Hydraulic lift in three shrub species from the Chilean coastal desert

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Abstract

Hydraulic lift is defined as the passive movement of water through roots from wetter, deeper soil layers into drier shallower layers along a gradient in soil water potential. This process is generally found in plant species with dimorphic root systems, which use water from both shallow and deep layers. We assessed the ability of three shrub species of the Chilean coastal desert, *Porlieria chilensis*, *Adesmia bedwellii* and *Proustia cuneifolia*, to act as hydraulic lifters. Our results showed evidences that the three species are hydraulic lifters with larger fluctuations of soil water potentials in summer 2004 and smaller fluctuations in winter 2004 and summer 2005. The soil water potential was higher beneath *P. chilensis* than beneath *P. cuneifolia* and *A. bedwellii*. Soils were significantly wetter at 60 cm than at 30 cm depth. The movement of water from wetter and deeper soil layers to drier and shallower soil layers through hydraulic lift may allow these shrubs to extend their metabolic activity into the lengthy drought period that characterizes the Chilean desert ecosystems.

1. Introduction

Roots have been largely recognized as key organs for water uptake by plants, playing an important role in arid environments where water is the principal resource limiting plant productivity (Ehleringer et al., 1999; Jackson et al., 2000; Noy-Meir, 1973). The main function of deep roots is to take up water from deep soil layers while shallow roots take up water and nutrients from the shallower soil layers. The presence of both deep and shallow roots in a plant defines the dimorphic root habit that maximizes both functions (Dawson and Pate, 1996; Mooney et al., 1980). In north-central Chile, dimorphic roots have been described for some shrubs growing in the coastal desert (León and Squeo, 2004) and this root morphology appears to make possible hydraulic lift. Hydraulic lift is defined as the passive movement of water through roots from wetter, deeper soil layers into drier shallower layers along a gradient in water potential (Caldwell et al., 1998; Horton and Hart, 1998; Richards and

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Caldwell, 1987). This process redistributes water to shallow soil layers where it can be taken up by plants and enhance transpiration. It occurs passively and is driven by the water demand from the atmosphere (Caldwell et al., 1998; Williams et al., 1993). Hydraulic lift may be an efficient mechanism to enhance transpiration rates and decrease the water stress of plants (Dawson, 1993). In desert zones, hydraulic lift can supply between 15% and 20% of daily water requirements of shrubs during the dry season (Wan et al., 1993; Ryel et al., 2002). In addition, hydraulic lift by maintaining a higher water potential could prevents root shrinkage and embolism that might inhibit rapid uptake of water the next time it becomes available (Tyree and Sperry, 1989).

A number of studies have shown that hydraulic lift enhances water availability for shrubs, communities and ecosystems (Filella and Peñuelas, 2003; Ishikawa and Bledsoe, 2000; Kurz-Besson et al., 2006; Lee et al., 2005; Ludwig et al., 2003; Moreira et al., 2003; Oliveira et al., 2005; Scholz et al., 2002; Smith et al., 1999; Yoder and Nowak, 1999). Hydraulic lift promotes more effective exploitation of subterranean waters, lowering water stress for plants in summer by maintaining enough water in the soil to support plant communities and promoting microbial processes which release nutrients from organic matter and soil minerals (Austin et al., 2004). Hydraulic lift also maintains the integrity of symbiotic mychorrizal associations during periods when soils would otherwise be dry (Caldwell et al., 1998; Horton and Hart, 1998; Pate and Dawson, 1999; Querejeta et al., 2003) highlighting its ecological role in facilitation processes (Hirota et al., 2004; Ludwig et al., 2003, 2004). Hydraulic lift enhances the nutrients availability in the upper soil layers (Caldwell et al., 1998; Dawson, 1993, 1998; McCulley et al., 2004) because of the increase of microbial activity and absorption by fine roots triggered by the soil moisture (Junk, 1996).

Plant species that exhibit hydraulic lift may also act as nurse species by aiding seedling recruitment during dry months (Gutiérrez and Squeo, 2004). This facilitation has been described for wild tree and shrub species (Filella and Peñuelas, 2003; Ishikawa and Bledsoe, 2000; Ludwig et al., 2003; Moreira et al., 2003; Oliveira et al., 2005; Scholz et al., 2002; Smith et al., 1999; Yoder and Nowak, 1999) and also for agricultural crops (Corak et al., 1987; Hirota et al., 2004; Smart et al., 2005; Wan et al., 2000). Recently, reverse hydraulic lift has also been shown to occur. This is the downward flux of soil water through roots when upper layers have a higher soil water potential (Jackson et al., 2000).

The process of hydraulic lift has been demonstrated in more than 50 plant species from a variety of climates, including Mediterranean, cool regions, temperate regions, and seasonally dry tropical and subtropical habitats (Jackson et al., 2000). Hence, hydraulic lift by roots appears to be very common in vascular plants with dimorphic root systems. Few cases, however, have been reported for the extensive shrubland communities of north-central Chile (León and Squeo, 2004; Squeo et al., 1999).

The shrub species of north-central Chile are either evergreen (with leaves present year round) or drought deciduous (with leaves absent during dry months). Evergreen shrubs are photosynthetically active all year while deciduous shrubs are photosynthetically active only during the wet season. The contrast of these phenological habits likely translates to differences in hydraulic lift properties (if present) as well as responses to water input (precipitation). Olivares and Squeo (1999) showed that deciduous shrubs with dimorphic roots systems in north-central Chile started their vegetative growth soon after the first winter rainfalls, which could be indicative of their high dependency on this water source.

In the Parque Nacional Bosque Fray Jorge (protected as a National Park since 1941 and as a Biosphere Reserve since 1972) in north-central Chile, the dominant species of the scrub community are the shrubs *Porlieria chilensis*, *Adesmia bedwellii* and *Proustia cuneifolia* (Gutiérrez et al., 1993a). These species have dimorphic root systems (Morales et al., unpublished data). The aim of this study was to find out whether or not these species are hydraulic lifters, and if the deciduous shrubs (*A. bedwellii* and *P. cuneifolia*) differ from the evergreen shrub *P. chilensis* with regard to hydraulic lift.

2. Materials and methods

2.1. Study site

The study site is located in an interior valley (Quebrada de Las Vacas, 200 m elevation) in the Parque Nacional Bosque Fray Jorge, in north-central Chile (30°38′S, 71°40′W). The park is about 5 km east of the Pacific coast, on the eastern side of the coastal range, which reaches about 600 m elevation here. The park lies

on the northern fringe of the Chilean Mediterranean zone and on the southern edge of the Pacific Coastal Desert. The climate is semiarid Mediterranean with 90% of annual precipitation falling in the cool austral winter months (May–September). Summer months are warm and dry. Underground water is at 5–10 m depth depending on location in the landscape (W. Canto, personal communication).

Between 1989 and 2003, mean annual precipitation in Fray Jorge was 145.4 ± 31.3 mm (1 SE). Rainfall in 2003, the year preceeding this study, was relatively low (96.7 mm) while that during the study period was slightly above average in 2004 (168.3 mm) and below average in 2005 (90.2 mm).

The flora of the region is a combination of elements from the dry western Andean slopes with a few species from the Monte Desert on the opposite side of the Andes (Sarmiento, 1975). The general plant community is characterized by spiny drought-deciduous and evergreen shrubs, with an herbaceous understory, and generally unvegetated sandy areas between shrubs (Gutiérrez et al., 1993a, 2004). The specific community occupying the valley floor where the study was conducted has been called the *P. chilensis–A. bedwellii–Proustia pungens* (= *cuneifolia*) association (Muñoz and Pisano, 1947). The dominant species is the thorny evergreen shrub *P. chilensis* (25–35% cover), followed by the woody drought-deciduous shrubs *A. bedwellii* (2.6–5.7% cover) and *P. cuneifolia* (2.0–9.5% cover). The three shrub species have dimorphic root systems. However, *P. chilensis* and *A. bedwellii* have a higher root biomass in the first 40 cm of soil (82.5% and 72.1%, respectively) than *P. cuneifolia* (43.8%) (Morales et al. unpublished data).

2.2. Hydraulic lift measurements

To test for hydraulic lifting, the amplitude of soil water potentials ($\Delta\psi_s$) were measured in the soil under each shrub. Five shrubs per species were randomly chosen in an area of 1600 m^2. In January 2004 (the austral summer season) the soil at least 2 m apart from each shrub was excavated up to 1 m depth and then through horizontal cylindrical cores, thermocouple psychrometers (Wescor, Inc. model PST-55) were installed at 30 and 60 cm in the soil under shrubs. The psychrometers were connected to a data logger (Campbell Scientific, Inc. model CR7). The same procedure was repeated in five soil samples without shrubs as a control. Fourteen measures were recorded per day for each psychrometer, and $\Delta\psi_s$ was estimated according to Ludwig et al. (2003). Data were taken between the 2nd and 16th day of each month.

2.3. Pre-dawn water potential of shrubs

Pre-dawn water potentials (ψ_{pd}) of three apical stems (7–10 cm) for each of the five shrubs per species were measured between 0400 and 0600 local time in September 2004 and February 2005. Measurements were made with a Scholander-type Pressure Chamber (PMS Instrument Co.).

2.4. Statistical analyses

The $\Delta\psi_s$ was analyzed using repeated measures ANOVA, and pre-dawn water potential of shrub stems was analyzed using two-way ANOVA with species and seasons as factors. We compared the dry season of 2004 (February), the spring season four weeks after the last rain of 2004 (September) and the dry season of 2005 (February) for $\Delta\psi_s$, and the last two seasons for pre-dawn water potential of stems. For mean comparisons we used *a posteriori* Tukey's tests.

3. Results

3.1. Hydraulic lift

The daily variations in soil water potentials ($\Delta\psi_s$) associated with a day–night cycle (Fig. 1) suggest that the three shrub species: *P. chilensis, P. cuneifolia* and *A. bedwellii* are hydraulic lifters. Rains in winter 2004 (June–September) lowered the amplitude of $\Delta\psi_s$ for the three species, i.e. $\Delta\psi_s$ values were smaller in September 2004 (Fig. 2). The deciduous species *A. bedwelli* and *P. cuneifolia* showed faster increases of $\Delta\psi_s$ as compared to the evergreen *P. chilensis*.
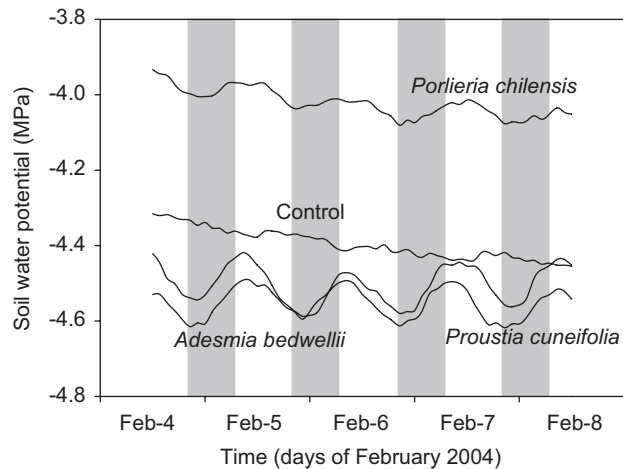
Fig. 1. Soil water potentials, associated to four consecutive night–day cycles, taken under three shrub species and in open (control) sites in February 2004 at 30 cm depth. Gray areas correspond to nighttime. In the night, soil water potentials under shrub species were higher than in the day demonstrating the hydraulic lift. Note that in the controls these fluctuations were not present.

In July 2004 (winter) the soil under the three shrub species showed similar behavior but differed from soil in the open. At 60 cm depth in the open the moisture supplied by recent precipitation took an additional week to appear compared to soils under the canopy of the three shrub species (Fig. 2).

The hydraulic lift in these shrubs showed seasonal differences ($F_{(2,20)} = 601.1$; $P < 0.001$). In summer 2004, the amplitude of $\Delta\psi_s$ was four times higher than in spring 2004 and summer 2005 (Fig. 3). The three species did not differ in $\Delta\psi_s$ but did differ for soil water potential ($F_{(2,10)} = 6.00$; $P < 0.05$). The soil water potential was higher beneath *P. chilensis* than *P. cuneifolia* and *A. bedwellii*. Soils were significantly wetter at 60 cm (-2.7 ± 0.4 MPa) than at 30 cm (-3.1 ± 0.4 MPa).

3.2. Pre-dawn water potentials of shrubs

The pre-dawn water potentials of shrubs showed significant differences for species ($F_{(2,12)} = 52.3$; $P < 0.001$), season ($F_{(1,12)} = 494.3$; $P < 0.001$) and species × season interaction ($F_{(2,12)} = 46.4$; $P < 0.001$). Across species the pre-dawn water potentials of stems were higher in spring 2004 than in summer. At the species level the pre-dawn water potentials were higher for the stems of *A. bedwellii* than for the stems of *P. cuneifolia*, and the lowest value was for the evergreen *P. chilensis* (Table 1).

4. Discussion

The Chilean leguminous tree *Prosopis tamarugo* was the first species in the world reported to be a hydraulic lifter, however, at that time the phenomenon was ascribed to the singular characteristics of the Atacama Desert (Mooney et al., 1980). The three shrub species studied showed fluctuations in soil water potentials that were associated with a day and night cycle, suggesting their ability to act as hydraulic lifters. This is the first report of hydraulic lift activity for these species, adding to the growing number of shrub species from north-central Chile (*Pleocarphus revolutus*, *Senna cumingii*, and *Flourensia thurifera*) in which hydraulic lift has been described (León and Squeo, 2004). These results strongly suggest that hydraulic lift is a common physical phenomenon of shrubs with dimorphic root systems in the Chilean coastal desert.

Fluctuations of soil water potentials were verified at 30 and 60 cm where most of the lateral and fine roots were concentrated. The tap roots of these shrub species reach over 2 m deep. Hydraulic lift was clearly detected in summer 2004 but not in summer 2005, which is likely related to the lower canopy of these species in the summer of 2005 (Tracol et al., unpublished data). A lower canopy would affect the water taken up from the deeper soil layers. Snyder and Williams (2003) showed that a decrease of *Prosopis velutina* canopy by
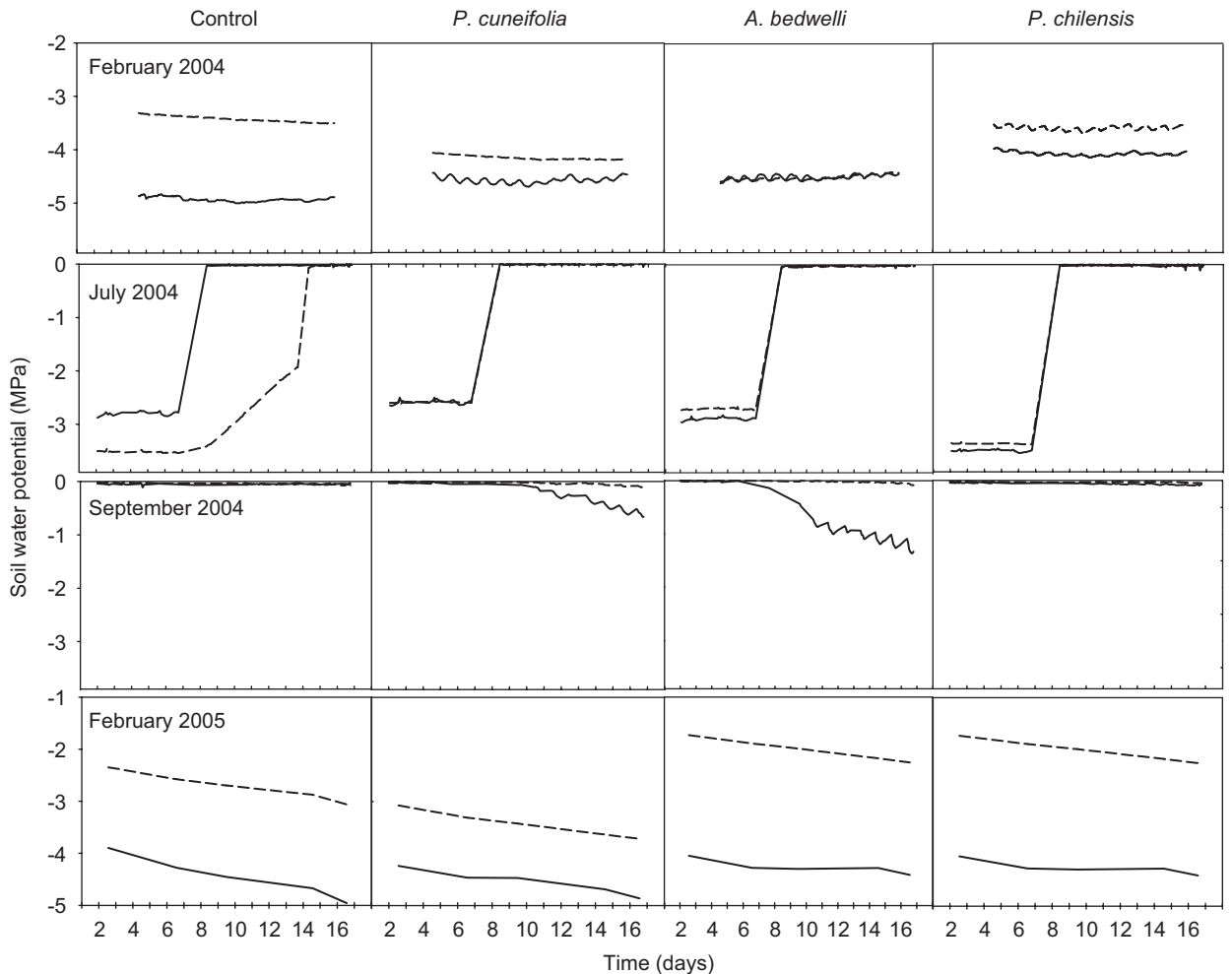
Fig. 2. Soil water potential measured under three shrub species and in open (control) sites for the first 15 days of February, July, and September 2004, and February 2005 at 30 cm (solid line) and 60 cm (dashed line) depth. Vertical lines indicate mid-night time.

defoliation inhibited the water taken up by deep roots, and water was only taken up from the upper soil layers through the shallower roots. In the Chilean shrubs, larger canopies in summer 2004 could be the outcome of a large rainfall in winter 2002 (356.4 mm) associated with an El Niño/Southern Oscillation event (Gutiérrez et al., 2007; Holmgren et al., 2006). In contrast, the low foliar canopy cover seen in summer 2005 was likely the result of low rainfall in winter 2003 (96.7 mm), which suggests that shrub responses are delayed by one year. Delayed responses of shrubs to precipitation are common in arid and semiarid zones (Ogle and Reynolds, 2004). Another possible explanation for the differences observed in hydraulic lift between the summers of 2004 and 2005, is that perhaps in rainy years enough underground water accumulates in shallower soil layers which can be reached and lifted more easily by shrub roots.

Fluctuations in soil water potentials after rainfall appeared first in the deciduous shrubs *A. bedwellii* and *P. cuneifolia* and then in the evergreen *P. chilensis*. This process occurred a few weeks after the water pulses coming from precipitation. In July 2004, water first appeared at 30 and 60 cm depth beneath shrubs, and then in the open. This suggests faster water infiltration for soils beneath shrubs than for soils in the open where they are probably more compacted. In addition, there may be reverse hydraulic lift by shrubs, i.e. the downward flux of soil water through roots when upper layers have a higher water potential (Schulze et al., 1998). Because the three shrubs studied are dominant in this system, they could be playing a major role in the water recharge
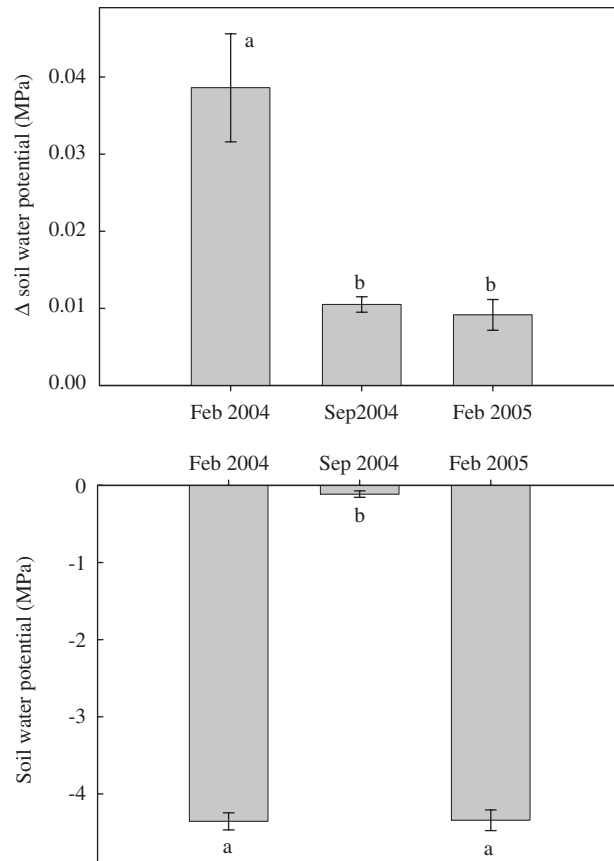
Fig. 3. Δ soil water potential (top plate) and soil water potential (down plate) under the canopy of the shrubs (data pooled) in February 2004, 2005, and September 2004. Data were taken at 30 and 60 cm depth for 30 days each month.

Table 1
Means (± 1 SE, $n = 5$) of pre-dawn water potentials (in MPa) for shrub species and seasons in north-central, Chile

Species/season	Spring 2004	Summer 2005	Means for species
Adesmia bedwellii	-0.64 ± 0.05 a	-1.32 ± 0.12 a	-0.98 ± 0.13 a
Porlieria chilensis	-1.15 ± 0.14 b	-3.45 ± 0.16 b	-2.30 ± 0.40 c
Proustia cuneifolia	-0.64 ± 0.03 a	-2.88 ± 0.11 b	-1.76 ± 0.38 b
Means for seasons	-0.81 ± 0.08 a	-2.55 ± 0.25 b	

Means in a column followed by different letters indicate significant differences at $\alpha = 0.05$.

of deep soil layers. This important ecosystem service has been proposed for other site of north-central Chile (Squeo et al., 1999, 2006).

Unlike *P. chilensis*, soil water potentials for *A. bedwellii* and *P. cuneifolia* were slightly lower than in the control (Fig. 1), which suggests that competition for water with the shrubs could outweigh the value of lifted water to other plants. Although, hydraulic lift enhances the soil water potentials of the rhizosphere (Dawson, 1993), the roots making hydraulic lift also actively uptake water, decreasing the soil water potential limiting the benefit of hydraulic lift for plants underneath shrub canopies (Ludwig et al., 2003).

The nocturnal water translocation from plant roots enhances the soil nutrient availability in the shallower soil layers (Caldwell et al., 1998; Dawson, 1993, 1998; McCulley et al., 2004) due to an increase of the microbial activity and the absorption by fine roots promoted by the higher soil moisture of this layer

(Junk, 1996), i.e. the changes induced by roots in the nitrogen (Griffiths and Robison, 1992) and micronutrient mineralization (Marschner and Römhekd, 1996). Beneath shrub canopies there are higher nutrient concentrations and microorganisms than in the open areas (Herman et al. 1995; Pugnaire et al., 1996; Schlesinger et al., 1990; Titus et al., 2002). In the Chilean coastal desert, soils under the canopies of *P. chilensis* and *A. bedwellii* contain more nutrients than the surrounding open areas (Aguilera et al., 1999; Gutiérrez et al., 1993b). Hydraulic lift could be importantly contributing to the formation of these ''fertility islands''.

Acknowledgments

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