Water stress effects on the seedling growth of *Prosopis argentina* and *Prosopis alpataco*

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Abstract

The expansion of the *Prosopis* genus from the Chaco region towards drier and colder areas would involve several morphological and physiological adaptations that allow these species to occupy different ecological niches. *Prosopis argentina* and *Prosopis alpataco* (Fabaceae, Mimosoideae) are good examples of shrubs adapted to highly stressed environments. *P. argentina* reaches its ecological optimum in sandy soils while *P. alpataco* attains it in clayish, saline and periodically flooded soils. We analysed the effects of water stress on the early seedling growth of *P. argentina* and *P. alpataco*; in addition we discussed the importance of these effects in the ecological success of these species. We used a completely randomized experimental design with two fixed factors: species (*P. argentina* and *P. alpataco*), and two levels of water supply (350 and 1400 mm). Water stress produced a detrimental effect in the seedling growth of both species, which was evident from the reduction in leaf area, seedling height, and above-ground and root biomass. However, plant growth in *P. alpataco* was more strongly affected by water stress than it was in *P. argentina,* as suggested by the significant species-irrigation interactions ($P < 0.05$) found in the height and biomass variables. The proportional growth (biomass reach in water stress in relation to control treatment) was lower in *P. alpataco* (0.14) than in *P. argentina* (0.32). These results indicate that *P. argentina* has a greater tolerance to water deficit during plant establishment. Our results, and the

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morphological features of each species, are consistent with the previous findings that have described *P. argentina* as a xerophyte able to cope with harsh sand-dune conditions, and *P. alpataco* as a phreatophytic species with more mesomorphic features.

1. Introduction

The expansion of the genus *Prosopis* from the Chaco region towards colder and drier zones would involve several morphological and physiological adaptive processes that allow these species to occupy different ecological niches (Burkart, 1976; Burkart and Simpson, 1977; Roig, 1993). Germination and seedling establishment constitute the most critical periods in the life cycle of desert plants (Rathcke and Lacey, 1985; Solbrig and Cantino, 1975; Sosebee and Wan, 1987). Consequently, the presence of adaptations during these stages can determine their natural distribution. Several works (Catalán et al., 1994; Peinetti et al., 1992; Peláez et al., 1994) have studied some ecological and physiological aspects of the establishment of arboreal species of the genus, however little is known about shrub species (López Villagra and Galera, 1992; Vilela et al., 2003; Villagra and Cavagnaro, 2000), despite their importance from an evolutionary point of view.

Prosopis argentina and *Prosopis alpataco* (Fabaceae, Mimosoidea) are shrub species distributed over the Monte Phytogeographical province, in the arid zone of Argentina (Morello, 1958; Villagra and Roig, 2002). These species are good examples of shrubs adapted to highly stressed environments. *P. argentina* reaches its ecological optimum in the loose sandy soils of active dunes; while *P. alpataco* achieves it in heavy, clayish, saline and periodically flooded soils (Villagra and Roig, 2002). In the area where these species are sympatric, the climate is extremely arid. Mean annual rainfall ranges between 80 and 200 mm and mean annual temperature between 15 and 17 °C (Villagra and Roig, 2002).

In a previous study, we analysed the effects of soil type on seedling growth in the absence of water stress, and found that the marked decrease in growth shown by *P. alpataco* in sandy soils could be critical to the survival of this species. In contrast, previous results cannot explain the exclusion of *P. argentina* from clayish environments, which appears to be related to other factors (Villagra and Cavagnaro, 2000). One of these factors is salinity, which strongly affects the establishment of *P. argentina*, especially in clayish soil (Villagra and Cavagnaro, 2005). Frequently, salt tolerance is associated with tolerance to water stress. However, when salt toxicity is the main cause of the effect of salinity, salt tolerance is not necessarily linked to water stress tolerance. In fact, some halophytes can tolerate salt stress but not drought, and some xerophytes can tolerate drought but not salt stress (Zhao et al., 2003; Zhao and Harris, 1992). In the case of *P. argentina*, salt toxicity, rather than the osmotic effects, appears to be the cause of the stronger effect of salinity on

P. argentina (Villagra and Cavagnaro, 2005); therefore, it is possible that this species could tolerate water stress in absence of saline stress.

In this study, we analysed the effects of water stress on the early seedling growth of *P. argentina* and *P. alpataco*; in addition we discussed their importance in the ecological success of these species. We postulated that water stress tolerance is another adaptive factor in the niche differentiation of these species; we expected *P. argentina* to be more tolerant to water stress than *P. alpataco*. We tested the prediction that the growth and biomass allocation in *P. alpataco* is more affected by water stress than in *P. argentina*.

2. Materials and methods

The assay was performed in the experimental field of CRICYT, Mendoza, Argentina (32°53′S; 68°57′W) in the summer of 1996 (January–April), over a period of 100 days. We used seeds collected from habitats where both species grow naturally: *P. argentina* from the Telteca Reserve (Lavalle, Mendoza, Argentina) (32°21′S, 67°55′W) and *P. alpataco* from Asunción (Lavalle, Mendoza, Argentina) (32°34′S, 68°14′W) in January and February of 1994. Seeds were manually separated from their pods and preserved following the methodology proposed by Cony (1993) for other species of the genus. Broken and insect-damaged seeds were discarded. Seeds were scarified with sandpaper in order to break dormancy, and then disinfected by immersion in 70% ethanol for 7 min, followed by 7 min in commercial hypochlorite (60 gl-1 active Cl) diluted to 15% (Villagra, 1995). Finally, they were washed repeatedly with distilled water.

Soil used in the experiment was a loam-clayish soil classified as Typic Torripfluvent Entisols (Moscatelli, 1990) and was obtained from the locality of Asunción where *P. alpataco* is the dominant species. In a previous work, we observed that *P. alpataco* does not grow in sandy soil, so we did not include this type of soil in the experiment (Villagra and Cavagnaro, 2000).

Pots of 10 cm in diameter and 85-cm deep with six 5 mm-holes at the bottom were filled with 9 l (11.5 kg) of air-dried, sieved (5-mm mesh) soil and distributed under a 100 μm-thick yellow polyethylene rain shelter. Light level was 70–85% of the outside light intensity. Two seeds were planted in each pot and, once seedlings became established, pots were thinned to one plant per pot.

We used a completely randomized experimental design with two fixed factors: species (*P. argentina* and *P. alpataco*), and two levels of water supply (350 and 1400 mm). For each of the four treatments, we used seven replicates of 12 plants each, i.e. a total of 84 plants per treatment and 336 plants in all. As logistical constraints prevented us from measuring all variables in all plants, each variable was measured in only some (and different) randomly selected plants in each of the seven replicates. We used the mean value of these measurements as the single entry representing the replication.

Pots were watered with tap water (electrolytic conductivity = 850 (μS cm^{-1}). No nutrient was added to the soil. In the treatment without water stress, each pot

received 1 l of water per week (equivalent to 1400 mm over the 100 days of the assay); in the water stress treatment, each pot was watered with 250 ml of water (350 mm during the assay, a little higher than the mean rainfall of the region). To determine the differences in water conditions between treatments, we measured the predawn and noon water potential (ψ_a) with a pressure chamber (Scholander et al., 1965) in one randomly selected plant from four randomly selected replicates between February 6 and March 6, 1996.

At the beginning of the experiment, we randomly selected six plants per replicate. The height of these seedlings was measured periodically (every 6–15 days). At the end of the experiment (100 days after sowing) leaf, stem and root dry matter, as well as the number of leaves and leaf area were registered for one randomly selected plant in each of the seven replicates. Roots were obtained after washing the soil. Root and shoot dry weights were recorded after oven-drying at 60 °C for 72 h. Leaf area was determined with a leaf area meter LI-COR, model 3000. We estimated the specific leaf area as the ratio between leaf area and leaf biomass (Hunt, 1978).

To compare the effect of water stress on both species, we calculated the "proportional growth" of each species as the ratio between the mean biomass reached in the water stress treatment and that of the control treatment. We used this calculation based on Munns (2002), who reported that stress tolerance is usually assessed as the proportion of biomass production under stress conditions in relation to that produced under control conditions.

Growth data were subjected to a two-way analysis of variance (ANOVA), and water potential data to an analysis of variance for repeated measure. Tukey's test was used for comparison of means (Zar, 1984). As seedling height and biomass data did not meet the ANOVA assumption of variance homogeneity, a $\ln(x+1)$ transformation was applied (Zar, 1984).

3. Results

The lower water potential observed at both pre-dawn and noon in the water stress treatment indicates that irrigation with 350 mm of water was efficient to generate water stress in both species (Fig. 1, Table 1).

The level of water supply affected the growth of *P. argentina* and *P. alpataco* plants in all variables evaluated. The height of *P. alpataco* decreased more than that of *P. argentina* under water stress conditions (species-irrigation level interaction: $F = 7.98$; $P = 0.0096$) (Table 2, Fig. 2).

Plants of both species showed a decrease in total biomass, biomass of leaves, stems and roots, leaf area, and number of leaves under water stress conditions (Table 3). This decrease was stronger in *P. alpataco* than in *P. argentina* as indicated by the significant species-irrigation level interactions and the higher proportional growth reached by *P. argentina* compared to *P. alpataco* under water stress (Table 3). The specific leaf area was not affected by water stress and was higher in *P. alpataco* than in *P. argentina* under both irrigation conditions (Table 3).
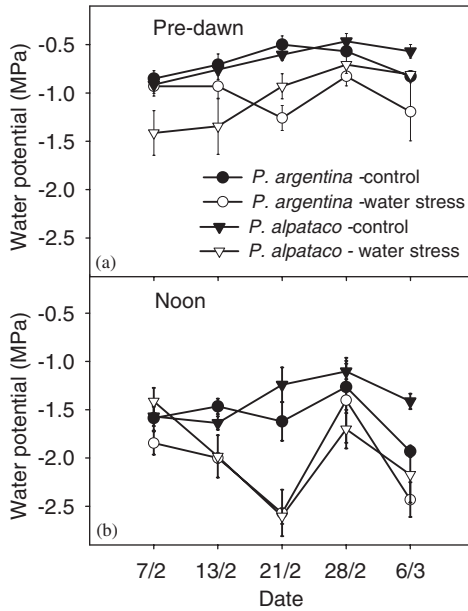
Fig. 1. Water potential of *P. argentina* and *P. alpataco* in the control treatment (1400 mm) and under water stress (350 mm) measured at pre-dawn and noon. Points represent means and vertical lines the standard error.

Table 1
Results of the analysis of variance for repeated measures performed on pre-dawn and noon water potentials

Effects	Pre-dawn				Noon			
	df	MS	*F*	*p*	df	MS	*F*	*p*
(A) Species	1	0.01	0.15	0.70	1	0.31	1.85	0.21
(B) Irrigation levels	1	2.06	23.15	<0.001	1	3.8	22.4	0.001
A × B	1	0.04	0.43	0.53	1	0.09	0.51	0.49
Error	11	0.09			8	0.17		
(C) Date	4	0.30	4.16	0.006	4	0.79	7.41	<0.001
C × A	4	0.20	2.72	0.041	4	0.07	0.65	0.63
C × B	4	0.08	1.15	0.34	4	0.59	5.52	0.002
C × A × B	4	0.09	1.17	0.33	4	0.24	2.28	0.08
Error	44	0.07			32	0.11		

The shoot–root ratio decreased equally in both species under water stress conditions (Table 3). The proportion of leaf and stem biomass decreased, whereas the proportion of root biomass increased with water stress in both species. *P. argentina* allocated a higher proportion of biomass to stems, and a lower proportion to leaves, than *P. alpataco* under both water conditions (Table 2, Fig. 3).

Table 2
Results of the analysis of variance performed on seedling height 96 days after sowing, and on percentage of biomass allocated to leaves, stems and roots

| Variables	Effects	df	MS	F	P
Final height	(A) Species	1	0.02	2.06	0.1647
	(B) Irrigation levels	1	4.98	458.36	<0.0001
	A × B	1	0.09	7.98	0.0096
	Error	23	0.01		
Leave percentage	(A) Species	1	0.04	21.03	0.0001
	(B) Irrigation levels	1	0.03	19.03	0.0002
	A × B	1	0.0001	0.03	0.87
	Error	24	0.0018		
Stem percentage	(A) Species	1	0.02	5.42	0.03
	(B) Irrigation levels	1	0.14	33.22	<0.0001
	A × B	1	0.0015	0.36	0.55
	Error	24	0.0043		
Root percentage	(A) Species	1	0.0004	0.06	0.81
	(B) Irrigation levels	1	0.28	42.65	<0.0001
	A × B	1	0.0016	0.25	0.62
	Error	24	0.01		
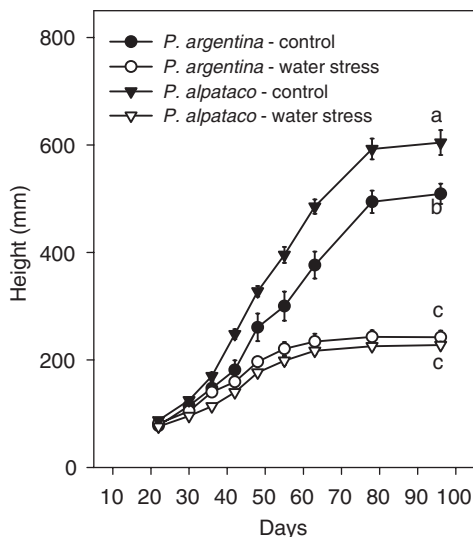
Fig. 2. Effects of irrigation level on the height of *P. argentina* and *P. alpataco* seedlings. Points represent means and vertical lines the standard error. Different letters between treatment combinations indicate significant differences at $P < 0.05$.

Table 3
Effects of the irrigation level on the growth variables measured in *P. argentina* and *P. alpataco*

Species	P. argentina		P. alpataco		Anova results		
Irrigation	Control	Water stress	Control	Water stress	Species	Irrigation	Species × irrigation
Biomass							
Leaves (mg)	297.4 b	66.2 d	1152.9 a	131.4 c	$F = 120; P < 0.001$	$F = 383; P < 0.001$	$F = 11.9; P < 0.002$
Stems (mg)	1120.5 b	260.1 c	2795.3 a	305.3 c	$F = 22.6; P < 0.001$	$F = 237; P < 0.001$	$F = 8.29; P < 0.001$
Roots (mg)	578.1 b	309.3 b	1675.2 a	404.2 b	$F = 20.5; P < 0.001$	$F = 39.8; P < 0.001$	$F = 6.48; P < 0.02$
Total (mg)	1996.0 b	635.6 c	5623.4 a	840.8 c	$F = 35.6; P < 0.001$	$F = 177; P < 0.001$	$F = 10.0; P < 0.004$
Proportional growth							
Shoot/root ratio	2.85	1.18	2.45	1.16	Not analysed	$F = 30.9; P < 0.001$	$F = 0.49\ P = 0.49$
Leaf area (cm²)	34.3 b	8.12 d	165.3 a	19.6 c	$F = 0.65; P = 0.42$	$F = 151; P < 0.001$	$F = 13.9; P < 0.001$
Number of leaves	14.7 b	6.7 c	64.1 a	16.1 b	$F = 177; P < 0.001$	$F = 151; P < 0.001$	$F = 13.9\ P = 0.001$
Specific leaf area	0.11	0.11	0.14	0.15	$F = 24.8; P < 0.001$	$F = 0.14; P = 0.7$	$F = 0.51; P = 0.48$

Measures were taken on day 96 after sowing. Different letters in each variable indicate significant differences at $P < 0.05$.
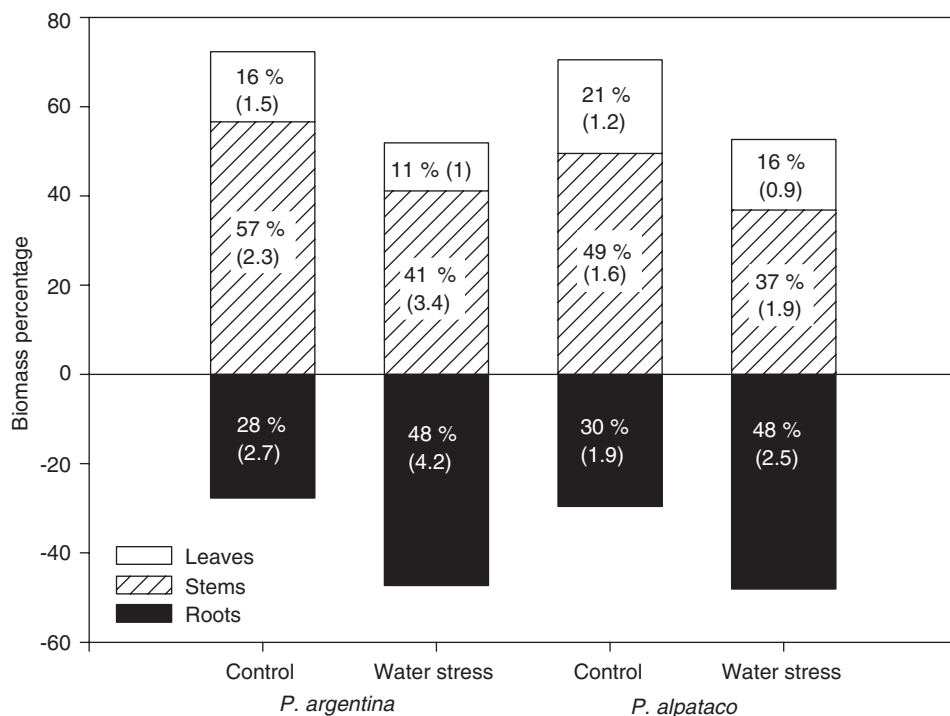
Fig. 3. Biomass allocation by *P. argentina* and *P. alpataco* seedlings growing under different irrigation levels (control: 1400 mm and water stress: 350 mm). Values represent mean (standard error) percentages of dry matter allocated to leaves, stems and roots.

4. Discussion

Stress-tolerant plants have a suite of morpho-physiological traits that allow them to survive in stress conditions, but reduces potential growth in the absence of stress (Chapin III et al., 1993; Grime, 1977; Orians and Solbrig, 1977). Therefore, those species with adaptive mechanisms to stress conditions usually show lower phenotypic plasticity than non-adapted species. As a consequence, the proportion of biomass reduction under stress in relation to control conditions can be used to estimate stress tolerance in a species (Munns, 2002). In the *Prosopis* genus, Vilela et al. (2003) found that *Prosopis alba*, a species from relatively high-resource environments, took advantage of increased water while *Prosopis strombulifera,* from poor environments, showed no differences in growth among different water availabilities. In this study, the response of each species to water stress treatments was different as suggested by the lower proportional growth of *Prosopis alpataco*. In addition the significant species-irrigation interactions in most of the variables measured (leaf, stem and total biomass, leaf area, and leaf number). *P. alpataco* was more affected by water stress than *P. argentina,* in agreement with the postulated hypothesis.

P. argentina should then have mechanisms allowing it to survive under stress conditions but preventing it from taking advantage of water availability. The analysis of morphological and anatomical features suggests that this species presents "drought tolerance with high water potential of the tissues", characterized by a conservative use of water through different morphological adaptations (Jones et al., 1981; Turner, 1979). One adaptation that we observed is that *P. argentina* shows a marked xeromorphism, evidenced by a smaller leaf area, a lower number of leaves and a smaller specific leaf area. In addition, other authors have reported thick cuticles (Burkart, 1976), greater leaf pubescence (Vilela, 1996), the presence of green photosynthetic stems, and a higher number of small grouped vessels in the wood maximizing the safety of the hydraulic system (Villagra and Roig Juñent, 1997). In contrast, *P. alpataco* shows more mesophytic features, such as a larger leaf area, a larger specific leaf area, thinner cuticles, lower leaf pubescence, and big solitary vessels (Vilela, 1996; Villagra and Roig Juñent, 1997).

In a previous study we suggested that the higher salt tolerance of *P. alpataco* could be related to its ability to counteract the toxic effect rather than the osmotic effect of salt (Villagra and Cavagnaro, 2005). This idea is reinforced by the lower tolerance of *P. alpataco* to water stress observed in this paper, which suggests that this species would be even more affected than *P. argentina* by the osmotic effect of saline solutions. This agrees with conclusions of other authors that have postulated that physiological and ecological responses are different in halophytes versus xerophytes (Zhao et al., 2003; Zhao and Harris, 1992).

The presence of adaptations that induce higher drought tolerance in *P. argentina* could be important to the survival of this species in sand dunes, where it uses the scarce rainfall water accumulated in the deep soil layers. In contrast, the higher effects of water stress on *P. alpataco* could contribute to the exclusion of this species from sand dunes, when water stress interacts with the strong detrimental effects of sandy soils, as observed for this species in a previous work (Villagra and Cavagnaro, 2000). The mesophytic features shown by *P. alpataco* suggest that this species needs wet periods to become established, perhaps after the flooding events that are typical of the environments where it naturally grows (Villagra, 1998). Additionally, in these areas, established plants can take advantage of water complement if their roots reach the water-table. This is consistent with the postulates of Roig (1987) and Villagra (1998) suggesting that it is a phreatophytic species.

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