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" "$= 1 - f_U$):

$$\delta D_X = f_U \delta D_U + f_L \delta D_L \tag{1}$$

From which:

$$f_U = (\delta D_X - \delta D_L)/(\delta D_U - \delta D_L) \tag{2}$$

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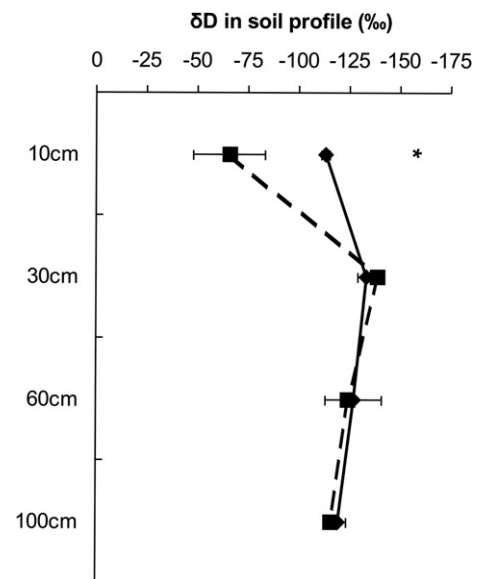
Fig. 1. Deuterium (‰ vs. SMOW) in soil as a function of depth 14 d after adding 10 mm of isotopically enriched water. Squares: treatment; diamonds: control. Bars show SE; $N = 3$; * indicates $P < 0.05$, Kruskal Wallis test.