

Resource economics and coordination among above- and below-ground functional traits of three dominant shrubs from the Chilean coastal desert

Joaquín Morales¹, Francisco A. Squeo^{1,2,3},
Yann Tracol¹, Cristina Armas^{1,2,*} and Julio R. Gutiérrez^{1,2,3}

¹ Facultad de Ciencias, Universidad de La Serena, Casilla 554, La Serena, Chile

² Institute of Ecology and Biodiversity (IEB), Casilla 653, Santiago, Chile

³ Center of Advanced Studies in Arid Zones, Casilla 554, La Serena, Chile

*Correspondence address. Facultad de Ciencias, Universidad de La Serena, Casilla 554, La Serena, Chile.
Tel: +56-51-2334650; Fax: +56-51-2204383; E-mail: carmas@userena.cl

Abstract

Aims

Plant functional traits determine how plants respond to environmental factors and influence ecosystem processes. Among them, root traits and analyses of relations between above and below-ground traits in natural communities are scarce. Methods we characterized a set of above- and below-ground traits of three dominant shrub species in a semiarid shrub-steppe that had contrasting leaf phenological habits (deciduous, semideciduous and evergreen). We analysed if there was coordination among above- and below-ground resource economics patterns: i.e. patterns of biomass allocation, construction costs and lifespan.

Important Findings

Above- and below-ground traits and their resource economics relations pointed to species-specific functional strategies to cope with drought and poor soils and to a species ranking of fast to slow whole-plant strategies in terms of resource uptake, biomass construction costs and turnover. The deciduous shrub, *Proustia cuneifolia*, had relatively deep and even distribution of roots, and high proportion of short-lived tissues of low C construction costs: it had high fine to coarse root and high leaf-to-stem biomass ratios, high

specific leaf area (SLA), and stems of low wood density. This strategy allows *Proustia* to maximize and coordinate above- and below-ground resources uptake as long as the most limiting factor (water) is available, but at the cost of having relative high plant biomass turnover. The evergreen *Porlieria chilensis*, instead, displayed a more conservative and slow strategy in terms of resource economics. It had ~80% of the roots in the 40 cm topsoil profile, low proportion of fine compared with coarse roots and low leaf-to-stem ratios, low SLA and stems of high wood density, i.e. it invested in C costly tissues that, overall, persist longer but probably at the cost of having lower plant resource uptake rates. Traits in the semideciduous *Adesmia bedwellii* were in between these two functional extremes. Our results revealed high functional diversity and above- and below-ground complementarity in resource economics among these three codominant species in the Chilean coastal desert.

Keywords: drought, functional diversity, mass fractions, root distribution, specific leaf area

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INTRODUCTION

Plants have functional characteristics (traits hereafter) at tissue-to-organismal scales that reflect their evolutionary history and shape their performance (Reich 2014 and cites

therein). Such traits give clues regarding the responses to the environment the plant may have (e.g. how it interacts with other species, where can it grow or its effects on its surrounding environment). It is now known that plant traits are usually correlated in functional syndromes or plant ecological

strategies within and across communities and biomes (Westoby et al. 2002), and the identification of such general syndromes has gained considerable importance in ecology (Mommer and Weemstra 2012; Wright et al. 2004). A classic example is the tradeoff between the leaf area per leaf mass (specific leaf area (SLA)) and leaf lifespan. Species with lower SLA have usually thicker laminas and higher tissue density (Westoby et al. 2002 and cites therein). SLA is negatively related to leaf lifespan and positively related to leaf nitrogen content per leaf area, maximum photosynthesis and respiration (Poorter et al. 2009; Wright et al. 2004). Plants with high SLA can achieve fast growth by rapid assimilation, driven by high leaf N content and a large leaf area with low biomass investment. But they are also less mechanically robust and usually short lived, suggesting that longer leaf lifespans requires extra structural strength (Poorter et al. 2009; Reich et al. 1992; Westoby et al. 2002).

This and other general plant functional syndromes are now well established (Poorter et al. 2009, 2012; Reich 2014; Westoby et al. 2002; Wright et al. 2004) and explain much about species performance and community assembly for different species, being also applicable at different scales (within and across communities, climate zones and biomes; e.g. in Reich 2014; Westoby et al. 2002). However, they have been largely built upon analyses of plant above-ground functional traits, whereas there is poor knowledge on below-ground traits strategies, integrated above- and below-ground syndromes or whole-plant resource economics spectrum (Fortunel et al. 2012; McCormack et al. 2012; Mommer and Weemstra 2012; Tjoelker et al. 2005). Total plant biomass allocated to roots is as high as 47% in shrublands and 56% in deserts, with worldwide minimum and maximum values among biomes ranging from 20 to 70% (Poorter et al. 2012). However, despite their potential relevance, studies on roots traits and patterns of biomass allocation to different roots are still rather scarce (Lavorel 2013), particularly for woody species growing in natural conditions (Poorter et al. 2012; Schenk and Jackson 2002a). Overall, root traits are underrepresented in global functional traits databases (Kattge et al. 2011), and it seems that root traits may not always be well correlated with leaf traits (Fortunel et al. 2012).

In a recent forum, Reich (2014) hypothesizes that the ubiquity of strong selection along trait and life-history tradeoff axes, in tandem with biophysical constraints, results in convergence for any taxon on a uniformly fast, medium or slow strategy; i.e. having high, medium or low rates, respectively, of resource acquisition and processing for all plant organs and all resources. He hypothesized that there is coordination among above- and below-ground traits, organs, tissue biomass construction costs and uptake of resources that results in a general spectrum of fast to slow whole-plant strategies in terms of resource economics, i.e. a fast or slow strategy requires similar sets of leaf, root and stem traits regardless of whether the main limiting factor is light, N, P, water or temperature. For example, as Mommer and Weemstra (2012) hypothesized,

leaf traits that allow rapid photosynthesis, such as high leaf N and high maximum photosynthetic rate (and as an indirect measure, high SLA), will probably increase water and nutrient demand below-ground. Above- and below-ground traits might be thus functionally coupled and an investment on high SLA with high photosynthetic rates would probably require a dense root system with thin roots ensuring a large root-absorptive surface.

In arid environments, coexisting species have to cope with harsh conditions such as the scarce and pulsed availability of water (and nutrients) that controls the primary productivity, species function and ecosystem processes (Ehleringer et al. 1999; Ogle and Reynolds 2004). Thus, it may be expected that plant species belonging to similar big functional groups (e.g. shrubs) may share a set of common functional trait values, particularly those related to maximize the acquisition of the most limiting resource (water) or to drought survival (e.g. relatively large root to shoot ratios compared to species from more humid environs; Chapin et al. 1993; Schenk and Jackson 2002b). However, an intriguing observation in these arid environments is the fact that traits values may vary widely among coexisting species of similar functional groups, pointing to a stable mixture of different ecological strategies within the community (Westoby et al. 2002). This is the case of the shrub species in a semiarid coastal thorn scrub in the southern limit of the Atacama Desert. The three dominant species (~60% of total shrub cover) greatly differ in their leaf habit. One species, *Proustia cuneifolia*, is a drought-deciduous shrub that loses its leaves on a yearly basis. Another species, *Adesmia bedwellii*, is a drought semideciduous shrub and depending on water availability and precipitation patterns, it may or may not shed its leaves yearly (JR Gutiérrez, personal observation). The third species, *Porlieria chilensis*, is evergreen. Below-ground, the three species are engaged in the phenomenon of hydraulic lift—the passive movement of water through roots from wetter, deeper soil layers into drier shallower layers along a gradient in soil water potential (Muñoz et al. 2008), suggesting that all have dimorphic root systems that redistribute water among soil layers (Prieto et al. 2012) and that all may share some common below-ground traits such as root depth distribution.

The three species may certainly share common functional traits typical from perennial woody species (Poorter et al. 2012) and may also show convergence in traits values of central importance in terms of selection and persistence under the harsh conditions of arid environments (May et al. 2013). However, following the hypothesis stated by Reich (2014) and the observation that the three species greatly differ in leaf habit and, thus, probably in leaf construction costs and life span, we asked: (i) if within each species, there was coordination among traits and between different organs above- and below-ground in respect to biomass allocation and construction costs, i.e. if there is convergence in resource economics above- and below-ground and (ii) if this coordination differ among species in such a way that they could be ranked

in a whole-plant fast–slow plant economics spectrum. We expected to find the drought-deciduous species having a fast functional strategy in terms of biomass allocation and construction costs. We expected this species to allocate more biomass to fast-growing and short-lived tissues above- and below-ground that maximize resources acquisition while they are available and to have overall less dense tissues. On the opposite side would be the evergreen species, which would display a slow strategy characterized by the allocation of more biomass to relatively slow-growing, dense and long-lasting organs both above- and below-ground; these organs would be able to persist and be active during the long dry spells typical of these arid environments. Finally, the semideciduous species would be in-between this two extremes in the fast–slow plant economics spectrum.

For this purpose, we characterized different functional traits of shrubs of the three species growing in field conditions. We first analysed the depth distribution of roots, the percentage of biomass allocated to different type of roots (from fine to coarse roots) and then related these below-ground traits to above-ground traits such as leaf habit, SLA, leaf area index (LAI) and wood density, as well as calculated different biomass allocation ratios and fractions for each species.

METHODS

Study site

The study site is in an interior valley (Quebrada de Las Vacas, 230 m elevation) in Bosque Fray Jorge National Park (30°38'S, 71°40'W), north-central Chile. Climate is semiarid Mediterranean, with 90% of annual precipitation occurring in winter months (May–September). Average annual precipitation for 1989–2012 was 140 mm, with high interannual variation. The mean maximum temperature in the warmest month (January) is 24°C, while the mean minimum temperature in the coolest month (July) is 4°C.

The plant community is characterized by drought-deciduous and evergreen spiny shrubs of 2–3 m in height and an annual herbaceous plant community layer in rainy years. The dominant shrub species is the evergreen *P. chilensis* I. M. Johnst. (Zygophyllaceae, 25–35% cover; *Porlieria* hereafter), followed by the drought-semideciduous *A. bedwellii* Skottsb. (Fabaceae, 2.6–5.7% cover; *Adesmia* hereafter) and the drought-deciduous *P. cuneifolia* D. Don (Asteraceae, 2.0–9.5% cover; *Proustia* hereafter). The three species are engaged in the phenomenon of hydraulic lift (Muñoz *et al.* 2008), suggesting that all have dimorphic root systems. In another study, Tracol *et al.* (2011) measured marked differences in plant area index and microclimatic conditions underneath the three shrub species that point to vast differences in above-ground traits among species.

Below-ground traits: distribution and biomass of roots

Because our study was carried out in a National Park and because the methodology to estimate root distribution and

biomass allocation is destructive, we were just allowed to study three shrubs per species. These shrubs were randomly chosen in an area of 100 m². Beginning from the main stem of each shrub, we dug a trench in the soil 1 m deep and 1.6 m long outwards the shrub, and collected soil samples on increments of 20×20×10 cm (length, width and depth, respectively) to determine root biomass. A total of 80 soil samples per shrub were collected. Depending on their diameter, roots were separated into fine, medium or coarse roots ($\emptyset < 1$, 1–2 and >2 mm, respectively), dried in an oven for 48 h at 70°C and then weighed. To estimate total root mass of each shrub, we considered the root mass within the trench to be a proportion (~4%) of the total root biomass in the cylinder (radius 1.6 m and depth 1 m).

With this data in hand, we calculated the depth distribution of roots, referred as root biomass or length along soil depth. It can be characterized by the β index, which is estimated from the asymptotic equation:

$$Y = 1 - \beta^d \quad (1)$$

where Y is the accumulated proportion of root biomass from the soil surface down to d depth (Gale and Grigal 1987). β values usually range between 0.91 and 0.98 (Jackson *et al.* 1996). High β values correspond to greater proportion of roots deep in the soil and lower β values imply greater proportion of roots near the soil surface. This depth distribution of roots is one of the variables that best reflects root architecture (Lynch 1995). It is a good indicator of the relative reliance of plants on different depths for soil resources and resource niche partitioning among species, and it defines the vertical distribution of plant's influence on soil activity (Pérez-Harguindeguy *et al.* 2013).

Above-ground traits: LAI, biomass, wood density and SLA

Plant above-ground parts were harvested, separated into leaves and stems, dried in an oven for 48 h at 70°C and then weighed. We also estimated wood density on three basal stems per plant. In each stem we collected the first 15 cm in length from the base and discarded the first 5 cm. Wood density was estimated as the stem dry weight divided by its fresh volume. We estimated volume by submerging fresh stem in water and recording the water volume displaced.

Leaves were collected at two locations within a branch length: the most exposed to sunlight (leaves at the branch tip) as well as those far away of the branch tips (i.e. shaded leaves). In both branch locations, all fully expanded leaves within an area of 15 cm² were collected and pooled together to estimate their mean SLA (in m² kg⁻¹), measured as the ratio between fresh leaf area and leaf dry mass. Leaf samples were wrapped in wet paper and put inside sealed bags in a cooler. The area of each leaf was determined using a portable leaf area measurer (CI-203, CID Bio-Science Inc., Camas, WA, USA). Leaves were oven-dried for 48 h at 70°C and then weighed.

We measured LAI of five plants per species (the three plants harvested for biomass estimations and two other randomly selected nearby) using a LAI-2000 Plant Canopy Analyzer (Li-Cor, Nebraska, USA). Above- and under-canopy measurements allowed us to determine the solar radiation intercepted at five angles; LAI was calculated using a radiation transmission model for plant canopies (Tracol et al. 2011).

Data analysis

Differences among shrub species in root biomass distribution with depth, above-ground traits and biomass allocation fractions (or ratios) were analysed using general linear models (GLMs). For all analyses, species was the fixed factor. In the particular case of the analysis of root biomass distribution with depth (percentage of below-ground biomass along the soil profile), species, root diameter, depth and their interactions terms were the fixed factors. For this variable we also included in the model a correlation structure (corCompSymm) to take into account that there was spatial dependence among root samples at different soil depths within the same profile (same plant). This corCompSymm structure represents a compound symmetry structure corresponding to uniform correlation applied to soil depth within each plant individual.

To meet the assumptions of a normal distribution, biomass variables (roots, stems and leaves) were transformed using the natural logarithm. If necessary, different variance structures were tested to achieve homocedasticity and the best model was selected by comparing them via Akaike information criterion (Akaike 1974): we selected an exponential structure (varExp) for SLA and root biomass (percentage of below-ground biomass along the soil profile) and a varIdent

structure for above-ground biomass variables; varIdent represents a variance structure with different variances for different strata (species). Significant differences were further determined using Fisher's Least Significant Difference (LSD) *post hoc* tests. Non-parametric Kruskal–Wallis analysis was performed to analyse differences in β coefficients among species, as suggested by Gale and Grigal (1987). Analyses were performed in Infostat (Di Rienzo et al. 2013). Values throughout the text, tables and figures are means \pm 1 SE.

RESULTS

Root biomass and root distribution

The three shrub species had dimorphic root systems with lateral roots extending horizontally and one or more descendent deep tap roots (Figs 1 and 2). Root biomass peaked at 30–40 cm in all species, and the depth distribution of roots was similar among species (β coefficients were 0.964 ± 0.006 , 0.955 ± 0.007 and 0.951 ± 0.011 for *Proustia*, *Adesmia* and *Porlieria* respectively; Kruskal–Wallis $H = 1.67$, $P = 0.43$).

The accumulated root biomass at 30, 40 and 60 cm depths showed a tendency to be higher in the evergreen species *Porlieria* and the semideciduous species *Adesmia* than in the deciduous species *Proustia*. These differences were significant at 0–40 cm depth ($F_{2,6} = 9.75$, $P = 0.01$; Fig. 3) and marginally significant at 0–60 cm depth ($F_{2,6} = 4.35$, $P = 0.07$). The amount of root biomass of *Porlieria* and *Adesmia* increased with depth along the first centimetres of topsoil (0–40 cm) and then decreased with soil depth. Instead, the deciduous species *Proustia* had a more uniform distribution of root biomass along most of the soil profile (first 20–80 cm depth; Fig. 2, Table 1, Supplementary Table A1. Soil sections deeper

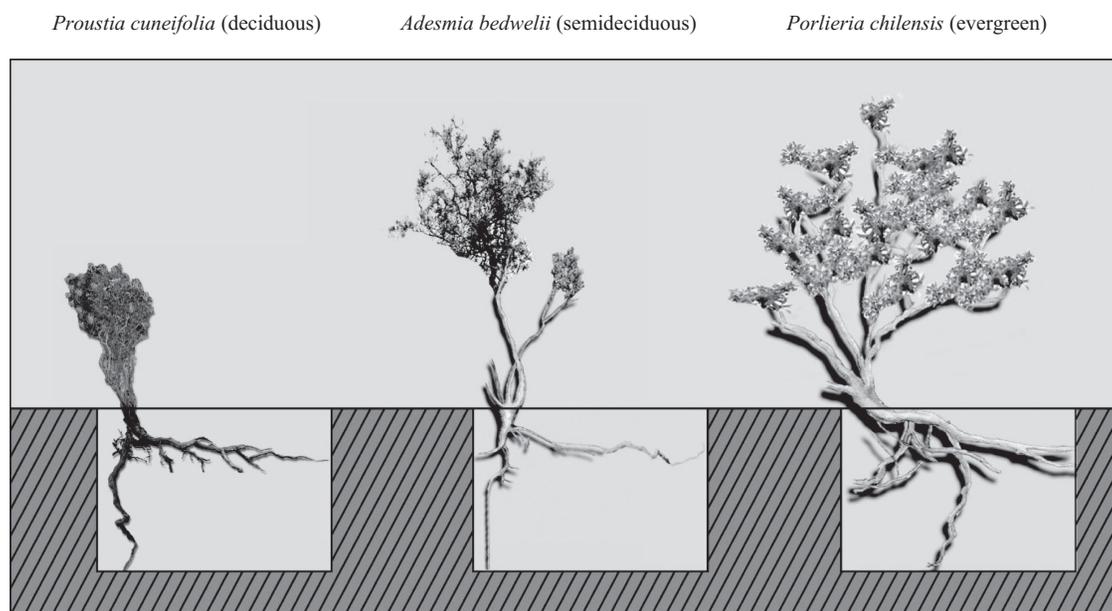


Figure 1: images of above-ground parts and main roots of *Proustia* (drought-deciduous), *Adesmia* (semideciduous) and *Porlieria* (evergreen). Photos were taken from field samples.

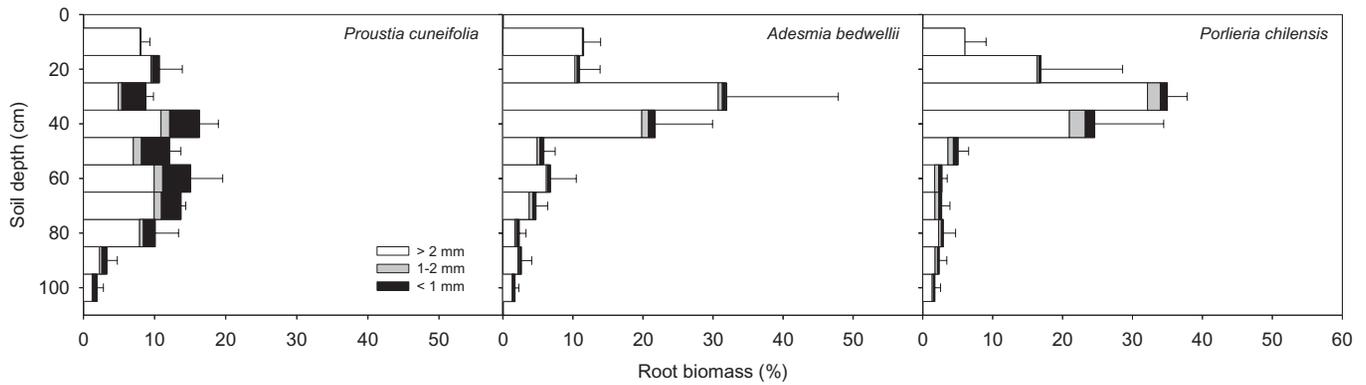


Figure 2: depth distribution of roots of different diameters in *Proustia* (drought-deciduous), *Adesmia* (semideciduous) and *Porlieria* (evergreen). Data are mean \pm SE; $n = 3$.

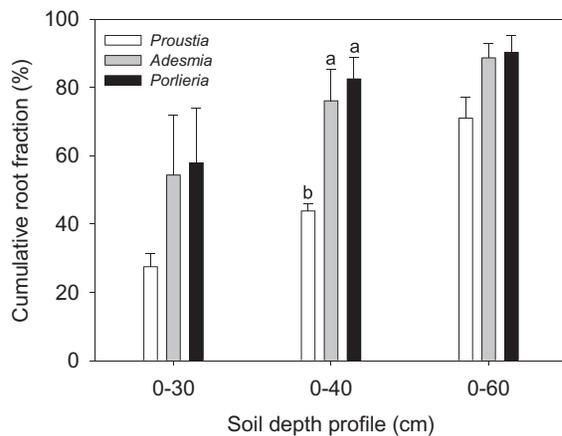


Figure 3: cumulative root fraction in *Proustia* (drought-deciduous), *Adesmia* (semideciduous) and *Porlieria* (evergreen) at different soil depth profiles (0–30; 0–40; 0–60 cm). Bars with different letters within a soil depth profile are significantly different (no letters within a soil depth profile indicate no differences among species; *post hoc* Fisher's LSD after GLM analyses, $P < 0.05$). Data are mean \pm SE; $n = 3$.

than 80 cm and between 0 and 20 cm deep had the lowest root biomasses). *Porlieria* and *Adesmia* displayed relative big amounts of lateral roots in the upper 40 cm soil layers (Fig. 2).

For all species, fine roots ($\varnothing \leq 2$ mm) were almost absent in the 10 cm topsoil. The percentage of root biomass allocated to fine- medium roots ($\varnothing < 2$ mm) and to coarse ones ($\varnothing > 2$ mm) were significantly higher (fine roots) and lower (coarse) in *Proustia* than in the other two species ($F_{2,6} = 26.90$, $P = 0.001$; Table 2, data on total root biomass also included), while there were no differences between *Porlieria* and *Adesmia*.

LAI, above-ground biomass, wood density and SLA

The three species had similar LAI ($F_{2,12} = 2.79$, $P = 0.10$, Table 2), and LAI was positively related to SLA and total leaf biomass (Supplementary Fig. A1; $F_{2,6} = 6.64$, $P = 0.02$, $r^2 = 0.71$). Biomass of leaves and stems was greater in the evergreen *Porlieria* than in the other two species that had

Table 1: statistical analysis of the percentage of below-ground biomass in each shrub species along the soil profile ($n = 3$)

	df	F
Intercept	1	302.19***
Species (S)	2	4.15*
Root diameter (R)	2	73.47***
Soil depth (D)	9	9.39***
S \times R	4	20.85***
S \times D	18	0.98 ^{ns}
R \times D	18	2.61***
S \times R \times D	36	1.61*

Statistical models are GLMs with species (*Proustia*, *Adesmia* and *Porlieria*), root diameter (<1, 1–2 and >2 mm), soil depth (10 depth intervals of 10 cm each from 0 to 1 m deep) and their interactions terms as fixed factors. A compound symmetry correlation structure on soil depth and plant individual was selected to account for spatial dependence among samples. An exponential variance structure (varExp) on soil depth was selected to correct for heterocedasticity. F values are shown in the last column; *, *** indicate $P < 0.05$, 0.001, respectively; ns indicates no significant differences.

similar above-ground biomass ($F_{2,6} = 9.17$, $P = 0.02$ for leaves; $F_{2,6} = 11.72$, $P = 0.01$ for stems, Table 2). The same occurred for wood density. It was highest in *Porlieria* than in the other species ($F_{2,6} = 12.90$, $P = 0.01$; Fig. 4a) that had similar wood density. SLA differed among species ($F_{2,12} = 44.56$, $P < 0.001$) and between sun exposed and shaded leaves ($F_{1,12} = 10.50$, $P < 0.01$). SLA values could be ranked according to species leaf-lifespans: leaves of the drought-deciduous *Proustia* had the highest SLA followed by *Adesmia* (semideciduous), whereas leaves of *Porlieria* (evergreen) had the lowest SLA values (Fig. 4b). Sun-exposed leaves had, on average, lower SLA than shaded leaves, but this difference was only significant for *Adesmia* (Fig. 4b).

Biomass allocation and correlations among traits

In general, the three species allocated most of the biomass to woody structures (stems and coarse roots, Fig. 5). *Proustia* (drought-deciduous) allocated higher biomass fraction to fine

Table 2: different traits of shrub species *Proustia* (drought-deciduous), *Adesmia* (semideciduous) and *Porlieria* (evergreen)

	Species		
	<i>P. cuneifolia</i>	<i>A. bedwellii</i>	<i>P. chilensis</i>
Below-ground			
Fine-to-medium root biomass (%)	25.91 ± 3.16b	8.00 ± 2.10a	12.02 ± 1.15a
Coarse root biomass (%)	71.61 ± 3.16b	92.67 ± 2.10a	87.98 ± 1.50a
Below-ground biomass (kg)	3.46 ± 0.52b	5.01 ± 1.06b	15.41 ± 6.26a
Above-ground			
LAI (m ² m ⁻²)	2.12 ± 0.34a	1.30 ± 0.11a	2.15 ± 0.44a
Total leaf biomass (kg)	0.45 ± 0.13b	0.49 ± 0.04b	1.57 ± 0.38a
Total stem biomass (kg)	3.41 ± 0.78b	7.16 ± 1.57b	22.77 ± 6.27a
Above-ground biomass (kg)	3.86 ± 0.89b	7.64 ± 1.53b	24.34 ± 6.64a

Below-ground: relative percentage of fine ($\varnothing < 2$ mm) and coarse root biomass and total root biomass in the first 1 m of soil depth. Above-ground: LAI; total leaf, total stem and above-ground biomass. Values within a row with different letters are significantly different (*post hoc* Fisher's LSD after GLM analyses, $P < 0.05$). For biomass variables, homoscedasticity was achieved including in the model a variance structure with different variances for different strata (varIdent). Data are mean ± SE; $n = 3$.

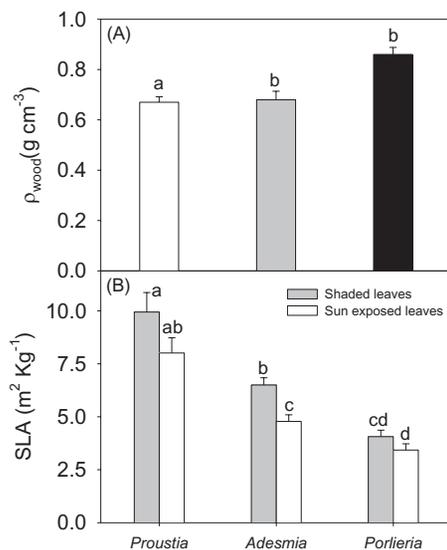


Figure 4: stem wood density (ρ_{wood}) (A) and SLA of canopy sun exposed and shaded leaves (B) in *Proustia* (drought-deciduous), *Adesmia* (semideciduous) and *Porlieria* (evergreen). Bars with different letters are significantly different (*post hoc* Fisher's LSD or Tukey after GLM analyses, $P < 0.05$). For SLA, homoscedasticity was achieved including in the model an exponential variance structure (varExp). Data are mean ± SE; $n = 3-6$.

roots (Fig. 5), and it also invested more biomass in leaves per stem unit (Table 3) than the other two species. Other mass fractions or biomass allocation ratios were similar among species.

Some traits were correlated, notably SLA with root-to-shoot (R/S), leaf-to-stem ratio and fine root mass fraction (positively correlated with SLA), and total mass of leaves, stems, coarse roots, above- and below-ground parts and stem mass fraction (all negatively correlated with SLA) (Supplementary Table A2).

DISCUSSION

Our results reveal a spectrum of plant functional strategies suited to cope with the harsh environmental conditions in this semiarid shrubland, suggesting there is functional complementary among the three co-dominant shrub species in the community. The three species had a dimorphic root system, similar rooting distribution depth and LAI, they had relative high root-to-shoot ratio and shared most of above- and below-ground mass fractions and ratios values. However, they differed in some functional traits related to above- and below-ground resource acquisition, maintenance and processing, displaying coordination between construction costs of above- and below-ground biomass. The drought-deciduous species allocated a significant higher proportion of plant biomass to short-living organs of relative high turnover ratios and low biomass construction costs (fine roots and high SLA) and it also had low density stems. Meanwhile, the evergreen allocated most of the above- and below-ground biomass to long living tissues of high biomass construction costs: coarse roots and stems of high wood density. It displayed relative low leaf-to-stem and fine-to-coarse root ratios and had low SLA and long-living leaves and roots, all pointing to relative slow whole-plant resource acquisition and biomass turnover of plant parts.

The three species had dimorphic root systems and are able to uplift water from deeper to shallower soil layers (Muñoz et al. 2008). This allows the shrubs to take advantage of rainfall pulses that infiltrates shallow soils along with soil water stored in deeper profiles as well as to maximize water use in time and space (Dawson and Pate 1996; Schwinning et al. 2002). They also shared similar root distribution depth with β values similar to other sclerophyllous (Jackson et al. 1996) and desert shrubs (Reynolds et al. 2004). This high overlap in their root distribution is probably determined not only by water but also by soil nutrient availability (Reynolds et al. 2004). Nonetheless,

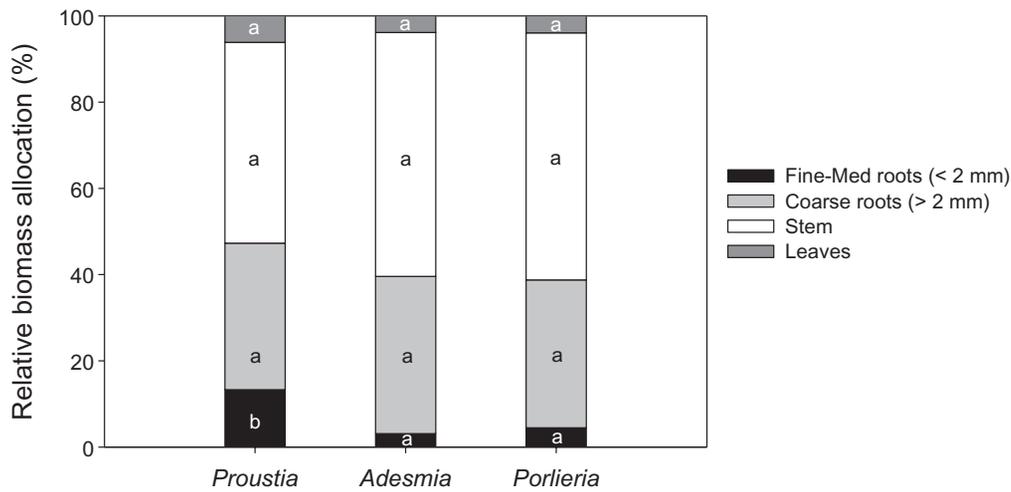


Figure 5: leaf, stem, coarse roots ($\varnothing > 2$ mm) and fine root mass fractions in *Proustia* (drought-deciduous), *Adesmia* (semideciduous) and *Porlieria* (evergreen). Data are expressed in relative percentage. Within each tissue, stacked bars with different letters indicate differences in biomass allocation among species (*post hoc* Fisher's LSD or Tukey after GLM analyses, $P < 0.05$). Data are mean \pm SE; $n = 3$.

Table 3: different mass fractions in *Proustia* (drought-deciduous), *Adesmia* (semideciduous) and *Porlieria* (evergreen)

	Species			$F_{2,6}$
	<i>P. cuneifolia</i>	<i>A. bedwellii</i>	<i>P. chilensis</i>	
R/S	1.04 \pm 0.37a	0.66 \pm 0.05a	0.69 \pm 0.21a	0.54 ^{ns}
Leaf/stem	0.13 \pm 0.01b	0.08 \pm 0.01a	0.07 \pm 0.01a	5.95*
Leaf/fine roots	0.51 \pm 0.18a	1.91 \pm 0.81a	1.02 \pm 0.29a	2.25 ^{ns}
Leaf/coarse roots	0.21 \pm 0.07a	0.12 \pm 0.07a	0.15 \pm 0.07a	0.48 ^{ns}
Stem/fine roots	3.96 \pm 1.26b	16.71 \pm 9.70a	14.22 \pm 4.18a	3.49 [‡]
Stem/coarse roots	1.54 \pm 0.60a	1.55 \pm 0.14a	2.21 \pm 0.93a	0.18 ^{ns}

R/S, leaf-to-stem, leaf-to-fine roots, leaf-to-coarse roots, stem-to-fine roots and stem-to-coarse roots ratios. Values within a row with different letters are significantly different (*post hoc* Fisher's LSD test after GLM analyses). F values are shown in the last column; * indicates $P < 0.05$; ns indicates no significant differences and [‡] marginally significant differences $P < 0.1$. Data are mean \pm SE; $n = 3$.

our results showed some relevant differences in below-ground traits among species. *Adesmia* and *Porlieria* had higher root biomass in the first 40 cm of soil (82.5 and 72.1%, respectively) than the drought-deciduous *Proustia* (43.8%). *Proustia* had a more even vertical distribution of roots and a higher proportion of fine roots than the other two species. These root patterns of *Proustia* are typical from species growing in soils with low water availability and that restrict their growth to periods with low evapotranspiration demand (Heilmeyer *et al.* 1997). By investing a greater proportion of root biomass to fine roots (particularly very fine roots of $\varnothing < 1$ mm) compared with the other species, *Proustia* allocate more below-ground biomass to the organs most active in water and nutrient uptake and in roots of low construction costs but that have greater turnover (Padilla *et al.* 2013). Non-suberized fine roots usually lose activity or die during dry spells (Jha and Prasad Mohapatra 2010; López *et al.* 2001), and, in general, they have lower survivorship under harsh abiotic conditions than medium to coarse roots (Chen and Brassard 2013; Eissenstat *et al.* 2000).

Interestingly, above-ground biomass allocation and investment costs mirrored below-ground patterns: compared with the other species, *Proustia* invested in short-lived leaves of high SLA, and in a higher proportion of above-ground biomass to leaves than stems. The fact that the drought-deciduous *Proustia* had higher SLA than the evergreen *Porlieria* and the semideciduous *Adesmia* is in agreement with metadata of species with different leaf habits, or lifespans, and leaf economics spectrum (Poorter *et al.* 2009, 2012; Westoby *et al.* 2002; Wright *et al.* 2004). Short-lived leaves with high SLA have to invest less biomass per leaf area unit, and thus it has been suggested that lower leaf longevity or deciduous habit is associated to lower nitrogen use efficiency (Falster *et al.* 2012) and smaller lifetime leaf carbon gain by photosynthesizing faster but for a shorter period (Falster *et al.* 2012; Westoby *et al.* 2002). SLA is positively correlated with leaf N and negatively correlated with leaf longevity, resource use efficiency (Wright *et al.* 2004) and relative growth rate (Poorter *et al.* 2009). Species with high SLA values lose turgor at higher (less negative) water potentials

than species with low SLA (but see Bartlett *et al.* 2012; Bucci *et al.* 2004; Poorter *et al.* 2009).

All this is in accordance with the leaf economic spectrum and leaf phenological habit of the three species under study, and also with the differences we found in wood construction costs. In all species, almost half of the biomass was allocated to stems and most of the biomass was above- or below-ground woody tissue, a typical pattern of species living in water-limited ecosystems (Poorter *et al.* 2012). In general, woody plants that allocate more biomass to stems (water transport) than to leaves (transpiration) improve their water relations by reducing the probability of xylem cavitation (Tyree and Dixon 1986), and resistance to xylematic embolism is positively correlated with wood density (Hacke *et al.* 2001). Species from water-limited ecosystems with shallow root systems tend to have higher wood density and resistance to cavitation than relatively deeper-rooted ones (Ackerly 2004; Bucci *et al.* 2004). Hence, although the three species have dimorphic root systems and similar depth distribution of roots, the evergreen *Porlieria* allocated below-ground biomass mainly to shallower roots, which might have promoted the development of a dense wood resistant to xylem cavitation that allows water transport and photosynthesis even at low soil moisture levels (Sperry *et al.* 2002). This might have also favoured its evergreen habit of leaves with low SLA values and that lose turgor only at low water potentials, as well as it is in accordance with its higher coarse-to-fine root ratio (i.e. higher investment in long-lived roots in charge of resource transport and that are less vulnerable to root cavitation than fine ones, Chen and Brassard 2013; Eissenstat *et al.* 2000). On the other end, the deciduous *Proustia* produced wood tissues of lower density, being thus potentially more vulnerable to xylem cavitation and producing leaves with high SLA that lose turgor at relative less negative soil water potentials than the evergreens. Overall this determines its deciduous leaf habit and relatively low tolerance to drought (Choat *et al.* 2006). Interestingly, trait values in the semideciduous species, *Adesmia*, were in between the two other species. Although wood density of *Adesmia* was similar to the drought-deciduous *Proustia*, SLA values and most mass fractions did not differ from any species, while leaf-to-stem and fine-to-coarse root mass fractions as well as root system distribution was similar to the evergreen *Porlieria*, overall explaining its intermediate strategy and leaf habit.

In conclusion, the set of functional trait values within each species suggests that the three species under study could be ranked in a fast–slow spectrum in terms of whole plant economics. We found an evergreen species that favoured whole plant relative long-lived, dense tissues of high construction costs, drought resistant and with probably high resource use efficiency that, overall, can be identified as a slow species following Reich's (2014) plant economic spectrum proposal. On the opposite side, the drought-deciduous species favours above- and below-ground short-lived, lighter tissues of low construction costs, growing faster by constructing less C costly tissues and favouring those organs more active and

fast in resource uptake (high SLA and fine roots). The species restricts its growth to favourable periods when higher amounts of soil water and nutrients are available and gets rid of leaves and, probably, fine roots once the most limiting resources are depleted, becoming dormant and maintaining those drought-resistant organs for the next favourable season. Thus, it can be identified as a fast species. The fact that these dominant species could be ranged in a single 'fast–slow' plant economics spectrum that integrates across leaves, stems and roots reveals high functional diversity and complementary in this community and may help to explain community assembly and the functioning of semiarid ecosystems.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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