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MAGNITUDE AND MECHANISMS OF DISEQUILIBRIUM BETWEEN PREDAWN PLANT AND SOIL WATER POTENTIALS

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Abstract. Predawn plant water potential (Ψ_w, measured with leaf psychrometers) and surrogate measurements made with the pressure chamber (termed Ψ_{pc} here) are used to infer comparative ecological performance, based on the expectation that these plant potentials reflect the wettest soil Ψ_w accessed by roots. There is growing evidence, however, that some species exhibit substantial predawn disequilibrium (PDD), defined as plant Ψ_w or Ψ_{pc} at predawn substantially more negative than the Ψ_w of soil accessed by roots. In the western Great Basin desert, the magnitude of PDD calculated as soil Ψ_w minus predawn leaf Ψ_w was as large as 1.4 and 2.7 MPa for two codominant shrub species, *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus*, respectively. The magnitude of PDD calculated as soil Ψ_w minus predawn Ψ_{pc} was smaller, up to 0.6 and 2.1 MPa for *Chrysothamnus* and *Sarcobatus*, respectively. For both species, mechanisms contributing to PDD included nighttime transpiration and putative leaf apoplastic solutes, but not hydraulic conductance limitations. Hydraulic lift also occurred in both species and likely contributed to PDD for *Sarcobatus*. Finding large magnitude PDD in field populations emphasizes that species differences in predawn plant Ψ_w or Ψ_{pc} do not necessarily reflect differences in accessible soil Ψ_w and rooting depth, nor does a low predawn plant Ψ_w or Ψ_{pc} value necessarily mean that soil Ψ_w is also low. Mechanisms contributing to PDD affect relationships between plants and soil resources, as well as the potential for plant–plant interactions.

Key words: apoplastic solutes; Chrysothamnus nauseosus; *Great Basin desert, California; hydraulic conductance; hydraulic lift; nighttime transpiration; predawn water potential;* Sarcobatus vermiculatus; *water relations.*

INTRODUCTION

Water is a primary factor limiting plant physiological and ecological performance in many habitats. Plant water potential (Ψ_w; typically measured with a leaf psychrometer) and a surrogate measurement made with a pressure chamber on the stem of leafy shoots (termed Ψ_{pc} here), are generally accepted as biologically meaningful measures of plant water status, soil water availability, and components of the driving force for water transport through the soil–plant–atmosphere continuum. Diurnal patterns of plant Ψ_w reflect transpirational water loss controlled by the degree of stomatal opening and leaf microenvironment. Plant Ψ_w values for C_3 or C_4 plants are generally most negative during the day when stomata open for CO_2 uptake and recover to least negative values overnight after stomata close. Predawn plant Ψ_w, or more commonly Ψ_{pc}, are widely used to estimate soil Ψ_w, and thus the accessible soil moisture, based on the assumption that plant Ψ_w equilibrates with the "wettest" soil layer around active roots (Hinckley et al. 1978, Boyer 1995, Kramer and Boyer 1995, Richter 1997, Améglio et al. 1999). The assumption of predawn plant–soil equilibration explicitly or implicitly underlies ecological interpretations of species or treatment differences in predawn plant Ψ_w or Ψ_{pc} as differences in rooting depth, habitat partitioning, water source, water stress, or competitive ability (e.g., Davis and Mooney 1986, Romo and Haferkamp 1989, Donovan and Ehleringer 1994, Bréda et al. 1995, Le Roux and Bariac 1998, Hamerlynck et al. 2000, McCarron and Knapp 2001). Additionally, predawn plant Ψ_w or Ψ_{pc} is often used to estimate soil Ψ_w when calculating soil–leaf hydraulic conductance, as part of efforts to understand controls on whole plant water use (Brisson et al. 1993, Hubbard et al. 1999, Nardini and Salleo 2000).

Much evidence challenges the use of predawn plant Ψ_w or Ψ_{pc} to infer soil Ψ_w (reviews in Améglio et al. 1999, Donovan et al. 1999, 2001, Sellin 1999). The difference between soil Ψ_w around roots and predawn plant Ψ_w or Ψ_{pc} quantifies the magnitude of predawn disequilibrium (PDD). Literature reviews suggest that PDD is nonexistent or small for herbaceous plants and some woody plants, but can be as large as 2.0 MPa for other woody plants and halophytes (Donovan et al. 2001). The magnitude of PDD must be quantified in field populations to refine ecological interpretations of predawn plant water potential measurements, Ψ_w, or Ψ_{pc}.

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Various mechanisms may contribute to PDD. One ecologically important situation occurs when plants are hydraulically isolated from dry soil by breaks in soil–root hydraulic contact (Nobel and Cui 1992). Our research, however, has documented other mechanisms that produce substantial PDD, even under well-watered conditions (Donovan et al. 1999, 2001). Nighttime transpirational water loss and limitations on the conductance of water from roots have long been recognized as factors that may prevent or slow down complete recovery of plant Ψ_w overnight (Blake and Ferrell 1977, Ourcival and Berger 1995, Sellin 1996, 1999). Soil moisture heterogeneity may also play a role, although Améglio et al. (1999) demonstrated that this effect is likely to be small unless only a very small percentage of roots are in wet soil. Substantial concentrations of apoplastic solutes in leaf intercellular spaces have also been proposed as a mechanism contributing to PDD, based on unexpectedly large differences between stem Ψ_{pc} and leaf Ψ_w (see model by Donovan et al. 1999). Preliminary results with cation-binding fluorescent dyes support this interpretation (J. James, K. Mühling, A. Läuchli, and J. Richards, *unpublished data*). Mechanisms contributing to PDD need to be identified and quantified in field populations to understand more fully how plants interact with their soil moisture environment and with each other.

We investigated the magnitude and mechanisms of PDD in natural populations of two C_3 cool-desert shrub species. *Sarcobatus vermiculatus* (Hook.) Torrey (Chenopodiaceae, greasewood) is a deep-rooted, Na-accumulating halophyte. *Chrysothamnus nauseosus* (Palla.) Britt. ssp. *consimilis* (E. Greene) H.M. Hall and Clements (Asteraceae, rabbitbrush) is a co-occurring, deep-rooted, Na-excluding non-halophyte. For these species, PDD was initially suggested by field data (Donovan et al. 1996). Glasshouse experiments with smaller plants confirmed large magnitude PDD under well-watered conditions, attributable to nighttime transpiration and putative apoplastic solutes, but not hydraulic conductance limitations (Donovan et al. 1999, 2001). The process of hydraulic lift has been documented in *Sarcobatus* (Caldwell et al. 1998) and may also contribute to PDD under field conditions given that the nighttime loss of water from shallow roots is analogous to nighttime transpirational water loss from leaves (Donovan et al. 1999). In this first experimental investigation of PDD in natural populations, we examined (1) the magnitude of PDD, and (2) whether nighttime transpiration, hydraulic lift, putative apoplastic solutes, and hydraulic limitations contribute to PDD.

MATERIALS AND METHODS

The research site was located in the cool-desert shrubland north of Mono Lake, California, USA (38°5′ N, 118°58′ W, 1958 m elevation). Healthy reproductive *Chrysothamnus* and *Sarcobatus* shrubs (1.30 ± 0.05 and 1.34 ± 0.07 m height [mean ± 1 SE], respectively) were selected in the "Diverse Dunes" area, where these species have similar root-depth distribution to groundwater at 3–5 m depth (Donovan et al. 1996, Donovan and Richards 2000). Annual precipitation is 163 mm (Toft 1995). During the study (1 April–21 September 2000), precipitation was 26 mm; 150% of normal for this period.

We used 60 shrubs: 12 replicates for each of 5 species–irrigation combinations. The species–irrigation combinations were blocked (1 replicate/block) to account for environmental gradients across the site. Both *Chrysothamnus* and *Sarcobatus* received natural rainfall (no irrigation, NA) and surface irrigation (SIR) treatments. Because *Sarcobatus* is capable of hydraulic lift, it also received a deep irrigation (DIR) treatment to maximize the soil Ψ_w gradient driving hydraulic lift. Pressure-compensating drippers delivered irrigation water to the surface for the SIR treatment and to 1.1 m depth (via PVC tubing) for the DIR treatment. Each of the 36 irrigated plants received 3126 L, applied periodically from 28 April to 18 September, which is ~1.6 times the long-term average annual precipitation. Repeated measurements of volumetric soil moisture (neutron probe, Campbell Pacific Nuclear, Martinez, California, USA) confirmed the effectiveness of the irrigation treatments. Soils around NA plants were dry to >1.0 m depth (0.05–0.08 m^3 H_2O/m^3 soil) and increasingly moist to a maximum ~0.15 m^3 H_2O/m^3 soil at 2.0 m and deeper. The SIR treatment brought the soil to near field capacity (~0.20 m^3 H_2O/m^3 soil) from the surface to 1.5 m depth. The DIR treatment brought the soil to field capacity from 1.3 to 2.0 m depth.

Some of the objectives required shrub crowns to be "bagged" overnight to eliminate nighttime transpiration. Half (6) of the replicates in each species–irrigation treatment were randomly assigned to bagging for June diurnal measurements. The same plants were bagged for July and September measurements. However, the bags were not adequately sealed in June, so only data from the later two dates are presented and analyzed. Bagged plant crowns were covered with a wetted fabric tarp (humidification) and polyethylene film, held up by a PVC frame. Crown bags were sealed around the margin with sand when installed 1 h before sunset, opened and resealed as needed for sampling (e.g., predawn), and removed shortly after sunrise.

Methods for soil Ψ_w, plant Ψ_{pc} and Ψ_w, and plant gas exchange measurements

From 21 March to 20 September, soil Ψ_w was calculated (Brown and Bartos 1982) from the output of 120 individually calibrated screen-cage thermocouple soil psychrometers (Series 74, Merrill Specialty Equipment, Logan, Utah, USA) that were logged hourly (CR7, Campbell Scientific, Incorporated, Logan, Utah, USA). Each shrub had one soil psychrometer at 2.0 m depth. Most shrubs also had one soil psychrometer at

0.3 m, except for four *Chrysothamnus* and four *Sarcobatus* in the SIR treatment. Eight *Sarcobatus* shrubs (3 NA, 2 SIR, 3 DIR) had a replicate psychrometer at 0.3 m depth to accommodate a concurrent study of hydraulic lift. Psychrometers at 0.3 m depth were expected to measure soil Ψ_w adjacent to shallow roots, based on high root length density at this depth (Donovan et al. 1996), the observation of roots excavated during installation, and the insertion of psychrometers into the undisturbed soil in the side of the installation hole. Psychrometers at 2.0 m were expected to measure soil Ψ_w adjacent to deep roots based on the occurrence of roots of both species at this depth and the relatively uniform soil water content. Psychrometer outputs were removed from the analyses when soil Ψ_w dropped below detection levels (∼6.0 MPa) or when psychrometers demonstrated unacceptable electronic noise.

Stem Ψ_{pc} was measured on terminal leafy stems (5–10 cm) with a pressure chamber (PMS Instrument Company, Corvallis, Oregon, USA) at predawn and several additional times to determine diurnal courses on 21–23 June, 22–25 July, and 14–17 September. Rigorous procedures were followed to minimize errors (Turner 1988). Because pressure chamber measurements were made on plants with and without canopy bagging (see *Materials and methods*) we distinguish $\Psi_{pc\ bagged}$ and $\Psi_{pc\ unbagged}$, as they require somewhat different interpretations (Ritchie and Hinckley 1971, 1975, Turner 1981, Melcher et al. 1998). $\Psi_{pc\ bagged}$ is interpreted as a direct measure of stem and leaf xylem pressure potential, when plants were not transpiring and shoot water potentials had equilibrated between compartments. $\Psi_{pc\ unbagged}$ is a volume-weighted average of the water potentials of compartments of the measured shoot, including stems and leaves. When unbagged and losing water, incomplete equilibration between stem xylem and leaf compartments prevents using stem $\Psi_{pc\ unbagged}$ as a direct measure of xylem pressure potential.

In September, predawn leaf Ψ_w was also measured for each plant using excised leaves (from stems comparable to those sampled for stem Ψ_{pc}) and individually calibrated psychrometers (Donovan et al. 1999, 2001). Although neither species excretes salt onto leaves, the leaves were rinsed with deionized water the day before measurements were taken to remove any dust and salt spray. Entire leaves were placed in chambers within 1 min of excision, and the chambers were suspended in a water bath to minimize temperature gradients. Psychrometer outputs were logged hourly, and leaf Ψ_w was determined after equilibration (generally between 12 and 20 h).

Concurrent with diurnal stem Ψ_{pc} measurements, leaf stomatal conductance was measured on unbagged plants in the NA and SIR treatments with a field gas exchange system (LI-COR 6400, LI-COR Incorporated, Lincoln, Nebraska, USA). For each set of measurements, the light level was set at ambient for that time of day, chamber CO_2 was held at 360 ppm, and temperature and humidity tracked ambient. Empty chamber measurements confirmed equipment performance.

Experimental design and analyses for each objective and mechanism

The magnitude of PDD was calculated as soil Ψ_w minus predawn stem Ψ_{pc} or leaf Ψ_w. For each shrub, soil Ψ_w was the least negative value (0.3 or 2.0 m depth) at dawn on the morning of the stem Ψ_{pc} or leaf Ψ_w measurement. PDD was considered significant when repeated-measures ANOVA (PROC GLM, time as repeated factor; SAS 1989) demonstrated that soil Ψ_w was less negative than predawn stem Ψ_{pc} across sampling dates. Univariate analyses and Huynh-Feldt adjusted P values were used for within-subject effects because there were no significant departures from compound symmetry. Data were analyzed separately for each species–irrigation combination and bagged/unbagged subset.

The contribution of nighttime transpiration to PDD was measured as the difference in predawn stem Ψ_{pc} between unbagged ($\Psi_{pc\ unbagged}$) and bagged ($\Psi_{pc\ bagged}$) plants within each treatment (repeated-measures ANOVA, time as repeated factor). Stomatal conductance of unbagged NA and SIR plants was also measured, concurrent with stem $\Psi_{pc\ unbagged}$ measurements, to confirm nighttime transpiration.

Hydraulic lift was determined from appropriate diurnal soil Ψ_w fluctuations with magnitudes >0.1 MPa (Caldwell et al. 1998). For *Sarcobatus*, the contribution of hydraulic lift to PDD was assessed by comparing PDD in the DIR treatment (soil Ψ_w gradients driving hydraulic lift expected to be experimentally maximized by uniformly moist deep soil) to PDD in the SIR treatment (soil Ψ_w gradients minimized). Only bagged plants were used so the effect of hydraulic lift was quantified in the absence of nighttime transpiration. Although soil water potential gradients in the NA treatment could drive hydraulic lift, direct comparisons to the DIR and SIR treatment plants are not appropriate. In the DIR and SIR treatments, roots and psychrometers were in irrigated soil, assuring good estimates of soil Ψ_w in the wettest rooted soil volume, and thus the best estimates of PDD. In contrast, the roots of plants in the NA treatment may have accessed wetter soils at depths greater than the 2.0 m psychrometer. Thus, the estimated PDD in the NA treatment is just a minimum estimate. This precludes its use in a sensitive test for the contribution of hydraulic lift to PDD. In July and September, predawn stem $\Psi_{pc\ bagged}$ (interpreted as xylem pressure potential) from the diurnal courses (n = 6 bagged plants for each DIR and SIR treatment) were used. Because of sample size concerns, an additional comparison, separate from the diurnal courses, was subsequently made in July using 10 bagged plants/treatment.

TABLE 1. Soil Ψ_w (mean ± 1 SE) in NA (natural rainfall, unirrigated), SIR (surface irrigated), and DIR (deep irrigated) treatments, for 0.3- and 2.0-m soil depths for the two study species in the western Great Basin desert, California, USA.

Treatment	21–23 June		22–25 July		14–17 September	
	0.3 m	2.0 m	0.3 m	2.0 m	0.3 m	2.0 m
Chrysothamnus						
NA	−0.43 ± 0.07	−0.29 ± 0.10	−0.63 ± 0.10	−0.28 ± 0.08	−0.99 ± 0.16	−0.27 ± 0.07
SIR	−0.05 ± 0.01	−0.09 ± 0.02	−0.05 ± 0.01	−0.10 ± 0.03	−0.05 ± 0.01	−0.10 ± 0.02
Sarcobatus						
NA	−1.96 ± 0.37	−0.40 ± 0.09	−1.99 ± 0.63	−0.68 ± 0.15	−2.99 ± 0.52	−1.00 ± 0.11
SIR	−0.08 ± 0.02	−0.29 ± 0.10	−0.06 ± 0.03	−0.28 ± 0.08	−0.05 ± 0.01	−0.27 ± 0.07
DIR	−2.14 ± 0.55	−0.31 ± 0.11	−1.97 ± 0.50	−0.34 ± 0.13	−2.79 ± 0.50	−0.39 ± 0.18

Notes: For *Chrysothamnus nauseosus,* $n = 6$ for SIR at 0.3 m, and $n = 11–12$ for SIR at 2.0 m, and for NA at 0.3 and 2.0 m. For *Sarcobatus vermiculatus,* $n = 8–13$ for all treatments and depths. The dates correspond to the plant Ψ_{pc} and gas exchange measurement periods.

The contribution of putative apoplastic solutes to PDD was calculated as predawn stem Ψ_{pc} minus leaf Ψ_w (Donovan et al. 1999), and evaluated with two-way ANOVA (block and Ψ) for each species–irrigation–bagging combination in September. Hydraulic conductance limitations were assessed by comparing stem Ψ_{pc} at predawn to Ψ_{pc} of the same plants two hours earlier with a two-way ANOVA (Ψ_{pc} and block) for each species–irrigation combination in July and September.

RESULTS

Soil Ψ_w was less negative at 2.0 m depth than 0.3 m for NA and DIR treatments on all plant sampling dates. Much smaller soil Ψ_w gradients and soil Ψ_w near field capacity were observed in the SIR treatment (Table 1).

TABLE 2. Repeated-measures ANOVA results for predawn diseqilibrium (PDD) for *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus* in each irrigation treatment.

Species	Treatment	PDD (soil Ψ_w vs. predawn plant Ψ_{pc})	Time	Time × Ψ
		F	*F*	*F*
Unbagged plants (soil Ψ_w vs. predawn plant $\Psi_{pc\ unbagged}$)				
Chrysothamnus	NA	22.39***	6.69**	0.22
	SIR	375.15***	2.08	5.04*
Sarcobatus	NA	101.95***	10.80***	1.43
	SIR	394.87***	13.67***	11.95**
	DIR	30.88***	17.67***	9.38**
Bagged plants (soil Ψ_w vs. predawn plants $\Psi_{pc\ bagged}$)				
Chrysothamnus	NA	11.03**	15.17**	1.96
	SIR	131.21***	9.02*	4.01
Sarcobatus	NA	17.96**	1.93	2.57
	SIR	60.99**	1.72	9.12*
	DIR	252.13***	5.44*	10.34**

Notes: A significant soil Ψ_w vs. predawn plant Ψ_{pc} difference indicates PDD. Unbagged plants were measured three times (June, July, and September), and df (numerator, denominator) are 1, 10 for PDD, and 2, 20 for time and Ψ × time. Bagged plants were measured twice (July and September), and df are 1, 10 for PDD, time, and Ψ × time. See Fig. 1 for data, treatments, and sampling dates.

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Predawn stem Ψ_{pc} was significantly more negative than the wettest soil Ψ_w measured for roots of these species, for all species–irrigation treatment combinations (Table 2, Fig. 1), indicating substantial PDD. For unbagged plants at the field site, the magnitude of PDD between soil Ψ_w and plant $\Psi_{pc\ unbagged}$ was as large as 0.6 MPa for *Chrysothamnus* and 2.1 MPa for *Sarcobatus*.

Nighttime transpiration increased PDD 0.1 MPa for *Chrysothamnus* and 0.6 MPa for *Sarcobatus*, averaged across irrigation treatments (Table 3). Stomata of both species were partially open at night (Fig. 2).

Hydraulic lift was detected as small diurnal fluctuations (generally 0.1–0.2 MPa) in soil Ψ_w at 30 cm depth. It was prevalent for both species in the NA treatment and *Sarcobatus* in the DIR treatment, but was not detected in the SIR treatment (Fig. 3). For bagged plants, PDD in *Sarcobatus* DIR plants (hydraulic lift) tended to be greater by an average of 0.3 MPa than in SIR plants (no hydraulic lift) (for two July comparisons, $n = 10$, $P = 0.07$, and $n = 6$, $P = 0.06$; for the September comparison, $n = 6$, $P = 0.02$).

In September, predawn leaf Ψ_w was significantly more negative than predawn stem Ψ_{pc} for each species–irrigation–bagging combination (df = 1, $F > 7.94$, $P < 0.05$, for all comparisons; Fig. 1). For the bagged plants (i.e., no transpiration), the difference suggests that intercellular apoplastic solutes contributed 0.7 and 0.9 MPa to PDD for *Chrysothamnus* and *Sarcobatus*, respectively. The magnitude of difference was similar for unbagged plants, indicating no apparent interaction of apoplastic solute accumulation and nighttime transpiration. When PDD was estimated using leaf Ψ_w instead of stem Ψ_{pc}, PDD was larger: up to 1.4 MPa for *Chrysothamnus* and 2.7 MPa for *Sarcobatus*.

Stem Ψ_{pc} at predawn did not differ from Ψ_{pc} of the same plants two hours earlier (df = 1, $F < 4.31$, $P > 0.09$, for every comparison shown in Fig. 2). Given that transpiration had been suppressed in the bagged plants, this plateau of stem Ψ_{pc} before dawn is consistent with no hydraulic conductance limitation contributing to PDD. Diurnal stem Ψ_{pc} patterns were normal.

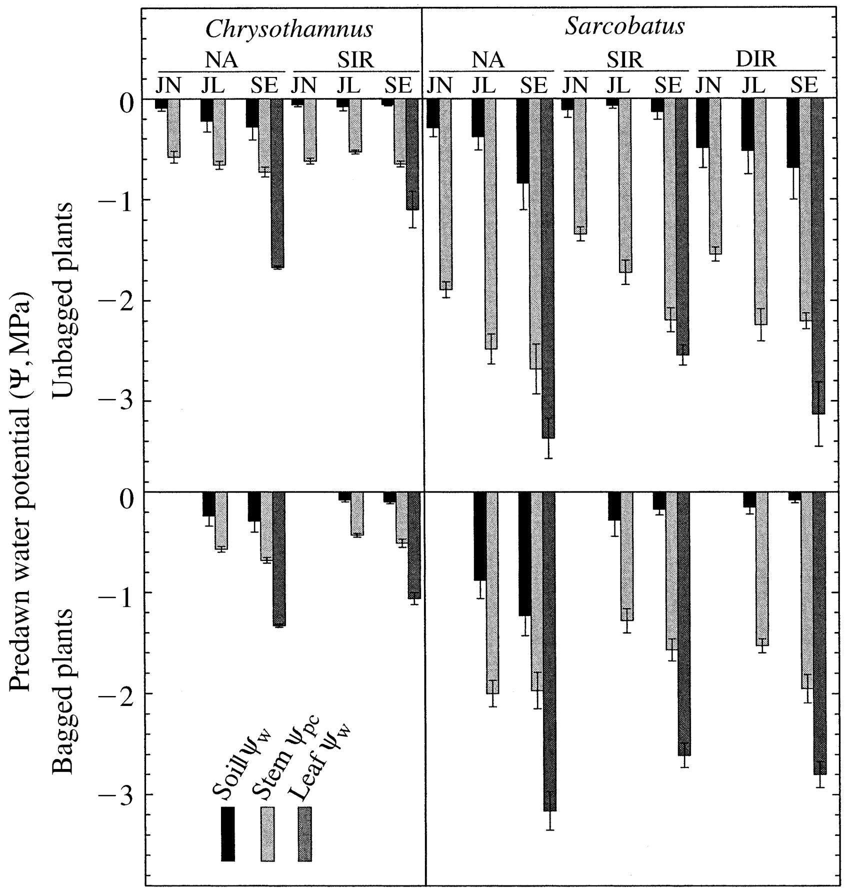

FIG. 1. Soil Ψ_w, predawn stem Ψ_{pc}, and predawn leaf Ψ_w (mean ± 1 SE, n = 5–6 plants/mean) for (top panel) unbagged plants and (bottom panel) bagged plants of *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus* in the western Great Basin desert, California, USA, on (JN) 21–23 June, (JL) 22–25 July, and (SE) 14–17 September 2000. Bagged plants had shrub crowns covered overnight during the July and September sampling to prevent nighttime transpiration. Treatments were natural rainfall (no irrigation, NA), surface irrigation (SIR), and deep irrigation (DIR). Soil Ψ_w was less negative than stem Ψ_{pc} for each species–irrigation combination (see Table 2) indicating predawn disequilibrium (PDD). In addition, stem Ψ_{pc} was significantly less negative than leaf Ψ_w for each comparison in September ($P < 0.05$).

TABLE 3. Repeated-measures ANOVA results comparing predawn stem Ψ_{pc} of bagged and unbagged plants for *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus* in each irrigation treatment.

		Predawn $\Psi_{pc\ bagged}$ vs. predawn $\Psi_{pc\ unbagged}$	Time	Time × Ψ_{pc}
Species	Treatment	*F*	*F*	*F*
Chrysothamnus	NA	2.03	14.3**	0.68
	SIR	11.5**	27.65***	1.11
Sarcobatus	NA	7.24*	0.41	0.67
	SIR	18.71**	11.37**	0.65
	DIR	12.45**	3.5	5.22*

Notes: The comparison was made on two dates (July and September), so time is the repeated factor. The df (numerator, denominator) are 1, 10 for predawn Ψ_{pc}, time, and time × Ψ_{pc}. See Fig. 1 for data, treatments, and sampling dates.
* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

DISCUSSION

In natural populations, *Chrysothamnus* and *Sarcobatus* had PDD with magnitudes similar to reports for these and other desert shrubs, and for halophytes from glasshouse studies (Donovan et al. 1999, 2001). The estimated magnitude of PDD depended on whether stem Ψ_{pc} or leaf Ψ_w was used. With stem Ψ_{pc}, PDD was as large as 0.6 MPa for *Chrysothamnus* and 2.1 MPa for *Sarcobatus*. Using leaf Ψ_w, and thus including the effect of leaf intercellular apoplastic solutes, PDD was greater: up to 1.4 MPa for *Chrysothamnus* and 2.7 MPa for *Sarcobatus*. For these species, predawn Ψ does not reflect the wettest soil Ψ_w in the root zone, and species differences in predawn stem Ψ_{pc} or leaf Ψ_w cannot be used to infer ecological differences in soil moisture access, rooting depth, or soil water stress.

By experimentally isolating individual mechanisms, our field experiments showed that several mechanisms simultaneously contributed to PDD in these desert

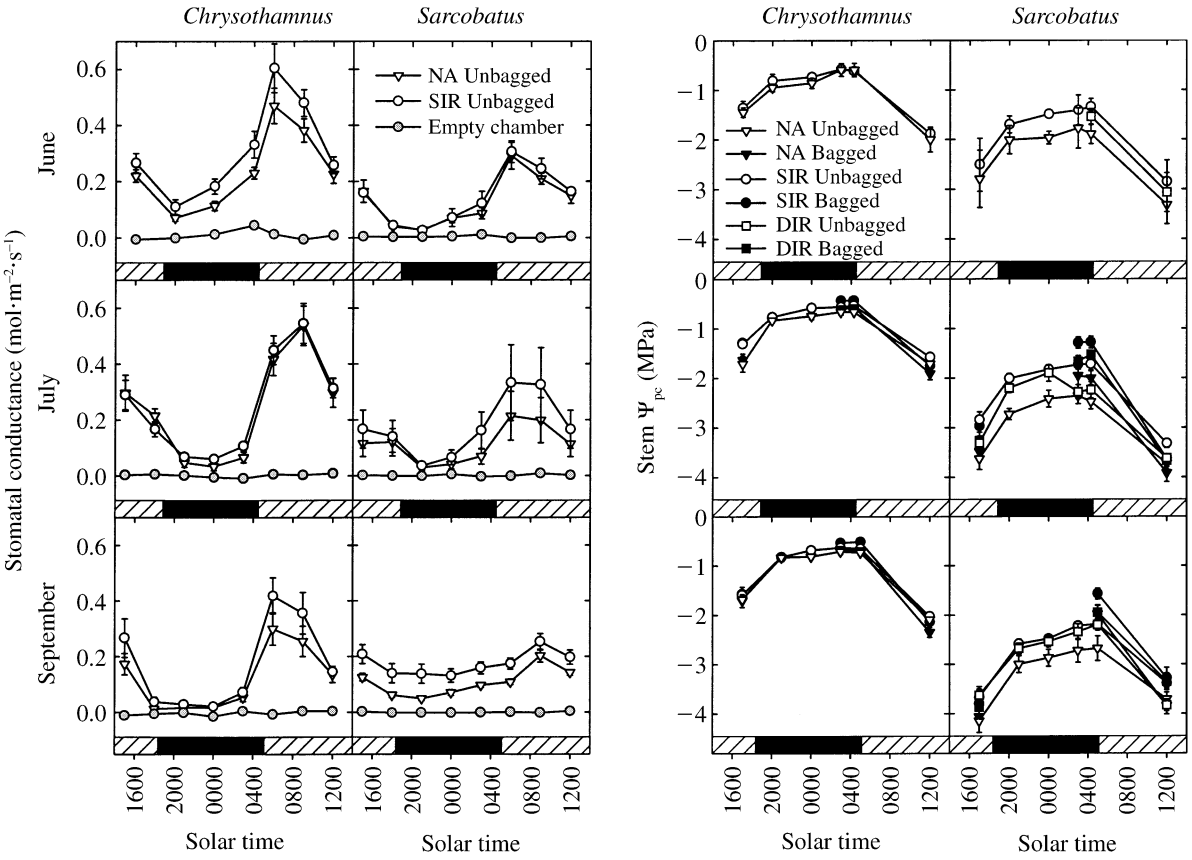

FIG. 2. Diurnal stem Ψ_{pc} and plant stomatal conductance (mean ± 1 SE, $n = 6$ plants/mean) for *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus*. Solid symbols = bagged plants (shrub crowns covered overnight to prevent nighttime transpiration); open symbols = unbagged plants. Black bars on *x*-axes indicate nighttime. See Fig. 1 for treatments and sampling dates. For stomatal conductance, empty chamber error bars were always less than symbol size.

shrubs in their natural environment. Nighttime transpiration contributed to PDD for *Chrysothamnus* (~0.1 MPa) and *Sarcobatus* (~0.6 MPa). Putative apoplastic solutes also contributed to PDD (~0.7 and ~0.9 MPa, respectively). For both species, predawn stem $\Psi_{\text{pc bagged}}$ and $\Psi_{\text{pc unbagged}}$ both reached plateaus before dawn, indicating no contribution of hydraulic conductance limitations. The occurrence and magnitude of these PDD mechanisms in the heterogeneous field conditions are remarkably consistent with results from more controlled glasshouse studies with uniform soil moisture conditions (Donovan et al. 1999, 2001).

As expected, *Sarcobatus*, but also *Chrysothamnus*, exhibited small magnitude hydraulic lift. We only had the experimental setup (i.e., DIR treatment with uniformly moist deep soil) to assess the contribution of hydraulic lift to PDD for *Sarcobatus*. We interpret the ~0.3 MPa difference in PDD for the DIR and SIR treatments as contribution of nighttime water loss from roots via hydraulic lift, the first such report in the literature. An alternative interpretation would attribute the PDD difference to greater soil moisture heterogeneity in the DIR treatment, even in the absence of hydraulic lift. However, the heterogeneity effect is expected to be minimal, unless only a very small percentage of roots are in wet soil and hydraulic conductance limits the speed of overnight recovery (Améglio et al. 1999). Although plants in the NA treatment also exhibited hydraulic lift, this treatment was not used to ascertain the effect of hydraulic lift on PDD because the roots in this nonirrigated treatment may have accessed even wetter soils than measured at 2.0 m, resulting in an underestimate of soil Ψ_w and PDD.

The sums of the estimated contributions of individual mechanisms for *Chrysothamnus* and *Sarcobatus* (1.1 and 1.8 MPa, respectively; assuming similar hydraulic lift contribution in both species) approach the overall magnitude of PDD for these species (1.4 and 2.7 MPa, respectively). However, the experimental treatments in this study do not allow us to assess whether the mechanisms are additive. In some cases, such as with nighttime transpiration and hydraulic lift, a trade-off is more likely than is an additive effect.

Plants with open stomata or transpiration at night have been reported (Blake and Ferrell 1977, Wieser and Havranek 1993, Matyssek et al. 1995, Hogg and Hurdle 1997, Benyon 1999, Donovan et al. 1999, Lasceve et al. 1999, Sellin 1999, Oren et al. 2001), but

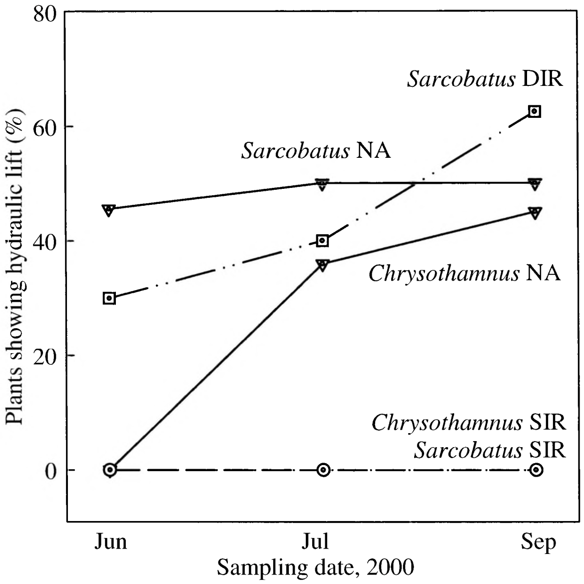

FIG. 3. Percentage of *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus* plants exhibiting hydraulic lift at 0.3 m depth during the 10-d interval centered on each of the plant Ψ_{pc} sampling dates; $n = 8–11$ shrubs per treatment. See Fig. 1 for treatments and sampling dates.

potential costs or benefits remain unclear. If our leaf level measurements scale up to whole shrubs, then nighttime stomatal conductances reported here translate to 5–15% of the 24-h water loss occurring at night without concomitant CO_2 fixation, potentially a large cost for desert plants. Ecologically, nighttime transpiration may affect plant water use, nutrient uptake (Sellin 1999), turgor and hydraulic resistance regulation (Zwieniecki et al. 2001), and gaseous pollutant exposure (Wieser and Havranek 1993, Matyssek et al. 1995). We are investigating relationships of nighttime sap flow to leaf-to-air vapor pressure deficit (e.g., Benyon 1999) to better understand stomatal control and plant water loss at night.

Nighttime transpiration and hydraulic lift both contribute to PDD by decreasing predawn plant Ψ_{pc} and Ψ_w, and may also provide nutrient acquisition benefits (Richards and Caldwell 1987, Matzner and Richards 1996, Caldwell et al. 1998). For example, hydraulic lift potentially enhances root growth, root and mycorrhizae maintenance, and rhizosphere processes in drying soil. Nighttime transpiration could improve nutrient acquisition from deep sources. These potential benefits may be significant in nutrient-poor habitats, such as our study site (Donovan and Richards 2000). We are currently investigating interactions of hydraulic lift, nighttime transpiration, and N uptake.

The contribution of putative apoplastic solutes to PDD, first documented in glasshouse plants under well-watered conditions (Donovan et al. 1999, 2001), is also substantial under field conditions. If intercellular solutes can be accumulated and dissipated on an appropriate temporal scale, they might provide desert shrubs and halophytes with an additional means to regulate turgor. While it is well documented that leaf cells accumulate compatible solutes and/or ions in order to maintain turgor when soil Ψ_w becomes more negative, intercellular solutes could dissipate excess turgor for leaves that still contain substantial compatible solutes and ions when soil Ψ_w is closer to zero.

Awareness of the existence and potential magnitude of PDD allows refinement of ecological and physiological interpretations of predawn stem Ψ_{pc} and leaf Ψ_w. More important, however, is the recognition that mechanisms contributing to PDD are a coordinated suite of plant interactions with the soil and atmospheric moisture environment. We need to explore mechanisms that may individually and collectively contribute to PDD in different species and habitats. Is PDD a restricted phenomenon or relatively widespread? Are individual mechanisms more prevalent in particular functional or taxonomic groups? What are the costs and benefits for each mechanism, and do they change seasonally or when acting simultaneously with other mechanisms? Are the mechanisms additive? Answers to these questions will further understanding of how plants interact with their soil and atmospheric moisture environment and with each other.

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LITERATURE CITED

Améglio, T., P. Archer, M. Cohen, C. Valancogne, F. Daudet, S. Dayau, and P. Cruiziat. 1999. Significance and limits in the use of predawn leaf water potential for tree irrigation. Plant and Soil **207**:155–167.

Benyon, R. G. 1999. Nighttime water use in an irrigated *Eucalyptus grandis* plantation. Tree Physiology **19**:853–859.

Blake, J., and W. K. Ferrell. 1977. The association between soil and xylem water potential, leaf resistance, and abscisic acid content in droughted seedlings of Douglas-fir (*Pseudotsuga menziesii*). Plysiologia Plantarum **39**:106–109.

Boyer, J. D. 1995. Measuring the water status of plants and soils. Academic Press, San Diego, California, USA.

Bréda, N., A. Granier, F. Barataud, and C. Moyne. 1995. Soil water dynamics in an oak stand. I. Soil moisture, water potentials and water uptake by roots. Plant and Soil **172**: 17–27.

Brisson, N., A. Olioso, and P. Clastre. 1993. Daily transpiration of field soybeans as related to hydraulic conductance, root distribution, soil potential and midday leaf potential. Plant and Soil **154**:227–237.

Brown, R. W., and D. L. Bartos. 1982. A calibration model for screen-caged Peltier thermocouple psychrometers. USDA Forest Service Research Paper INT-293.

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

Davis, S. D., and H. A. Mooney. 1986. Water use patterns of four co-occurring chaparral shrubs. Oecologia **70**:172–177.

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

Donovan, L. A., D. J. Grisé, J. B. West, R. A. Pappert, N. N. Alder, and J. H. Richards. 1999. Predawn disequilibrium between plant and soil water potentials in two cold-desert shrubs. Oecologia **120**:209–217.

Donovan, L. A., M. J. Linton, and J. H. Richards. 2001. Predawn plant water potential does not necessarily equilibrate with soil water potential under well-watered conditions. Oecologia **129**:328–335.

Donovan, L. A., and J. H. Richards. 2000. Juvenile shrubs show differences in stress tolerance, but no competition or facilitation, along a stress gradient. Journal of Ecology **88**: 1–16.

Donovan, L. A., J. H. Richards, and M. W. Muller. 1996. Water relations and leaf chemistry of *Chrysothamnus nauseosus* ssp. *consimilis* (Asteraceae) and *Sarcobatus vermiculatus* (Chenopodiaceae). American Journal of Botany **183**:1637–1646.

Hamerlynck, E. P., J. R. McAuliffe, and S. D. Smith. 2000. Effects of surface and sub-surface soil horizons on the seasonal performance of *Larrea tridentata* (cresotebush). Functional Ecology **14**:596–606.

Hinckley, T. M., J. P. Lassoie, and S. W. Running. 1978. Temporal and spatial variations in the water status of forest trees. Forest Science Monograph **20**:1–72.

Hogg, E. H., and P. A. Hurdle. 1997. Sap flow in trembling aspen: implications for stomatal responses to vapor pressure deficit. Tree Physiology **17**:501–509.

Hubbard, R. M., B. J. Bond, and M. G. Ryan. 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. Tree Physiology **19**:165–172.

Kramer, P. J., and J. S. Boyer. 1995. Water relations of plants and soils. Academic Press, San Diego, California, USA.

Lasceve, G., J. Leymarie, M. A. Olney, E. Liscum, J. M. Christie, A. Vavasseur, and W. R. Briggs. 1999. Arabidopsis contains at least four independent blue-light-activated signal transduction pathways. Plant Physiology **120**: 605–614.

Le Roux, X., and T. Bariac. 1998. Seasonal variations in soil, grass and shrub water status in a West Africa humid savanna. Oecologia **113**:456–466.

Matyssek, R., M. S. Günthardt-Goerg, S. Maurer, and T. Keller. 1995. Nighttime exposure to ozone reduces whole-plant production in *Betula pendula*. Tree Physiology **15**: 159–165.

Matzner, S. L., and J. H. Richards. 1996. Sagebrush (*Artemisia tridentata* Nutt.) roots maintain nutrient uptake capacity under water stress. Journal of Experimental Botany **47**:1045–1056.

McCarron, J. K., and A. K. Knapp. 2001. C_3 woody plant expansion in a C_4 grassland: are grasses and shrubs functionally distinct? American Journal of Botany **88**:1818–1823.

Melcher, P. J., F. C. Meinzer, D. E. Yount, G. Goldstein, and U. Zimmermann. 1998. Comparative measurements of xylem pressure potential in transpiring and non-transpiring leaves by means of the pressure chamber and the xylem pressure probe. Journal of Experimental Botany **49**:1757–1760.

Nardini, A., and S. Salleo. 2000. Limitation of stomatal conductance by hydraulic traits: sensing or preventing xylem cavitation? Trees **15**:14–24.

Nobel, P. S., and M. Cui. 1992. Hydraulic conductances of the soil, the root-soil air gap, and the root: changes for desert succulents in drying soil. Journal of Experimental Botany **43**:319–326.

Oren, R., J. S. Sperry, B. E. Ewers, D. E. Pataki, N. Phillips, and J. P. Megonigal. 2001. Sensitivity of mean canopy stomatal conductance to vapor pressure deficit in flooded *Taxodium distichum* L. forest: hydraulic and non-hydraulic effects. Oecologia **126**:21–29.

Ourcival, J. M., and A. Berger. 1995. Equilibrium between soil water potential and predawn water potential of two pre-Saharan shrub species of Tunisia. Journal of Arid Environments **30**:175–183.

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

Richter, H. 1997. Water relations of plants in the field: some comments on the measurement of selected parameters. Journal of Experimental Botany **48**:1–7.

Ritchie, G. A., and T. M. Hinckley. 1971. Evidence for error in pressure bomb estimates of stem xylem potentials. Ecology **30**:534–536.

Ritchie, G. A., and T. M. Hinckley. 1975. The pressure chamber as an instrument for ecological research. Advances in Ecological Research **9**:165–254.

Romo, J. T., and M. R. Haferkamp. 1989. Water relations of *Artemisia tridentata* ssp. *wyomingensis* and *Sarcobatus vermiculatus* in the steppe of southeastern Oregon. American Midland Naturalist **121**:155–164.

SAS Institute. 1989. SAS STAT user's guide, version 6. Fourth edition, volume 2. SAS Institute, Cary, North Carolina, USA.

Sellin, A. 1996. Base water potential of *Picea abies* as a characteristic of soil water status. Plant and Soil **184**:273–280.

Sellin, A. 1999. Does pre-dawn water potential reflect conditions of equilibrium in plant and soil water status? Acta Oeologica **20**:51–59.

Toft, C. A. 1995. A 10-yr demographic study of rabbitbrush (*Chrysothamnus nauseosus*): growth, survival and water limitation. Oecologia **101**:1–12.

Turner, N. C. 1981. Correction of flow resistances of plants measured from covered and exposed leaves. Plant Physiology **68**:1090–1092.

Turner, N. C. 1988. Measurement of plant water status by the pressure chamber technique. Irrigation Science **9**:289–308.

Wieser, G., and W. M. Havranek. 1993. Ozone uptake in the sun and shade crown of spruce: quantifying the physiological effects of ozone exposure. Trees **7**:227–232.

Zwieniecki, M. A., P. J. Melcher, and N. M. Holbrook. 2001. Hydrogel control of xylem hydraulic resistance in plants. Science **291**:1059–1062.