

Water status, drought responses, and growth of *Prosopis flexuosa* trees with different access to the water table in a warm South American desert

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Received: 15 March 2010 / Accepted: 27 December 2010 / Published online: 8 January 2011
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Abstract *Prosopis flexuosa* trees dominate woodlands in the Central Monte Desert (Mendoza, Argentina), with <200 mm rainfall, exploiting the water table recharged by Andean rivers, and also growing in dunes with no access to the water table. *Prosopis* woodlands were extensively logged during development of the agricultural oasis, and surface and groundwater irrigation could lower the depth of the water table in the future. We evaluated tree populations with decreasing access to the water table: valley adult trees, valley saplings, and dune adult trees, in order to assess their ecophysiological response to water table accessibility. High and seasonally stable pre-dawn leaf

water potentials (-2.2 ± 0.2 to -1.2 ± 0.07 MPa) indicated that valley adults utilize larger and more stable water reservoirs than valley saplings and dune adults (-3.8 ± 0.3 to -1.3 ± 0.07 MPa), with higher midday leaf conductance to water vapor (valley adults ~ 250 ; dune adults <60 $\text{mmol m}^{-2} \text{s}^{-1}$), potentially higher CO_2 uptake, and increased radial growth rate (valley adults 4.1 ± 0.07 ; dune adults 2.9 ± 0.02 mm year^{-1}). Trees with poor access to the water table exhibited drought tolerance responses such as midday stomata closure, leaflet closure, and osmotic adjustment. Stomata density decreased in response to drought when leaf expansion was restricted. The combination of phreatophytism and drought tolerance would enlarge *P. flexuosa* habitats and buffer populations against changes in rainfall dynamics and water table depth.

Electronic supplementary material The online version of this article (doi:10.1007/s11258-010-9892-9) contains supplementary material, which is available to authorized users.

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Keywords Dunes · Groundwater · Monte · Phreatophytes

Introduction

Woody phreatophytes play particular ecological and economic roles in deserts, related to their ability to use constantly saturated soil water reservoirs in environments where rainfall is intra and inter-annually variable and scarce (Noy-Meir 1973). They often possess dimorphic root systems where deep roots access groundwater, while lateral roots search for surface moisture and nutrients. They produce higher annual biomass than that predicted by precipitation (Sharifi et al. 1982), and are dominant components of their community, with central roles in ecosystem interactions (Rossi and Villagra 2003; Zou et al. 2005; Simmons et al. 2008), biogeochemical (Schade and Hobbie 2005; Alvarez et al. 2009), and hydrological cycles (Burgess et al. 2000; Hultine et al. 2004).

Prosopis flexuosa D.C. (Fabaceae, Mimosoidae, 'algarrobo dulce') is a phreatophytic tree that dominates open woodlands in the Central Monte Desert, Argentina (Morello 1958), whose presence in a warm arid region is supported by the contribution of groundwater derived from Andean rivers (Torres and Zambrano 2000). *Prosopis* woodlands have historically provided local indigenous people descendant from the *Huarpes* with goods for survival, and were extensively exploited in the twentieth century for vineyard and urban development in the oasis. They were also indirectly affected by human activity, as irrigation with river water has reduced river flows into barren lands and riparian woodlands (Abraham 2000). Increased irrigation supplemented by groundwater extraction could lower the depth of the water table beneath *Prosopis* woodland areas in the future.

Despite the ecological and economic importance of *Prosopis* species, information about their water use and drought responses to surface and groundwater availability in arid South America is scarce (Mooney et al. 1980; Villagra and Cavagnaro 2006; Villagra et al. 2010) compared to the information on *Prosopis* species from North American deserts (e.g., Nilsen et al. 1984; Ansley et al. 1992; Stromberg et al. 1992;

Resco et al. 2009). It has been suggested that receiving less than 350 mm mean annual rainfall *P. flexuosa* needs access to constantly saturated soil water reservoirs (Morello 1958; González Loyarte et al. 2000). However, it has been recently demonstrated from the analysis of stable isotopes of xylem water that it can grow without access to groundwater, using only rainwater from the unsaturated soil of 20-m-high dune slopes receiving <200 mm mean annual rainfall in the Central Monte Desert (Jobbágy et al. 2010), although there is no physiological or growth-related evidence of ground and rainwater use by this species.

In this paper, we ask what consequences water table accessibility and rainfall dynamics have on water use, drought tolerance responses and growth of *P. flexuosa* trees at the mostly arid end of its range of distribution. We compare three *P. flexuosa* populations that, due to their topographical position (valley or dune) or size (adult or sapling), could have different access to the water table and, consequently, differing dependence on rainfall. We determine physiological and growth indicators of water table accessibility in valley and dune adult trees based on previous xylem water isotopic composition data that indicated differential use of groundwater by both populations (Jobbágy et al. 2010). We also infer whether or not young valley trees (for which we have no xylem water isotopic information) access the water table, based on their physiological behavior. Finally, we discuss the likely effects on *P. flexuosa* populations of variations in water table depth and rainfall dynamics.

Materials and methods

Study site

It is located in the Central Monte Desert on the eastern foothills of the Andes, NE Mendoza city, Argentina, within the Telteca Natural Reserve (32°20'S; 68°00'W). The climate is arid with mean annual rainfall of 156 mm (1972–2007), mostly concentrated in the austral summer (October–March), with mean annual temperature of 18.5°C (Alvarez et al. 2006). The region comprises a NNW–SSE oriented valley-dune system, with a 6–15 m deep subterranean watershed that is remotely replenished by Andean

river infiltration, with local recharge by rainfall drainage being negligible (Jobbágy et al. 2010; Arani-bar and Gomez, personal communication).

Experimental design

Our experimental site comprised a valley and an adjacent 20 m high dune in Puesto La Penca (32°25'42"S 68°00'33"W). The depth of the water table was 7.1 m below the valley surface (assessed by a hand-dug well) with 25% w/w water in the 1.5-m wide capillary fringe (Jobbágy et al. 2010). The dune held ~3% w/w rainwater in 1–4 m deep water reservoirs, and both landscape units had a homogeneous sandy soil profile in the root zone (Jobbágy et al. 2010; Guevara et al. 2010). We studied three populations of *P. flexuosa* trees that due to their topographical position (valley-dune) or size (adult-sapling) could have variable access to the water table and thus, varying dependence on rainfall: adult trees in the valley and the dune, for which we had isotopic evidence indicating different access to the water table (Jobbágy et al. 2010), and saplings in the valley [non-reproductive tree-type individuals, base diameter 1.5–4.5 cm (Table 1), 4–10 years old], for which we have no isotopic data with which to distinguish water sources. We selected five similar-sized adult individuals at each landscape unit, and four saplings in the valley (14 individuals in total; Table 1). Leaf water status, conductance, osmolality and leaflet closure were measured in two consecutive growing seasons on dates: 21/12/2007, 08/02/2008, 13/03/2008, 17/12/2008, and 05/03/2009.

Table 1 Dimensions of individuals selected for field measurements

Population	DB ^a (cm)	Height (m)	Crown area (m ²)
Valley sapling	3.0 (0.65)	1.53 (0.30)	2.27 (1.13)
Valley adult	14.54 (1.36)	4.08 (0.29)	12.91 (1.81)
Dune adult	15.35 (2.7)	3.34 (0.32)	13.56 (3.9)
<i>P</i> value ^b	0.82	0.13	0.88

Values are means ± s.e.m. between brackets

^a Diameter at the tree base

^b From the two tailed *t*-test between valley and dune adult trees, *N* = 10

Rainfall

Rainfall was recorded with a data logging rain gauge (Hobo Event, Onset Computer Corporation, Bourne, MA, USA).

Leaf water status

We measured pre-dawn (PD, 3:00 to 5:00 h) and midday (MD, around local solar noon: 13:30 h) leaf water potential (Ψ_w) in two branches ≤ 2 mm diameter that supported expanded sun-exposed leaves with a pressure chamber (PMS Instruments Co., Corvallis, OR, USA) based on Scholander et al. (1965). Cut branches were placed in sealed nylon bags in the dark and measured within 1–2 min.

Leaf conductance to water vapor

We measured adaxial and abaxial leaf conductance to water vapor (g_l) with a steady-state diffusion porometer (SC-1, Decagon Devices, Pullman, WA, USA). Daily g_l profiles were obtained from two adult trees, one from the valley and one from the dune in wet and dry periods. Seasonal midday g_l was measured in the 14 selected individuals from all three populations. In all cases we measured three expanded sun-exposed leaves per tree, added up adaxial and abaxial g_l , and used the averaged data for further analyses.

Leaf osmolality

We measured osmolality (mol kg⁻¹) in three frozen leaves per tree collected at midday. Because thawed leaves yielded a low volume of cellular juice by pressing, we disrupted the cells by smashing them in liquid N₂ and sonicating (50 mg) in 200 μ l of potassium phosphate buffer 50 mM (pH 7), in an ultrasonic bath at room temperature (Bransonic 1510RMT, 42 kHz, Branson Ultrasonic, Danbury, CT, USA) for 7 min. We centrifuged the samples at 10,000 rpm for 5 min, and measured osmolytes in the supernatant with a vapor pressure osmometer (Wescor, Logan, UT, USA). Leaf osmolality was calculated by correcting for the dilution by the potassium phosphate buffer and for the amount of liquid in a subsample of smashed leaves after drying at 60°C for 2 days.

Leaf movements

We measured *P. flexuosa* leaf movements that alter the fraction of total leaf area and stomata exposed to air and sun (three leaves per tree).

Leaflet closure

We measured the angle between the adaxial faces of opposite leaflet laminas with a portable protractor.

Leaf orientation

Using a compass, we recorded the cardinal direction of an imaginary vector perpendicular to the plane determined by the adaxial surface of leaflets.

Stomatal density and amphistomy

Stomata were counted in optical microscope (Axio-star Plus, Carl Zeiss International, Göttingen) photographs of epidermal prints (Boccalandro et al. 2009) obtained at 400 \times magnification from middle portions of leaflet laminas. We evaluated three mid laminas per leaf and three leaves per tree, and used averaged data for further analyses.

Stomata density (SD)

$$= \text{no. of stomata per leaf area (mm}^{-2}\text{)}$$

Amphistomy = SD adaxial / SD abaxial.

Early (harvested in December) and late (harvested in March) cohorts of leaves were evaluated.

Leaf surface area

We harvested five expanded sun-exposed leaves, scanned them with a reference area, and calculated surface area per leaf (without the petiole) using Adobe Photoshop (v. 7.0). Early and late leaf cohorts were evaluated.

Tree growth

We took transverse core samples at the base of seven adult trees from the valley and six from the dune with a gas-powered drill (TED_262R, Tanaka Kogyo Co. Ltd, Chiba, Japan) in June 2008. We measured the width of all growth rings from the pith to the

outermost ring with a precision of 0.01 mm using a Velvex system, and cross-dated them using the COFECHA program (Holmes 1999a), following Fritts (1976). We constructed curves of cumulative radial growth vs age for each sampled tree with DPL-AGE program (Holmes 1999b) and estimated individual growth curves by linear regression. We calculated the rate of radial growth per year, as the slope of each individual curve. Growth curves for each population (valley adults and dune adults) were constructed using the data of all measured trees and adjusting to a line by linear regression.

Statistical analysis

Dimensions of trees from the dune and the valley were compared with a two tailed *t*-test. Leaf Ψ_w (PD and MD), g_1 , osmolality, and leaflet angle mean comparison in time among the three populations (valley adults, dune adults, and valley saplings) were analyzed with repeated measures (rm) ANOVA. Comparison of population means on each sampling date was done with Tukey post-hoc test on the rm-ANOVA. Variation in g_1 and leaflet angles as a function of Ψ_{wPD} or midday g_1 was evaluated with linear regression. SD, amphistomy, and leaf area of valley and adult trees and two leaf cohorts were analyzed with two-way ANOVA. We evaluated differences in annual growth rates between both populations comparing the slopes of the growth curves of dune and valley adult trees with *t*-test. We used Infostat (v.2008, InfoStat, Córdoba, Argentina) and Statistica (v.6, StatSoft, Tulsa, OK, USA). $\alpha = 0.05$.

Results

Climate conditions and rainfall dynamics

The 2007–2008 growing season received more rainfall (250.6 mm) than the 2008–2009 growing season (154.9 mm), exceeding the annual average for the region, and with contrasting dry (October–December) and wet (January–March) periods (Fig. 1 a). In 2008–2009, rainfall was close to the average for the region and concentrated in two huge events in December and January (Fig. 1b).

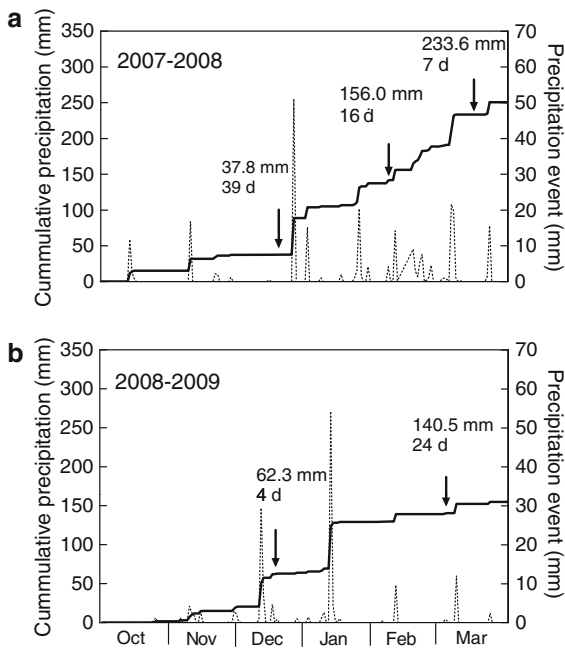


Fig. 1 Rainfalls during 2007–2008 (a) and 2008–2009 (b) growing seasons. Cumulative rainfall (solid line) and rainfall events (dotted line) are plotted from 1st October to 31st March. Vertical arrows indicate measurement dates; captions above indicate cumulative precipitation and days (d) since the last precipitation event ≥ 10 mm

Leaf water status

Pre-dawn leaf water potential (Ψ_{wPD}) varied seasonally with tree population (interaction $P < 0.0001$, time $P < 0.0001$, population $P < 0.0001$ rm-ANOVA; Fig. 2). Dune adult trees showed the lowest Ψ_{wPD} values and highest seasonal fluctuation associated with rainfall dynamics (e.g., low Ψ_{wPD} in dry periods and high Ψ_{wPD} following rains), indicating a strong dependence on rainfall as a source of water. Valley adult trees showed the lowest seasonal fluctuation and highest values of Ψ_{wPD} , associated with the exploitation of a groundwater reservoir of greater magnitude and seasonal stability than rainfall. Ψ_{wPD} values for valley saplings were intermediate between those of valley and dune trees during the relatively dry periods, indicating access to an additional water reservoir besides current rainfall, although of lower magnitude than that exploited by valley adult trees. On the other hand, midday leaf water potential (Ψ_{wMD}) varied in time with similar values among tree populations (interaction $P = 0.58$, time $P < 0.0001$, population

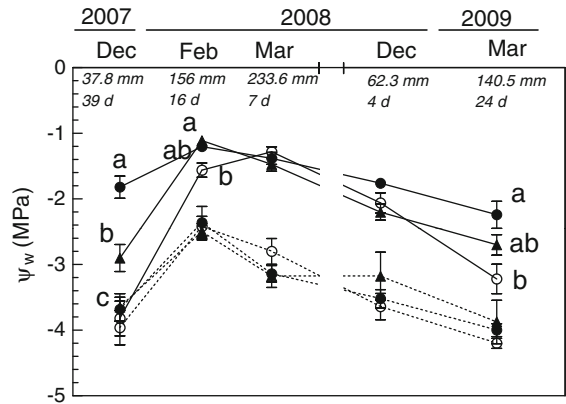


Fig. 2 Pre-dawn (solid line) and midday (dotted line) leaf water potential (Ψ_w) of valley adult trees (closed circles) valley saplings (triangles) and dune adult trees (open circles) during two consecutive growing seasons. Accumulated rainfall and days (d) since the last precipitation event ≥ 10 mm are indicated. Symbols are means and vertical lines \pm s.e.m. Different letters indicate differences among tree populations on each sampling date and type of measurement (pre-dawn or midday), tested by Tukey's post-hoc test on the rm-ANOVA

$P = 0.56$), indicating that Ψ_{wPD} is a better physiological indicator of groundwater accessibility than Ψ_{wMD} . Leaf Ψ_w morning fluctuation ($\Psi_{wMD} - \Psi_{wPD}$) during dry periods (December 2007 and March 2009) can be arranged as: valley trees $>$ valley saplings $>$ dune adults, indicating higher water movement through trees and gas exchange in populations with higher accessibility to the water table. In December 2007, Ψ_w morning fluctuation of dune trees was nearly 0, suggesting poor or null water transport and gas exchange in dunes during the driest period.

Leaf conductance to water vapor

Prosopis flexuosa trees showed the highest leaf conductance to water vapor (g_l) during the morning, with peak values approximately 2.5 h following sunrise and a steep decrease toward midday and afternoon (Online Resource 1). The dune tree showed lower g_l than the valley tree, with greater differences during the driest period, and midday stomata closure clearly promoted leaf rehydration after the steep decrease of about 2.5 MPa in leaf Ψ_w from pre-dawn values after morning transpiration (Online Resource 1).

Midday g_l evaluated across seasons showed a fluctuation that varied with tree population

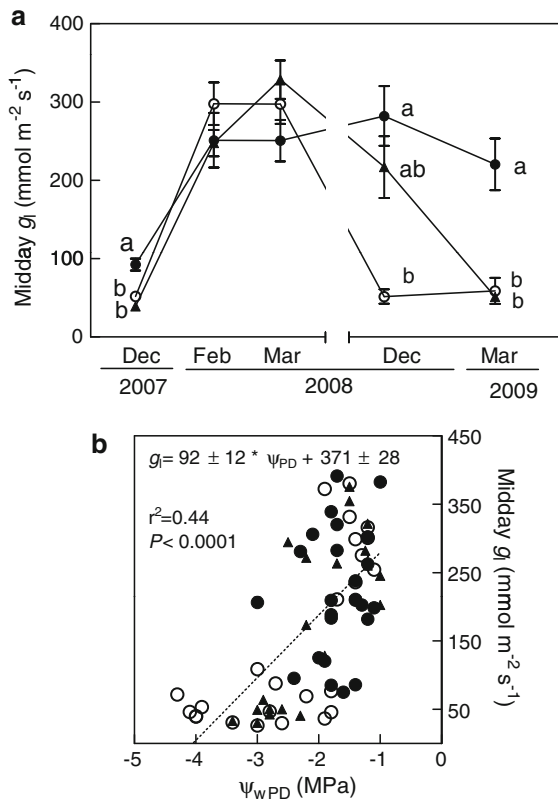


Fig. 3 (a) Midday leaf conductance to water vapor (g_1) of valley adult trees (closed circles) valley saplings (triangles) and dune adult trees (open circles) during two consecutive growing seasons. Symbols are means and vertical lines \pm s.e.m. Different letters indicate differences among tree groups on each sampling date tested by Tukey's post-hoc test on the rm-ANOVA. (b) Midday g_1 versus pre-dawn leaf water potential (Ψ_{wPD}). Symbols represent single measurements; dotted line is the trend of the linear regression, and line equation, P and r^2 values are indicated in each graphic

(interaction $P < 0.0001$, time $P < 0.0001$, population $P = 0.006$ rm-ANOVA, Fig. 3a). Valley adult trees showed the most seasonal stability and highest values of g_1 which is in keeping with their having access to a stable groundwater reservoir. During the dry December 2007, they had the lowest midday g_1 suggesting an effect of extreme surface drought despite groundwater accessibility. Dune adult trees showed a greater seasonal fluctuation and lower midday g_1 than valley trees ($<60 \text{ mmol m}^{-2} \text{ s}^{-1}$ in 3/5 dates), which relates to their dependence on rainfall. Valley saplings showed midday g_1 values intermediate between dune and valley adult populations, or similar to that of dune trees, suggesting that they are more sensitive to

surface drought than valley adults. During wet periods (February and March 2008), differences associated with groundwater accessibility disappeared. Midday g_1 varied significantly and positively with Ψ_{wPD} ($r^2 = 0.44$, $P < 0.0001$; Fig. 3b), which relates to the magnitude of the water reservoir used by each population.

Leaf osmolality

Prosopis flexuosa populations displayed seasonal osmotic adjustment associated with rainfall dynamics and groundwater accessibility (interaction $P = 0.006$, time $P < 0.0001$, population $P = 0.14$ rm-ANOVA; Fig. 4). During the driest period (December 2007), a high concentration of osmolytes in leaves of dune trees would favor water absorption (Fig. 4).

Leaflet closure and leaf orientation

Prosopis flexuosa leaves close their leaflets at different angles, with lowest daily angles at midday (Online Resource 2). Midday leaflet angle varied across seasons and among tree populations (interaction $P = 0.002$, time $P < 0.0001$, population $P = 0.06$ rm-ANOVA; Fig. 5a). Valley adult trees maintained their leaflets more open at midday than valley saplings and dune trees on most of the dates. Dune adult trees

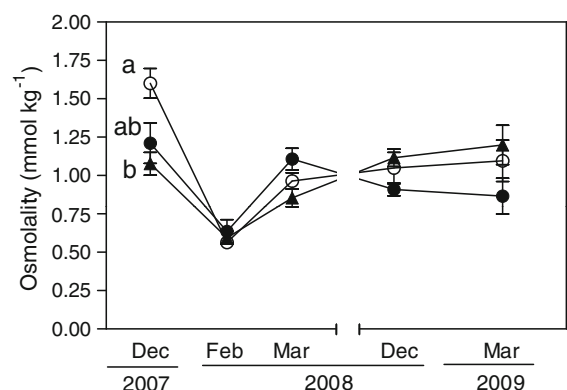
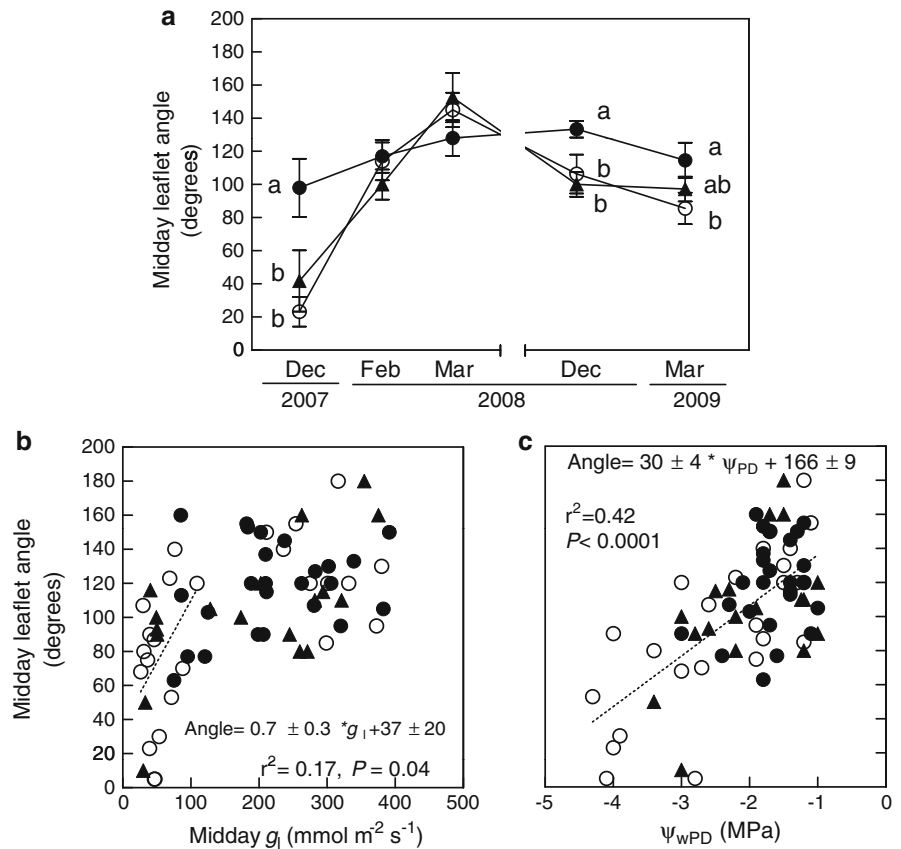


Fig. 4 Leaf osmolyte concentration of valley adult trees (closed circles), valley saplings (triangles), and dune adult trees (open circles) during two consecutive growing seasons. Symbols are means and vertical lines \pm s.e.m. Different letters indicate differences among populations on each sampling date tested by Tukey's post-hoc test on the rm-ANOVA

Fig. 5 (a) Midday leaflet angle in valley adult trees (closed circles), valley saplings (triangles), and dune adult trees (open circles) during two consecutive growing seasons. Symbols are means and vertical lines \pm s.e.m. Different letters indicate differences among populations on each sampling date tested by Tukey's post-hoc test on the rm-ANOVA. (b) Midday leaflet angle vs. midday leaf conductance to water vapor (g_1), and (c) Midday leaflet angle vs. pre-dawn leaf water potential (Ψ_{wPD}). Symbols represent single measurements; dotted lines are the trend of linear regressions, and line equation, P and r^2 values are indicated in each graphic



and valley saplings presented a higher seasonal variation and more closed leaflets than valley adults. Differences among populations were evident during 'average' and dry periods (December 2007, December 2008, and March 2009) and disappeared during wet periods (February and March 2008) when leaflets remained open. Midday leaflet angles between 80° and 180° were recorded within a wide range of midday g_1 ($100\text{--}400 \text{ mmol m}^{-2} \text{ s}^{-1}$, Fig. 5b) and a steep decrease in leaflet angles with decreasing g_1 occurred at $g_1 \leq 100 \text{ mmol m}^{-2} \text{ s}^{-1}$ ($r^2 = 0.17$, $P = 0.04$). Midday leaflet closure increased with decreasing Ψ_{wPD} ($r^2 = 0.42$, $P < 0.0001$, Fig. 5c).

We detected constitutive diurnal solar tracking by *P. flexuosa* leaves that move from an eastern position in the morning to a western orientation in the afternoon (Fig. 6). The combination of constitutive leaf solar tracking plus leaflet closure reduces the leaf area perpendicularly exposed to sun rays and conceals adaxial stomata when water is scarce and g_1 is very low (Fig. 5b, c).

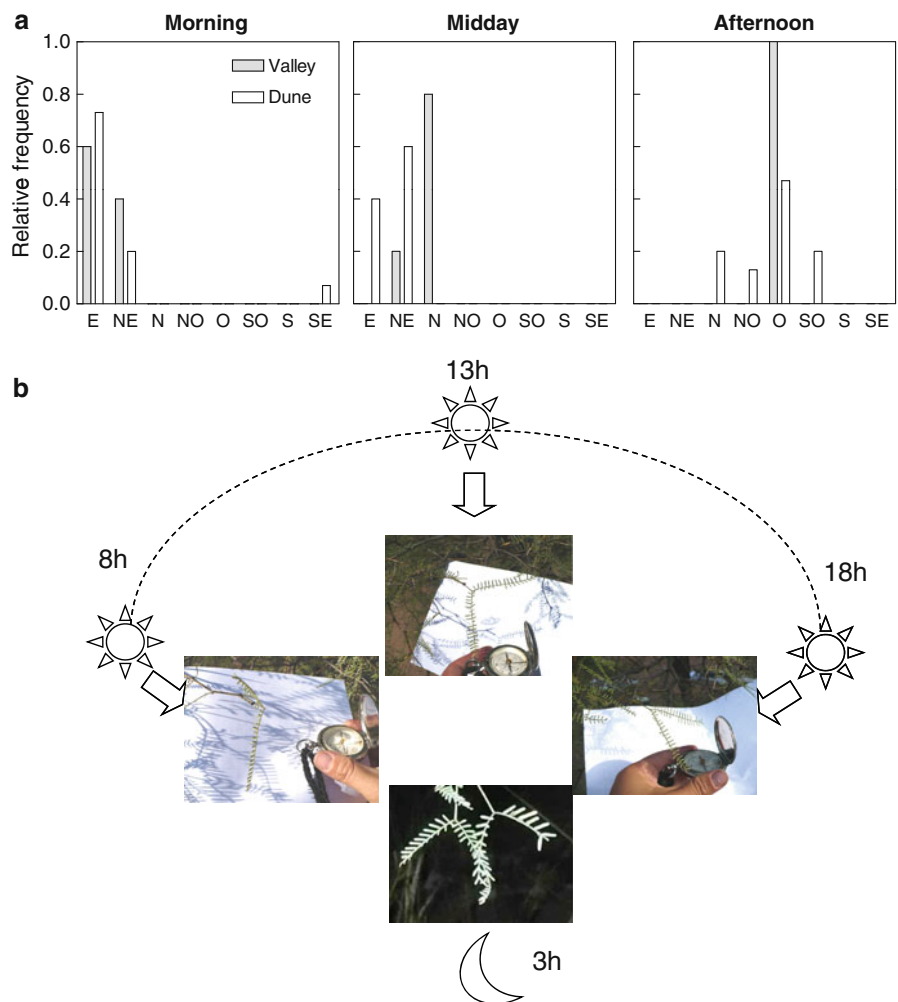
Stomatal density and amphistomy

Prosopis flexuosa leaves presented higher SD in the adaxial than in the abaxial leaf surface (amphistomy >1 , Table 2), more pronounced in the late cohort of leaves in both growing seasons. Total SD (contribution of both leaf surfaces) was lower in valley trees than in dune trees in both growing seasons and in the early cohort of leaves in 2007–2008 (Table 2).

Leaf area

During 2007–2008 there was a marked difference in surface area per leaf between early and late cohorts; the small leaves from the early cohort coincided with a dry period of expansion (Table 3). During 2008–2009, early and late leaves had similar surface area, with intermediate values between the extremes recorded for the previous growing season. We found no differences in leaf expansion associated with groundwater accessibility.

Fig. 6 (a) Leaf solar tracking movement in valley (grey bars) and dune (white bars) adult trees, indicated by the relative frequency of leaves found in the cardinal positions of the *abscisas*. (b) Photographs of leaves taken from the northern side of the tree crown at different hours; note that the sun is tilted toward the north in the southern hemisphere



Tree growth

Radial growth curves for valley and dune adult tree populations, estimated from individual cumulative growth curves, indicated that throughout their life-span, valley trees grew at a faster rate (4.6 ± 0.05 mm year⁻¹) than dune trees (2.9 ± 0.03 mm year⁻¹, $P < 0.02$, t -test, Fig. 7).

Discussion

Access to the water table was determinant of the frequency and degree of drought experienced by *P. flexuosa* populations in the Monte Desert (Fig. 2). Valley adult trees exploited a larger and more stable water reservoir than dune adult trees, avoiding

drought caused by rainfall shortage (Figs. 1, 2). On the other hand, water status of the dune population was linked to rainfall, and trees were frequently subjected to drought (Fig. 2). This confirms that *P. flexuosa* behaves as a facultative phreatophyte at the mostly arid end of its distribution, with the capacity to access groundwater and to survive entirely on rainfall, as suggested by previous xylem water isotopic analyses (Jobbágy et al. 2010). We have previously demonstrated that *P. flexuosa* trees extend their surface roots deeper into the ground in the dune than in the valley which, coupled with a higher frequency of primary branches, would allow them to access subsurface rainfall-derived water reservoirs in the dune and thus compensate for inaccessibility of the water table (Guevara et al. 2010), as occurs in *Banksia attenuata* dune

Table 2 Amphistomy and stomatal density (SD) in early and late cohorts of leaves from valley (V) and dune (D) adult tree populations during consecutive growing seasons

	2007–2008				2008–2009				P value					
	Early		Late		Early		Late		Int.	Pop	Cohort	Int.	Pop	Cohort
	V	D	V	D	V	D	V	D						
Amphistomy	1.12 (0.07)	1.21 (0.09)	1.67 (0.17)	1.65 (0.09)	0.60	0.73	0.0004***	1.36 (0.10)	1.55 (0.13)	1.76 (0.10)	0.91	0.10	0.04*	
SD (no. mm ⁻²)	262 (39)	395 (52)	414 (19)	453 (36)	0.24	0.04*	0.01**	368 (25)	467 (35)	443 (2)	0.29	0.03*	0.15	

Numbers are means ± s.e.m. between brackets. P values from the two-way ANOVA are reported

Pop = population

communities in western Australia (Zencich et al. 2002). However, lower leaf Ψ_{wPD} in dune trees than in valley trees in dry periods indicates that plasticity of the former trees' surface roots is insufficient to avoid drought. High Ψ_w morning fluctuation ($\Psi_{wMD} - \Psi_{wPD}$, ~1.8 MPa during drought, Fig. 2) and midday g_1 (Fig. 3) in valley trees suggest higher water transport and potentially higher CO₂ uptake through them than through dune individuals across seasons. This agrees with an isotopic and soil/sediment survey that indicates groundwater-fed *P. flexuosa* woodlands as areas of groundwater discharge (Jobbágy et al. 2010). Besides being vehicles for groundwater flux into the atmosphere, *P. flexuosa* adult trees from valleys would potentially redistribute groundwater from saturated deep soil into unsaturated shallow soil through their roots as described for phreatophytes including other *Prosopis* species (Caldwell et al. 1998; Hultine et al. 2004).

Under severe drought, growth of the dune population could be challenged because there is almost no water movement and no gas exchange in dune trees (December 2007 in Figs. 2, 3). The negative effect of groundwater inaccessibility on growth is evident from the 1.5-fold slower annual radial growth of dune trees compared to valley trees (Fig. 7). Although contribution of groundwater promotes radial growth and wood production of *P. flexuosa* trees in this ecosystem, severe drought can still negatively affect growth of adult valley populations by restricting leaf expansion (Table 2) and limiting gas exchange (Fig. 3a), which indicates that water table connected trees are not completely decoupled from rainfall dynamics.

Several drought tolerance responses displayed by *P. flexuosa* could explain its capacity to grow without accessing the water table in dune habitats: osmotic adjustment, modulation of g_1 and stomata density, and leaf movements. Osmotic adjustment capacity, also reported for North American *Prosopis* species (Nilsen et al. 1984), could be crucial to maintain water absorption in dune trees subjected to extremely low leaf Ψ_w under severe drought (Fig. 4). In turn, a daily course of g_1 characterized by stomata opening during the morning, when low temperatures and high relative humidity minimize water loss per CO₂ fixed, could enhance daily water use efficiency (Online Resource 1), a pattern common to North American and Asian *Prosopis* species (Changgui and Sosbee

Table 3 Leaf surface area of early and late cohorts from valley (V) and dune (D) adult tree populations during consecutive growing seasons

Leaf surface area (cm ²)	Early		Late		P value		
	V	D	V	D	Int.	Population	Cohort
2007–2008	4.98 (0.27)	4.37 (0.41)	9.55 (0.80)	8.25 (1.04)	0.63	0.19	<0.0001***
2008–2009	7.58 (0.50)	8.15 (1.07)	7.58 (0.73)	8.10 (1.02)	0.97	0.54	0.97

Numbers are means \pm s.e.m. between brackets. P values from the two-way ANOVA are reported

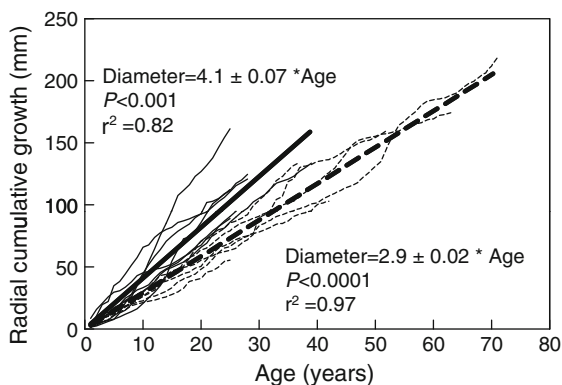


Fig. 7 Individual curves of cumulative radial growth versus tree age of valley (solid line) and dune (dotted line) adult trees. Data in the ordinate axis is expressed as tree diameter in each year, calculated from the growth ring width values. Growth curves for each population were estimated by linear regressions indicated in the graphic

1991; Ansley et al. 1992; Elfadl and Luukkanen 2006) and other desert taxa (Szarek and Woodhouse 1978). In addition, drought-induced stomata closure reduces water loss during hot afternoons and facilitates leaf rehydration (Fig. 3 and Online Resource 1).

While g_1 is mainly controlled by stomata aperture, it could be also affected by stomata density that varies from changes in leaf area (e.g. increased SD with decreased leaf area) and/or from adjustments in the number of epidermal cells that differentiate into stomata in response to water availability and other environmental factors (Casson and Gray 2008; Boccacalandro et al. 2009). Increased SD in the dune adult tree population with respect to the valley population (Table 2) was not related to leaf area reductions (Table 3), suggesting an adjustment in stomata differentiation. Across seasons, the greater SD in dune trees than in valley trees resulted in a 3% (2007–2008) to 15% (2008–2009) higher total amount

of stomata per individual leaf (SD per average leaf area), which is counterintuitive as one should reasonably expect a reduction rather than an increment in the proportion of epidermal cells that differentiate into stomata under drought in dune populations. However, dune trees presented lower g_1 than valley trees during dry periods (Fig. 3a), indicating an efficient control of stomata aperture despite differences in SD. During the infrequent periods when water is available and stomata are open, a higher SD in dune trees would enhance gas exchange per leaf area and biomass production. The early leaf cohort that developed under the 2007 drought experienced a half-fold reduction in leaf area and also a lower SD with respect to the later cohort in both valley and dune populations, resulting in a 300% reduction in total stomata per individual leaf. This leaf cohort also exhibited a smaller proportion of stomata on the adaxial leaf surface (Table 2), which would contribute to water loss reduction during the first half of the growing season, usually drier than the second (peak rains are in January–February). The plasticity of *P. flexuosa* for stomata differentiation could prevent increments in SD and regulate amphistomy when leaf growth is reduced, a novel drought tolerance response reported for *Prosopis* species. Water flux and drought resistance in valley and dune populations could be further improved by reducing xylem hydraulic conductance (and improving cavitation resistance) in response to drought, as observed during the early life stages of *P. flexuosa* (Villalba 1985) and under higher aridity within its habitat range (Giantomassi et al. 2009).

Stomata closure in a dry, hot, and highly irradiated environment raises the risk of oxidative and thermal stress, since reactive oxygen species increase under low availability of electron acceptors of the photosynthetic electronic chain (Foyer et al. 2006), and leaf refreshing is reduced due to reduced transpiration.

The combination of midday leaf closure when g_1 is very low (Fig. 5b) with leaf solar tracking (Fig. 6) minimizes light interception, for closed leaves are oriented parallel to the sun's rays thus potentially reducing oxidative risk and energy load. At the same time, the adaxial leaf surface with the highest SD is hidden, reducing adaxial transpiration, while the exposed abaxial surface would continue to evaporate water and refresh the leaf. In turn, solar tracking by open leaves assures maximal light interception under optimal water conditions when CO₂ uptake can take place (Mooney and Ehleringer 1978). Midday leaflet closure under water stress (Fig. 5b, c) appeared as a different movement from the 'sleeping' (day and night cycles of leaf opening and closure) and solar tracking movements displayed by legumes, including *Prosopis* species, which are governed by light (Ehleringer and Forseth 1980; Prichard and Forseth 1988; Koller 1990). The natural selection of relatively broad leaves with multiple movements that vary the sunlight-exposed leaf area in response to multiple signals, including water availability, could improve drought tolerance as well as photosynthesis during the dry–wet cycles typical of desert habitats.

Physiological indicators of groundwater use, Ψ_{wPD} , g_1 , midday leaflet angle and osmotic adjustment during extreme drought allow us to infer water reservoirs used by valley saplings with fivefold smaller DB and threefold lower height than adult trees (Table 1). Valley saplings seem to have access to an additional water reservoir besides current rainfall, although not as stable as the constantly saturated capillary fringe of the water table. So, individuals <10 years might not have developed as long or profuse tap roots as to fully exploit the groundwater under an annual rainfall regime of <200 mm, suggesting that juveniles are more vulnerable than valley adult trees to drought events or descent of the water table level.

Under scenarios of global climate change and expanding agricultural oases, *P. flexuosa* populations in the Central Monte Desert should be differently affected by changes in rainfall regime or water table depth. The increase in summer rainfall predicted for the region (Labraga and Villalba 2009) might promote *P. flexuosa* growth and establishment, with relatively more important effects on dune and sapling populations which are currently water restricted. A hypothetical deepening of the water table due to oasis

expansion could negatively affect valley populations, but would have no effects on dune populations acclimated to survive without groundwater. The combination of phreatophytism and drought resistance responses might buffer *P. flexuosa* populations against changes in either of the water sources exploited by this species in the Monte Desert.

Acknowledgments We thank the Dirección de Recursos Naturales Renovables of Mendoza province for their permission to work in Telteca Natural Reserve. We are grateful to Silvana Piccone and 'Husky' park rangers, Hugo Debandi, Julieta Aranibar, Diego Odales, Victoria Salomón, and Ana Antúnez for field assistance; to Mariano Morales and Lidio López for help with dendrochronology; to Mercedes Fucili for help in stomata counting; to Bruno Cavagnaro, Mariana Combina, and Walter Manucha for porometer, microscope and osmometer facilities, respectively; to Nelly Horak for English correction; and to anonymous reviewers for suggestions on how to improve an earlier versions of the manuscript. We are thankful to Mariano, Chicho, Valeria, and Cecilia for their warm hospitality. This research was supported by Agencia Nacional de Promoción Científica y Tecnológica PICT 2007-01222 to PEV and PICT 2007-00492 to HEB.

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