Plant and Soil **215:** 93–102, 1999.
© 1999 *Kluwer Academic Publishers. Printed in the Netherlands.*

Hydraulic lift among native plant species in the Mojave Desert

Carolyn K. Yoder* and Robert S. Nowak
Ecology, Evolution and Conservation Biology Program, University of Nevada, Reno, NV 89557-0013, USA
**Corresponding author: Department of Rangeland Resources and the Ecology Center, Utah State University, Logan, UT 84322-5205, USA*

Key words: CAM and C_3 plants, hydraulic lift, Mojave Desert shrubs and grasses, root-soil contact, soil texture

Abstract

Hydraulic lift was investigated among native plants in the Mojave Desert using in situ thermocouple psychrometers. Night lighting and day shading experiments were used to verify the phenomenon. Hydraulic lift was detected for all species examined: five shrub species with different rooting depths and leaf phenologies and one perennial grass species. This study was the first to document hydraulic lift for a CAM species, *Yucca schidigera*. The pattern of diel flux in soil water potential for the CAM species was temporally opposite to that of C_3 species: for the CAM plant, soil water potential increased in shallow soils during the day when the plant was not transpiring and decreased at night when transpiration began. Because CAM plants transport water to shallow soils during the day when surrounding C_3 and C_4 plants transpire, CAM species that hydraulically lift water may influence water relations of surrounding species to a greater extent than hydraulically lifting C_3 or C_4 species. A strong, negative relationship between the percent sand in the study site soils at the 0.35 m soil depth and the frequency that hydraulic lift was observed at that depth suggests that the occurrence of hydraulic lift is negatively influenced by coarse-textured soils, perhaps due to less root–soil contact in sandy soils relative to finer-textured soils. Differences in soil texture among study sites may explain, in part, differences in the frequency that hydraulic lift was detected among these species. Further investigations are needed to elucidate species versus soil texture effects on hydraulic lift.

Introduction

Water is the primary factor limiting plant growth in arid ecosystems (Smith and Nowak, 1990), and soil nutrients are often second-order regulators of plant productivity (Marschner, 1986). Hydraulic lift may be very important in desert ecosystems because this phenomenon may enhance or prolong uptake of water and nutrients by roots during periods of water stress (Caldwell and Richards, 1989; Caldwell et al., 1998; Horton and Hart, 1998; Richards and Caldwell, 1987). During hydraulic lift, which occurs when stomata are closed and the plant is not transpiring, water is absorbed by plant roots in moist subsoil and transferred to shallow roots in drier topsoil where the water then exits the roots and enters the drier soil due to a water potential gradient. The water remains in the shallow soil until stomata open and the transpirational stream for water movement from the soil through the plant and into the atmosphere is reinstated. Hydraulic lift has been documented for several species with different growth forms and in different climates. For example, hydraulic lift occurs in at least two Great Basin species: *Artemisia tridentata*, a deep-rooted shrub (Richards and Caldwell, 1987), and *Agropyron desertorum*, a perennial grass (Caldwell, 1990). In addition, hydraulic lift has been documented in a shallow-rooted half shrub, *Gutierrezia sorothrae*, in West Texas (Wan et al., 1993), and in sugar maple, *Acer saccharum*, in more mesic climates during periods of drought (Dawson, 1993).

Although hydraulic lift could significantly increase the effectiveness of water and nutrient uptake in desert ecosystems by increasing the efficiency of deep roots and by facilitating nutrient uptake, the occurrence of hydraulic lift in warm deserts, such as the Mojave Desert in southwestern USA, has not been documented. Also, the occurrence of hydraulic lift in succulent species with the crassulacean acid metabolism

---

* FAX No: +1-435-797-3872. E-mail: cyoder@cc.usu.edu

(CAM) photosynthetic pathway has not been investigated previously. Several factors might limit or preclude the occurrence of hydraulic lift in desert environments, including: lack of sufficient deep soil water to drive the process, poor root–soil contact, xylem embolisms, or low radial root hydraulic conductivity. Low radial root hydraulic conductivity may be important for limiting water losses from succulent species into surrounding dry soil (Nobel and Sanderson, 1984) and may subsequently limit hydraulic lift. For instance, average radial root hydraulic conductivity coefficients of three desert succulents, *Agave deserti*, *Ferocactus acanthodes*, and *Opuntia ficus-indica*, decreased about 3-fold as ambient potential decreased from −0.01 to −10 MPa (Nobel, 1994). A 3-fold decrease in radial root hydraulic conductivity alone, however, is not sufficient to account for the small losses of water from *A. deserti* to dry soils; rather, the conductance of the root–soil system must decrease 10^5-fold to account for the small losses of water from *A. deserti* (Nobel, 1994). Therefore, the hydraulic conductivity of soil and root–soil air gaps must also play a large role in limiting water efflux from roots and hence, hydraulic lift. Because soil hydraulic conductance and root–soil contact are influenced greatly by soil texture, soil texture may determine, to a large degree, whether hydraulic lift can occur when soil water potentials are low.

The objectives of this study were to: (1) determine if hydraulic lift occurs among Mojave Desert species with different growth forms, rooting depths, and leaf phenologies and (2) determine if hydraulic lift occurs in a species with the CAM photosynthetic pathway. Because soil texture varied among study sites and depths, the relationship between soil texture and the frequency of hydraulic lift observations among the study sites at two soil depths was also examined.

Methods

Study site

Research was conducted at the Nevada Test Site (NTS), which is located between 36°35′ and 37°15′N latitude and 115°55′ and 116°35′W longitude. The NTS is 350 000 ha of arid and semiarid terrain that straddles the transition zone between the Mojave and Great Basin deserts of western North America. In 1993, the NTS was designated as a National Environmental Research Park in order to support ecological research and to study the impacts of energy development on the environment. Excellent descriptions of vegetation patterns, climate gradients and variability, and physical geography for the region are given by Rundel and Gibson (1996).

Six sites within the Mojave Desert vegetation zone in the southern part of the NTS were chosen for this study. Each site was selected such that a monoculture of one of the six study species occurred within 3 m of the psychrometer installation sites. Annual plants growing under or near target plant canopies were removed on a regular basis. Elevation of the sites ranges from 950 to 1150 m. Yearly rainfall at the NTS is highly variable but generally ranges from 85 to 160 mm and rarely exceeds 250 mm at elevations below 1000 m (Rundel and Gibson, 1996). Soil classification maps were not available for our study sites, but soils located at similar elevations on the NTS belong to the Thermic family and would be classified as Entisols with an ochric epipedon and showing no pedogenic horizons (Rundel and Gibson, 1996). Soil texture measurements at the study sites are discussed below.

Study species

Six species were examined that differed in rooting depth and leaf longevity. *Larrea tridentata* was chosen as a deep-rooted species (Freckman and Virginia, 1989) with evergreen leaves and *Ephedra nevadensis* as a more shallow-rooted species (Wallace and Romney, 1972) with evergreen stems. *Ambrosia dumosa* was selected as a shallow rooted species (Wallace et al., 1980) with drought deciduous leaves and *Lycium pallidum* as a drought deciduous species with a fairly uniform root distribution (Ackerman et al., 1980; Wallace et al., 1980). *Yucca schidigera*, which is a long-lived CAM species with stomatal opening at night, strong diurnal fluctuations of malic acid (LaPre, 1979), and $\delta\ ^{13}$C values of ca. −13.9‰ (Smith and Madhaven, 1982), was chosen to test for the occurrence of hydraulic lift in a CAM species. In addition to these shrub species, hydraulic lift was investigated in the perennial grass, *Achnatherum hymenoides*.

Psychrometer installation and measurement

Prior to field installation, Peltier thermocouple psychrometers (J.R.D. Merrill Specialty Equip., Logan, UT, USA) were calibrated in the lab using methods outlined by Brown and Bartos (1982). Field installation of psychrometers involved digging a trench to a depth of approximately 1 m at the edge of the plant canopy. Horizontal access holes that were the same diameter as the screen-cage of the psychrometers were then made by inserting a steel rod into the trench wall horizontally for a distance of 0.3 m. The psychrometers were guided gently into the access tunnels with their lead wires for the entire length of the tunnel, thus providing a relatively undisturbed soil environment around each psychrometer sensing head. A 0.3–0.5 m length of the remaining lead wire was coiled and draped below the access tunnel in order to provide a similar thermal environment for the wire near the sensing head and to prevent water from traveling from the soil surface along the lead wire to the sensing head during wet periods (Brown and Chambers, 1987). Psychrometers were installed at two soil depths, 0.35 and 0.75 m, for three plants of each species in order to measure in situ soil water potential (Ψ_s) and to determine if diel fluctuations in soil water potential ($\Delta\Psi_s$) occurred. These depths were chosen because diel temperature fluctuations at these depths were weak, and thus temperature gradients within the psychrometers were small enough to be corrected by a calibration model (Brown and Bartos, 1982). Two psychrometers were installed at each depth as a precaution against psychrometer failure. When both psychrometers functioned properly, the two measurements were averaged together. A data logger (model CR7, Campbell Scientific, Inc., Logan, UT, USA) was used to monitor all psychrometers for one species at hourly time intervals for a period of $\geq$2 days. Because only one data logger was available, the data logger would then be moved to another species. Measurements were made at intermittent periods throughout the year, beginning in June 1994 for the C_3 shrubs and in February 1995 for the CAM plant *Y. schidigera* and the perennial grass *A. hymenoides*. Psychrometer measurements continued through August 1996.

Night lighting/day shading experiments

Night lighting/day shading experiments were used during the summer of 1996 to help verify the occurrence of hydraulic lift. Because 1996 was an exceptionally dry year, the plots were irrigated with the equivalent of a 127 mm rainfall event 1–2 months prior to the experiments. The shrub *L. pallidum* responded quickly to the irrigation treatment, producing a flush of leaves and dropping the leaves within a 2-week period. Because *L. pallidum* did not maintain a leaf canopy, night lighting/day shading experiments were not conducted on this species. In addition, night lighting/day shading experiments were not conducted on the perennial grass *A. hymenoides* because of poor survival of this species at our study site. For the remaining C_3 plants, night lighting experiments were used to prevent nighttime stomatal closure and circumvent conditions under which hydraulic lift might occur. Shading of C_3 plants during the day was used to suppress transpiration, thus enhancing conditions under which hydraulic lift might occur. For the CAM plant, night lighting should facilitate stomatal closure and induce hydraulic lift activity; day shading should prevent stomatal closure and the occurrence of hydraulic lift in the CAM plant.

Day shading was achieved by constructing a 3.6×3.6×3.6-m shelter consisting of PVC pipe and rigid board, foam insulation. The insulation had a silver coating that reflected solar radiation and thus prevented extreme temperatures within the shelter. Night lighting was achieved by suspending a 1-kW metal halide lamp from a tripod placed over the target plant. A second lamp, identical to the one suspended above the plant, was placed on the ground facing the plant. The temperature and relative humidity within the shelter were monitored hourly with a thermistor and relative humidity probe attached to a data logger (21X, Campbell Scientific).

Relationship between soil texture and hydraulic lift

Soil samples were collected in 0.2-m depth increments from the surface to 1 m at each site and analyzed for soil texture by the particle size distribution method (Bouyoucos, 1962) and bulk density by the core method (Blake, 1965).

The relationship between soil texture and hydraulic lift was investigated by simple linear regression of the frequency of times hydraulic lift was detected at a study site (i.e., the number of times hydraulic lift was observed at a study site divided by the number of Ψ_s data collection periods for that study site) versus the percent sand at the study site at a given soil depth; only one species was present at each study site. Data collection periods when $\Delta\Psi_s$ indicated drainage or infiltration of soil water were not included in this analysis because hydraulic lift could not have occurred at these depths when these soil layers were saturated (i.e., when drainage or infiltration of soil water were occurring).

Results

Psychrometer data

To interpret the psychrometer data, we first determined if the diurnal change in soil water potential ($\Delta\Psi_s$) was $\geq$0.05 MPa. 0.05 MPa was chosen as a threshold because this was the lowest $\Delta\Psi_s$ for which consistent, diurnal $\Delta\Psi_s$ were observed. Measurements of $\Delta\Psi_s \geq 0.05$ MPa indicated one of three processes: (1) drainage of water through the soil profile, (2) infiltration of water into a given soil depth, or (3) hydraulic lift. $\Delta\Psi_s$ indicated drainage if Ψ_s was near saturation and if Ψ_s consistently became more negative. $\Delta\Psi_s$ indicated infiltration if the upper soil profile was saturated and if Ψ_s at a given depth below the surface soil consistently became less negative. $\Delta\Psi_s$ indicated hydraulic lift if a cyclic, diurnal variation in Ψ_s occurred with increases in Ψ_s corresponding to periods when plant transpiration would be reduced. Because the unsaturated hydraulic conductivity of sandy loam soils at the test site ranges from 10^{-15} to 10^{-13} m s^{-1} (Albright, 1995), lateral migration of water into root depletion zones in these sandy soils is expected to be very low (Hunt and Nobel, 1987) and would therefore have contributed little, if any, to the diel Ψ_s fluctuations in this study. Further, vertical Ψ_s gradients, which are the driving force for hydraulic lift, were at least an order of magnitude greater than expected lateral Ψ_s gradients.

Hydraulic lift was detected at each of the study sites at least once during the duration of the study (Fig. 1), although there were differences in the timing and frequency of hydraulic lift observations among species (Table 1). For instance, during June 1994, hydraulic lift was detected only for *A. dumosa*. However, during the spring and summer of 1995, which were preceded by an exceptionally wet winter, hydraulic lift was detected for all of the study species.

The frequency of hydraulic lift observations at the two different soil depths also varied among species (Table 1). The number of occurrences at the 0.35-m soil depth was similar to the number of occurrences at the 0.75-m soil depth for *E. nevadensis* and *L. pallidum*. However, for *L. tridentata* and *A. hymenoides*, approximately two-thirds of the observed occurrences of hydraulic lift were at the 0.35-m soil depth and one-third were at the 0.75-m soil depth. Hydraulic lift was never detected at the 0.75-m soil depth for *Y. schidigera*, and hydraulic lift was detected at the 0.75-m soil depth on only one date (June 1995) for *A. dumosa* (13% of all measured occurrences for *A. dumosa*).

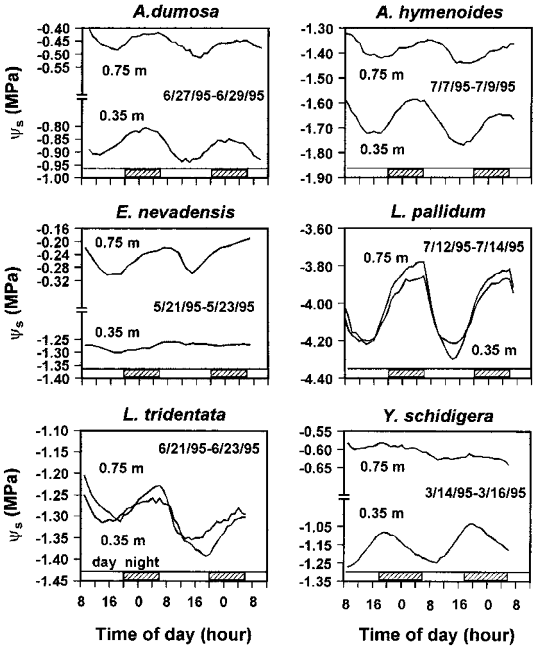

Figure 1. Examples of changes in Ψ_s at two soil depths that indicate hydraulic lift for the six study species during spring and summer 1995. Values are means of measurements collected beneath three plants of each species, except for *Lycium pallidum* where *N*=1. Day/night periods are indicated by open/shaded areas along the *x*-axis.

For the CAM species, *Y. schidigera*, the pattern of hydraulic lift was temporally opposite to that of the C3 species (Fig. 1). At the *Y. schidigera* site, Ψ_s increased in shallow soils during the day when the plants were not transpiring and decreased at night when transpiration resumed. This pattern of $\Delta\Psi_s$ reflects the CAM photosynthetic pathway of *Y. schidigera*.

Although hydraulic lift was detected for all study species, hydraulic lift was not detected for all plants at a site at a given time. For example, in June 1995, hydraulic lift was detected at both depths beneath only one *L. pallidum* shrub (Fig. 2). Hydraulic lift was not detected at either soil depth beneath the other two *L. pallidum* plants. This same pattern was repeated in July 1995. Soil temperatures beneath all of the plants were similar (Fig. 2), indicating that the $\Delta\Psi_s$ beneath the one plant was not an artifact due to temperature variation. Also, the $\Delta\Psi_s$ could not have been induced by another species because this site was a *L. pallidum* shrub monoculture, and annual plants under the shrubs were removed. However, note that failure to detect hy-

Table 1. Results of psychrometer measurements for June 1994 through August 1996: ‘d’ indicates drainage; ‘i’ indicates infiltration; ‘hl’ indicates hydraulic lift with the magnitude of $\Delta\Psi_S$ (MPa) indicated in parentheses after ‘hl’; ‘–’ indicates $\Delta\Psi_S < 0.05$ MPa during the measurement period. If spaces are blank then no data were collected during that period

		Jun-94	Mar-95	Apr-95	May-95	Jun-95	Jul-95	Aug-95	May-96	Jun-96	Jul-96	Aug-96
A. dumosa												
0.35 m Plant	1	hl (0.20)	d		d	hl (0.05)		–		–	d	hl (0.05)
	2	hl (0.30)	d		d	hl (0.25)		hl (0.20)		–	hl (0.10)	hl (0.15)
	3	hl (0.10)	d		d	hl (0.10)		hl (0.10)		–	hl (0.10)	hl (0.15)
0.75 m Plant	1	–	d		i	–		–		–	–	d
	2	–	d		i	hl (0.05)		–		–	–	–
	3	–	d		i	hl (0.20)		–		–	–	–
A. hymenoides												
0.35 m Plant	1		d	d		hl (0.35)	hl (0.30)					
	2		d	d		hl (0.15)	hl (0.20)					
	3		d	d		hl (0.40)	hl (0.40)					
0.75 m Plant	1		d	d		–	–					
	2		d	d		hl (0.10)	hl (0.08)					
	3		d	d		–	hl (0.10)					
E. nevadensis												
0.35 m Plant	1	–	d		–	–		–	–	hl (0.10)	–	–
	2	–	d		–	–		–	–	hl (0.05)	hl (0.10)	hl (0.05)
	3	–	d		–	–		–	–	hl (0.10)	–	–
0.75 m Plant	1	–	d		hl (0.10)	–		–	–	hl (0.10)	hl (0.10)	hl (0.15)
	2	–	d		–	–		–	–	–	hl (0.08)	–
	3	–	d		hl (0.20)	–		–	–	–	–	–
L. pallidum												
0.35 m Plant	1	–	d		d	–	–					
	2	–	d		d	–	–					
	3	–	d		–	hl (0.50)	hl (0.60)					
0.75 m Plant	1	–	i		hl (0.10)	–	–					
	2	–	i		–	–	–					
	3	–	i		–	hl (0.35)	hl (0.38)					
L. tridentata												
0.35 m Plant	1	–	d	d		hl (0.15)	hl (0.50)		hl (0.05)	hl (0.18)	hl (0.10)	
	2	–	d	d		hl (0.05)	hl (0.20)		hl (0.10)	hl (0.10)	hl (0.15)	
	3	–	d	hl (0.15)		hl (0.20)	hl (0.20)		hl (0.05)	hl (0.15)	hl (0.10)	
0.75 m Plant	1	–	d	i		hl (0.25)	hl (0.20)		hl (0.05)	–	–	
	2	–	d	hl (0.05)		–	hl (0.30)		–	–	–	
	3	–	d	hl (0.50)		–	–		–	–	–	
Y. schidigera												
0.35 m Plant	1		hl (0.20)			hl (0.20)			hl (0.10)			
	2		hl (0.20)			hl (0.05)			hl (2.20)			
	3		hl (0.20)			hl (0.20)			hl (0.10)			
0.75 m Plant	1		–			–			–			
	2		–			–			–			
	3		–			–			–			

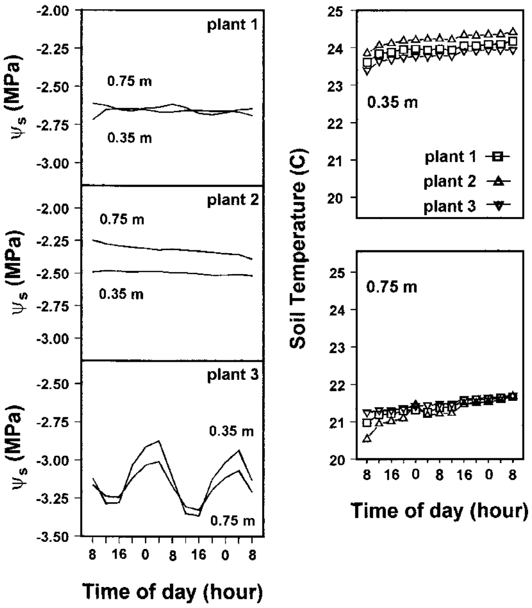

Figure 2. Ψ_s and soil temperatures at two depths beneath individual *Lycium pallidum* plants, June 25–27, 1995.

draulic lift does not necessarily mean that hydraulic lift did *not* occur: rather, it is possible that psychrometers placed beneath the other two shrubs were not in close enough proximity to functioning roots to detect plant-induced changes in Ψ_s.

Night lighting/day shading experiments

Night lighting/day shading experiments were conducted for *Y. schidigera*, *L. tridentata*, *A. dumosa* and *E. nevadensis* (Fig. 3). For each of these species, the experiments stopped or greatly decreased the diurnal $\Delta\Psi_s$. However, the experiments were not successful in reversing the $\Delta\Psi_s$. Failure to achieve reversal of the $\Delta\Psi_s$ is likely due, in part, to inadequate light during the night lighting portion of the experiment. Photon flux density (PFD) for sun and sky is $\geq$2.0 mmol m^{-2} s^{-1} during most of the day. In contrast, mean PFD inside the night lighting shelter was only 0.4 mmol m^{-2} s^{-1}. In addition, endogenous circadian rhythms in stomatal conductance (Gorton et al., 1993; Hagemeyer and Waisel, 1987) may have influenced stomatal responses and subsequent transpiration patterns. Regardless of the nonreversal of $\Delta\Psi_s$, return of the diurnal $\Delta\Psi_s$ upon cessation of the night lighting/day shading experiments verified that the $\Delta\Psi_s$ were plant induced.

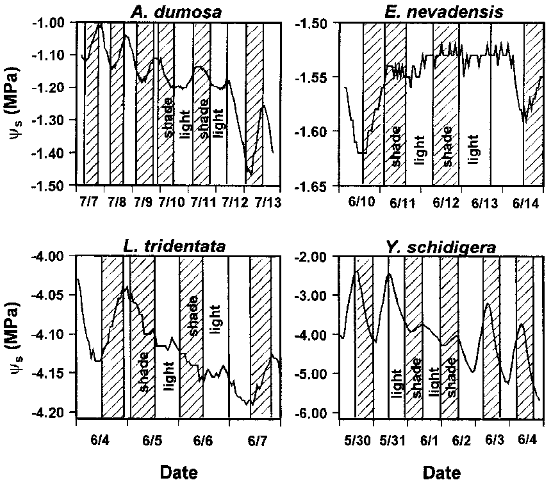

Figure 3. Examples of Ψ_s at the 0.35-m soil depth during night lighting and day shading experiments for *Ambrosia dumosa, Ephedra nevadensis, Larrea tridentata*, and *Yucca schidigera*. Periods when plants were exposed to light are open and periods where plants were in the dark have diagonal lines. Natural diel cycles are unlabeled, whereas times when the diel cycle was reversed (i.e., night lighting/day shading experiments) are labeled.

Mean daily maximum air temperature inside the shelter was 43°C and mean daily maximum relative humidity inside the shelter was 15%. These values are within the normal range reported for the southern region of the Mojave Desert (Rundel and Gibson, 1996).

Relationship between soil texture and hydraulic lift

With the exception of the *A. hymenoides* site at the 0.35-m depth, all of the soils at the study sites were $>$70% sand (Table 2), and would therefore be classified as sands or loamy sands according the U.S. Department of Agriculture Soil Textural Triangle. Soil at the 0.35-m depth at the *A. hymenoides* site would be classified as sandy loam.

The frequency of hydraulic lift observations at the 0.35-m soil depth was negatively related ($P<0.01$; $r=-0.92$) to the percent sand in the study site soils at the 0.35-m depth (Fig. 4). No significant relationship ($P>0.05$) was found between the frequency of hydraulic lift observations at the 0.75-m soil depth and the percent sand at that depth.

Discussion

The results of this study indicate that given sufficient soil water, hydraulic lift occurs in Mojave Desert

Table 2. % Sand, silt, clay, and bulk densities (Mg m^{-3}) for soils at the six study sites. '–' indicates missing data

Species	Soil Depth (m)	% Sand	% Silt	% Clay	B.D.
Achnatherum hymenoides	0.35	62	32	6	1.5
	0.75	83	10	7	1.5
Ambrosia dumosa	0.35	79	16	5	1.5
	0.75	74	23	3	1.6
Ephedra nevadensis	0.35	92	5	2	1.6
	0.75	87	12	1	1.7
Lycium pallidum	0.35	93	2	5	1.5
	0.75	72	22	6	1.6
Larrea tridentata	0.35	78	13	9	1.7
	0.75	83	8	9	1.7
Yucca schidigera	0.35	75	14	11	1.6
	0.75	–	–	–	–

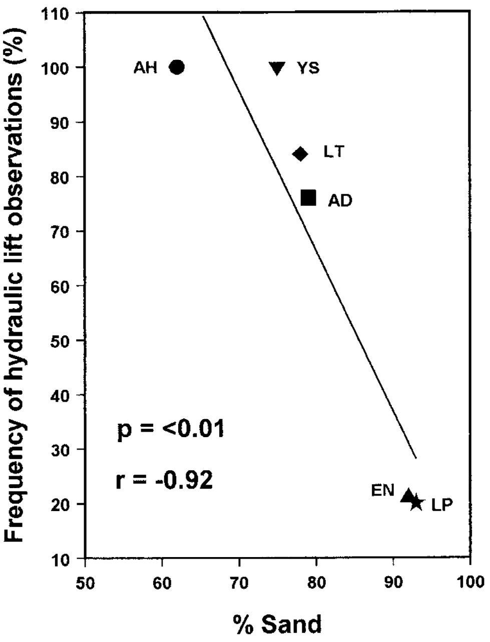

Figure 4. Linear regression of the frequency of hydraulic lift observations at the 0.35-m soil depth (i.e., number of times hydraulic lift was detected divided by the number of Ψ_s data collection periods; data collection periods when $\Delta\Psi_s$ indicated drainage 'd' or infiltration 'i' were not included in this analysis because hydraulic lift could not have occurred at these depths when these soil layers were saturated) versus the percent sand at the 0.35-m soil depth at each study site for *Achnatherum hymenoides* (AH), *Ambrosia dumosa* (AD), *Ephedra nevadensis* (EN), *Larrea tridentata* (LT), *Lycium pallidum* (LP), and *Yucca schidigera* (YS).

plants with different leaf phenologies, rooting depths, and growth forms. Hydraulic lift was detected in all six species studied: two evergreen shrubs, *L. tridentata* and *E. nevadensis*; two drought deciduous shrubs, *A. dumosa* and *L. pallidum*; one perennial grass, *A. hymenoides*; and a CAM species, *Y. schidigera*.

The patterns of diel $\Delta\Psi_s$ corresponded closely to reported patterns of stomatal conductance and transpiration for desert plants. For example, our Ψ_s data suggested that during the spring when soil water contents were relatively high, stomata of *Y. schidigera* opened at ca. 20:00 h and closed at ca. 09:00 h. This pattern of stomatal opening is consistent with findings by LaPre (1979), who found little indication of daytime stomatal opening for *Y. schidigera* except during early morning hours. For the C_3 shrubs, our Ψ_s data suggested that during periods of moderate soil water availability (i.e., $\Psi_s -0.4$ to -4.4 MPa) stomata opened during early morning hours (05:00 to 07:00 h) and closed in late afternoon (~16:00 h). These diurnal patterns of stomatal conductance inferred from $\Delta\Psi_s$ correspond well with diurnal patterns of conductance and transpiration reported in the literature for *L. tridentata* (Franco et al., 1994) and other desert species (Kappen et al., 1975; Nilsen et al., 1983). During the summer, as soil water became more limiting, periods of Ψ_s stasis were frequently observed around midday (i.e., ~noon to 16:00 h), which correspond to reported midday depressions in stomatal conductance during periods of low soil water availability for *L. tridentata* (Lajtha and Whitford, 1989) and other desert plants (Tenhunen et al., 1987). Many desert plants limit their transpiration rates during periods of summer water stress by limiting stomatal opening to periods when leaf water potentials are the highest (Monson and Smith, 1982; Smith et al., 1995; Tenhunen et al, 1987).

The night lighting/day shading experiments helped to verify that the diurnal $\Delta\Psi_s$ were plant induced. Delayed responses in $\Delta\Psi_s$ at the onset of the night lighting/day shading experiments for*A. dumosa*, *L. tridentata* and *Y. schidigera*, and following cessation of the experiment for *E. nevadensis*, may be indicative of endogenous circadian rhythms in stomatal control. Although we know of no studies that have investigated circadian rhythms in stomatal control in these study species, circadian rhythms of stomatal movement have been found in several species under various conditions (e.g., Gorton et al., 1989; Hagemeyer and Waisel, 1987; Meidner and Mansfield, 1968). Regardless of our inability to reverse the pattern of $\Delta\Psi_s$, we were able to alter the diel $\Delta\Psi_s$. Cessation of the night lighting/day shading experiments resulted in the return of normal diurnal $\Delta\Psi_s$; i.e., Ψ_s increased during periods when transpiration would be reduced and decreased during periods when transpiration would occur. These results indicate that the $\Delta\Psi_s$ observed in this study were plant induced.

This study is the first to document hydraulic lift in a CAM species. The pattern of diel flux in Ψ_s for *Y. schidigera* was temporally opposite to that of C_3 species, as would be expected given the temporally opposite patterns of stomatal aperture. Because CAM plants transfer water from moist subsoils to dry, shallow soils during the day when C_3 and C_4 plants are transpiring, water that is hydraulically lifted by CAM plants may significantly influence water relations of surrounding species. The potential for utilization of hydraulically lifted water by neighboring plants in the field was first demonstrated by Caldwell and Richards (1989). Dawson (1993) later demonstrated the magnitude of water utilization by neighboring plants by utilizing the natural abundance of deuterium in xylem water to identify sources of plant water uptake. Dawson found that the proportion of water hydraulically lifted by maple trees and then utilized by neighboring plants varied from 3 to 60% and that the growth of some of the neighboring plants was influenced positively by hydraulically lifted water. Thus, neighboring species can benefit from hydraulically lifted water, even if the species have similar patterns of stomatal conductance. Because *Y. schidigera* transfers water to shallow soils during the day when C_3 and C_4 plants are transpiring, hydraulically lifting *Y. schidigera* plants may influence the water relations of surrounding plants to a greater degree than hydraulically lifting C_3or C_4 plants. Whether water that is hydraulically lifted by CAM plants is more beneficial to surrounding plants than water lifted by C_3 or C_4 plants needs to be investigated.

The objective of this current study was to determine if hydraulic lift occurs for Mojave Desert plants with different rooting depths, leaf phenologies, growth forms, and photosynthetic pathways. Hydraulic lift was detected for all of the study species, however, the frequency that hydraulic lift occurred among these species varied greatly. Analysis of particle size distributions indicated that soil texture also varied among these study sites. Because only one species was present at each study site, we were unable to distinguish between species and soil texture effects on the frequency of hydraulic lift observations. However, a strong, negative relationship ($P<0.01$; $r=-0.92$) between the frequency of hydraulic lift observations at the 0.35-m soil depth, where root densities of these species are high (Cody, 1986; Wallace et al., 1980), and the percent sand at that depth, suggested that hydraulic lift is influenced negatively by coarse-textured soils. Because root–soil contact is influenced strongly by soil structure (Passioura, 1991), the negative effect of coarse-textured soils on hydraulic lift was possibly a consequence of less root–soil contact in coarse soils relative to more finely textured soils. Failure to identify a significant relationship between the frequency of hydraulic lift observations and the percent sand in the study site soils at the 0.75-m depth was likely due to: (1) sparse rooting at that depth (discussed below) and subsequently, fewer psychrometers in close enough proximity to active roots to detect plant induced changes to Ψ_s; and (2) less deep soil water (i.e., water below 0.75 m) to drive hydraulic lift at the 0.75-m depth. Although additional studies are needed to elucidate species and soil texture effects on hydraulic lift, lower frequencies of hydraulic lift at the 0.75-m depth relative to the 0.35-m depth were likely due, in large part, to lower root length densities at the 0.75-m depth. The majority of the root systems (95% of total root biomass) of *A. dumosa*, *E. nevadensis*, *L. pallidum*, and *L. tridentata* were distributed in the top 0.5 m of soil in a sandy wash area of the northern Mojave Desert (Wallace et al., 1980). Also, Cody (1986) reported a rooting depth of only 0.5 m for *Y. schidigera*. Although we did not quantify root length densities in this study, we observed only sparse rooting at the 0.75-m depth for *Y. schidigera* and for

A. dumosa at our study sites when trenches were dug for psychrometer installation. Low root length densities at the 0.75-m depth likely explain why hydraulic lift was rarely, or never detected for *A. dumosa* and *Y. schidigera*, respectively. The remaining study species had more roots at the 0.35-m depth than at the 0.75-m depth, but also had more roots than either *A. dumosa* or *Y. schidigera* at the 0.75-m depth. Relatively higher root densities at the 0.75-m depth for *L. tridentata*, *E. nevadensis* and *L. pallidum* are consistent with reported rooting depths of 1–3 m for *L. tridentata* (Freckman and Virginia, 1989) and 1–2 m for *E. nevadensis* and *Lycium* spp. (Wallace and Romney, 1972). Also, Reynolds and Fraley (1989) reported that the root system of *A. hymenoides* may extend to 1.5 m.

In summary, we have documented the occurrence of hydraulic lift in desert species with different rooting depths, growth forms, and photosynthetic pathways. A strong, negative relationship between the percent sand at the study sites at the 0.35-m soil depth and the frequency of hydraulic lift observations at that depth suggests that coarse-textured soils negatively influenced the occurrence of hydraulic lift, presumably due to poor root–soil contact and low soil hydraulic conductance under dry conditions. Additional studies are needed to distinguish between soil texture and species effects on hydraulic lift. Other factors that likely control hydraulic lift in the Mojave Desert include availability of deep soil water and root density distributions. Because CAM plants transfer water to shallow soils while C_3 and C_4 plants are transpiring, hydraulically lifting CAM plants may significantly influence water relations of surrounding annuals and potentially aid the establishment and survival of more shallow rooted species. However, the potential influence of hydraulic lift by CAM plants on surrounding C_3 and C_4 plants still needs to be investigated.

Acknowledgements

Authors thank Craig Biggart, Will Amy, Tony Giglini and Alan Kirk for field assistance; Ray Brown for technical assistance with psychrometers. We also appreciate logistical and technical support at the Nevada Test Site by employees of the United States Department of Energy-Nevada Operations Office (especially Bob Furlow) and Bechtel Nevada. Financial support for this project was provided through a cooperative agreement between the University of Nevada, Reno and the Department of Energy-Nevada Operations Office (DE-FC08-93 NV11359), and the Nevada Agricultural Experiment Station; sabbatical leave support to RSN is gratefully acknowledged.

References

Ackerman T L, Romney E M, Wallace A and Kinnear J E 1980 Phenology of desert shrubs in southern Nye County, Nevada. Great Basin Natur. Mem. 4, 4–23.

Albright W H 1995 Physical and Hydrologic Characteristics of an Amended Soil Proposed as a Low Permeability Component of a Radioactive Waste Landfill Cover. Master of Science Thesis, University of Nevada, Reno, NV.

Blake G R 1965 Bulk density. *In* Methods of Soil Analysis, Part 1. Ed. C A Black. pp 374–390. Am. Soc. Agron. Madison, WI.

Bouyoucos G J 1962 Hydrometer method improved for making particle size analysis of soil. Agron. J. 54, 464–465.

Brown R W and Bartos D L 1982 A Calibration Model for Screen-caged Peltier Thermocouple Psychrometers. USDA Forest Service, Intermountain Research Station, Research Paper INT-293, Ogden, UT.

Brown R W and Chambers J C 1987 Measurements of in situ water potential with thermocouple psychrometers: A critical evaluation. *In* Proceedings of International Conference on Measurement of Soil and Plant Water Status. Volume 1, Soils. July 6–10, 1987, Logan, UT.

Caldwell M M 1990 Water parasitism stemming from hydraulic lift: a quantitative test in the field. Isr. J. Bot. 39, 395–402.

Caldwell M M and Richards J H 1989 Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. Oecologia 79, 1–5.

Caldwell M M, Dawson T E and Richards J H 1998 Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113, 151–161.

Cody M L 1986 Structural niches in plant communities. *In* Community Ecology. Eds J Diamond and T J Case. pp 381–405. Harper & Row, New York.

Dawson T E 1993 Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. Oecologia 95, 565–574.

Franco A C, deSoyza A G, Virginia R A, Reynolds J F and Whitford W G 1994 Effects of plant size and water relations on gas exchange and growth of the desert shrub *Larrea tridentata*. Oecologia 97, 171–178.

Freckman D W and Virginia R A 1989 Plant-feeding nematodes in deep-rooting desert ecosystems. Ecology 70, 1665–1678.

Gorton H L, Williams W E, Binns M E, Gemmell C N, Leheny E A and Shepherd A C 1989 Circadian stomatal rhythms in epidermal peels from *Vicia faba*. Plant Physiol. 90, 1329–1334.

Gorton H L, Williams W E and Assmann S M 1993 Circadian rhythms in stomatal responsiveness to red and blue light. Plant Physiol. 103, 399–406.

Hagemeyer J and Waisel Y 1987 An endogenous circadian rhythm of transpiration in *Tamarix aphylla*. Physiol. Plant. 70, 133–138.

Horton J L and S C Hart 1998 Hydraulic lift: a potentially important ecosystem process. Trends Ecol. Evol.13, 232–235.

Hunt E R and Nobel P S 1987 A two-dimensional model for water uptake by desert succulents: implications of root distribution. Ann. Bot. 59, 559–569.

Kappen L, Oertli J J, Lange O L, Schulze E D, Evenari M and Buschbom U 1975 Seasonal and diurnal courses of water relations of the arido-active plant *Hammada scoparia* in the Negev Desert. Oecologia 21, 175–192.

Lajtha K and Whitford W G 1989 The effect of water and nitrogen amendments on photosynthesis, leaf demography, and resource-use efficiency in *Larrea tridentata*, a desert evergreen shrub. Oecologia 80, 342–348.

LaPre L 1979 Physiological Ecology of *Yucca schidigera*. Ph.D. Diss. University of California, Riverside, CA.

Marschner H 1986 Mineral Nutrition of Higher Plants. Academic Press. New York.

Meidner H and Mansfield T A 1968 The role of rhythms in stomatal behavior. *In* Physiology of Stomata. Ed. M B Wilkins. pp 102–169. McGraw-Hill, New York.

Monson R K, Smith S D 1982 Seasonal water potential components of Sonoran Desert plants. Ecology 63, 113–123.

Nilsen E T, Sharifi M R and Rundel P W 1983 Diurnal and seasonal water relations of the desert phreatophyte *Prosopis glandulosa* (honey mesquite) in the Sonoran Desert of California. Ecology 64, 1181–1193.

Nobel P S 1994 Root-soil responses to water pulses in dry environments. *In* Exploitation of Environmental Heterogeneity by Plants: Ecophysiological Processes Above- and Below-Ground. Eds R W Pearcy and M M Caldwell. Academic Press, New York.

Nobel P S and Sanderson J 1984 Rectifier-like activities of roots of two desert succulents. J. Exp. Bot. 35, 727–737.

Passioura J B 1991 Soil structure and plant growth. Aust. J. Soil Res. 29, 717–728.

Reynolds T D and Fraley L 1989 Root profiles of some native and exotic plant species in southeastern Idaho. Environ. Exp. Bot. 29, 241–248.

Richards J H and Caldwell M M 1987 Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia 73, 486–489.

Rundel P W and Gibson A C 1996 Ecological Communities and Processes in a Mojave Desert Ecosystem: Rock Valley, Nevada. Cambridge University Press, Cambridge.

Smith B N and Madhaven S 1982 Carbon isotope ratios in obligate and facultative CAM plants. *In* Crassulacean Acid Metabolism. Eds I P Ting and M Gibbs. pp 231–243. Proceedings of the Fifth Annual Symposium in Botany, January 1982. University of California, Riverside.

Smith S D and Nowak R S 1990 Ecophysiology of Plants in the Intermountain Lowlands. *In* Ecological studies, Vol. 80. Plant Biology of the Basin and Range. Eds C B Osmond, L F Pitelka and G M Hidy. pp 179–241. Springer-Verlag, Heidelberg.

Smith S D, Herr C A, Leary K L and Piorkowski J M 1995 Soil–plant water relations in a Mojave Desert mixed shrub community: a comparison of three geomorphic surfaces. J. Arid Environ. 29, 339–351.

Tenhunen J D, R W Pearcy and Lange O L 1987 Diurnal variations in leaf conductance and gas exchange in natural environments. *In* Stomatal Function. Eds E. Zeiger, G D Farquhar and I R Cowan. pp 323–351. Stanford University Press, Stanford, CA.

Wallace A and E M Romney 1972 Radioecology and Ecophysiology of Desert Plants at the Nevada Test Site. U.S. Atomic Energy Commission Report TID-25954, National Technical Information Service, U.S. Department of Commerce, Springfield, VI.

Wallace A, Romney E M and Cha J W 1980 Depth distribution of roots of some perennial plants in the Nevada Test Site area of the northern Mojave Desert. Great Basin Natur. Mem. 4, 201–207.

Wan C, Sosebee R E and McMichael B L 1993 Does hydraulic lift exist in shallow-rooted species? A quantitative examination with a half-shrub *Gutierrezia sarothrae*. Plant Soil 153, 11–17.

Section editor: H Lambers