

# The effect of radiation on seedling growth and physiology in four species of *Prosopis* L. (Mimosaceae)

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Domestication of wild plants needs efforts focused particularly on the development of the theoretical basis of plant responses to environmental conditions. The objective of this study was to assess the effect of radiation on seedling growth and physiology of *Prosopis alba*, *P. chilensis*, *P. flexuosa* and *P. glandulosa*. Seedlings were grown in a greenhouse and randomly assigned to three light environments: full-sun, 52% sun, and 38% sun. No significant differences were found in the rate of leaf appearance and plant height 60 days after the light treatments began. Instantaneous  $CO_2$  uptake was not affected by the light environment during leaf development and did not differ among species. Variations in radiation availability resulted in significant differences in biomass accumulation, shoot/root ratio, protein and total non-structural carbohydrates contents. The practice of shading seedlings reduces the chances of survival of *Prosopis* due to an increase of the shoot/root ratio and a reduction of total biomass, stored carbohydrates, and the C:N balance.

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# Introduction

The genus *Prosopis* L. is distributed throughout America, Asia and Africa. Most species (29 of 44) are native to Argentina and six of them have potential for commercial cultivation. Although *Prosopis* trees are among those species that hold great promise for the conservation and development of drylands (Sene, 1996) and many of them are extensively used for timber and fodder, no commercial plantations currently exist in Argentina.

Indigenous trees like *Prosopis alba*, *P. chilensis* and *P. flexuosa*, whose products have traditionally been gathered from natural forests, can be integrated into designed agroforestry or silvopastoral systems. According to Nair (1998), and Leakey & Simons (1998), domestication, improvement and exploitation of indigenous trees should be a major focus of agroforestry research in the 21st century, because the use of these trees,

which provide important environmental services or economically valuable products, should result in land use that is both sustainable and productive.

Domestication of wild plants needs efforts focused particularly on the development of the theoretical basis of the physiological responses of plants to environmental stresses, since agroforestry systems are intended mostly for areas with environmental limitations to plant growth.

Few attempts, in this respect, have been undertaken to understand the performance of *Prosopis* species under the constraints imposed by the environment in arid and semi-arid lands: Villagra (1995) studied the effect of temperature on the germination of *P. argentina* and *P. alpataco*; Cony & Trione (1998) computed the salt concentration that lowered germination of *P. flexuosa* and *P. chilensis*; Imo and Timmer (1992) determined the N level required for optimum growth in *P. chilensis*; and Ortiz *et al.* (1995) discussed the physiological implications of the responses of *P. chilensis* to temperature stress. The effect of light on growth and establishment of mesquite has been indirectly suggested by Stromberg (1993) and Mooney *et al.* (1977).

The objective of this study was to assess the effect of radiation on seedling growth and physiology of four species of *Prosopis*: *P. alba*, *P. chilensis* (trees), *P. flexuosa* and *P. glandulosa* (shrubs and trees). We evaluated potential assimilation, rate of leaf appearance, plant height, biomass partition and composition 60 days after seed germination. This information could help in the understanding of seedling establishment in native stands, as well as aid in the design of proper propagation techniques for nurseries and reforestation programmes.

#### Materials and methods

Seeds of *Prosopis alba*, *P. chilensis* and *P. flexuosa*, obtained from ripe pods collected in the Monte phytogeographic region of Argentina, and seeds of *P. glandulosa*, provided by the Desert Legume Program of the University of Arizona, collected in Tucson, AZ, U.S.A., were mechanically scarified (Ffolliott & Thames, 1983) and planted in tree tubes  $(40 \times 150 \text{ mm})$  filled with commercial nursery mix (ground sphagnum, peat moss and vermiculite). Voucher specimens of South American species are deposited in BAFC.

Seedlings were grown in a greenhouse at 14/38°C (night/day). Plants were assigned to one of three light environments: (1) direct solar radiation (hereafter referred to as full-sun); (2) 47% reduction in direct solar radiation (hereafter referred to as 53% sun); and (3) 62% reduction in direct solar radiation (hereafter referred to as 38% sun). The shade was provided by black 100% polypropylene fabric; this fabric did not alter the red/far-red ratio of the incoming radiation (Ballaré *et al*, 1991). On selected days, photosynthetic photon flux density (PPFD) was measured hourly from dawn to dusk using a LI-189 Quantum meter (LICOR Inc., Lincoln, Nebraska), and integrated through 24-h periods for each light environment.

All plants were irrigated three times a week and fertilized once  $(9:45:15, NH_4:P_2O_5:K_2O)$  in a randomized complete block design (three blocks and 10 reps/block). The rate of leaf appearance was recorded up to 56 days after seeded (DAS). Net CO<sub>2</sub> uptake (A) was measured using an LCA-3ADC portable infrared analyser open gas exchange system (Analytical Development Co, Hoddesdon, U.K.). Gas exchange was measured from 09 00 to 15 00. At the end of the experiment (60 DAS) the total height of every plant was recorded, plants were harvested, and leaves, stems and roots separated and weighed (10 plants per species and light treatment). Total non-structural carbohydrates (TNC) were extracted by autoclaving (0·1 MPa, 15 min) 50 mg of biomass in 100 ml of distilled water. Samples were homogenized in 100 ml of water and in every case the solubilized sugars were determined by the anthrone method (Yemm & Willis, 1954). Nitrogen determination was based on the Kjeldahl method.

A protein Digestion System G 1007 (Tekator, Höganäs, Sweden) with a Kjeltec System 1002 nitrogen determinator was used. The C:N ratio was determined by computing the amount of TNC (C) and nitrogen (N) content, respectively.

Statistical analysis of the data was performed using the Duncan's Multiple Range Test with significance at p = 0.05. The number of replicates was 10 per treatment except for gas exchange measurements in which n = 3.

### **Results and discussion**

No significant differences were found in the rate of leaf appearance (RLA) among radiation treatments (data not shown). For all species, the first true leaf appeared 12 DAS (Fig. 1). RLA was similar among species up to leaf number 3 (7 days and 2·7 days for leaves numbers 2 and 3, respectively). From leaf number 4 on, *P. alba* showed a significantly lower RLA than *P. chilensis* and *P. glandulosa*, while *P. flexuosa* presented the highest rate (6·7, 5·8, 5·6, and 4·8 days leaf<sup>-1</sup> for *P. alba*, *P. chilensis*, *P. glandulosa*, and *P. flexuosa*, respectively, for leaf numbers 1 to 8, p < 0.01; Fig. 1). This pattern resulted in a significantly different final number of leaves when plants were harvested 56 days after the experiment was initiated (p < 0.01; data not shown).



**Figure 1.** Rate of leaf appearance of four *Prosopis* species: ( $\blacktriangle$ ) *P. flexuosa*, ( $\blacksquare$ ) *P. alba*, ( $\blacklozenge$ ) *P. chilensis*, and (X) *P. glandulosa.*. Mean  $\pm$  S.E. for 25 plants.



**Figure 2.** Total dry weight (g plant<sup>-1</sup>) of 60-day plants of four *Prosopis* species: ( $\blacktriangle$ ) *P. flexuosa*, ( $\blacksquare$ ) *P. alba*, ( $\blacklozenge$ ) *P. chilensis*, and (X) *P. glandulosa*. Mean  $\pm$  S.E. for 10 plants.

Radiation availability did not affect plant height at harvest-time. Plant height showed a trend (p < 0.01) from the tallest *P. flexuosa* (21.2 cm) to *P. glandulosa* (11.2 cm), with intermediate *P. chilensis* and *P. alba* (17.6 and 13.9 cm, respectively). Lee *et al.* (1992) reported that the seedlings obtained from the progeny of one *P. flexuosa* tree were taller than those from several *P. alba* and *P. glandulosa* trees at 8 months, but *P. glandulosa* and *P. alba* were taller and accumulated more biomass when measured at 27 months of age.

Instantaneous CO<sub>2</sub> uptake measured under full-sun conditions was not affected by the light environment in which leaves grew and did not differ among species (between 9·9 and 11·7  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>). Similar A values have been reported for establishing *P. glandulosa* seedlings growing under well-watered field conditions (Soyza *et al.*, 1996).

Differences in radiation availability resulted in significant differences in biomass accumulation (p < 0.01; Fig. 2). Total biomass was reduced 24% and 38% on average for plants under 52% sun and 38% sun. *P. chilensis* accumulated significantly more biomass in all radiation environments than the other species (p < 0.01; Fig. 2), while *P. glandulosa* and *P. alba* gained the least biomass.

The shoot/root ratio significantly increased with reductions in radiation availability considering all species together (1.9, 2.0, and 2.3, for full sun, 52% sun, and 38% sun,



**Figure 3.** Biomass allocation to roots ( $\blacksquare$ ), stems ( $\blacksquare$ ) and leaves ( $\square$ ) of four *Prosopis* species grown under three light environments: full-sun (FS), 52% sun and 38% sun.

respectively; p < 0.05). Within each species, only in *P. chilensis* did light availability significantly increase the shoot/root ratio between full-sun, 52% sun and 38% sun (p < 0.01). *P. alba* showed the lowest shoot/root ratio and *P. chilensis* and *P. flexuosa* the highest (Fig. 3; p < 0.01). While there was no effect of radiation, the species differed on the proportion of leaves in the shoot (p < 0.01; 1.4, 1.2, and 0.8 for *P. chilensis*, *P. flexuosa*, and *P. glandulosa* respectively). The combined effect of higher shoot/root ratio with no changes in leaf/stem ratio resulted in a slight increase in the proportion of leaf biomass under shading conditions only for *Prosopis alba* and *Prosopis chilensis*. In general, although shading tends to increase the proportion of total dry matter allocated to leaves, the influence is small (Bjorkman, 1981).

Protein content was about half in stems and roots compared to in leaves (Table 1). The reduction in light availability increased the protein content in leaves in *P. glandulosa* and *P. flexuosa* from full-sun to 52% sun, and in *P. chilensis* and *P. alba* throughout the range of radiation. Protein content increased throughout the range of light availability in stems of *P. alba* and *P. flexuosa*, as well as in the roots of *P. glandulosa*, *P. alba*, and *P. chilensis*. TNC content in shoots decreased with reductions in light availability in all

Species	Plant part	Protein content (% of D.W.)		
		Full-sun	52% sun	38% sun
Prosopis alba	Leaves	14·6	20·1	20.2
	Stem	6·6	9·3	10·1
	Roots	7·0	7·7	7·9
Prosopis chilensis	Leaves	12·0	16·9	20·2
	Stem	8·2	6·8	8·4
	Roots	6·1	6·5	7·1
Prosopis <i>flexuosa</i>	Leaves	12·8	17·3	14·9
	Stem	7·7	8·2	8·4
	Roots	6·5	7·6	7·2
Prosopis glandulosa	Leaves	18·2	19·6	18·6
	Stem	9·6	9·3	10·0
	Roots	8·0	10·1	11·1

**Table 1.** Protein content of leaves, stems and roots (% of D.W.) for four Prosopis species. Four plants harvested 56 days after seeded were pooled in each sample

species except *P. chilensis* (Table 2). The decrease in TNC between full-sun and 52%-sun plants and between full-sun and 38%-sun plants, was smaller in *P. alba* and *P. glandulosa* than that found for biomass. Similarly, root TNC was lower for *P. alba* and *P chilensis* grown under reduced light availability, although the decrease was less than that found for biomass (Table 2). In *P. glandulosa* a similar reduction in TNC was found for 52%-sun and 38%-sun plants compared to that of control (full-sun) plants (Table 2). Only small changes in TNC were found in roots of *P. flexuosa* associated to radiation availability (Table 2). Fluctuations in root TNC between 35% and 15% have been reported for *P. glandulosa*, the lowest values found 45 days after bud-break (during the period of active growth) and during flowering and fruit-set (Wan & Sosebee, 1990). Recharge periods have been associated with high water availability and the completion of pod formation and seed filling. In other tree species TNC availability is related to plant vigour and defense mechanisms (Landsberg & Gower, 1997). For example, in

Species	Plant Part	TNC (% of D.W.)		
		Full-sun	52% sun	38% sun
Prosopis alba	Shoot	26.9	24.9	20.6
	Root	24.5	22.0	17.4
Prosopis chilensis	Shoot	26.7	28.2	26.0
	Root	26.6	23.1	18.0
Prosopis flexuosa	Shoot	26.4	25.8	16.0
1 5	Root	20.7	22.0	20.1
Prosopis glandulosa	Shoot	29.3	23.8	22.5
	Root	25.8	22.1	23.5

 Table 2. Total non-structural carbohydrates content (TNC) of shoots and roots (% of D.W.) for four Prosopis species. Four plants harvested 56 days after seeded were pooled in each sample

Species	C:N ratio (TNC/Total N content)				
	Full-sun	52% sun	38% sun		
Prosopis alba	2.8	1.9	1.5		
Prosopis chilensis	3.0	2.6	1.9		
Prosopis flexuosa	2.8	2.3	1.7		
Prosopis glandulosa	2.4	1.9	1.7		

**Table 3.** C: N ratio (whole plant) for four species of Prosopis

*Prunus dulcis* grown under arid conditions, higher TNC availability could have been responsible for early bud-break in older tress (Heilmeier *et al.*, 1997). These trees were able to assimilate  $CO_2$  during a period of lower atmospheric VPD and extend the length of the season for photosynthesis that resulted in higher water use efficiency. Also, plants grown under full-sun conditions have a higher content of carbohydrate reserves, which are important for new leaf expansion in case of leaf shedding under water stress (Hartmann *et al.*, 1990, p. 161).

Changes in TNC were balanced with changes in protein contents, resulting in similar C: N ratios among species. On the other hand, there was a clear reduction in C: N with reduced radiation availability (Table 3). Changes in C:N related to light availability, as well as its effect on secondary metabolism, have been reported for other species and are the base for the carbon/nutrient balance hypothesis (Bryant *et al.*, 1983; Herms & Mattson, 1992). Concentrations of C-based secondary metabolites decline as the limited available carbon is allocated to growth. Exudated gums (C-based secondary metabolites) have been suggested as a defense mechanism against invading microorganisms (Marques *et al.*, 1982). As for other C-based secondary metabolites, their production should be related to the C:N ratio (Herms & Mattson, 1992). The reduction in C:N found in our experiment should decrease the defense capability of plants grown under reduced radiation.

## Conclusion

Although shading is a common practice in plant nurseries, when used in *Prosopis* it not only reduced the total biomass, TNC reserves and C:N ratio, but also increased the shoot/root ratio. All these characteristics should lessen the chances of *Prosopis* survival under field conditions since vigour and survival of seedlings and many of the responses to environmental stresses are directly related to size, biomass allocation and amount of stored carbohydrates (Puttonen, 1986).

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