

Effects of clayish and sandy soils on the growth of *Prosopis argentina* and *P. alpataco* seedlings

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ABSTRACT. *Prosopis alpataco* Burk. and *P. argentina* Phil. occupy areas with different soil characteristics within the arid zone of Argentina. *Prosopis alpataco* occurs in periodically flooded, clayish and saline soils, whereas *P. argentina* occurs in non-saline sand dunes. The capability to occupy these different habitats might be related to the presence of different adaptive features in these two species. We analyzed seedling growth of both species on clayish and sandy soils. Their emergence percentages, seedling height, biomass, and leaf area were measured in a factorial experiment (species x soils) carried out in a greenhouse. Both species showed a higher growth rate (height, biomass, leaf area and number of leaves and shoot-root ratios) in clayish soils. In sandy soils, the growth rate of *P. alpataco* was lower than that of *P. argentina*, indicating that the detrimental effects of sandy soils were greater for *P. alpataco*. We suggest that soil effects on growth could be due to the differences in nutrient (especially nitrogen) availability, and that *P. argentina* shows adaptations to sandy soils which are absent in *P. alpataco*. These results could explain the exclusion of *P. alpataco* from sandy soils but not that of *P. argentina* from clayish soils. Exclusion of this last species should be associated with other environmental factors like flooding or salinity, or with biological factors such as competition.

RESUMEN. Efecto de los suelos arcillosos y arenosos en el crecimiento de plántulas de *Prosopis argentina* y *P. alpataco*: *Prosopis alpataco* Burk. y *P. argentina* Phil. ocupan áreas con características edáficas diferentes dentro de la zona árida Argentina. *Prosopis alpataco* se encuentra en suelos arcillosos y salinos, sometidos a inundaciones esporádicas, mientras que *P. argentina* se encuentra en los suelos arenosos, no salinos, de los médanos. La capacidad de ocupar estos ambientes estaría relacionada con la presencia de diferentes adaptaciones en estas dos especies. En este trabajo, analizamos comparativamente el crecimiento de plántulas de ambas especies en suelos arenosos y arcillosos. El porcentaje de emergencia, la altura, la biomasa y el área foliar de las plántulas fueron medidos en un experimento factorial (especies x suelos) llevado a cabo en condiciones de invernáculo. Las dos especies muestran una mayor velocidad de crecimiento en (altura, biomasa, área foliar, número de hojas y relación vástago-raíz) en suelos arcillosos. En suelos arenosos, la tasa de crecimiento de *P. alpataco* fue menor que el de *P. argentina*, indicando que el efecto perjudicial de los suelos arenosos fue mayor en *P. alpataco*. Sugerimos que los efectos del suelo sobre el crecimiento podrían deberse a las diferencias en la disponibilidad de nutrientes, especialmente nitrógeno, y que *P. argentina* tiene adaptaciones a los suelos arenosos que están ausentes en *P. alpataco*. Estos resultados podrían explicar la exclusión de *P. alpataco* de los suelos arenosos pero no la exclusión de *P. argentina* de los suelos arcillosos. En este caso la exclusión debe relacionarse con otros factores como el anegamiento, la salinidad o con el efecto de interacciones biológicas como la competencia.

INTRODUCTION

The great morphological diversity of the South American *Prosopis* species and their pattern of flavonoid chemistry (Carman 1973) suggest that this genus had a radiation center

in the Argentinean-Paraguayan Chaco. From there, by speciation, it may have spread over more xeric areas toward the south and west (Burkart 1976; Burkart & Simpson 1977; Roig 1993). Probably this expansion involved several adaptive processes, such as the change from tree to shrub form, leaf reduction, and the capacity for seed germination and seed-

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ling establishment under the harsh conditions of arid lands.

In arid zones, water availability is the most important factor limiting seedling establishment (Noy-Meir 1973) and, consequently, the structure and dynamics of ecosystems. In these areas, edaphic factors operate almost always by modification of the water regime. However, soil texture can also act as a mechanical factor that controls root penetration (Brar & Palazzo 1995). In addition, soils differ in the amount, quality, and spatial and temporal distribution of nutrients. The occupation of different edaphic environments by plants implies the presence of adaptations that allow species to reproduce and grow in the particular conditions of each soil type.

Prosopis argentina Burk. and *P. alpataco* Phil. (Fabaceae, Mimosoideae) are good examples of species adapted to extreme edaphic conditions. At the regional scale, both species are sympatric in a part of their distribution area within the Monte desert, located in the arid zone of western Argentina (average annual rainfall <350 mm) (Figure 1). However, at the community or local scale, these species occupy clearly differentiated edaphic niches. No communities have been found with both species coexisting (Villagra 1998). *Prosopis argentina* reaches its ecological optimum, with the highest densities and the largest individuals, in the loose sandy soils of active dunes, while *P. alpataco* achieves its ecological optimum in heavy, clayish, saline and periodically flooded soils. 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 is between 15 and 17 °C (Villagra 1998). Aside from texture, the main difference between soils is the higher concentration of salts and nitrogen observed in clayish soils (Table 1). In addition to xeric climatic conditions, both edaphic environments display very adverse conditions for the establishment and growth of most plant species (Noy-Meir 1973; Miller 1986; Danin 1991; Brar & Palazzo 1995).

Adaptations to adverse conditions could be found on any stage of the life cycle of a plant and in many functional processes. However, since germination and establishment stages are considered the most critical periods in the life cycle of desert plants (Solbrig & Cantino

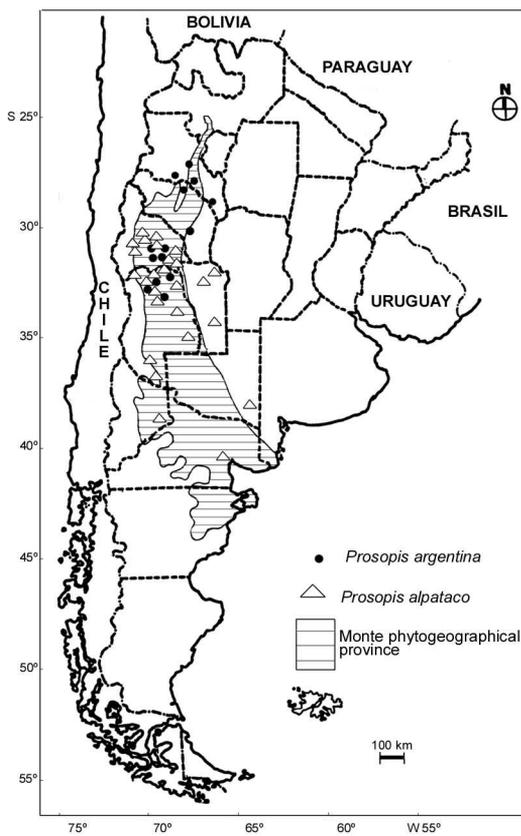


Figure 1. Geographical distribution of *Prosopis argentina* and *P. alpataco* in Argentina (adapted from Villagra 1998).

Figure 1. Distribución geográfica de *Prosopis argentina* y *P. alpataco* en Argentina (adaptado de Villagra 1998).

1975; Rathcke & Lacey 1985; Sosebee & Wan 1987), the presence of adaptations during these stages can determine their natural distribution. In the case of *Prosopis* species, establishment and early growth could be affected by soil conditions such as nutrient (especially nitrogen) availability (Van Auken & Bush 1989; Jarrel & Virginia 1990; Imo & Timmer 1992) and salinity (Felker et al. 1981; Villagra 1997). However there is little information about the effect of soil texture on the establishment of *Prosopis* species (Cox et al. 1993).

Considering that soil characteristics seem to be a crucial factor in determining the niche separation of *P. argentina* and *P. alpataco*, we evaluated the effects of the soil type on the establishment and growth of *P. argentina* and *P. alpataco* seedlings, and discussed the possible relations with the distribution of these species.

Table 1. Physical and chemical properties of sandy and clayish soils where *P. argentina* and *P. alata* reach their greater development (Lavalle, Mendoza, Argentina). Values are the min. and max. of four samples taken, except for the texture analysis where a pool from the four samples was used (Villagra 1998). AEC: Actual Electrical Conductivity.

Tabla 1. Propiedades físicas y químicas de los suelos arenosos y arcillosos donde *P. argentina* y *P. alata* alcanzan su mayor desarrollo (Lavalle, Mendoza, Argentina). Los valores son el mín. y máx. de cuatro muestras, excepto para el análisis de la textura, donde se agruparon las cuatro muestras (Villagra 1998). AEC: conductividad eléctrica.

Origin	Asunción	Telteca Reserve
Environment	Clayish soil periodically flooded	Sand dunes
Dominant species	<i>P. alata</i>	<i>P. argentina</i>
Soil classification	Typic Torrifluvent Entisol	Typic Torripsament Entisol
Texture	Clayish	Sandy
Sand (%)	21.31	47.10
Internat. silt (%)	30.18	18.15
American silt (%)	41.60	27.50
Clay (%)	6.43	2.86
Field capacity (%)	33	8.5
AEC ($\mu\text{S}/\text{cm}$)	2551–7280	321–382
Ca ⁺⁺ (me/l)	29.8–44.4	2–2.5
Mg ⁺⁺ (me/l)	4.4–6.8	0.2–0.3
Na ⁺ (me/l)	13.2–14.5	0.63–1.2
RAS	2.86–4.2	1.03–1.14
pH	7.02–7.5	8.03–8.15
N (ppm)	392–735	84–171
P (ppm)	5.53–8.36	6.01–7.96
K (ppm)	236–626	230–782
Organic matter (%)	0.52–1.25	0.16–0.39

We wonder if the type of soil is the sole factor determining niche separation, or if it requires interaction with other factors such as water stress or competition. Should it be the principal factor, we would expect *P. argentina* to grow faster (in length and biomass) than *P. alata* in sandy soils, and the converse to occur in clayish soils.

MATERIALS AND METHODS

The assay was performed in the experimental field of CRICYT, Mendoza (32°53'S; 68°57'W) in the summer of 1996 (January to

April), over a period of 100 days. We used *P. argentina* seeds collected from Telteca Reserve (Dpto. Lavalle, Mendoza, Argentina) and *P. alata* seeds collected from Asunción (Dpto. Lavalle, Mendoza, Argentina) 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 ones 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 hypochloride (60 g/L active Cl) diluted to 15% (Villagra 1995). Finally they were washed repeatedly with distilled water.

The two types of soil for the experiment were obtained from the same places where the seeds were collected: sandy soil (classified as Typic Torripsament Entisols; Moscatelli 1990) from dunes in Telteca Reserve where the dominant species is *P. argentina*, and clayish soil (classified as a Typic Torrifluvent Entisols; Moscatelli 1990) from the locality of Asunción where *P. alata* is the dominant species. Table 1 shows the physical and chemical characteristics of these soils from composite samples taken at four different sites for each locality. Texture was analyzed from a pool of the four sites samples (Villagra 1998).

Pots of 10 cm in diameter and 85-cm deep with six 5 mm holes at the bottom were filled with 9 L of air-dried, sieved (5-mm mesh) soil (14.5 kg for sandy soil and 11.5 kg for clayish 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.

A completely randomized experimental design with two factors (species and soils) was followed. For each treatment combination we used 84 plants, divided into seven groups of 12 plants each. Each group was a replication for the different observations made but, as logistical constraints prevented us from measuring all variables in all plants, each variable was measured in only some (and different) plants in each repetition ($n = 7$ in all cases). We use the mean value of these measurements as the single entry representing the replication.

Table 2. Final percentage and rate of emergence of *P. argentina* and *P. alpataco* in the two types of soils. Different letters indicate significant differences at $P < 0.05$.

Tabla 2. Porcentaje final y tasa de emergencia de *P. argentina* y *P. alpataco* en los dos tipos de suelo. Las letras diferentes indican diferencias significativas con $P < 0.05$.

Species - Soil type	Emergence percentage	Emergence rate
<i>P. argentina</i>		
Sandy	60.7 b	9.6 b
Clayish	48.2 b	6.7 b
<i>P. alpataco</i>		
Sandy	69.0 a	16.3 a
Clayish	68.4 a	14.5 a
Species-soil interactions	$F = 1.316$ $P = 0.262$	$F = 0.202$ $P = 0.656$

Pots were periodically watered to maintain the water content near field capacity. We made sure that water availability was the same for all plants by measuring seedling water potential once a week, by using a pressure chamber (Scholander et al. 1965) at pre-dawn and mid-day, in four plants randomly selected in each treatment combination. For these measures we used a total of four plants per replicate.

Seedling emergence, defined as the development of the first true leaf, was daily recorded in every pot throughout the first 10 days, and expressed as percentage of seeds sown in each of the seven replicates. The emergence rate was calculated using Maguire's equation (M) (Naylor 1981):

$$M = \frac{n_1}{t_1} + \frac{n_2}{t_2} + \dots + \frac{n_{10}}{t_{10}},$$

where n_1, n_2, \dots, n_{10} represent the number of seedlings emerged at times t_1, t_2, \dots, t_{10} (in days).

Seedling height was measured periodically (every 6–15 days) in six randomly-selected plants per replicate.

At the end of the experiment (100 days after sowing), leaf, stem and root dry matter, the number of leaves and leaf area were registered in one randomly-selected plant in each of the seven replications. Root biomass was measured at different depths. In order to do this,

each pot was divided into four 20-cm long cylinders from which roots were obtained by washing. 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.

Data were subjected to a two-way analysis of variance (ANOVA) with species and soils as factors. Tukey's test was used for comparison of means. As some data did not meet the ANOVA assumptions, they were previously transformed according to the following criteria: arcsin(square root (x)) transformation was applied to emergence percentages (x), and log ($x + 1$) transformation was applied to seedling height (x) and root biomass (x) (Zar 1984).

RESULTS

Both the final percentage and the rate of emergence in *P. alpataco* were significantly higher ($P < 0.05$) than in *P. argentina* regardless of the type of soil (species-soil interactions not significant at $P < 0.05$). These parameters showed no differences between soils (Table 2).

Seedling height at day 100 showed significant species-soil interaction ($F = 63.72$; $P < 0.0001$), indicating that the type of soil affected the growth of *P. argentina* and *P. alpataco*

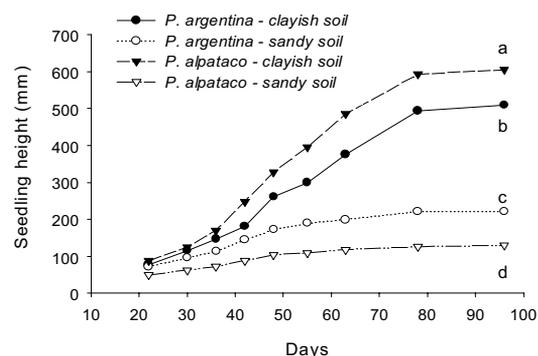


Figure 2. Soil effects on seedling height of *P. argentina* and *P. alpataco*. Different letters indicate significant differences at $P < 0.05$. Species-soil interaction was significant ($F = 63.72$; $P < 0.00001$).

Figure 2. Efecto del tipo de suelo sobre la altura de plántulas de *P. argentina* y *P. alpataco*. Las letras diferentes indican diferencias significativas con $P < 0.05$. La interacción especie-suelo fue significativa ($F = 63.72$; $P < 0.00001$).

Table 3. Leaf area, number of leaves and internode length (mean \pm SE) of seedlings of *P. argentina* and *P. alpataco* growing in different soils. Different letters in leaf area and in number of leaves indicate significant differences at $P < 0.05$. For internode length, different small letters indicate significant differences at $P < 0.05$ between species, and capital letters indicate differences between soils.

Tabla 3. Área foliar, número de hojas y largo de entrenudos (promedio \pm EE) de plántulas de *P. argentina* y *P. alpataco* creciendo en diferentes suelos. Las letras diferentes en área foliar y en número de hojas indican diferencias significativas con $P < 0.05$. Para el largo de entrenudos, diferentes letras minúsculas indican diferencias significativas entre especies con $P < 0.05$, mientras que las letras mayúsculas indican diferencias entre suelos.

Species - Soil type	Leaf area (cm ²)	Number of leaves	Internode length (mm)
<i>P. argentina</i>			
Sandy	5.8 \pm 0.8 a	6.29 \pm 0.4 a	29.7 \pm 0.7 aB
Clayish	32.7 \pm 2.8 b	12.00 \pm 1.5 b	36.3 \pm 0.9 aA
<i>P. alpataco</i>			
Sandy	4.4 \pm 0.5 a	13.83 \pm 1.0 b	10.7 \pm 0.2 bB
Clayish	165.3 \pm 16.2 c	64.14 \pm 7.1 c	17.0 \pm 0.6 bA
Species-soil interactions	$F = 66.48$ $P < 0.00001$	$F = 22.03$ $P = 0.0001$	$F = 0.048$ $P = 0.83$

differently. Seedlings were taller in clayish soils for both species, but each species grew taller than the other in the type of soil where it naturally grows (Figure 2).

Total leaf area was larger in clayish than in sandy soil for both species (Table 3). In clayish soil, *P. alpataco* showed a greater leaf area than did *P. argentina*, while no differences were ob-

served between species in sandy soil. The type of soil affected the leaf area and the number of leaves of *P. alpataco* more intensely than those of *P. argentina*, as significant species-soil interactions indicate. Leaf area of *P. alpataco* in sandy soil was 37 times less than it was in clayish soil, while in *P. argentina* it was only 5 times less. *Prosopis argentina* had fewer leaves than *P. alpataco* in both soils, and internodes of *P. argentina* were longer than those of *P. alpataco* in both soils (Table 3).

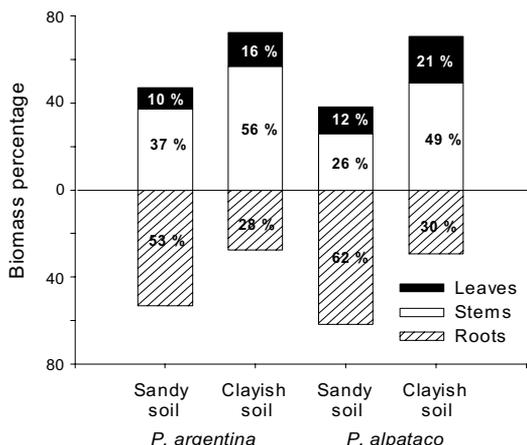


Figure 3. Biomass allocation in *P. argentina* and *P. alpataco* seedlings growing in different soils. Values represent the percentage of dry matter allocated to leaves, stems and roots.

Figura 3. Partición de biomasa en plántulas de *P. argentina* y *P. alpataco* creciendo en suelos diferentes. Los valores representan el porcentaje de materia seca en hojas, tallos y raíces.

In both species, shoot and root biomass was greater in clayish soil (Table 4). However, in this type of soil plant biomass was greater in *P. alpataco* than in *P. argentina*, whereas in sandy soil differences were no significant (species-soil interaction significant at $P < 0.05$). This indicates that the soil effect was greater in *P. alpataco* than in *P. argentina*; thus, this species produced approximately 40 times more leaf biomass, 45 times more shoot biomass and 10 times more root biomass in clayish soil, while *P. argentina* only increased 6, 7 and 4.2 times more, respectively (Table 4). The shoot-root ratio was higher in clayish soil in both species and no differences were found between species (species-soil interaction not significant: $F = 0.06$, $P = 0.81$) (Table 4 and Figure 2). *Prosopis alpataco* allocated more biomass to leaf formation than *P. argentina*, while *P. argentina* allocated a greater proportion to shoot formation than *P. alpataco* (Figure 3). No differences between species were observed in the propor-

Table 4. Leaf, stem, root and total biomass, shoot-root ratio and leaf-stem ratio of *P. argentina* and *P. alpataco* seedlings growing in different soils. Different letters within the same variable indicate significant differences at $P < 0.05$.

Tabla 4. Biomasa de hoja, tallo, raíz y total, relación vástago-raíz y relación hoja-tallo de plántulas de *P. argentina* y *P. alpataco* creciendo en suelos diferentes. Letras diferentes en una misma variable indican diferencias significativas con $P < 0.05$.

Species - Soil type	Biomass (mg)				Shoot-root ratio	Leaf-stem ratio
	Leaves	Stems	Roots	Total		
<i>P. argentina</i>						
Sandy	47.8 c	177.9 c	227.2 c	465.2 c	0.93 b	0.26 b
Clayish	297.4 b	1120.5 b	578.1 b	1995.9 b	2.86 a	0.28 b
<i>P. alpataco</i>						
Sandy	28.8 c	61.9 d	153.8 c	244.5 c	0.66 c	0.47 a
Clayish	1152.9 a	2795.3 a	1675.2 a	5623.4 a	2.45 a	0.42 a
Species-soil interactions	$F = 21.8$ $P = 0.0001$	$F = 54.4$ $P < 0.0001$	$F = 31.7$ $P < 0.0001$	$F = 57.7$ $P < 0.0001$	$F = 0.06$ $P = 0.81$	$F = 0.69$ $P = 0.41$

tion of biomass allocated to root formation. In clayish soil both species presented a greater proportion of root biomass in the upper 20-cm than in deeper layers (Figure 4). However, in sandy soil, root biomass was distributed more homogeneously in the whole soil profile. In clayish soil, *P. alpataco* showed more root biomass in the upper layers than *P. argentina* (0–20 cm and 20–40 cm) while no differences between species were found in the deeper layers (40–60 cm and >60 cm).

DISCUSSION

Both the final percentage and the rate of emergence were higher in *P. alpataco* regardless of the type of soil. These differences could be related to the observations of Villagra (1995), who found that *P. alpataco* have more vigorous seedlings in spite of its smaller seeds (18 mg for *P. alpataco* and 34.5 mg for *P. argentina*). In contrast with the observations of Cox et al. (1993), who found that clayish soils diminish the seedling emergence of *P. velutina* and prevent that of *Acacia constricta*, the type of soil did not affect seedling emergence in *P. argentina* and *P. alpataco*.

The type of soil affected the growth of *P. argentina* and *P. alpataco*: differences in height, number of leaves, leaf area, shoot and root biomass, and root distribution were observed between the seedlings of these species growing in different soils. This effect of soil type on growth was different for the two species.

Consistently with the postulated hypothesis, each species showed greater growth (in height and biomass) than the other in the soil where it naturally grows. This suggests that the type of soil is an important factor in determining the different distribution of these species. However, both species attained greater growth in clayish soil, even *P. argentina* that has never been found in environments with this type of soil (Villagra 1998). It is then evident that the physiological optimum of *P. argentina*, regarding to soil type, markedly differs from its ecological optimum (Crawley 1997). This suggests that the role of the interactions with other species (such as competition) or with other physical factors (such as salinity) may be crucial in limiting at least the distribution of *P. argentina*.

In arid zones, water availability is the major factor limiting ecosystem productivity; edaphic factors operate almost always by modifying the water regime (Noy-Meir 1973). In this study water availability was not an environmental constraint; consequently, the greater growth observed in clayish soils may be the result of differences in nutrient availability between both soils, especially in nitrogen content (Table 1). In this case, since soils affected both species differentially, *P. alpataco* would be less tolerant to nutrient limitations than *P. argentina*, which could be due to differences in their nutrient absorption capacity or in use efficiency (Chapin et al. 1987). In other *Prosopis* species, nitrogen availability has been observed to have several effects on both

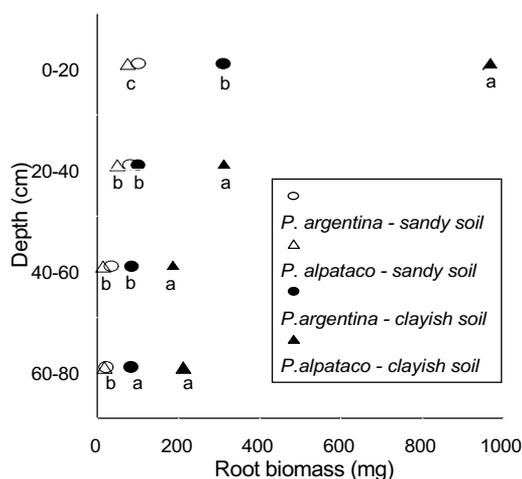


Figure 4. Root biomass distribution in the soil profile of *P. argentina* and *P. alpataco* seedlings growing in different types of soils. Different letters at the same depth indicate significant differences at $P < 0.05$. Species-soil interactions were significant in the 0–20-cm ($F = 25.17$, $P = 0.00005$) and the 20–40-cm-deep layers ($F = 11.69$, $P = 0.02$), and not significant in the 40–60-cm ($F = 1.98$, $P = 0.17$) or the >60-cm-deep layers ($F = 2.77$, $P = 0.19$).

Figura 4. Distribución de la biomasa radical en el perfil del suelo de plántulas de *P. argentina* y *P. alpataco* creciendo en diferentes tipos de suelos. Letras diferentes a la misma profundidad indican diferencias significativas con $P < 0.05$. La interacción especie-suelo fue significativa con $P < 0.05$ en las profundidades 0–20 cm ($F = 25.17$, $P = 0.00005$) y 20–40 cm ($F = 11.69$, $P = 0.02$), y fue no significativa en las profundidades 40–60 cm ($F = 1.98$, $P = 0.17$) y >60 cm ($F = 2.77$, $P = 0.19$).

plant growth and biological interactions. For example, increased nitrogen availability results in increased growth rate and final biomass in *P. chilensis* (Imo & Timmer 1992) and *P. glandulosa* (Van Auken & Bush 1989; Jarrel & Virginia 1990), reduced competitive capacity in *P. glandulosa* (Van Auken & Bush 1989), and increased susceptibility to salinity in *P. glandulosa* (Jarrel & Virginia 1990). Besides, various species of the genus are capable of fixing nitrogen through their symbiosis with N-fixing bacteria (Felker & Clark 1980, 1982; Diagne & Baker 1994; Aiazzi et al. 1995). *Prosopis argentina* and *P. alpataco* are able to develop nodules in both soils (PE Villagra, pers. obs.) but the potential amount of N fixed by these species is totally unknown. The analysis of nitrogen dynamics in these species is beyond the scope of this study and could be the aim of another experiment.

Grime (1977) and Chapin et al. (1993) suggested that plants with adaptations to some environmental stress show their adaptive features even though they grow in absence of such stress, and termed this suite of features a “stress resistance syndrome”. *Prosopis argentina* retained, even in clayish soil, typical characteristics of plants from low-resource environments as leaf reduction, a greater proportion of stem biomass, and lower growth rate. The lesser phenotypic plasticity of *P. argentina* could be the result of the adaptation of this species to sandy soils and can represent a stress resistance syndrome.

Several authors (Miller 1986; Brar & Palazzo 1995) proposed that in sandy soils roots penetrate deeper than in clayish soils, while in the latter roots accumulate near the soil surface. In agreement with these authors, we found a greater root concentration in the upper 20 cm of clayish soils, whereas in sandy soils roots were more homogeneously distributed down the whole soil profile. However, *P. alpataco* showed a greater proportion of root biomass in the upper 40-cm than *P. argentina* regardless of soil type. This can be interpreted as an adaptation to clayish soils where available water is near the surface, since water infiltration to deeper layers is very low (Noy-Meir 1973, Solbrig et al. 1977). In contrast, the adaptive mechanism of *P. argentina* would be to develop a deep root system that allows it to use the water accumulated in deeper layers by percolation.

The present assay did not reproduce some of the main constraining factors occurring in sand dunes, such as plant burial in sites of sand accumulation, root exposure at deflation sites, injury of aerial parts by particle impact, or extremely high surface temperatures (Danin 1991). Thus, the marked decrease in growth shown by *P. alpataco* in sandy soils could be critical to the survival of this species when such factors occur. In this sense, the longer internodes of *P. argentina* can be an advantage allowing plants to reduce the buried leaf biomass and to overcome sand burial.

Finally, it is evident that clayish soils do not limit the growth of *P. argentina*, at least under no water limitation. Therefore, the exclusion of this species from environments with clayish soils should be related to other factors like flooding or excessive salinity, or to some biological factors such as competition.

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