

Soil water availability and rooting depth as determinants of hydraulic architecture of Patagonian woody species

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Abstract Adaptations of species to capture limiting resources is central for understanding structure and function of ecosystems. We studied the water economy of nine woody species differing in rooting depth in a Patagonian shrub steppe from southern Argentina to understand how soil water availability and rooting depth determine their hydraulic architecture. Soil water content and potentials, leaf water potentials (Ψ_{Leaf}), hydraulic conductivity, wood density (ρ_w), rooting depth, and specific leaf area (SLA) were measured during two summers. Water potentials in the upper soil layers during a summer drought ranged from -2.3 to -3.6 MPa, increasing to -0.05 MPa below 150 cm. Predawn Ψ_{Leaf} was used as a surrogate of weighted

mean soil water potential because no statistical differences in Ψ_{Leaf} were observed between exposed and covered leaves. Species-specific differences in predawn Ψ_{Leaf} were consistent with rooting depths. Predawn Ψ_{Leaf} ranged from -4.0 MPa for shallow rooted shrubs to -1.0 MPa for deep-rooted shrubs, suggesting that the roots of the latter have access to abundant moisture, whereas shallow-rooted shrubs are adapted to use water deposited mainly by small rainfall events. Wood density was a good predictor of hydraulic conductivity and SLA. Overall, we found that shallow rooted species had efficient water transport in terms of high specific and leaf specific hydraulic conductivity, low ρ_w , high SLA and a low minimum Ψ_{Leaf} that exhibited strong seasonal changes, whereas deeply rooted shrubs maintained similar minimum Ψ_{Leaf} throughout the year, had stems with high ρ_w and low hydraulic conductivity and leaves with low SLA. These two hydraulic syndromes were the extremes of a continuum with several species occupying different portions of a gradient in hydraulic characteristics. It appears that the marginal cost of having an extensive root system (e.g., high ρ_w and root hydraulic resistance) contributes to low growth rates of the deeply rooted species.

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Introduction

Physiological processes in plants from cold arid environments such as the Patagonian steppe are influenced by low soil water availability during periods when temperatures are favorable for growth (Soriano and Sala 1983; Sala et al. 1989; Jobbagy and Sala 2000; Austin and Sala 2002; Golluscio

and Oosterheld 2007). Several studies of Patagonian ecosystems indicate that shrubs and grasses differ in their adaptations to cope with limited water availability (Soriano and Sala 1983; Sala et al. 1989). According to this paradigm, grasses tap water resources from upper soil layers (above 30 cm depth) following both short and long duration rainfall events in the growing season, while shrubs mostly use water from deeper soil layers (below 40 cm depth) (e.g., Soriano and Sala 1983; Golluscio and Sala 1993; Aguiar and Sala 1998; Golluscio et al. 1998, 2005). However, in another study which employed hydrogen and oxygen isotope ratios of xylem and soil water, it was found that, even though roots of woody species growing near the foothills of the Patagonian Andes reached water-saturated soil layers at 2–3 m deep, they mostly used water deposited by recent rain events in the upper soil layer (Schulze et al. 1996). Arid ecosystems in the southwestern United States with general environmental conditions similar to some areas of Patagonia contain plant species that obtain moisture from either pulse-dominated shallow soil layers or from deeper soil layers with abundant and stable soil moisture (Schwinning and Ehleringer 2001). Consequently, woody species of the Patagonian steppe should not necessarily be expected to rely on a single soil layer for acquiring their water resources.

Rooting depth can differ substantially depending on site conditions. Global studies of rooting depths show that desert plants reach a maximum rooting depth of about 13 m with 50% of the total root biomass below 0.27 m soil depth, while trees from temperate forests have an average of maximum rooting depth of only 3.7 m with 50% of the root biomass below 0.21 m (Canadell et al. 1996; Schenk and Jackson 2002). This information provides a general picture of the potential capacity of roots to capture water resources across two different ecosystem types but does not reveal the important differences across species in a particular environment. Our preliminary observations of a relatively large group of woody species growing in the western Patagonian steppe indicate that rooting depths can range from shallow to deep. Understanding the resulting species-specific differences in patterns of water uptake and some of their physiological consequences is of importance for predicting the outcome of grass and shrub competition and consequences of man-made interventions.

Species-specific differences in wood density were central to the present research because wood density is a strong predictor of variations in a suite of traits related to stem water storage capacity, leaf specific hydraulic conductivity, regulation of leaf water status, avoidance of turgor loss, and growth rates in woody plants (Roderick 2000; Bucci et al. 2004a; Meinzer 2003; Scholz et al. 2007). Species with low wood density tend to exhibit both high leaf-specific hydraulic conductivity (Bucci et al. 2004a; Santiago et al. 2004)

and stem water storage capacity (Scholz et al. 2007; Meinzer et al. 2008). Trade-offs between growth rate and allocation of biomass to stems in woody plants result in species that allocate less biomass to xylem tissue (light woods) and rapid increases in basal diameter compared to species that allocate more biomass to stems (dense woods) but grow more slowly (Enquist et al. 1999; Muller-Landau 2004).

The objective of this study was to understand how soil water availability and rooting depths determine some hydraulic architecture traits of dominant woody plants in the Patagonian shrub steppe. Precipitation in the study area is less than 200 mm per year and most rainfall events tend to be of very short duration. We predicted that shallow- and deep-rooted shrub species would have contrasting hydraulic traits, consistent with their reliance on different types of soil water resources (recent rain pulses, soil water from a previous rainy season, and groundwater). Specifically, shallow-rooted species should have adaptations that permit them to utilize small rainfall events. These adaptations include low wood density and efficient water transport systems to exploit ephemeral pulses of water in the upper soil layers, permitting rapid growth following small rain events. On the other hand, deeper-rooted shrubs would have stems with denser wood and lower water transport efficiency, would have slower and more stable growth rates and would maintain similar minimum leaf water potentials during rainless and rainy periods. To test these predictions, we measured soil water content and water potentials, leaf water potential, stem hydraulic conductivity, rooting depths, wood density, and specific leaf area of nine shrub species during two consecutive summer periods.

Materials and methods

Site and species description

The research was carried out at La Dora Ranch in northwest Santa Cruz, Argentina (46°31'S, 71°03'W), at an elevation of 400–420 m a.s.l. The study sites are located in an area characterized by rolling small hills where the vertical distance between the top of the hills and the lower part of the topography is less than 10 m. Mean annual rainfall is 188 mm falling mostly in the fall and winter (April–September), sometimes in the form of snow, and the mean annual air temperature is 9.0°C. Average summer (December–February) and winter (June–August) temperatures are 14 and 3°C, respectively. Percolation is frequent in Patagonia because most precipitation occurs during winter when plant growth and transpiration are low (Paruelo and Sala 1995). Soils are generally either gravelly sandy loams or gravelly loamy sands (Douglas and Bockheim 2006). Upper horizons typically contain fine sand (0.10–0.25 mm)

Table 1 Life form, leaf phenology, maximum rooting depth, average height, and ratio of leaf area to sapwood area ($A_L:A_S$) for all studied species

Species	Family	Life form	Leaf phenology	Root depth (cm)	Height (cm)	$A_L:A_S$ ($m^2\ cm^{-2}$)
<i>Brachyclados caespitosus</i>	Asteraceae	Cushion shrubs	Evergreen	<100	15 ± 2	0.086 ± 0.005
<i>Euphorbia collina</i>	Euphorbiaceae	Dwarf shrub	Deciduous	<100	15 ± 2	0.100 ± 0.006
<i>Mulinum spinosum</i>	Apiaceae	Cushion shrub	Deciduous	<100	40 ± 6	0.0081 ± 0.009
<i>Senecio filaginoides</i>	Asteraceae	Small shrub	Evergreen	<100	55 ± 4	0.074 ± 0.008
<i>Adesmia boronioides</i>	Fabaceae	Tall shrub	Evergreen	<200	90 ± 7	0.080 ± 0.002
<i>Colliguaya integerrima</i>	Euphorbiaceae	Tall shrub	Evergreen	<200	105 ± 11	0.110 ± 0.009
<i>Lycium chilense</i>	Solanaceae	Tall shrub	Deciduous	<200	88 ± 5	0.066 ± 0.003
<i>Berberis heterophylla</i>	Berberidaceae	Tall shrub	Evergreen	>200	170 ± 9	0.057 ± 0.006
<i>Schinus johnstonii</i>	Anacardiaceae	Tall shrub	Evergreen	>200	210 ± 15	0.050 ± 0.014

Heights and $A_L:A_S$ are mean ± SE ($n = 5$)

and subsurface soil horizons have greater percentages of coarse sand (0.5–1.0 mm) within a matrix of gravel. There is a calcareous stony layer at 80–100 to 120–150 cm below the soil surface that some roots can penetrate.

Vegetation is typical of a Patagonian shrub steppe from the Occidental District (Soriano 1956) characterized by tussock grasses and shrubs. It comprises a two-phase mosaic formed by individual shrubs encircled by rings of grasses dispersed in a matrix of scattered tussock grasses. (Aguiar and Sala 1998). The dominant shrub species are *Mulinum spinosum* (Cav.) Pers, *Adesmia boronioides* J. D. Hooker, *Senecio filaginoides* De Candolle and *Colliguaja integerrima* Gilles et Hooker ex Hooker and the most conspicuous grass species are *Stipa speciosus* Trinius et Ruprecht, *S. humilis* cayabilles and *Poa ligularis* Nees. In the Patagonian steppe growth is limited in winter by low temperatures and is restricted by low soil water availability in late spring and summer (Soriano and Sala 1983). Grasses are active most of the year and exhibit rapid leaf expansion in the early spring. Shrubs show a clear-cut cyclical pattern of growth and dormancy; most of them are inactive during winter and exhibit an active growth phase during the spring and summer. Nine dominant shrub species were selected, including tall shrubs (>55 cm height) (*A. boronioides*, *Berberis heterophylla* Jusieu Lam; *C. integerrima*, *Schinus johnstonii* Barkley, *Lycium chilense* Miers ex Bertero) and small shrubs (<55 cm height) (*Brachyclados caespitosus* (Phil.) Speg; *Euphorbia collina* Philippi, *M. spinosum* and *S. filaginoides*). *E. collina* is a hemicryptophyte with soil level apical buds and the aboveground part dying every year during the winter. In this study we considered *E. collina* as a woody plant because its basal portions and roots are lignified.

Root systems of three representative individuals of the nine species were excavated down to 250 cm to study their architectural features and rooting depth. The root systems of *S. johnstonii* and *B. heterophylla* have a prominent single axis (taproot) that reaches depths in excess of 250 cm. They also have smaller roots that tend to grow vertically as well

as smaller fibrous secondary roots running outward very close to the soil surface. *L. chilense* has numerous roots that reach depths of 150 cm but none of them constitute a prominent tap root. *A. boronioides* has a conspicuous tap root with some branching of smaller roots that tend to grow vertically and small surface roots that start to proliferate close to the soil surface. *C. integerrima* has a conspicuous tap root that penetrates to a depth of about 200 cm and a large number of smaller diameter roots that explore all the soil profile starting near the soil surface. *S. filaginoides* and *M. spinosum* have a tap root with long lateral roots growing outward close to the soil surface in *S. filaginoides*, while in *M. spinosum* the lateral roots start to grow horizontally 15 cm below the soil surface, consistent with the patterns of root systems observed by Fernandez and Paruelo (1988) for these two species. *B. caespitosus* and *E. collina* have a tap root and few short lateral roots. Leaf phenology, maximum rooting depth, height and the ratio of total leaf area to sapwood area of all species studied are shown in Table 1. All measurements were done between January 2007 and March 2008.

Soil water potential and water content

Soil psychrometers (PST-55; Wescor, Logan, UT) were used to continuously monitor soil water potential (Ψ_{soil}) at 25, 40, 60, 100, 150, 200, and 300 cm depths. Before placement in the field, the psychrometers were individually calibrated against salt solutions of known osmolality following the procedures of Brown and Bartos (1982). Soil water potential was measured every 30 min, in the psychrometric mode, with a 30-s cooling time, and data recorded by a data logger (CR-7; Campbell Scientific, Logan, Utah, USA) and corrected for potential temperature gradients according to Brown and Bartos (1982).

Soil volumetric water content was monitored continuously with ECH2O probes (Decagon Devices). The probes have an accuracy of $0.03\ m^3\ m^{-3}$ and a maximum temperature

sensitivity of $\sim 0.003 \text{ m}^3 \text{ m}^{-3}$ per 1°C . They were calibrated in the laboratory with soil samples obtained from the study site. Probes were installed at 25, 40, 60, 100, 200, and 300 cm depth.

Soil samples for gravimetric water content were collected with a Dutch auger during January 2007 and February 2008. Samples were obtained every 10 cm down to 100 and at 125, 150, 200, and 300 cm depth. During January 2007, samples were only collected down to 125 cm depth. Four profiles per date were obtained. Dry weights were obtained after placing the soil samples in an oven at 105°C for 72 h.

Leaf water potential

Leaf water potential (Ψ_{Leaf}) was measured with a pressure chamber (PMS Instruments, Corvallis, OR, USA). Eight sets of measurements were obtained during the course of a day for each species during January 2007 (dry season). For each species, three leaves or terminal branches from five different individuals of similar size were cut with a sharp razor blade and sealed immediately in small plastic bags containing moist paper towels and kept briefly in a cooler until balancing pressures were obtained. In addition, leaf samples were collected at predawn and at 1400 hours during February and March 2008 for all studied species. Predawn Ψ_{Leaf} of three covered (non-transpiring) leaves from five different plants per species was measured simultaneously with predawn Ψ_{Leaf} of exposed leaves. Leaves for non-transpiring Ψ_{Leaf} determinations were enclosed in plastic bags and aluminum foil during the late afternoon prior to the measurement day.

Wood density

Wood density (ρ_w) was measured on ten terminal branches from each species and/or population. After removal of bark and pith, ρ was calculated as: $\rho_w = M/V$, where M is the dry mass of the sample (oven dried at 60°C for 72 h) and V is the sample volume. Volume was estimated by submerging the sample in a container with distilled water resting on a digital balance with a 0.001-g precision. Wood samples of *E. collina* were taken from the lignified portion of the plant.

Hydraulic conductivity

Hydraulic conductivity (k_h) was measured on five large terminal branches excised before dawn (0600 hours) and in the afternoon (1400–1500 hours), in seven of the nine species, in January 2007 and February 2008. Whereas predawn k_h probably reflects the maximum attained during a 24-h cycle, the early afternoon measurements should detect any reductions in water transport efficiency due to embolism

formation during the morning. Immediately after excision, a small portion of the branch cut end was removed by re-cutting under water. The branches were then tightly covered with black plastic bags and transported to the laboratory with the cut ends of the branches under water. Immediately after arriving at the laboratory, within 1 h of sample collection, stem segments 15- to 30-cm-long, depending of the species, were rapidly cut under water and attached to a hydraulic conductivity apparatus filled with distilled, degassed water (Tyree and Sperry 1989). Maximum vessel length estimated using the method described by Zimmerman and Jeje (1981) varied from 4.5 to 17.3 cm (data not shown). Water exuding from the open end of the stem drained into graduated micro-pipettes. Following a short equilibration period, water flow generated by a constant hydraulic head of 50 cm, was measured volumetrically. Hydraulic conductivity ($\text{kg m s}^{-1} \text{ MPa}^{-1}$) was calculated as $k_h = J_v/(\Delta P/\Delta X)$, where J_v is the flow rate through the branch segment (kg s^{-1}) and $\Delta P/\Delta X$ is the pressure gradient across the segment (MPa m^{-1}). Specific hydraulic conductivity (k_s ; $\text{kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$) was obtained as the ratio of k_h and the cross sectional area of the active xylem, and leaf specific hydraulic conductivity (k_L , $\text{kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$) was obtained as the ratio of k_h and leaf surface area distal to the stem section. The active xylem area (A_s) for water transport measured in the middle of stem segments was obtained by introducing indigo carmine dye to stem segments from one cut end.

Specific leaf area

Fifty new, fully expanded leaves were collected from five individuals per species during the spring of 2007 and summer of 2008. Fresh leaf area was determined with a scanner. Leaves were oven-dried at 70°C until constant weight, and dry mass was used for leaf area per dry mass calculation (SLA, specific leaf area). Leaves of *M. spinosum* are semi-cylindrical. Consequently, instead of using projected leaf area for SLA calculations we took into account the three dimensional characteristics of the leaves.

Results

Annual rainfall during 2007 was only 130 mm, with eight very dry months with less than 10 mm per month (Fig. 1a). The absolute maximum and minimum temperatures during the study period were about 30 and -9°C , respectively (Fig. 1b). The summer of 2008 (January and February) was warmer and with lower precipitation than January and February 2007 (annual rainfall during 2006 was 226 mm). This difference was reflected in the soil gravimetric water content (Fig. 2a). Water content down to 120 cm depth was

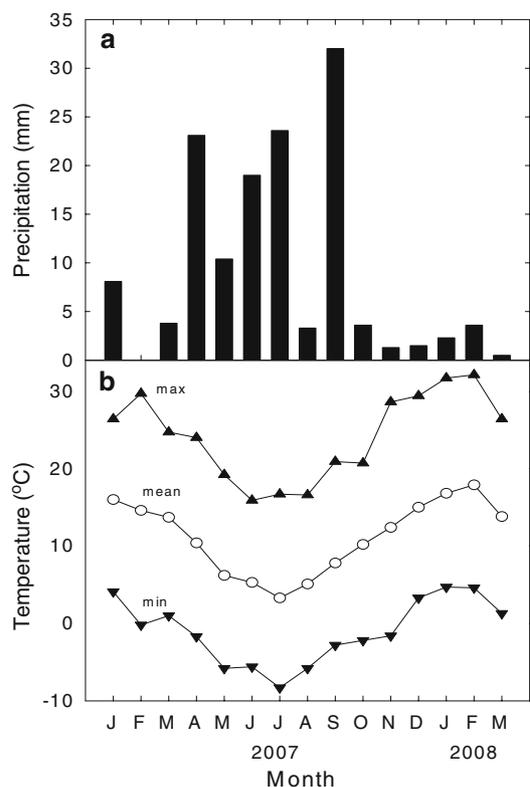


Fig. 1 **a** Seasonal variation in mean monthly precipitation and **b** mean air temperature, absolute maximum (*max*) and absolute minimum (*min*) temperatures from January 2007 to March 2008 from a weather station located 40 Km west of La Dora Ranch (Meteorological Station Los Antiguos, <http://www.inta.gov.ar>)

higher during the summer of 2007 than during the summer of 2008. Gravimetric and volumetric water contents were below 10% in the upper soil layers and relatively high at 300 cm depth (30 and 24%, respectively) (Fig. 2a, b). Consistent with the vertical pattern of variation in soil water content, Ψ_{soil} ranged from -3.6 to -2.3 MPa between 25 and 100 cm and increased to -0.13 MPa at 300 cm depth (Fig. 2c). Shortly after two consecutive rainfall events larger than 20 mm on 19 and 25 May 2008, Ψ_{soil} increased to -0.23 MPa at 25 cm depth, and to -0.16 MPa at 40 cm depth.

There were no significant differences between predawn Ψ_{Leaf} of covered and exposed leaves, suggesting that equilibration along the soil-to-leaf continuum was achieved at night. Consequently, predawn Ψ_{Leaf} was used as a surrogate for weighted mean water potential of the soil profile explored by functional roots (Bucci et al. 2004b). Because estimates of predawn Ψ_{Leaf} were obtained during a period without rainfall events, the differences in species-specific predawn Ψ_{Leaf} reflect differences in rooting depth and effective soil water availability, with more negative values of predawn Ψ_{Leaf} indicating that root systems were tapping shallower soil layers with lower water availability (Figs. 2, 3).

Differences in predawn Ψ_{Leaf} were consistent with rooting depths (Fig. 3), ranging from about -4.0 MPa for shallow-rooted shrubs (e.g. *M. spinosum* and *S. filaginoides*) to about -1.0 MPa for deep-rooted shrubs (e.g., *S. johnstonii* and *B. heterophylla*) during a summer drought.

Daily variation in Ψ_{Leaf} during the dry season for seven of the species studied exhibited a typical pattern with Ψ_{Leaf} decreasing (becoming more negative) during the morning and increasing (becoming less negative) in the afternoon (data not shown). Predawn Ψ_{Leaf} and minimum Ψ_{Leaf} differed significantly among species ($P < 0.0001$). Variations in species-specific predawn Ψ_{Leaf} were associated with variations in ρ_w (Fig. 4). Wood density was significantly different among the species studied ($P < 0.001$) ranging from 0.36 ± 0.01 g cm $^{-3}$ in *M. spinosum* to 0.91 ± 0.01 g cm $^{-3}$ in *S. johnstonii*. A family of linear relationships was fitted to the data, indicating that predawn Ψ_{Leaf} increased with increasing ρ_w across all species, however, the slopes of these relationships varied significantly ($P < 0.05$) according to soil water availability during the measurement period, with March 2008 being the driest period and consequently having the steepest linear relationship (Fig. 4). Species with deep roots (higher predawn Ψ_{Leaf} were able to maintain a more constant predawn Ψ_{Leaf} seasonally compared to species with shallow roots (more negative predawn Ψ_{Leaf}). For example, the predawn Ψ_{Leaf} of the shallow rooted *M. spinosum* changed from -2.85 MPa in January 2007 to -5.50 MPa in March 2008, whereas the predawn Ψ_{Leaf} of the deep rooted *S. johnstonii* only changed from -0.48 to -1.08 MPa during the same time period. Consistent with seasonal differences in predawn Ψ_{Leaf} , minimum Ψ_{Leaf} also remained relatively constant (isohydry) for the deep-rooted *S. johnstonii* and *B. heterophylla* while it differed substantially depending on water availability in the upper soil layers for the shallow-rooted species (e.g. *M. spinosum*) (Fig. 5). Wood density was a good predictor of maximum k_S and k_L measured on stems collected prior to dawn (Fig. 6). Although k_S appeared to decrease linearly with increasing ρ_w , k_L decreased exponentially. Species with low ρ_w and shallow roots such as *M. spinosum* and *S. filaginoides* had a more efficient water transport system (high predawn k_L) than species with high ρ_w and deep roots such as *S. johnstonii* and *B. heterophylla*. Depending on the species, k_S decreased by 22–7% from predawn to midday, with species attaining a more negative midday Ψ_{Leaf} experiencing a larger decrease in k_S compared to species able to maintain relatively high Ψ_{Leaf} (results not shown). Afternoon specific hydraulic conductivity was negatively correlated with soil–leaf water potential gradients ($\Delta\Psi$) across all species (Fig. 7) indicating, as expected, that species with higher k_S had lower $\Delta\Psi$ values compared to species with low k_S . There was no difference in $A_L:A_S$ between species with shallow roots and

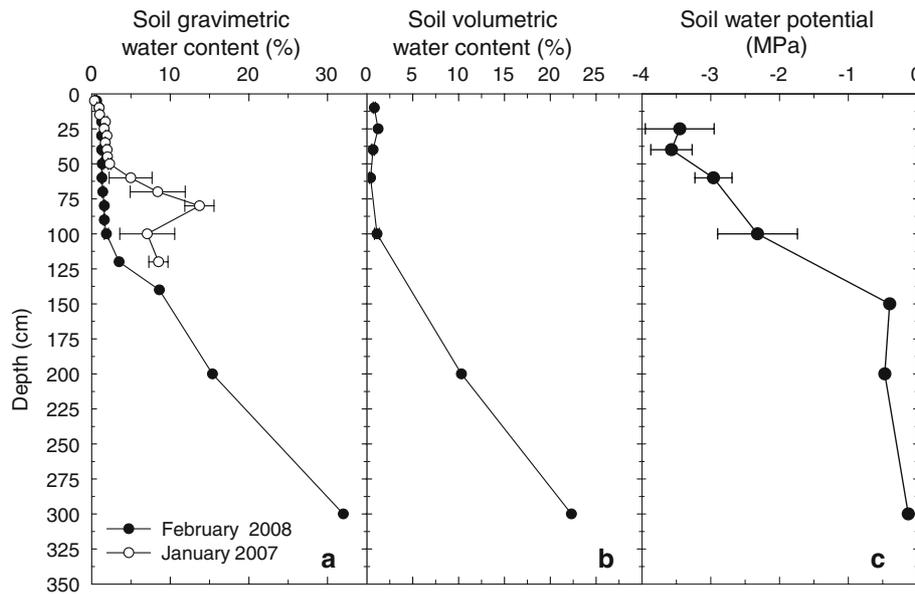


Fig. 2 **a** Soil gravimetric water content, **b** soil volumetric water content and **c** soil water potential at different soil depths. Values of gravimetric water content from samples obtained during January 2007 (*open symbols*) and February 2008 (*closed symbols*) are indicated in (**a**). Values in (**b**) and (**c**) were obtained during February 2008. Values of soil gravimetric water content are means (\pm SE) of three to four soil profiles

down to 120 cm depth and of two soil profiles for depths >120 cm. Values of volumetric water content are means (\pm SE) of two sensors per depth. Values in (**c**) are means (\pm SE) of three to five replicates at 25, 40, 60, 100 cm depth and of two replicates at 150, 200, and 300 cm depth

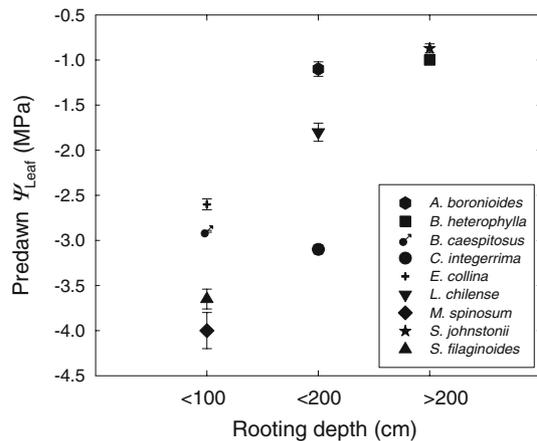


Fig. 3 Predawn leaf water potentials (predawn Ψ_{Leaf}) for non-transpiring leaves used to estimate species-specific weighted mean water potential of the rooting zone (see text), as a function of maximum rooting depth. Values of species-specific predawn Ψ_{Leaf} are means \pm SE of three individuals per species and three leaves per individual measured during February 2008. Rooting depth was obtained from excavations of three to five individuals per species

species with deep root systems (Table 1). The ratio $A_L:A_S$ is a morphological index of the water transport capacity of the stem in relation to the potential transpirational demand.

In addition to the strong linear relationships observed between ρ_w and both predawn Ψ_{Leaf} and k_S and k_L , specific leaf area (SLA) also decreased linearly with increasing

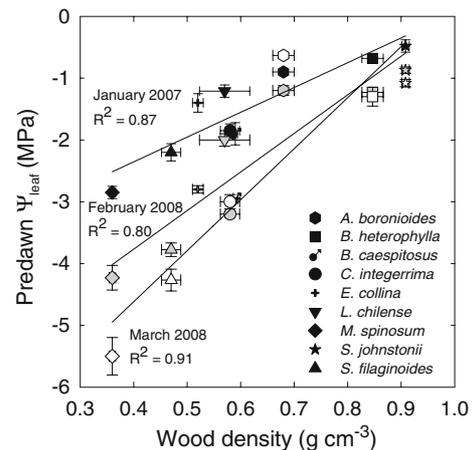


Fig. 4 Relationships between predawn leaf water potential (predawn Ψ_{Leaf}) and wood density of nine species obtained during January 2007 (*dark symbols*), of eight species during February 2008 (*gray symbols*) and of six species during March 2008 (*open symbols*). The *lines* are linear regressions fitted to the data (January 2007: $y = -3.9 + 4.0x$, $P < 0.001$; February 2008: $y = -6.2 + 6.2x$, $P < 0.005$; March 2008: $y = -7.9 + 8.2x$, $P < 0.05$). Each *point* represents the mean value (\pm SE) of five individuals per species and three leaves per individuals for predawn Ψ_{Leaf} ($n = 5$) and of ten individuals per species for wood density ($n = 10$)

wood density across species (Fig. 8). Species such as *M. spinosum* and *E. collina* with low wood density had thinner leaves (high SLA), compared to species such as *S. johnstonii* and *B. heterophylla* with denser wood and thicker leaves.

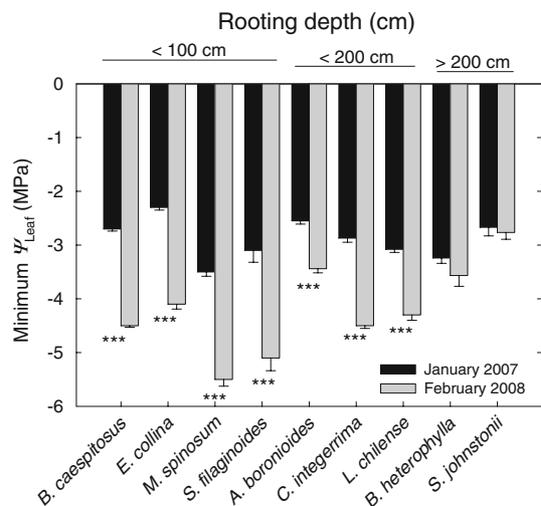


Fig. 5 Minimum leaf water potentials (minimum Ψ_{Leaf}) of nine woody species measured during a relatively wet period (January 2007) and a relatively dry period (February 2008). Each bar represents the mean value (\pm SE) of five individuals per species and three leaves per individual. *** indicate significant differences between periods at $P < 0.001$

Discussion

We found strong evidence of species-specific differences in the rooting depth of shrubs and in their potential ability to tap moisture from soil layers differing in water availability and residence time. This is not consistent with results of earlier studies suggesting that most woody species in the Patagonian shrub steppe had similar rooting depths, either exploring deeper soil layers compared to grasses or perennial herbs (e.g., Golluscio and Sala 1993; Golluscio and Oesterheld 2007), or using water from recent rain events in the topsoil where roots of most grasses preferentially occur (Schulze et al. 1996). Hydraulic architecture and water relations traits such as wood density, efficiency of water transport, and predawn or minimum Ψ_{Leaf} , were consistent with patterns of soil water uptake. Shallow-rooted species had low wood density, efficient water transport systems and midday Ψ_{Leaf} that exhibited strong seasonal changes, and apparently used moisture deposited in the upper soil by small rain events, while deeply rooted shrubs maintained similar Ψ_{Leaf} throughout the year, had stems with high wood density and low hydraulic conductivity and used water from deeper stable water sources. These two hydraulic syndromes were the extremes of a continuum with several species occupying intermediate portions of a gradient in hydraulic traits.

Temporal and spatial dynamics of soil water availability

In arid ecosystems, soil water potential is extremely variable in time and space, particularly in shallow soil layers. In contrast, the water potential of deeper soil layers is less

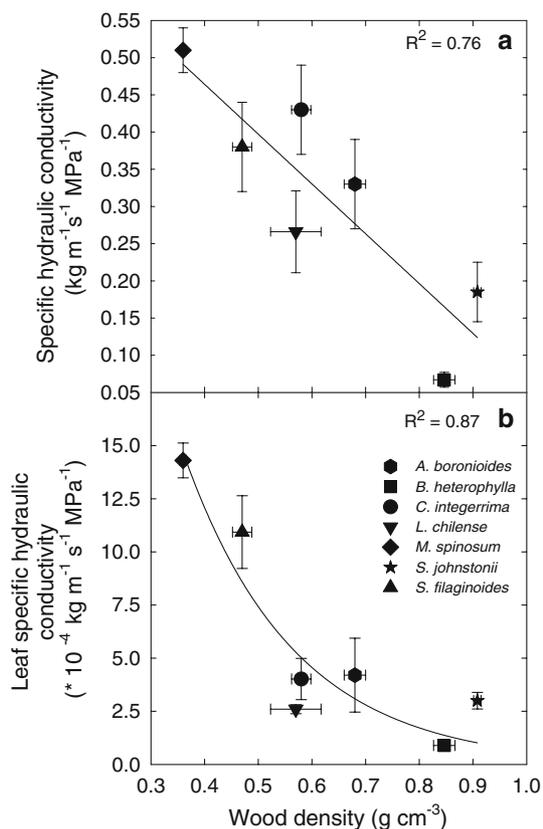


Fig. 6 Specific hydraulic conductivity and leaf-specific hydraulic conductivity as a function of wood density during January 2007. Each point represents the mean value (\pm SE) of five terminal branches per species measured at predawn and ten individuals per species for wood density. The line in **a** represents a linear relation fitted to the data $y = 0.73 - 0.67x$, $P < 0.005$. In **b**, an exponential decay function was fitted to the data [$y = 84.7 \times \exp(-4.9x)$, $P < 0.005$]

variable and its rate of change is slower (e.g., Noy-Meir 1973). In shallow soils, every rain event generates a pulse of moisture, which, depending on the amount of rainfall and evaporation, can last from a few hours to many weeks (Sala et al. 1981). Single events (larger than trace amounts) do not usually recharge the soil at depths greater than 20–30 cm (Sala and Lauerth 1982). Rainfall pulses translate into usable soil moisture depending on pulse size (mm of precipitation per event), evaporative demand conditions and soil physical properties (Reynolds et al. 2004). In North American deserts, most precipitation is received as small events (≤ 5 mm) and with most of the intervals between events being of short duration (≤ 10 days). In our study site, for the year 2007, only 23 of the 72 rain events were larger than 2 mm.

During the summer season in the study area, two distinct soil layers were discernible, with the upper 100 cm characterized by low water content and highly negative water potentials (around -3 MPa) and a deeper soil layer below 150 cm, with soil water potentials in the -0.8 to -0.1 MPa

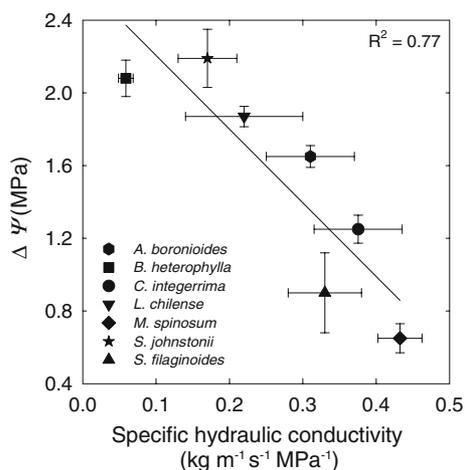


Fig. 7 Differences between predawn and minimum leaf water potential ($\Delta\Psi$) as a function of specific hydraulic conductivity of terminal branches measured in the afternoon during January 2007 in seven species. Each point represents the mean value (\pm SE) of five terminal branches of five different individuals per species ($n = 5$) for specific hydraulic conductivity and of five individuals per species and three leaves per individual for $\Delta\Psi$ ($n = 5$). The line is a linear regression fitted to the data ($y = 2.6 - 4.1x$, $P < 0.05$)

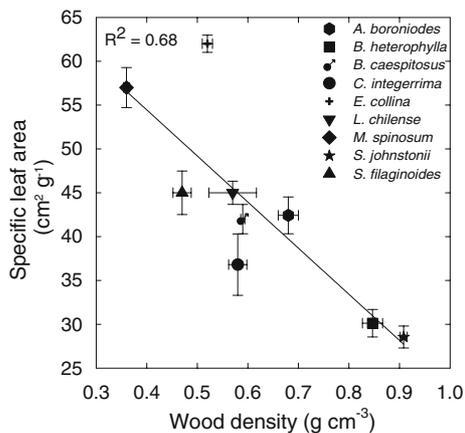


Fig. 8 Relationship between specific leaf area and wood density. Values for the seven species are means (\pm SE) of ten individuals per species ($n = 10$). The line is a linear regression fitted to the data ($y = 75 - 51x$, $P < 0.01$)

range. The presence of available moisture at depth in the study area is consistent with earlier observations that wet soil layers or ground water occurs at 2–3 m soil depth in the Patagonian steppe (Soriano et al. 1987; Soriano 1990; Schulze et al. 1996).

Leaf water potential, rooting depths and weighted mean soil water potentials

Reliable estimates of Ψ_{soil} and its spatial variation along with information on root distribution are key to calculating the driving forces for water movement along the soil–plant

atmosphere continuum. The presence of roots in a given soil layer is not by itself a reliable indicator of the potential activity of the roots in terms of water uptake unless their hydraulic conductivity is known. If leaf and soil water potential equilibrate before dawn, as with the nine species in this study, predawn Ψ_{Leaf} can be used as a surrogate for the weighted mean soil water potential (Davis and Mooney 1986; Brisson et al. 1993; Donovan and Ehleringer 1994). Excavation of root systems showed that shrub species differed in their rooting depth and that these variations were consistent with the pattern of daily and seasonal variations in Ψ_{Leaf} . Species with shallow roots had more negative predawn water potentials, and their seasonal fluctuations in Ψ_{Leaf} were larger than in species with deeper roots.

Wood density, growth rates and hydraulic conductivity

Density of woody stems has a theoretical upper limit of 1.5 g cm^{-3} (density of cell wall material; Siau 1984) and often varies from 0.1 to 1.0 g cm^{-3} across species. Even though ρ_w is typically considered to be a species-specific trait, it can vary under different growing conditions and between different parts of the same plant. Density is an excellent predictor of wood mechanical properties; both modulus of rupture and elasticity are positively correlated with density of woody stems (Niklas 1992; Van Gelder et al. 2006). Thus, high density wood offers better resistance to various environmental forces. In our study, taller shrub species had stems with higher ρ_w compared to shorter shrub species, and were more exposed to the strong winds common in Patagonia.

Wood density is also a good predictor of growth rate (Enquist et al. 1999; Roderick 2000; King et al. 2005). The relationship between growth rate and ρ_w may be universal with species having light wood growing faster than heavy wooded species (Enquist et al. 1999). In our study species, ρ_w ranged from 0.36 to 0.91 g cm^{-3} , a wide range of variation across species growing in the same habitat. Patagonian shrubs with low ρ_w have adaptations to make use of water pulses added to shallow soil layers and to grow fast during the short periods of time when soil water availability is high after a rainfall event or a sequence of small rainfall events. On the other hand, deep-rooted species with high ρ_w apparently grow slowly over a longer period of time and do not make use of water pulses as intensively as the other group of species because the hydraulic conductivity of their stems is low. These arguments may appear to be counterintuitive. Our previous work in seasonally dry tropical savannas showed just the opposite: wood density increased linearly with decreasing soil water potentials (across the entire profile) experienced by individual plants during the peak of the dry season (Bucci et al. 2004a). Following this line of

reasoning, it can be argued that because shallow-rooted species are under more stress they would have higher ρ_w associated with reduced cell expansion and thicker vessel walls. Savanna ecosystems typically receive 1,500 mm of rainfall annually and most of the species expand their stems during the wet season (Prior et al. 2004) when CO_2 assimilation rates are high (Franco et al. 2005). Woody plants in the Patagonian steppe, however, receive less than 200 mm of rainfall annually either in the form of snow during the winter and/or in short rainfall events during the spring and summer. It appears that shallow-rooted Patagonian plants behave opportunistically by growing fast and expanding their stems only when water is available for short periods of time in upper soil layers during the growing season. Deeper-rooted plants, on the other hand, appear to grow slowly and expand their stems continuously using water sources that are more stable in time.

Wood density is often linked to xylem cavitation resistance (Hacke et al. 2001; Ackerly 2004; Jacobsen et al. 2005) k_s and mean diurnal variation in Ψ_{Leaf} or minimum Ψ_{Leaf} (Meinzer 2003; Bucci et al. 2004a; Scholz et al. 2007). Species with high ρ_w are generally more resistant to cavitation have lower k_s (Bucci et al. 2004a; Pittermann et al. 2006; Meinzer et al. 2008) and experience more negative values of Ψ_{Leaf} . These trends have been observed in plants of different arid and semiarid ecosystems (Hacke et al. 2001; Jacobsen et al. 2007) or across different communities (Jacobsen et al. 2008). Results of our studies in Patagonian steppe shrubs, however, were not consistent (indeed opposite for the relationship between ρ_w and Ψ_{Leaf}) with these findings. Species with shallow roots and low ρ_w exhibited the most negative predawn and minimum Ψ_{Leaf} during the dry season compared with species with high ρ_w and deep root systems. This suggests that ρ_w should not be considered as a predictor of minimum Ψ_{Leaf} unless the relationship between ρ_w and Ψ_{Leaf} has been determined. Although we have not determined the resistance to cavitation and its relationship with minimum Ψ_{Leaf} and ρ_w the species with lighter wood probably have low xylem resistance to cavitation despite reaching lower Ψ_{Leaf} and may show a higher degree of native embolism. In the same sense and also as suggested by Jacobsen et al. (2008) for Mojave Desert species, it is possible that ρ_w and minimum Ψ_{Leaf} of Patagonian shrubs are not predictive of vulnerability to cavitation.

Some deeply rooted species also have abundant small roots near the soil surface (dimorphic root systems) that probably are functional for a short period of time after a rain event, but may undergo rapid rectification, a decrease in axial and radial root hydraulic conductivity (Nobel and Sanderson 1984; North and Nobel 1996) soon after water is depleted in the upper soil layers. Additional studies on axial and radial hydraulic conductivity of roots are needed to

determine whether shallow roots of species with deep tap roots are more sensitive to changes in soil water status and exhibit a more rapid decrease in hydraulic conductivity when soil water potentials decrease after a rainfall event, than comparable roots of shallow rooted plants.

In individuals with high ρ_w and consequently relatively low leaf-specific hydraulic conductivity, a larger driving force (difference in water potential between the soil-root interface and the leaf: soil-leaf $\Delta\Psi$) is required to transport a given amount of water to the leaves. This compensatory response was observed in our study because shallow-rooted species with higher specific hydraulic conductivity had lower values of soil-leaf $\Delta\Psi$ compared to deeply rooted species with low specific hydraulic conductivity. The larger soil-leaf $\Delta\Psi$ and low specific hydraulic conductivity of deeply rooted shrubs may negatively affect growth rates of tap roots, decreasing or limiting water uptake from deep soil layers. Another factor that may affect root growth into deeper soil layers could be related to water logging. Roots of many plant species do not tolerate anoxic conditions causing their growth to decrease or stop in water-saturated soils (Naumburg et al. 2005). More information is needed to solve the puzzle of why Patagonian shrub species apparently do not fully utilize the large amount of available water at depth.

Species-specific allocation patterns at the individual level often result in enhancement of a particular function at the expense of another, particularly in water-limited environments such as arid and semiarid ecosystems. Examples of these trade-offs include building thicker leaves (low SLA) that may help in protection against herbivores, but have a cost in terms of low photosynthetic capacity (Reich et al. 1997; Wright and Cannon 2001; Taylor and Eamus 2008). Specific leaf area is functionally related to photosynthetic capacity of leaves with thin leaves having higher photosynthetic capacity per unit leaf area than thicker leaves (Reich et al. 1998, 1999; Franco et al. 2005; Shipley et al. 2005). In this study, a wide range of specific leaf areas was observed. High SLA should enhance growth rates under the assumption that the amount of carbon allocated to leaves and or photosynthetic structures is similar across species. Leaf-specific conductivity also differed across the species studied with shallow-rooted species having higher k_L . Even though photosynthesis was not measured in this study, it is expected that species with high k_L and SLA will also exhibit high photosynthetic capacity that is one of the prerequisites for high growth rates (e.g., Brodrribb et al. 2002; Santiago et al. 2004; Campanello et al. 2008). *M. spinosum* was the shrub species with lowest wood density and one of the species with highest SLA and k_L while *S. johnstonii*, was the species with the lowest SLA and k_L and the highest wood density. The first species had shallow root systems, low homeostasis with respect to seasonal variations in predawn Ψ_{Leaf} , highest k_s , and probably uses small rain pulses and grows fast

during a relatively short period of time. The second group has deep roots, high homeostasis in water potentials, and low k_s . It appears that there is a marginal cost in growing deeper: an increase in wood density and hydraulic resistance, a relatively low above ground biomass compared to below ground biomass, leaves with low SLA, and relatively large water potential gradients between soil and leaves, all of which should result in low growth rates maintained over relatively long periods of time. The rest of the species have distinct operating ranges between these two extreme species along common physiological response curves determined by hydraulic architectural traits (e.g., hydraulic conductivity and wood density) and leaf traits (e.g., specific leaf area).

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