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Short Communication

Differential utilization of a shallow-water pulse by six shrub species in the Patagonian steppe

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ABSTRACT

A field experiment was performed to improve understanding of the functional diversity of western Patagonian shrubs. *Anarthrophyllum rigidum*, *Adesmia volckmanni*, *Berberis heterophylla*, *Mulinum spinosum*, *Schinus poligamus* and *Senecio filaginoides* were compared in their capacity to absorb water from a 10-mm pulse enriched in deuterium and applied at the beginning of the dry summer. Xylem-water enrichment 14 days after watering was rather subtle, but the upper-soil signal was clear enough to distinguish shallow from deeper absorption. According to a linear mixing model, the proportion of surface-pulse water relative to total water uptake was maximum for *Senecio* (29–38%) and *Mulinum* (22–32%), both relatively shallow-rooted species, intermediate for *Berberis* (16–17%) and *Schinus* (6–9%), and negligible for the two N-fixing Fabaceae: *Adesmia* (<1%) and *Anarthrophyllum* (<3%), despite this last one having a dimorphic (tap + shallow) root system. It is hypothesized that shallow-water pulses may be more profitable in terms of nitrogen than of water, and thus constitute a higher-quality resource for those species only able to use N from soil sources.

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1. Introduction

In arid and semiarid ecosystems, water input is particularly variable in time and space, giving place to pulses of both resource availability and biological activity (Huxman et al., 2004; Reynolds et al., 2004). Plants' differential abilities to use inputs of a certain size and timing, and therefore location in the soil profile, contribute to diversity maintenance (Chesson et al., 2004). The first general proposal in this respect was Walter's (1971), classifying savanna species into shallow-rooted grasses, which tend to use water from the upper layers of the soil, and deep-rooted woody species, having exclusive access to lower layers. Later studies found different degrees of surface-water use by woody species (Ehleringer et al., 1991; Gebauer et al., 2002; Lin et al., 1996; Schwinning et al., 2002), and even a lack of partitioning of this resource between life forms (Reynolds et al., 2004; Schwinning et al., 2002).

Earlier observations for the western Patagonian steppe seemed to match Walter's simple two-layer model (Soriano and Sala, 1984), but later experiments revealed the complexities that could be expected from more realistic models (e.g. Emmerich and Verdugo, 2008; Ogle and Reynolds, 2004). For example, results for the same shrub species varied according to pulse size, timing, and preceding precipitation (Golluscio et al., 1998; Sala et al., 1989). In addition, Golluscio and Oesterheld (2007) found that western Patagonian shrubs constitute a life-form with large inter-specific heterogeneity in water-use efficiency.

This study reports a field experiment devised to improve our understanding of the functional diversity of Patagonian shrubs. A small, shallow, pulse of labeled water was added during the summer with the objective of assessing the ability of six different species to capitalize summer rainfall events. In order to shed light on potential explanations for inter-specific differences, responses were then related to life-history traits like rooting depth, foliage persistence, isotopic nitrogen concentration (indicative of N source; Lambers et al., 1998) and isotopic carbon concentration (indicative of water-use speed and efficiency; Jones, 1992). The studied species and their main traits are presented in Table 1.

2. Materials and methods

The Patagonian steppe as represented in SW Chubut, Argentina, is codominated by tussock grasses (*Stipa* spp. and *Poa ligularis*) and low-stature shrubs, mainly *Adesmia volckmanni*, *Mulinum spinosum* and *Senecio filaginoides* (Soriano et al., 1994); less frequent are *Schinus polygamus*, *Berberis heterophylla*, and *Anarthrophyllum*

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Table 1
Morpho-physiological traits of the studied species. Isotopic data obtained are from this study (see Methods), but no comparisons were made between treatments. Species order as in Table 2 (decreasing f_U-A).

Species	Family	Foliage	Root system	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
Senecio filaginoides De Candolle	Asteraceae	Evergreen	Shallow (Fernández and Paruelo, 1988)	2.35	−28.7
Mulinum spinosum (Cav.) Pers.	Apiaceae	Deciduous	Relatively shallow (Fernández and Paruelo, 1988)	2.87	−27.8
Berberis heterophylla Jussieu ex Poir.	Berberidaceae	Evergreen	>2 m deep (Bucci et al., 2009)	1.43	−26.7
Schinus polygamus (Cav.) Cabr.	Anacardiaceae	Evergreen	Probably very deep (see Bucci et al., 2009 for *Schinus johnstonii*)	2.42	−28.6
Adesmia volckmanni Phil.	Fabaceae	Deciduous	ca. 1.5 m deep (Golluscio et al., 2006)	−0.18	−25.4
Anarthropyllum rigidum Hieron.	Fabaceae	Evergreen	Dimorphic (Esteban Fernández, pers. comm.)	0.09	−24.6

rigidum, but the two last ones may become strongly dominant locally. Precipitation is concentrated in the autumn and winter months (April to September), with a 30-yr mean of 174 mm; average air temperature is 1 °C for July and 15 °C for January. Soils are of a coarse texture with a noticeable abundance of pebbles (Del Valle, 1998).

Work was performed at the Río Mayo Experimental Field Station from INTA (Instituto Nacional de Tecnología Agropecuaria), Argentina – 45.4° S 70.1° W, during the last days of 2002 and beginning of 2003. The year immediately preceding the experiment had been a Niño one, with above-average precipitation (206 vs. 174 mm), and virtually no rain during the last three months (6.3 mm total from October to December). Thus, we expected typical conditions for the season, with negligible moisture in the upper soil and relatively wet lower soil (Golluscio et al., 1998).

A large plot (ca. 4 ha) was selected in which individuals of the 6 species listed in Table 1 coexisted. Within this plot, we marked three areas containing at least two individuals of modal size of each population (i.e. 12 shrubs) growing between 3 and 10 m apart from each other. Pooled leaf samples for each species were then taken for isotopic analyses of C and N; these were air-dried and kept in paper bags.

Based on small differences in slope and aspect, each marked area was treated as a block in which one of the members of each same-species pair was randomly selected to be watered and the other kept as control. The former were irrigated on December 21st, 2002 (beginning of the Southern Hemisphere summer season) with the equivalent of a 10-mm precipitation with water highly enriched in deuterium (δD: $+49$ to $+51‰$ vs. Standard Mean Ocean Water [SMOW]; $n = 4$), covering an area centered at the main stem and extending ca. 0.4 m beyond the canopy edge. Immediately after irrigation, points were marked on which soil samples were going to be taken afterwards (one control and one treatment point per block).

Two weeks after irrigation, on January 4th, 2003, plant and soil samples were taken for stable-isotope content of hydrogen in water. This interval was chosen as a compromise between the need for allowing some response time of these slow-growing woody species (e.g. Golluscio et al., 1998) and the risk of water having been used by the time we sampled. In the early morning, four young suberized twigs were selected from each individual. These were defoliated and rapidly clipped and sealed in vials. Soil samples were taken at depths of 10, 30, 60 and 100 cm and placed in vials taking precautions to avoid evaporation. Samples were stored at −20 °C until analysis.

Isotopic H, N and C analyses were performed at DEVIL, the mass spectrometry facility at Duke University (U.S.A.). Water was extracted from soil and tissue samples by vacuum distillation. Isotope ratio analyses for D in water and ^{13}C and ^{15}N in tissues were quantified with a Finnigan-Mat delta S mass spectrometer, and expressed in parts per thousand vs. SMOW, V-PDB standard, and atmospheric N_2 respectively. A linear mixing model (Dawson, 1993) was used to estimate the proportion of surface-pulse water ("f_U"; U for upper soil) used by each individual relative to that coming from lower soil ("f_L" "$= 1 - f_U$):

$$\delta D_X = f_U \delta D_U + f_L \delta D_L \qquad (1)$$

From which:

$$f_U = (\delta D_X - \delta D_L)/(\delta D_U - \delta D_L) \qquad (2)$$

Being: δD_X: xylem deuterium isotopic signal; δD_L: signal from the lower-soil layers (average of 30, 60 and 100 cm depth); δD_U: signal from the upper-soil layer (10 cm depth).

Equation (2) was solved for each individual by two different approaches: (A) using the soil-water signal at each depth (δD_U, δD_L) resulting from the average across blocks or, alternatively, (B) using the δD_U and δD_L data for the soil sample of the block in which the individual was located. In both cases, results are reported as the average for each species.

3. Results

Fourteen days after experimental watering, there was a clear isotopic signal of the treatment in the upper soil and no detectable changes in the deeper soil. Water at 10 cm depth was enriched in deuterium, in average, by 47 per mil, whereas δD remained virtually constant for deeper layers (Fig. 1).

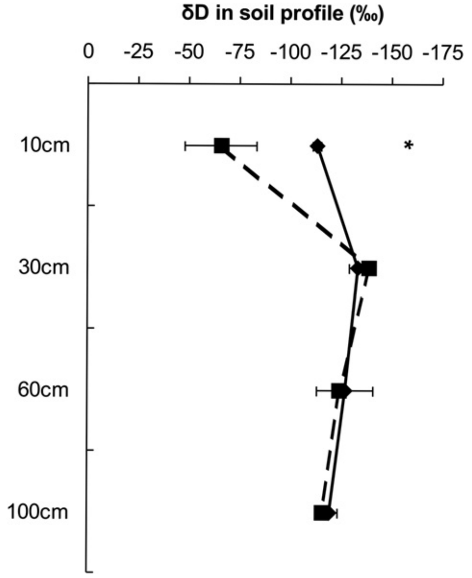

Fig. 1. Deuterium (‰ vs. SMOW) in soil as a function of depth 14 d after adding 10 mm of isotopically enriched water. Squares: treatment; diamonds: control. Bars show SE; $N = 3$; * indicates $P < 0.05$, Kruskal Wallis test.

Table 2
Xylem-water isotopic composition 14 days after treatment, ANOVA comparison, and results of mixing models (see text for approach A vs. B). Different letters indicate significant differences between species ($P < 0.1$). Ordered by decreasing f_U.

Species	Xylem δD (‰ above control) Average, [range]	Probability (treatm. vs. control)	Use of surface water (f_U)	
			Version A	Version B
Senecio filaginoides	+14 [+5, +21]	0.074	28.6%	38.2% a
Mulinum spinosum	+6 [+1, +10]	0.084	22.5%	31.7% a
Berberis heterophylla	+3 [−8, +16]	0.752	15.9%	16.6% ab
Schinus polygamus	−1 [−4, +3]	0.567	6.0%	9.4% b
Adesmia volckmanni	+3 [−1, +8]	0.214	0.6%	0.8% b
Anarthropyllum rigidum	−4 [−12, +5]	0.347	0.0%	2.8% b

Xylem water was clearly enriched by this treatment, relative to controls, for only two of the six species: *Senecio* and *Mulinum*, and much less or not at all for the other four species (Table 2; note large variability). Accordingly, these two were the ones for which the mixing models estimate the largest use of surface water relative to total use (f_U). regardless of the calculation approach (Table 2).

The two species making very little or no use of the added pulse water, *Anarthrophyllum* and *Adesmia* (both Fabaceae), had a nitrogen isotopic signal very close to zero, indicative of fixation from the atmosphere (Table 1). This contrasted with the values found for the other four species, none of them Fabaceae, which were using mainly N from soil sources.

Species also differed in their C isotopic signal: *Senecio*, *Mulinum* and *Schinus* had the lowest (more negative) δ^{13}C values (Table 1), indicative of a relatively fast water use at the leaf level (Jones, 1992). There was a trend for δ^{13}C to be correlated with f_U (rank correlation $P = 0.11$), suggesting that the potentially faster growers showed the largest response to the applied pulse.

4. Discussion

The shallow-water pulse produced at the beginning of the summer was used by Patagonian shrubs in different degrees. Most of the species seemed not to have taken advantage of this extra resource (clearly *Adesmia* and *Anarthrophyllum* did not; possibly neither *Schinus* nor *Berberis*), very likely because water was more available in the deeper soil. The complement of f_U numbers in Table 2 (i.e. f_L), indicates that the soil below ca. 15–20 cm provided almost all of the water (between 83 and 100%) for these non-responding species. Even for those species which did respond, *Senecio* and *Mulinum*, this source still accounted for the majority of total use (62–77%).

A relevant point is the influence that the chosen interval between treatments and sampling (2 weeks) may have had on our conclusions. The four species that appear as using little added water (*Berberis*, *Adesmia*, *Anarthrophyllum* and *Schinus*), could have already used it by the time we sampled? This seems unlikely, at least for the first three species, since carbon-isotope data show that they were slower in their use of water than *Senecio* and *Mulinum* (less negative δ^{13}C; Table 1), which is consistent with the relatively large specific leaf area of these last two species (Bucci et al., 2009). Given the high evaporation rates expected during this time of the year, neither seems likely that there was any usable pulse water left afterwards (e.g. Whythers et al., 1999).

Some of our results, although not all of them, are in agreement with what is known about the root systems of these species. Those having the largest upper-soil water uptake (*Mulinum* and *Senecio*) have relatively shallow root systems, with a peak at a depth of 30–40 cm; *Senecio* in particular has abundant roots above that layer (Fernández and Paruelo, 1988). *Adesmia*, instead, has a deeper system, with a peak between 40 and 60 cm and virtually no roots in the upper 20 cm (Golluscio et al., 2006). We are not aware on any published quantitative studies on the rooting patterns of *Schinus* and *Berberis*, although they are routinely referred to as deep-rooted species. *Anarthrophyllum*, in contrast, has a dimorphic system, with a strong tap root and thick, horizontally extended surface roots (Esteban Fernández, pers. comm.).

There are a number of reasons why an arid-zone plant may not respond to a water pulse that reaches active roots (e.g. Donovan and Ehleringer, 1994; Fernández et al., 1992; Golluscio et al., 1998; Snyder et al., 2004), but possibly the most common one is the existence of available water deeper in the profile (Fernández, 2007). The precipitation pattern in the study year, as explained above, guaranteed a dry upper soil, and our results (Table 2) show that there was some available water deeper in the lower soil. Then the question is why some of the species did respond to the shallow-water pulse at all. One possibility is that this allowed them to save deeper moisture, a source not subjected to direct evaporation and more protected from dense-root competition than shallower sources (Schwinning et al., 2002).

Another conceivable explanation focuses not in water but in nitrogen use, and we pose it here as our final hypothesis. Since most soil N is located in the upper soil and uptake of water and N can occur simultaneously in different parts of the root system (Gebauer and Ehleringer, 2000), species not having access to atmospheric N_2 would benefit by using surface-water pulses as a way of acquiring soil nitrogen (cf. Jeschke and Pate, 1995). The use of surface-soil N may not have been possible for *Adesmia* because of its rooting pattern (see above), but for *Anarthrophyllum* may not have been necessary (and, as long as there is a cost involved in acquiring it, may not have been profitable) because of its access to N from the atmosphere. Results may certainly have been different on a year or site with a drier deep soil (e.g., Fravolini et al., 2005 on *Prosopis*). Actually, our δ^{15}N data for *Adesmia* are very close to Golluscio et al.'s (2006) for a wet site, but very different from that for their drier site. Also, preliminary dendrochronological observations for *Anarthrophyllum* showed a smaller degree of growth dependence on precipitation at our site than at a sandier one located ca. 30 km away ("Cañadón Faquico"; Srur and Villalba, 2009).

In a comparison of 13 species from SW Spain, Zunzunegui et al. (2005) showed that the two leguminous ones showed very little variations in midday water potentials along the growing season, suggesting reliance on deep soil moisture. Our *Adesmia* and *Anartrophyllum* example highlights how strongly the availabilities for different resources can interact: These plants shared ability to use atmospheric nitrogen seems to be at least as important to predict their responses to water pulses than other, most obvious, differences, such as rooting patterns (deep vs. dimorphic) and leaf phenology (deciduous vs. evergreen).

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References

Bucci, S.J., Scholz, F.G., Goldstein, G., Meinzer, F.C., Arce, M.E., 2009. Soil water availability and rooting depth as determinants of hydraulic architecture of Patagonian woody species. Oecologia 160, 631–641.

Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., Sher, A., Novoplansky, A., Weltzin, J.F., 2004. Resource pulses, species interactions and diversity maintenance in arid and semi-arid environments. Oecologia 141, 236–253.

Dawson, T.E., 1993. Water sources of plants as determined from xylem-water isotopic composition: perspectives on plant competition, distribution, and water relations. In: Ehleringer, J.R., Hall, A.E., Farquhar, G.D. (Eds.), Stable Isotopes and Plant Carbon–Water Relations. Academic Press, San Diego, pp. 465–496.

Del Valle, H.F., 1998. Patagonian soils: a regional synthesis. Ecología Austral 8, 103–123.

Donovan, L.A., Ehleringer, J.R., 1994. Water stress and use of summer precipitation in a Great Basin shrub community. Functional Ecology 8, 289–297.

Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F., Sandquist, D.R., 1991. Differential utilization of summer rains by desert plants. Oecologia 88, 430–434.

Emmerich, W.E., Verdugo, C.L., 2008. Precipitation thresholds for CO_2 uptake in grass and shrub plant communities on Walnut Gulch experimental watershed. Water Resources Research 44, W05S16.

Fernández, R.J., 2007. On the frequent lack of response of plants to rainfall events in arid areas. Journal of Arid Environments 68, 688–691.

Fernández, R.J., Paruelo, J.M., 1988. Root systems of two Patagonian shrubs: a quantitative description using a geometrical method. Journal of Range Management 41, 220–223.

Fernández, R.J., Núñez, A.H., Soriano, A., 1992. Contrasting demography of two Patagonian shrubs under different conditions of sheep grazing and resource supply. Oecologia 91, 39–46.

Fravolini, A., Hultine, K.R., Brugnoli, E., Gazal, R., English, N.B., Williams, D.G., 2005. Precipitation pulse use by an invasive woody legume: the role of soil texture and pulse size. Oecologia 144, 618–627.

Gebauer, R.L.E., Ehleringer, J.R., 2000. Water and nitrogen uptake patterns following moisture pulses in a cold desert community. Ecology 81, 1415–1424.

Gebauer, R.L.E., Schwinning, S., Ehleringer, J.R., 2002. Interspecific competition and resource pulse utilization in a cold desert community. Ecology 83, 2602–2616.

Golluscio, R., Oesterheld, M., 2007. Water use efficiency of twenty-five co-existing Patagonian species growing under different soil water availability. Oecologia 154, 207–217.

Golluscio, R.A., Sala, O.E., Lauenroth, W.K., 1998. Differential use of large summer rainfall events by shrubs and grasses: a manipulative experiment in the Patagonian steppe. Oecologia 115, 17–25.

Golluscio, R.A., Faigón, A., Tanke, M., 2006. Spatial distribution of roots and nodules and $\delta^{15}N$ evidence of nitrogen fixation in *Adesmia volckmanni*; a Patagonian leguminous shrub. Journal of Arid Environments 67, 328–335.

Huxman, T.E., Snyder, K.A., Tissue, D., Leffler, A.J., Pockman, W., Ogle, K., Sandquist, D., Potts, D.L., Schwinning, S., 2004. Precipitation pulses and carbon balance in semi-arid and arid ecosystems. Oecologia 141, 254–268.

Jeschke, W.D., Pate, J.S., 1995. Mineral nutrition and transport in xylem and phloem of *Banksia prionotes* (Proteaceae), a tree with dimorphic root morphology. Journal of Experimental Botany 46, 895–905.

Jones, H.G., 1992. Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology, second ed. Cambridge University Press, Cambridge.

Lambers, H., Chapin, F., Pons, T., 1998. Plant Physiological Ecology. Springer, Berlin.

Lin, G., Phillips, S.L., Ehleringer, J.R., 1996. Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. Oecologia 106, 8–17.

Ogle, K., Reynolds, J.F., 2004. Plan responses to precipitations in deserts ecosystems: integrating functional types, pulses, thresholds and delays. Oecologia 141, 282–294.

Reynolds, J.F., Kemp, P.R., Ogle, K., Fernández, R.J., 2004. Modifying the 'pulse–reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. Oecologia 141, 194–210.

Sala, O.E., Galluscio, R.A., Lauenroth, W.K., Soriano, A., 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. Oecologia 81, 501–505.

Schwinning, S., Davis, K., Richardson, L., Ehleringer, J.R., 2002. Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. Oecologia 130, 345–355.

Snyder, K.A., Donovan, L.A., James, J.J., Tiller, R.L., Richards, J.H., 2004. Extensive summer water pulses do not necessarily lead to canopy growth of Great Basin and northern Mojave Desert shrubs. Oecologia 141, 325–334.

Soriano, A., Sala, O.E., 1984. Ecological strategies in a Patagonian arid steppe. Vegetatio 56, 9–15.

Soriano, A., Sala, O.E., Perelman, S.B., 1994. Patch structure and dynamics in a Patagonian arid steppe. Vegetatio 111, 127–135.

Srur, A.M., Villalba, R., 2009. Annual growth rings of the shrub *Anarthrophyllum rigidum* across Patagonia: interannual variations and relationships with climate. Journal of Arid Environments 73, 1074–1083.

Walter, H., 1971. Natural savannahs as a transition to the arid zone. In: Burnett, J.H. (Ed.), Ecology of Tropical and Subtropical Vegetation. Oliver and Boyd, London, pp. 238–265.

Whythers, K.R., Lauenroth, W.K., Paruelo, J.M., 1999. Bare-soil evaporation under semiarid field conditions. Soil Science Society of America Journal 63, 1341–1349.

Zunzunegui, M., Díaz Barradas, M.C., Ain-Lhout, F., Clavijo, A., García Novo, F., 2005. To live or to survive in Doñana dunes: adaptative responses of woody species under a Mediterranean climate. Plant and Soil 273, 77–89.