seeds in two sites placed within a single large paddock but at different distances from the watering point, and hence with different grazing pressure (Bailey et al. 1996): 0.5–2 km, heavy grazing and >7 km, light grazing. These watering points have been in place for at least 50 years, and cattle grazing has occurred continuously within the paddocks since then. Thus, in our study region, aridity is a long-term selective force, while grazing pressure is a relatively short-term one (nevertheless, studies have shown intraspecific differentiation in response to grazing in shorter time periods; Detling and Painter 1983, Jaramillo and Detling 1988, Painter et al. 1993, Loreti et al. 2001). Visual estimates (Cook and Stubbendieck 1986) in four 10 × 10 m plots at each collection site before the beginning of the 2002–2003 growing season (L. J. Blanco and F. N. Biurrun, *unpublished data*) allowed us to define the percentage of utilization (PU) of grass aerial biomass (the main source of forage for cattle in the region; Anderson 1983). Thus, we sampled seeds in four sites: "semiarid and heavily grazed" (31°24–25′ S, 66°46–47′ W; PU = 88% ± 3% [mean ± SE]), "semiarid and lightly grazed" (31°30–32′ S, 66°48–49′ W; PU = 3% ± 2%), "subhumid and heavily grazed" (29°57–59′ S, 64°28–29′ W; PU = 85% ± 2%), and "subhumid and lightly grazed" (29°49–54′ S, 64°27–28′ W; PU = 2% ± 1%). In each site we collected seeds from 10 "mother" plants, which were sufficiently distant from each other (at least 100 m) to assure they did not come from the same vegetatively propagated genotype.

The following southern hemisphere spring, we established a common garden at the experimental station of the Instituto Nacional de Tecnología Agropecuaria (INTA), Chamical county, La Rioja province, Argentina (30°22′ S, 66°17′ W). In September 2005, we planted seeds in 30 cm diameter × 30 cm height cylindrical pots, filled with a mixture of loamy soil and sand (2:1). To avoid frost incidence during September and October we covered pots with a transparent 200-μm polyethylene film, placed at 80 cm height. To maintain optimal soil water conditions, we watered pots during months of plant establishment (September–November).

Watering treatments started on 30 November 2005, when plants had a mean of 25 tillers, and finished at the end of the experiment, on 20 March 2006. Precipitation water input over the pots was avoided by covering them with a 7 × 13 m tarp placed at 1.5 m height, which was deployed before and removed after each rainfall event. We applied two contrasting watering levels: one without water stress (well watered control, W+), and other with water stress (low watered, W−). In W+, we watered each pot with 1 L three times per week (3 L/week). In W−, during the two first weeks we watered each pot with 1 L once per week (1 L/week), and from the third week onward we watered each pot twice per week, once with 1 L and once with 0.5 L, to avoid extreme desiccation (1.5 L/week). Hence, plants with low watering receive 33% as much water as control plants during the two first weeks and 50% from the third week onward. The imposed water stress reduced total biomass of droughted plants at the end of the experiment to 63% of that of undroughted plants in the well watered control; as an estimator of water stress severity (e.g., Fernández and Reynolds 2000), this ratio suggests that drought conditions in our experiment were as severe as those achieved in the field experiment of Greco and Cavagnaro (2002) comparing *T. crinita* populations.

Defoliation levels were without leaf blade removal (control, L+), and defoliation of 100% of leaf blades (L−; stem bases were left intact). Defoliation was applied on 9 January 2006 (40 days after the onset of watering treatments, when plants had not begun to bloom yet) by cutting plants at the height of their lowest ligule; thus, some small sheath portions may have been also removed. Since cattle preferentially consume leaf blades (Lemaire and Chapman 1996, Loreti et al. 2001), this reasonably mimics a severe defoliation event. The validity of our defoliation treatment to estimate defoliation tolerance relied on the removal of similar tissue proportions in plants of the four populations (Stowe et al. 2000). Regardless of watering level, at the end of our experiment non-defoliated plants of different origins presented similar biomass proportion over the defoliation height (~40% of total plant biomass [shoots + roots] and ~57% of shoot biomass; data not shown).

Measurements

We measured fitness-related variables in all experimental plants, but grazing-avoidance related ones only in well watered and non-defoliated plants (control level of watering and defoliation).

Fitness-related variables.—To assess sexual reproduction, we counted the *number of inflorescences* at the end of the experiment. In addition, with the purpose of estimating the production of seeds per plant, in 6–7 randomly selected plants of each one of the 16 treatments (4 origin sites × 2 watering levels × 2 defoliation levels), we assessed the biomass of seeds produced per inflorescence, removing and weighing mature seeds in one inflorescence per plant. For each treatment we estimated *plant seed biomass* (grams/plant) as the product of number of inflorescences per plant by mean seed biomass per inflorescence.

To assess leaf growth we measured two variables, *leaf elongation rate* and *leaf appearance rate* (Lemaire and Chapman 1996). We selected these variables taking into account that leaf expansion is very sensitive to drought (Greco and Cavagnaro 2002, Tardieu et al. 2005). We made measurements weekly, from defoliation to the end of the experiment, in a selected tiller per plant. When a selected tiller died or started flowering, we replaced it with another vegetative one (Peacock 1976). We measured blade elongation of the youngest leaf using the technique described by Golluscio et al. (1998). Leaf elongation rate (cm/day) was estimated by dividing total length of the elongated blade of youngest leaves by the time elapsed from defoliation to the end of the experiment (Golluscio et al. 1998). Leaf appearance rate (leaves/day) was estimated by dividing total leaves appearing by the same time period (Anslow 1966). In 10 of 160 plants, the selected tiller died and was not replaced opportunely; hence these plants were not included in leaf appearance rate and leaf elongation rate analysis.

To assess plant vegetative reproduction we counted the *number of live tillers* at the end of the experiment (Briske 1991). We also counted them at the beginning of the experiment for use as a covariate.

To assess *total biomass* (stems + leaf sheaths + leaf blades + inflorescences + roots) we took into account all plant biomass (green and senesced) harvested at the end of the experiment and at defoliation application. We sifted roots using a 2-mm mesh and washed them in water. We dried plant materials at 60°C during 72 hours before weighing (Greco and Cavagnaro 2002).

Grazing-avoidance related variables.—We determined *digestibility* separately in samples of green and senesced leaf blades harvested at experiment end. In each sample we assessed acid detergent fiber (ADF, dry matter percentage) by sequential digestion (Goering and Van Soest 1970). We estimated dry matter digestibility (percentage) of each sample from ADF content (Digestibility = 88.9 − [0.779 × ADF]) (Rohweder et al. 1978). Digestibility determinations were performed at the Laboratorio de Calidad de Forrajes—INTA La Rioja, La Rioja, Argentina.

We determined *starch concentration* and *soluble carbohydrate concentration* separately in stem bases (tissues over the connection point between stems and roots, and below the height of the lower ligule) and root samples (not dried previously) obtained at experiment end. An aliquot of each sample was freshly milled with dry ice for starch and soluble carbohydrates determination (ethanol 80%, Megazyme enzyme kit, AA/AMG; Megazyme, Wicklow, Ireland) (McCleary et al. 1994). We dried another aliquot of each sample at 105°C for dry matter content estimation. We expressed starch and soluble carbohydrates concentrations as dry matter percentage. Starch and soluble carbohydrates determinations were performed at CISNA (Centro de Investigación y Servicios en Nutrición Animal—Facultad de Agronomía, Universidad de Buenos Aires, Buenos Aires, Argentina).

To quantify *shoot : root ratio* we divided aerial biomass (stems + leaf sheaths + leaf blades + inflorescences) by the underground biomass (roots) harvested at the end of the experiment.

We measured *plant height* from soil to the uppermost portion of a totally expanded leaf (Painter et al. 1993), leaving the plant in its natural position.

Statistical analyses

To compare drought resistance and defoliation tolerance between populations with different aridity and grazing history we analyzed fitness-related variables using mixed model (MIXED procedure, $\alpha = 0.05$) in the SAS package (SAS Institute 1996). The MIXED procedure use the restricted maximum likelihood estimates (REML) method (Littell et al. 1996, Gil 2001). Analyses were performed considering the split-plot design in randomized complete blocks, with factorial structure in main plots (aridity history × grazing history) and subplots (drought × defoliation) (Littell et al. 1996; Fig. 1).

The statistical model included four fixed-effect factors: aridity history, grazing history, drought and defoliation, and their respective double, triple, and quadruple interactions. It also included random-effect factors: "mother" plant and block. We considered aridity history and grazing history as fixed-effect factors because we sampled only at two levels of their corresponding gradients (precipitation gradient, distance to watering point–grazing pressure gradient) (Littell et al. 1996). Each main plot consisted of four plants (subplots) obtained from seeds of the same mother, each one receiving as treatment one of the four combinations of drought and defoliation levels. The evaluation of some double interactions is crucial in testing the main predictions from our hypothesis (Table 1: predictions 1.a, 1.b, 2.a, and 2.b).

Even when none of our predictions were directly related to random-effect factors, their inclusion was

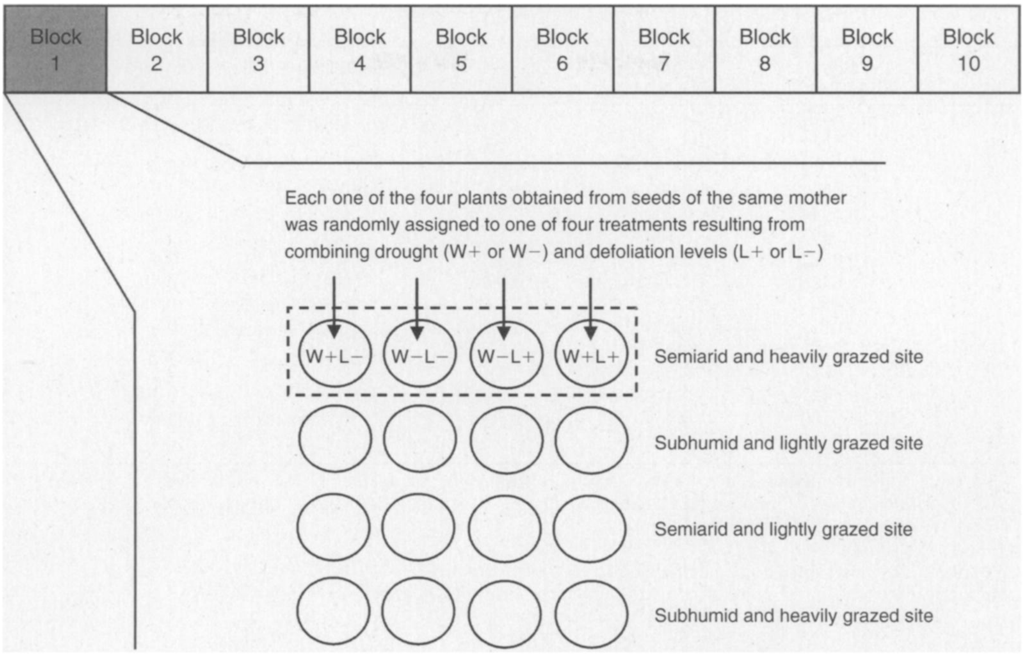

FIG. 1. Block schematization. Each plant is represented as a circle. To analyze fitness-related variables we consider the group of four plants obtained from seeds of the same mother as the main plot and each individual as a subplot. To analyze grazing avoidance, we consider as main plot one single plant (not subjected to drought and not defoliated) and tissue type as subplot.

necessary to correctly model experimental structure. We included block × aridity history × grazing history interaction as a random effect because it is the error term for main plot. We included "mother" as random effect factor and nested it in aridity history × grazing history because we randomly collected seeds from different mother plants on each of the four aridity × grazing history sites. We did not include mother × drought × defoliation interaction because of the lack of replicates within main plot. However, we included in the model mother × drought and mother × defoliation interactions to exclude the variation in drought and defoliation responses between progeny of different mothers from the error term.

The number of inflorescences was $\ln(x + 1)$-transformed to enhance their fitting to the normal distribution; the rest of variables were analyzed without transformation. To analyze the number of live tillers, we used the initial number of live tillers as covariate. When we detected significant effects of triple interactions that included double interactions of interest, we used the SLICE statement (Littell et al. 1996, Herrera 2000) to evaluate the double interaction of interest within the control level of the sliced factor, because we considered that in this way the test for drought resistance and defoliation tolerance would have an appropriate control (non-subjected to drought and non-defoliated plants). For example, if we wanted to evaluate aridity history × drought interaction, and we encountered that triple interaction aridity history × drought × defoliation was significant, we evaluated the desired interaction within non-defoliated plants.

We analyzed the effects of aridity history and grazing history on variables related to grazing avoidance (predictions 2.c and 2.d, respectively, in Table 1) using more simple versions of the mixed model used for fitness-related variables (MIXED procedure, $\alpha = 0.05$) in SAS package (SAS Institute 1996). We did not subdivide main plots into the four combinations of drought × defoliation treatments because we only used well-watered and non-defoliated plants (plants of control levels of watering and defoliation), and then we did not include the "mother" plant random factor (Littell et al. 1996). As a consequence, for shoot : root ratio and plant height we used a randomized complete block design. Instead, for leaf blade digestibility and starch and soluble-carbohydrate concentration, we considered the plant as the main plot, and subdivided it into two subplots: green or senesced leaves, and stem bases or roots.

RESULTS

Drought resistance and defoliation tolerance

In general, drought decreased ($P < 0.0001$) but defoliation increased ($P < 0.0001$) the *number of inflorescences*. However, significant effects of the interactions aridity history × drought × defoliation ($P = 0.0212$) and grazing history × drought × defoliation ($P = 0.0118$; Table 2), that involve double interactions of interest (listed in Table 1), deserve a more detailed analysis.

TABLE 2. Probability values of fixed-effect factors for fitness-related variables.

Fixed-effect factors	No. inflorescences†	Plant seed biomass	Leaf elongation rate	Leaf appearance rate	No. live tillers‡	Total biomass
A	0.5718	0.7871	0.0130*	0.3409	0.1832	0.0542
G	0.3611	0.8646	0.9518	0.3048	0.2212	0.2934
W	<0.0001***	<0.0001***	<0.0001***	<0.0001***	<0.0001***	<0.0001***
L	<0.0001***	0.0057**	0.1249	0.0036**	0.0120*	0.1855
A × W	0.1744	0.2003	0.9325	0.9255	0.0614	0.4460
A × L	0.4695	0.1238	0.1523	0.9219	0.2973	0.4301
A × G	0.6187	0.5201	0.4137	0.9096	0.4753	0.9495
G × W	0.0328*	0.0448*	0.9742	0.4553	0.8828	0.9342
G × L	0.8508	0.5739	0.1313	0.3697	0.9429	0.3906
W × L	0.0113*	0.0144*	0.5814	0.7001	0.4959	0.4304
A × W × L	0.0212*	0.0259*	0.0366*	0.1002	0.3351	0.9792
G × W × L	0.0118*	0.0392*	0.9131	0.5396	0.6524	0.9285
A × G × W	0.6027	0.4408	0.5305	0.9396	0.7491	0.5531
A × G × L	0.5700	0.5595	0.7961	0.1616	0.4078	0.2117
A × G × W × L	0.9425	0.2522	0.8386	0.3123	0.0745	0.1746

Notes: The table presents mixed-model analysis results, obtained by using the REML method in MIXED procedure (SAS Institute 1996). Complete tables of analysis results are provided in Appendix A. Abbreviations are as follows: A, aridity history; G, grazing history; W, drought; L, defoliation.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

† Variable $\ln(x + 1)$-transformed for analysis, due to lack of normality.

‡ Variable analyzed using initial number of live tillers as covariate ($P < 0.0001$).

In non-defoliated plants, we found significant interactive effects of aridity history × drought ($P = 0.0002$) and grazing history × drought ($P < 0.0001$). Aridity history × drought interaction showed, consistent with prediction 1.a in Table 1, that plants from semiarid sites decreased less their inflorescence production by drought than plants from subhumid sites (Fig. 2A). Also, grazing history × drought showed, consistent with prediction 1.b (Table 1), that plants from heavily grazed sites decreased less their inflorescence production by drought than plants from lightly grazed sites (Fig. 2B). Differences in response to drought between plants from semiarid and subhumid sites were similar to those for plants from heavily and lightly grazed sites.

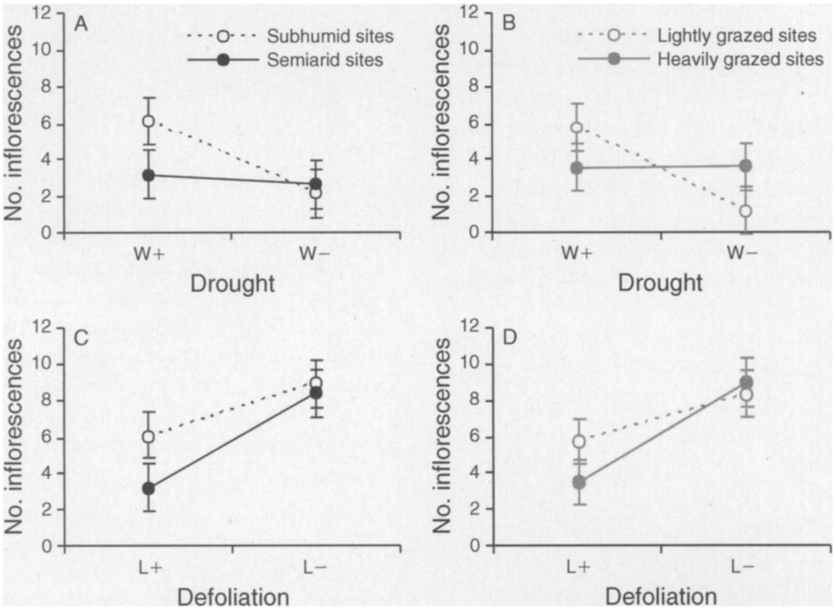

FIG. 2. Differential effect of drought (W+ [well watered] or W− [low watered]) and defoliation (L+ [non-defoliated] or L− [defoliated]) on the number of inflorescences of plants with different aridity (subhumid sites or semiarid sites) and grazing history (lightly grazed sites or heavily grazed sites): (A) aridity history × drought interaction ($P = 0.0002$); (B) grazing history × drought interaction ($P < 0.0001$); (C) aridity history × defoliation interaction ($P < 0.0001$); (D) grazing history × defoliation interaction ($P < 0.0001$). P values were obtained by using the SLICE statement (Littell et al. 1996, Herrera 2000) to enter within control level of factors defoliation (panels A and B) or drought (panels C and D) of significant triple interactions (aridity history × drought × defoliation, grazing history × drought × defoliation; Table 2). Results shown in panels A, B, C, and D were consistent with predictions 1.a, 1.b, 2.a, and 2.b from Table 1, respectively. Untransformed means ± SE are presented.

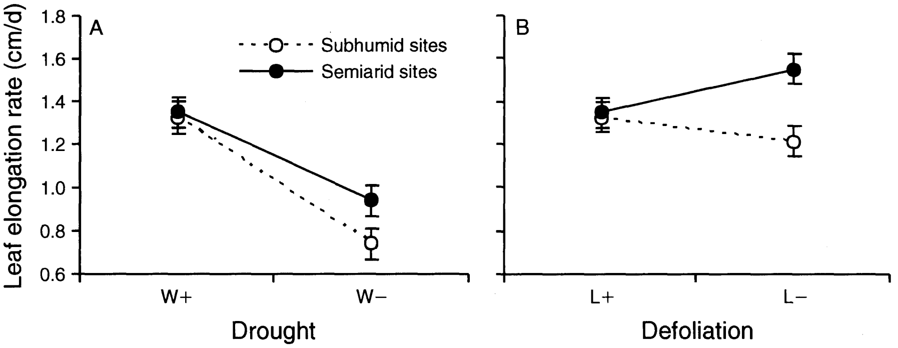

FIG. 3. Differential effect of drought (W+ [well watered] or W− [low watered]) and defoliation (L+ [non-defoliated] or L− [defoliated]) on leaf elongation rate of plants with different aridity history (subhumid sites or semiarid sites): (A) aridity history × drought interaction ($P < 0.0001$); (B) aridity history × defoliation interaction ($P = 0.0080$). P values were obtained using the SLICE statement to enter within control level of factors defoliation (panel A) or drought (panel B) significant triple interaction (aridity history × drought × defoliation; Table 2). Results shown in panels A and B were consistent with predictions 1.a and 2.a from Table 1, respectively. Means ± SE are presented.

In addition, for well watered plants we encountered significant interactive effects of aridity history × defoliation ($P < 0.0001$) and grazing history × defoliation ($P < 0.0001$). Aridity history × defoliation interaction showed, consistent with prediction 2.a (Table 1), that plants from semiarid sites increased more inflorescence production in response to defoliation than plants from subhumid sites (Fig. 2C). Also, grazing history × defoliation showed, consistent with prediction 2.b (Table 1), that plants from heavily grazed sites increased more inflorescence production in response to defoliation than plants from lightly grazed sites (Fig. 2D). Differences in response to defoliation between plants from semiarid and subhumid sites, were similar to those for plants from heavily and lightly grazed sites. *Plant seed biomass* showed similar patterns with number of inflorescences (Table 2), suggesting that the biomass of seeds per plant depends more on the number of inflorescences than on the biomass of seeds per inflorescence (data not shown, mean value for all treatments = 0.26 g/inflorescence, coefficient of variation = 21.5%).

Plants subjected to drought showed in general 35% lower *leaf elongation rate* than well-watered plants (0.89 vs. 1.36 cm/day, respectively; $P < 0.0001$). Strikingly, plants from semiarid sites had in general 17% higher leaf elongation rate than plants from subhumid sites (1.21 vs. 1.03 cm/day, respectively; $P = 0.0130$). However, there was a significant triple interaction aridity history × drought × defoliation ($P = 0.0366$; Table 2), involving the double interactions of interest (listed in Table 1). Consistent with prediction 1.a (Table 1), we found that non-defoliated plants from semiarid sites presented less decline in leaf elongation rate due to drought than those from subhumid sites (aridity history × drought; $P < 0.0001$; Fig. 3A). On the other hand, consistent with prediction 2.a (Table 1), we found that well-watered plants from semiarid sites increased leaf elongation rate in response to defoliation, while plants from subhumid sites decreased it (aridity history × defoliation; $P = 0.0080$; Fig. 3B).

Drought caused a decrease of 29% in *leaf appearance rate* and of 24% in the *number of live tillers* ($P < 0.0001$ in both cases; Table 2). Defoliation, instead, increased leaf appearance rate by 14% ($P = 0.0036$; Fig. 4A) and the number of live tillers by 12% ($P = 0.0120$; Fig. 4B). None of the interactions of interest had a significant effect on these variables.

Plants subjected to drought had 37% lower *total biomass* ($P < 0.0001$; Table 2) than well watered plants (52.2 vs. 83.0 g/plant, respectively). However, defoliation did not change total biomass (averaging both watering levels, defoliated plants were 65.7 g/plant and non-defoliated plants were 69.5 g/plant). None of interactions of interest had significant effect on total biomass.

Grazing avoidance

Consistent with prediction 2.d (Table 1), plants from heavily grazed sites showed lower leaf blade *digestibility* than plants from lightly grazed sites ($P = 0.0149$; Table 3). Despite the fact that green blades presented higher digestibility than senesced blades (tissue type; $P < 0.0001$), difference in digestibility between plants with different grazing history was consistent in both blade classes (grazing history × tissue type, $P = 0.3237$; Fig. 5A).

Starch concentration at the end of the experiment was affected by aridity history of plants ($P = 0.0149$), but not by grazing history (Table 3). We detected significant aridity history × tissue type interaction ($P = 0.0129$), and thus we compared starch concentration of plants of semiarid and subhumid sites separately for each tissue type. Consistent with prediction 2.c (Table 1), plants from semiarid sites had higher starch concentration in stem bases ($P = 0.0007$), but not in roots ($P = 0.9697$), than plants from subhumid sites (Fig. 5B). In general, stem bases had clearly a higher starch concentration than roots ($P < 0.0001$; Fig. 5B). *Soluble carbohydrate*

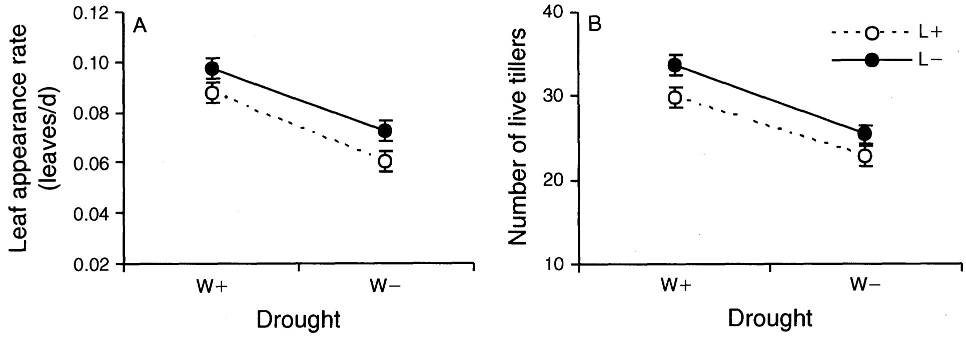

FIG. 4. (A) Drought (W+ [well watered] or W− [low watered]; $P < 0.0001$) and defoliation (L+ [non-defoliated] or L− [defoliated]; $P = 0.0036$) effects on leaf appearance rate. Drought × defoliation interaction was not significant ($P = 0.7001$). (B) Drought ($P < 0.0001$) and defoliation ($P = 0.0120$) effects on number of live tillers. Drought × defoliation interaction was not significant ($P = 0.4959$). Means ± SE are presented.

concentration in stem bases and roots did not change with aridity or grazing history of plants and was significantly higher in stem bases than in roots (0.76% vs. 0.26%, respectively; $P < 0.0001$; Table 3).

Consistent with prediction 2.c (Table 1), plants from semiarid sites presented lower *shoot : root ratio* ($P = 0.0171$; Table 3) than plants from subhumid sites (Fig. 5C). However, opposite to prediction 2.c (Table 1), plants from semiarid sites showed higher *plant height* than plants from subhumid sites ($P < 0.0001$; Table 3; Fig. 5D).

DISCUSSION

This study is, to the best of our knowledge, the first one to show direct, experimental evidence of convergence between aridity and grazing as selective pressures acting on both drought resistance and grazing resistance. Aridity selected *Trichloris crinita* individuals with not only higher drought resistance, but also higher defoliation tolerance, lower shoot : root ratio, and higher starch concentration in stem bases. In turn, grazing selected individuals with not only higher defoliation tolerance and lower leaf blades digestibility, but also higher drought resistance. The only variable in which we obtained a result opposite to predictions was plant height, as plants from semiarid sites were taller than plants from subhumid sites (Table 4). As all these results were obtained in a common garden experiment, they can be attributed to genetic differences between plants from different origins (Wu and Jain 1978).

The amount of variables showing higher plant drought and grazing resistance, increased with the aridity and grazing pressure at the site of origin. Plants from semiarid and heavily grazed site showed the highest number of variables related to drought and grazing resistance, while plants from subhumid and lightly grazed site showed the opposite pattern (Table 4). In our study, aridity seems to be more important than grazing history as a determinant of the number of drought- and grazing-resistance-related traits, perhaps because aridity acted upon these populations for a longer time than grazing did.

Previous investigation focused only on the idea that both aridity and grazing are forces that select higher grazing resistance in plants (Milchunas and Lauenroth 1993, Adler et al. 2004), but they did not explore their influence on drought resistance. Milchunas and Lauenroth (1993) found that resistance to grazing of plant communities, estimated as the difference of biomass production between grazed and ungrazed areas, increased with site aridity and grazing history. Adler et al. (2004) found that plants from arid ecosystems with

TABLE 3. Probability values of fixed-effect factors for variables related to grazing avoidance.

Fixed-effect factors	Digestibility	Starch	Soluble carbohydrates	Shoot : root ratio	Height
A	0.9644	0.0149*	0.4879	0.0171*	<0.0001***
G	0.0149*	0.9637	0.0644	0.1548	0.5344
A × G	0.4910	0.6349	0.4600	0.2844	0.7554
T†	<0.0001***	<0.0001***	<0.0001***		
A × T	0.5851	0.0129*	0.9557		
G × T	0.3237	0.7273	0.5306		
A × G × T	0.2778	0.6845	0.1176		

Notes: Variables were measured only in well-watered and non-defoliated plants. Mixed-model analysis results were obtained by using the REML method in MIXED procedure (SAS Institute 1996). Complete tables of analysis results are shown in Appendix B. Blank cells indicate model terms that were not evaluated. For those variables, tissue type was not included as a source of variation. Abbreviations are as follows: A, aridity history; G, grazing history; T, tissue type.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

† Tissue type was green or senesced leaf blades for digestibility, and stem bases or roots for starch and soluble carbohydrates.

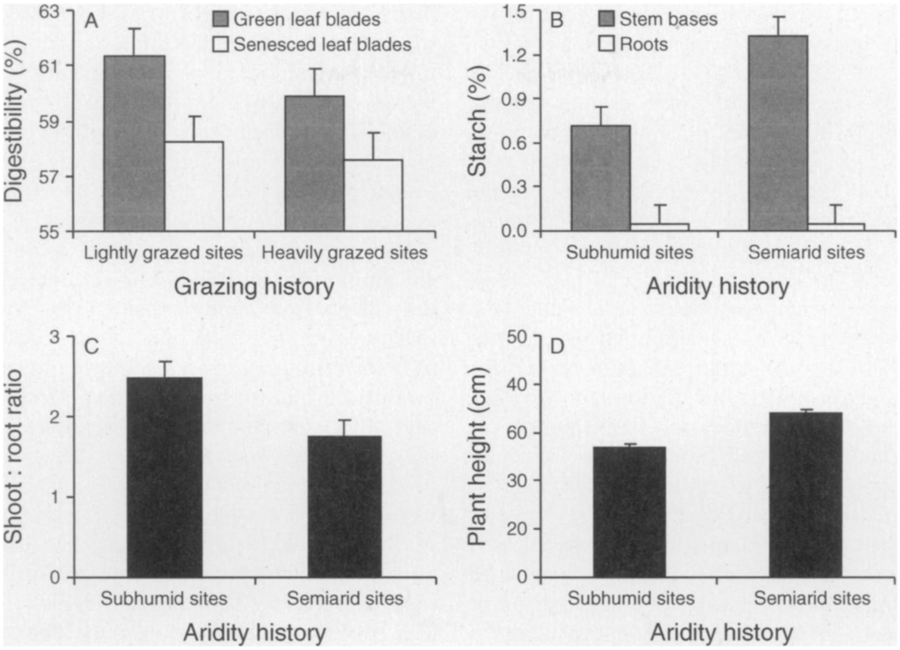

FIG. 5. (A) Variation in digestibility due to grazing history (lightly grazed sites or heavily grazed sites; $P = 0.0149$) and tissue type (green leaf blades or senesced leaf blades; $P < 0.0001$). Grazing history × tissue type interaction was not significant ($P = 0.3237$). (B) Aridity history (subhumid sites or semiarid sites) × tissue type (stem bases or roots) interactive effect on starch concentration ($P = 0.0129$). Slicing this interaction (using the SLICE statement), indicated that starch concentration differs between plants from subhumid and semiarid sites when considering stem bases ($P = 0.0007$) but not when considering roots ($P = 0.9697$). (C) Aridity history effect on shoot : root ratio ($P = 0.0171$). (D) Aridity history effect on plant height ($P < 0.0001$). The four variables were measured only in well-watered and non-defoliated plants. Results shown in panel (A) were consistent with prediction 2.d from Table 1; those shown in panels (B) and (C) were consistent with prediction 2.c from Table 1, and those shown in panel (D) were opposite to prediction 2.c in Table 1. Means + SE are presented.

high grazing pressure history were shorter, and then more able to evade grazing, than those from communities with low grazing pressure history. Also, they found that within communities subjected to high grazing pressure history, plants from arid sites had tissues with lower nutritional quality than plants from subhumid sites (Adler et al. 2004). However, none of these studies assessed the differences in response to drought and

TABLE 4. Synthesis of results obtained for drought resistance and grazing resistance (resulting from defoliation tolerance and grazing-avoidance-related characteristics) of plants of the four origin sites (HL, subhumid and lightly grazed; HH, subhumid and heavily grazed; AL, semiarid and lightly grazed; AH, semiarid and heavily grazed).

Variable	HL	HH	AL	AH	Reference
Drought resistance					
No. inflorescences and plant seed biomass†	−	+/−	+/−	+	Fig. 2A, B
Leaf elongation rate	−	−	+	+	Fig. 3A
Grazing resistance					
Defoliation tolerance					
No. inflorescences and plant seed biomass†	−	+/−	+/−	+	Fig. 3C, D
Leaf elongation rate	−	−	+	+	Fig. 3B
Grazing avoidance					
Leaf blade digestibility	−	+	−	+	Fig. 5A
Starch concentration in stem bases	−	−	+	+	Fig. 5B
Shoot : root ratio	−	−	+	+	Fig. 5C
Plant height	+	+	−	−	Fig. 5D

Notes: The last column indicates reference figures where the involved results can be observed. We excluded results in which we did not find differences in drought resistance, defoliation tolerance (leaf appearance rate, total biomass, number of live tillers), or grazing avoidance capacity (starch concentration in roots, soluble carbohydrate concentration in stem bases and roots) among populations. Sign representations are as follows: +, higher resistance, tolerance, or avoidance; −, lower resistance, tolerance, or avoidance; +/− intermediate resistance or tolerance.

† The variables "number of inflorescences" and "plant seed biomass" were considered together because results obtained for the second of them can be attributed to results obtained for the first (see *Results*).

defoliation between plants with different evolutionary history of grazing and aridity in a common environment.

In our study, regardless of plant origin, drought affected negatively all variables related to fitness, as would have been expected given the central role played by water in plant function. By contrast, the damage imposed by defoliation was fully compensated (biomass production) or overcompensated (number of inflorescences, plant seed biomass, and number of live tillers). As far as our experimental conditions mimic actual field grazing conditions, these results supported the hypothesis that herbivory in some situations can increase plant fitness (McNaughton 1993). In addition, for two key variables related to sexual reproduction (number of inflorescences and plant seed biomass) we found an interactive effect between drought and defoliation ($P < 0.05$; Table 2). There was a stronger positive response to defoliation in well watered plants than in water stressed plants; this agrees with Maschinski and Whitham's (1989) prediction of better chances of compensation of herbivory in plants under higher resource availability.

The aforementioned responses to drought and defoliation were different according to plant site history. Plants from semiarid sites and heavily grazed sites showed, respectively, higher inflorescence and seed biomass production in response to drought and defoliation than plants from subhumid sites and lightly grazed sites (Fig. 2A–D). However, no differences were observed between populations in response to drought and defoliation in terms of total biomass or number of live tillers. This suggests differential reproductive effort (key to the fecundity component of fitness) between plants from different origins in response to drought and defoliation. Vail (1992) and Agrawal (2000) argued that the maintenance of a large proportion of inactive reproductive meristems until an herbivory event occurs would be a strategy to enhance seed production in environments when the probability of herbivore damage is high, avoiding the consumption of the reproductive investment. These authors also pointed out that this strategy would imply a disadvantage for plants in the absence of herbivory, because it would imply lower reproduction. Our results are consistent with these concepts, since plants from heavily grazed sites presented better response to defoliation and lower inflorescence and seed biomass production in the absence of it (Fig. 2D). This pattern not only was repeated for the response to defoliation/no defoliation of plants from semiarid vs. subhumid sites (Fig. 2C), but also for the response to drought/no drought of plants from semiarid vs. subhumid (Fig. 2A) and heavily vs. lightly grazed sites (Fig. 2B). In line with Vail's (1992) and Agrawal's (2000) view, we think that the lower inflorescence and seed biomass production under no-stress conditions could be a cost paid by plants of semiarid or heavily grazed sites for their adaptation to drought or high grazing pressure. Our results led us to extend concepts of previous models in plant adaptation to herbivory (Vail 1992, Agrawal 2000) to models on plant adaptation to drought. We suggest that a mechanism involving inactivity of reproductive meristems in absence of aerial tissue damage (no defoliation or no drought) could be genetically selected in environments with high probability of herbivory, and also in environments with high probability of water-stress-induced damage to plant tissues.

Plants from semiarid sites also had higher leaf elongation rates in response to drought and defoliation than plants from subhumid sites (Fig. 3A, B), although they did not differ in response to drought or defoliation in terms of total biomass, leaf appearance rate, or tiller production. This suggests that plants from semiarid sites that were subjected to drought or defoliation would have a relatively higher resource allocation to leaf tissue production than plants from subhumid sites. Rapid recovery of photosynthetic surfaces, even at the expense of the growth of other organs, has been mentioned as a valuable adaptation to grazing and drought (McNaughton 1979, Coughenour 1985, Milchunas et al. 1988, Fernández and Reynolds 2000).

Plants of different origins also differed in variables related to grazing avoidance. Plants from heavily grazed sites showed lower leaf blade digestibility than plants from lightly grazed sites (Fig. 5A). Plants with lower leaf blade digestibility would have a comparative advantage in environments where herbivores are abundant, because they selectively consume high quality tissues (Mooney and Gulmon 1982, Coughenour 1985). As digestibility is inversely related to cellulose and lignin content (Rohweder et al. 1978), this trait is likely to contribute to aridity resistance (Stebbins 1981, Coughenour 1985). Higher cellulose and lignin concentration in leaf blades would be associated with high-density (low-water-content) tissues with a greater contribution of cell walls, a common drought-resistance trait (Grime 1977, Orians and Solbrig 1977, Chapin et al. 1993, Fernández and Reynolds 2000). These results underscore the difference between adaptive and plastic responses to grazing. Our data are an example of an adaptive response: populations coming from heavily grazed sites have lower leaf digestibility than those coming from lightly grazed sites (Fig. 5A). This contrasts with what have been found as a plastic response: that individuals of similar genotype have more digestible leaves when subjected to high grazing intensity than when subjected to light grazing intensity (e.g., Coppock et al. 1983).

On the other hand, plants from semiarid sites had a lower shoot : root ratio and higher starch concentration in stem bases than plants from subhumid sites (Fig. 5B, C). Maintaining lower shoot : root ratio would represent an advantage for plants in semiarid conditions (Orians and Solbrig 1977) and also under heavy grazing (Milchunas et al. 1988, Stowe et al. 2000), because it implies a proportionally smaller amount of transpiring and reachable tissues, and a greater amount of tissues for water absorption and reserve storing. Additionally, higher carbon reserves in stem bases would allow plants to improve their chances of survival during dry periods (Volaire and Thomas 1995) and to have more resources for regrowth after water stress or defoliation (Coughenour 1985, Hochwender et al. 2000). In accordance, we found that plants from semiarid sites, in comparison to those from subhumid sites, coped better with drought and defoliation in terms of leaf elongation rate and inflorescence and seed biomass production.

We did not find an effect of grazing history on plant height, which is at odds with previous studies which showed a decrease in plant height even with a short history of grazing (Detling and Painter 1983, Jaramillo et al. 1988, Painter et al. 1993). The larger height of plants from semiarid sites was contrary to our prediction 2.c (Table 1) and is an uneven result to that of Adler et al. (2004). In our study, the differentiation in plant height might have been a consequence of the selection exerted by the high solar radiation and soil temperatures of semiarid sites (e.g., much higher than those recorded in the Patagonian and Colorado steppes studied by Adler et al. [2004]). We found a positive correlation between plant height and tiller angle with respect to soil surface (data not shown), showing that taller plants had more erect tillers. Keeping aerial tissues at a near-vertical position can be a useful trait in dry and hot environments because it reduces solar radiation incidence in the warmest hours of the day, thus likely reducing heat load and transpiration requirements (Nobel 1999). In addition, bearing taller and more vertical tillers would allow plants to maintain more aerial tissues away from the soil surface, source of the highest temperatures in arid and semiarid environments (Campbell and Norman 1998), which also would reduce transpiration requirements.

Regardless of its theoretical importance, our work also has important applied consequences in terms of rangeland management. On the one hand, our results suggest the importance of grazing management as a control of tiller density, leaf tissue production, and plant reproductive effort in *T. crinita*. Both the absence of defoliation and intensive defoliation could be detrimental for the species. In the first case, sexual and vegetative reproduction might be constrained (defoliation promoted inflorescences and live tillers production); in the second case, the storage of reserves could be affected by total or partial removal of stem bases. On the other hand, our results provide relevant information about the influence of high/low water availability conditions on vegetative growth and seed production of the species, and thus it can be used to support rangeland management decisions during and after dry or rainy years. We have learned that when a dry growing season occurs it would be advisable to reduce grazing pressure, not only because plants would be less able to support defoliation but also because they are producing low quantities of seeds. In contrast, a rainy growing season offers us the opportunity of resting paddocks with poor rangeland condition to favor seedling establishment (key to colonization by the species; Pezzani and Montaña 2006, Quiroga et al. 2009) and concentrating animals in paddocks with good rangeland condition, taking into account that grasses there would be more able to support defoliation.

Results of our study also provide valuable information for the quest of plant materials with potential to be used in restoration. It seems important to consider the origin of the source when collecting plant material to restore vegetation in any environment, trying as much as possible to match environmental conditions of collecting and restoring sites (McKay et al. 2005). Rice and Emery (2003) further refine this recommendation, pointing out that when collecting plant material for restoration efforts, we also need to provide sufficient genetic variability (i.e., collecting seeds from a set of low-precipitation sites to restore a site with similar environmental characteristics) to permit restored populations to better face environmental challenges.

In addition, our work indicates that populations showed a set of adaptations that would be helpful in their home environment (productivity under no stress, responses to drought and defoliation, morphological and physiological characteristics), confirming the existence of ecotypes (sensu Huffon and Mazer 2003) within the species (Sal 1989, Greco and Cavagnaro 2002). Existent genetic variability could be used in breeding programs to obtain cultivars adapted to aridity and grazing conditions (Lee 1998, Humphreys et al. 2006). It is interesting to know that one could collect plant material in semiarid sites when searching for adaptation to grazing (and vice versa), and better results would be obtained if we collect plant material in semiarid and intensively grazed sites. Our results show the central role played by biotic and abiotic environmental factors on the genetic variability of native species, and highlight the importance for genetic resources conservation, of maintaining populations (in situ conservation) of native species through the range of environmental variability in which they can live (McKay et al. 2005).

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APPENDIX A

Tables with complete results of statistical analysis of variables related to fitness (*Ecological Archives* A020-069-A1).

APPENDIX B

Tables with complete results of statistical analysis of variables related to grazing avoidance (*Ecological Archives* A020-069-A2).