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Predawn disequilibrium between plant and soil water potentials in two cold-desert shrubs

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Abstract Classical water relations theory predicts that predawn plant water potential should be in equilibrium with soil water potential (soil Ψ_w) around roots, and many interpretations of plant water status in natural populations are based on this expectation. We examined this expectation for two salt-tolerant, cold-desert shrub species in glasshouse experiments where frequent watering assured homogeneity in soil Ψ_w and soil-root hydraulic continuity and where NaCl controlled soil Ψ_w . Plant water potentials were measured with a pressure chamber (xylem Ψ_p) and thermocouple psychrometers (leaf Ψ_w). Soil Ψ_w was measured with in situ thermocouple psychrometers. Predawn leaf Ψ_w and xylem Ψ_p were significantly more negative than soil Ψ_w , for many treatments, indicating large predawn soil-plant Ψ_w disequilibria: up to 1.2 MPa for *Chrysothamnus nauseosus* (0 and 100 mM NaCl) and 1.8 MPa for *Sarcobatus vermiculatus* (0, 100, 300, and 600 mM NaCl). Significant nighttime canopy water loss was one mechanism contributing to predawn disequilibrium, assessed by comparison of xylem Ψ_p for bagged (to minimize transpiration) and unbagged canopies, and by gas exchange measurements. However, nighttime transpiration accounted for only part of the predawn disequilibrium. Other mechanisms that could act with nighttime transpiration to generate large predawn disequilibria are described and include a model of how leaf apoplastic

solute could contribute to the phenomenon. This study is among the first to conclusively document such large departures from the expectation of predawn soil-plant equilibrium for C_3 shrubs, and provides a general framework for considering relative contributions of nighttime transpiration and other plant-related mechanisms to predawn disequilibrium.

Key words Apoplast · *Chrysothamnus* · Nighttime stomatal conductance · Salinity · *Sarcobatus*

Introduction

Classical expectations for diurnal patterns of soil, root, and shoot water status are founded on the assumption that predawn or maximum plant water potential should be in equilibrium with soil water potential in the rooting zone, based on thermodynamics and the Ohm's law analogy (see Fig. 9.13 in Nobel 1991, after Slatyer 1967, and older literature reviewed in Richter 1973). Leaf predawn water potentials have been measured directly with thermocouple psychrometers or indirectly with the Scholander-type pressure chamber [where xylem Ψ_p is generally considered to be a good approximation of leaf Ψ_w because xylem Ψ_s is usually negligible (Boyer 1995)]. Predawn water potentials are ecologically relevant. For example, differences in predawn xylem Ψ_p have been used to infer differences in rooting depth and habitat partitioning, based on the expectation that these values reflect equilibration with soil Ψ_w (Griffin 1973; Davis and Mooney 1986; Romo and Haferkamp 1989; Donovan and Ehleringer 1994a). Bréda et al. (1995) estimated the zone of oak root water uptake from the match of oak predawn Ψ_w with soil Ψ_w in the depth profile. Models that integrate plant transpiration responses to water stress and estimate hydraulic resistances also commonly assume that soil and plant Ψ_w equilibrate by dawn (Mishio and Yokoi 1991; Rambal 1992; Brisson et al. 1993). Predawn xylem Ψ_p has also been correlated with plant physiological processes in-

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cluding maximum stomatal conductance or transpiration (Reich and Hinckley 1989; Romo and Haferkamp 1989; Acherar and Rambal 1992; Améglio and Archer 1996) and growth (Mitchell et al. 1993). Thus, understanding the mechanisms that control plant predawn Ψ_w , knowledge of variation in this character, and assessment of the validity of the equilibrium assumption are critical to realistic interpretations of plant water use, plant adaptation to stress, water resource partitioning, and community water balance.

The pattern of least negative plant Ψ_w at predawn and more negative Ψ_w during the day, consistent with the classical expectation, is well documented in the literature but does not address whether plant Ψ_w recovers sufficiently overnight to approach equilibrium with the wettest soil layer in the rooting zone. Numerous studies, however, report differences between soil Ψ_w (around roots) and predawn leaf Ψ_w , suggesting that predawn leaf Ψ_w does not always equilibrate with the wettest soil layer (Hinckley and Ritchie 1973; Klepper et al. 1973; Hinckley et al. 1978a; Nilsen et al. 1983; Fahey and Young 1984; Küppers et al. 1987; Meinzer et al. 1988; Ourcival et al. 1994; Améglio and Archer 1996; Donovan et al. 1996). Some possible explanations discussed in the literature are soil moisture heterogeneity (i.e., difficulty in determining soil water potential directly adjacent to active roots) and poor hydraulic continuity between soil and root (Hinckley et al. 1978b; Storzaker and Passioura 1996; Schmidhalter 1997). In addition, various plant characteristics have been discussed such as nighttime transpiration, insufficient time for overnight recovery due to high internal resistances, and high capacitance or storage (Hinckley and Ritchie 1973; Hinckley et al. 1978b; Ourcival and Berger 1995; Richter 1997). In a glasshouse experiment where soil Ψ_w was uniformly near zero and soil-root hydraulic continuity was maintained, Ourcival and Berger (1995) found surprisingly large differences between psychrometric measurements of soil Ψ_w and predawn leaf Ψ_w for two Tunisian desert shrub species. Predawn leaf Ψ_w was 1.1–2.1 MPa more negative than soil Ψ_w , a substantial departure from the assumed equilibrium. Although factors such as soil moisture heterogeneity and soil-root hydraulic continuity are obviously important in understanding field patterns, this phenomenon of “predawn disequilibrium,” meaning predawn soil-plant water potential disequilibrium when soil-root hydraulic continuity is not a limiting factor, deserves further investigation.

In this study we investigated predawn disequilibrium under controlled conditions for two cold-desert phreatophytic shrubs: *Chrysothamnus nauseosus* (Palla.) Britt. ssp. *consimilis* (E. Greene) H.M. Hall & Clements (Asteraceae), and *Sarcobatus vermiculatus* (Hook.) Torrey (Chenopodiaceae). Large predawn disequilibria were noted in two field studies with these species. The first study compared these species at a marginally saline site near Mono Lake, Calif. (Donovan et al. 1996). Although both species had similar root distributions and access to non-saline groundwater ($\Psi_s \cong -0.06$ MPa),

plant predawn xylem Ψ_p was as low as -0.8 MPa for *Chrysothamnus* and -2.7 MPa for *Sarcobatus*. Thus, neither species equilibrated with the groundwater during the night and the species differed in magnitude of apparent predawn disequilibrium. In the second field study, predawn xylem Ψ_p in *Sarcobatus* was usually not in equilibrium with the wettest soil beneath the shrubs at four sites along a topographic salinity gradient (Donovan and Richards 1997). At each site, soil and capillary-fringe Ψ_w (soil psychrometers), and predawn and midday plant xylem Ψ_p (pressure chamber) were measured over two growing seasons. When *Sarcobatus* predawn xylem Ψ_p values were at their most negative during the 2-year study (August 1994), they were from 1.5 to 2.4 MPa more negative than soil Ψ_w of the wettest soil layer. Minirhizotron observations demonstrated growing roots near the psychrometers in the wettest soil layers. Because of the potential for soil moisture heterogeneity and poor hydraulic continuity between soil and root, however, these field studies do not yield conclusive evidence of large predawn disequilibria.

Our objectives in this glasshouse study were (1) to determine the existence and magnitude of predawn disequilibria for *Sarcobatus* and *Chrysothamnus* under conditions where soil Ψ_w was uniform, measured, and controlled by the salinity of the watering solution, and where good soil-root hydraulic continuity was assured, and (2) to investigate some of the likely plant-related mechanisms associated with predawn disequilibrium for these species.

Materials and methods

S. vermiculatus is a very salt tolerant, Na-accumulating shrub often associated with saline soils (Glenn and O'Leary 1984; Donovan et al. 1996, 1997). *C. nauseosus* is usually considered a non-salt-tolerant, glycophytic shrub, but subspecies *consimilis* is moderately salt tolerant and co-occurs with *Sarcobatus* at many marginally saline sites throughout the Great Basin. Both species are C_3 , winter-deciduous shrubs that produce leaves in spring, flower in late summer, and set and disperse seed in late autumn. Although these two species have similar root distributions in the upper meter of soil and deep roots penetrating to groundwater at 3–5 m, they differ greatly in water status and inorganic ion relations (Donovan et al. 1996, 1997). High leaf Na concentrations contribute to much lower water potentials for *Sarcobatus*, with Na sequestered predominantly in vacuoles.

In the experiments, the magnitude of the predawn disequilibrium was determined under conditions that eliminated uncertainties typical of field measurements. Predawn leaf Ψ_w , xylem Ψ_p , and soil Ψ_w were measured on plants whose roots were in well-watered soil of known Ψ_w to eliminate the possibility of poor soil-root hydraulic continuity which is unpredictable in soil dried to different matric potentials. Osmotic control of the soil solution allowed imposition of accurately known levels of water stress, while at the same time assuring good soil-root hydraulic continuity and homogeneity of soil moisture around the root system of the experimental plants. The levels of osmotic water stress imposed on each species were set within the limits of tolerance of any toxic ion effect that might accompany the osmotic effect of salt in the soil solution (Donovan et al. 1996, 1997; Dodd and Donovan 1999).

Experiments were conducted in a glasshouse at the University of Georgia, Athens. Seeds of *Sarcobatus* (from 13 plants) and *Chrysothamnus* (from 10 plants) were collected from Mono Dunes

Ecosystem Research Site north of Mono Lake, Calif. (Toft 1995; Donovan et al. 1996, 1997), air dried, and refrigerated until use. In autumn 1996, after scarifying *Sarcobatus* seeds with sandpaper, seeds of both species were germinated on wet filter paper in petri dishes. One-week-old seedlings at the cotyledon stage were transplanted to containers of washed river sand, and then to 2.5-l PVC pots of sand at 19 weeks. Seedlings received 1/4-strength modified Hoagland's solution (Epstein 1972) until the start of the salinity treatments, at 24 weeks.

Experiment 1 examined the role of nighttime transpiration on predawn water potential disequilibria. First, does predawn disequilibrium occur in the absence of nighttime canopy water loss? For this question, predawn leaf Ψ_w , xylem Ψ_p , and soil Ψ_w were compared for individual plants that had canopies enclosed in a plastic bag (i.e., bagged plants). The bags were secured around the base of the canopy approximately 1 h after nightfall and removed immediately before predawn sampling. Second, does the magnitude of the predawn disequilibrium increase when bags are removed and nighttime canopy water loss is allowed? For this question, bagged and unbagged plants were compared for xylem Ψ_p . Measurements were made 13–18 June 1997 (31-week-old plants). Each block was sampled during one predawn session (0430–0600 h) for leaf Ψ_w and xylem Ψ_p , and the three blocks were sampled sequentially at 2-day intervals. Sunrise was at \sim 0630 h. For selected plants from all blocks, midday xylem Ψ_p was also measured starting at 1400 h on the last day of predawn measurements.

Six species/salinity combinations, *Chrysothamnus* 0 and 100 mM NaCl, and *Sarcobatus* 0, 100, 300, and 600 mM NaCl, were used in experiment 1. Plants were randomly assigned to three experimental blocks to account for environmental variation in the glasshouse, with five replicates (individual potted plants) of each species/salinity combination in each block. The salinity treatments, NaCl added to 1/4 Hoagland's solution, were imposed incrementally to allow the plants to acclimate: 1/3 strength for 2 weeks, 2/3 strength for 2 weeks, and then full-strength salinity for 3 weeks prior to water potential measurements. Free-draining pots were watered to excess each day to prevent salt accumulation. During the week prior to and the week of plant water potential measurements, the pots were watered twice a day (morning and evening) with a volume sufficient to exchange all of the water in the pot assuring uniformity of water potential in the soil. Daylight in the greenhouse was supplemented with 400-W sodium vapor lamps for 14 h/day to simulate summer conditions in the native habitat. Air temperature in the glasshouse averaged 26°C during the day and 21°C at night.

Leaf Ψ_w was measured in stainless steel chambers with individually calibrated (Brown and Bartos 1982) chamber thermocouple psychrometers (83 series, Merrill Specialty Equipment, Logan, Utah) and a CR7 data logger (Campbell Scientific, Logan, Utah). Five to ten fully expanded leaves were plucked from an excised stem and inserted into a chamber within \sim 30 s of stem excision. Mature leaf tissue was used to minimize growth effects on leaf Ψ_w (Boyer 1995). Light for predawn sampling was provided by a green safety lamp with an intensity undetectable ($0 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation, PAR) by an LI-190 sensor (LiCor, Lincoln, Neb.). After filling, chambers were sealed and placed in an isothermal water bath. Psychrometer μV values (checked hourly) stabilized after \sim 8 h and were then used to calculate leaf Ψ_w . Although psychrometer measurements of excised stem Ψ_w were also attempted, equilibration times were exceptionally long, perhaps due to insufficient surface area in the chambers (Boyer 1995), and these data were not considered reliable. Predawn and midday stem xylem Ψ_p were measured using a pressure chamber (PMS, Corvallis, Ore.). Stems for predawn Ψ_p measurements were excised at the same time as leaves were sampled for leaf Ψ_w . Standard precautionary steps were followed to minimize errors, including enclosure of the stem in a plastic bag throughout the excision and measurement process (Turner 1988; Boyer 1995). After plants had been sampled for water potentials, mature fully expanded leaves were collected for determination of leaf fresh and dry biomass (after drying at 60°C), and then dried leaves were ground with a ball mill and combusted at 500°C for determination of ash content.

Soil Ψ_w was measured with individually calibrated screen-cage thermocouple psychrometers (74 series, Merrill Specialty Equipment) installed in the center of pots and monitored hourly with a CR7 data logger. Psychrometers were located in six replicate pots (two in each block) for each species/salinity combination. The value of soil Ψ_w for an individual pot used in the analysis was the mean of the 0400, 0500 and 0600 h readings for the week of plant water potential measurements. Zero offset values were generally $< 3 \mu\text{V}$, indicating minimal temperature-induced errors (Brown and Bartos 1982).

Statistical comparisons of water potentials were made within each species/salinity combination. For plants with bagged canopies, one-way ANOVA procedures (SAS 1989) were used to compare predawn leaf Ψ_w , xylem Ψ_p , and soil Ψ_w . One-way ANOVAs were also used to compare bagged and unbagged plants for xylem Ψ_p .

Experiment 2, conducted in April 1998, explored further the mechanisms contributing to predawn disequilibrium. It used a subset of plants from experiment 1 that had been transplanted to 12-l pots and continued to receive the salinity treatments. *Chrysothamnus* plants available for measurements were 0 mm ($n = 6$) and 100 mm ($n = 3$). *Sarcobatus* plants available for measurements were 0 mm ($n = 2$), 100 mm ($n = 4$), and 300 mm ($n = 5$).

Gas exchange was measured on 13–15 April 1998, using an LI-6400 portable gas exchange system (LiCor). Measurements were made on all available *Chrysothamnus* and *Sarcobatus* plants. For comparison, measurements were also made on four *Coleus* sp. (Labiatae) plants and four *Nicotiana tabacum* (Solanaceae) plants from the glasshouse teaching collection. Plant stems were sampled in random order with interspersed empty chamber measurements. Nighttime measurements were made from 0200 until 0500 h and chamber conditions were 22°C, $400 \mu\text{mol mol}^{-1} \text{CO}_2$ and $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR. Light for stem insertion into the chamber was provided by the green safety lamp. Daytime measurements were made on the same stems from 1000 to 1200 h; chamber conditions were 28°C, $350 \mu\text{mol mol}^{-1} \text{CO}_2$, and $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR. Leaf areas were measured with an LI-3100 leaf area meter (LiCor). To determine if nighttime leaf conductances (g_s) were significantly greater than zero, the g_s values for each species/salinity combination were compared to the empty chamber (i.e., control) with a one-way ANOVA and subsequent Tukey multiple-range tests.

Xylem Ψ_p was measured with a pressure chamber at 0300 and 0530 h, to determine if values had reached a plateau during the early morning hours before dawn. Soil psychrometers were used to measure soil Ψ_w . Double bagging minimized nighttime canopy water loss: each stem designated for xylem Ψ_p sampling was enclosed in an aluminum foil envelope, and each canopy was enclosed in a plastic bag containing a saturated paper towel. For each species/treatment combination with sufficient replication, a paired t -test was used to compare 0300 and 0530 h xylem Ψ_p values and a t -test was used to compare soil Ψ_w and xylem Ψ_p values.

Xylem Ψ_s was also determined for plants with sufficient stems containing leaves. Just after sunrise, xylem contents were expressed using a pressure chamber in a humidified box. The expressed sap was collected on filter paper strips, stored in microcentrifuge tubes, and subsequently measured in a SC10A Thermocouple Psychrometer System (Decagon Devices, Pullman, Wash.).

Results

When nighttime transpiration was eliminated, *C. nauseosus* and *S. vermiculatus* exhibited predawn disequilibria in all salinity treatments, with leaf Ψ_w significantly more negative than soil Ψ_w (Fig. 1). In addition, xylem Ψ_p was significantly more negative than soil Ψ_w for both species in the 0 mM NaCl treatment, and leaf Ψ_w was significantly more negative than xylem Ψ_p for *Chry-*

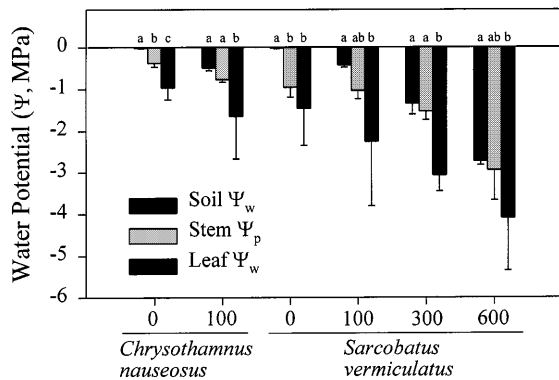


Fig. 1 Predawn soil Ψ_w ($n = 6$), stem xylem Ψ_p ($n = 8$), and leaf Ψ_w ($n = 3-8$) (MPa, means \pm SD) for *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus* growing in 0, 100, 300 and 600 mM NaCl salinity treatments. Canopies of all plants were bagged overnight to eliminate nighttime transpiration. Predawn leaf Ψ_w , xylem Ψ_p , and soil Ψ_w within a species treatment group were compared with one-way ANOVAs, and different letters within a group indicate significant differences using a multiple range test ($\alpha = 0.05$)

southamnis in 0 and 100 mM, and *Sarcobatus* in 300 mM NaCl.

Predawn xylem Ψ_p was significantly more negative for unbagged plants (with nighttime transpiration) than for bagged plants (without nighttime transpiration) for *Chrysothamnus* and *Sarcobatus* in 0 and 100 mM NaCl treatments (Fig. 2). The differences were 0.2 MPa for *Chrysothamnus* and 0.5–0.7 MPa for *Sarcobatus*. The means of unbagged and bagged plants followed the same pattern for *Sarcobatus* in the 300 and 600 mM NaCl treatments, but predawn xylem Ψ_p s were not significantly different.

Midday xylem Ψ_p (mean \pm SD, $n = 3$) for *Chrysothamnus* was -1.23 ± 0.10 and -1.70 ± 0.05 MPa for 0 and 100 mM NaCl, respectively. Midday xylem Ψ_p for *Sarcobatus* was -2.27 ± 0.20 , -2.80 ± 0.20 , -3.20 ± 0.22 , and -3.82 ± 0.33 MPa for 0, 100, 300,

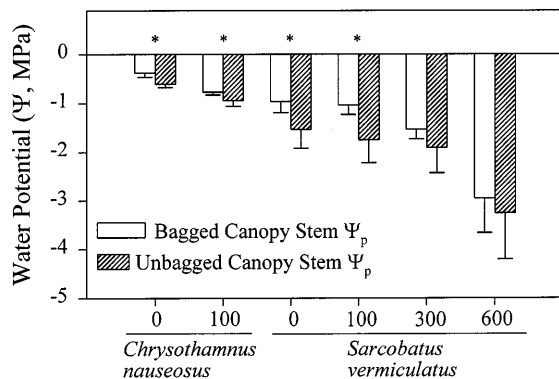


Fig. 2 Predawn stem xylem Ψ_p (MPa, mean \pm SD) for plant canopies bagged overnight ($n = 8$) and those remaining unbagged ($n = 7$), for *C. nauseosus* and *S. vermiculatus* growing in 0, 100, 300, and 600 mM NaCl salinity treatments. Predawn xylem Ψ_p for bagged and unbagged plants within a species treatment group were compared with one-way ANOVAs, and an asterisk within a group indicates a significant difference ($\alpha = 0.05$)

and 600 mM NaCl, respectively. The difference between predawn and midday xylem Ψ_p ranged from 0.85 to 0.93 MPa for *Chrysothamnus*, and from 0.87 to 1.76 MPa for *Sarcobatus*. *Chrysothamnus* leaves had fresh/dry biomass ratios of $4.6 \pm 0.2-4.1 \pm 0.3$, and ash contents of $9.2 \pm 3.7-10.1 \pm 1.0\%$. *Sarcobatus* leaves had fresh/dry biomass ratios of $6.6 \pm 0.8-8.8 \pm 0.5$, and ash contents of $28.1 \pm 3.5-45.0 \pm 1.9\%$.

In experiment 2, xylem Ψ_p values for 0300 h did not differ from those for 0530 h, for *Chrysothamnus* 0 mM ($t = 0.35$, $P = 0.741$, $df = 5$) and 100 mM NaCl ($t = 1.43$, $P = 0.289$, $df = 2$), and for *Sarcobatus* 100 mM NaCl ($t = 0.30$, $P = 0.783$, $df = 3$). For *Sarcobatus* 300 mM NaCl, however, the 0300 h xylem Ψ_p value (-1.79 MPa) was significantly more negative than the 0530 h value (-1.59 MPa) ($t = 3.51$, $P = 0.025$, $df = 4$). The differences between predawn and midday xylem Ψ_p , comparable to those in experiment 1, were 0.88 MPa for *Chrysothamnus* 0 mM NaCl and 1.70 and 0.92 MPa for *Sarcobatus* 100 and 300 mM NaCl, respectively. Also following the same trend found in experiment 1, predawn xylem Ψ_p was significantly more negative than soil Ψ_w for *Chrysothamnus* 0 mM ($t = 18.29$, $P < 0.001$, $df = 10$), *Chrysothamnus* 100 mM ($t = 3.76$, $P = 0.020$, $df = 4$), and *Sarcobatus* 100 mM NaCl ($t = 3.28$, $P = 0.013$, $df = 7$), by an average of 0.5 MPa. For *Sarcobatus* 300 mM NaCl, predawn xylem Ψ_p and soil Ψ_w were not significantly different ($t = 1.07$, $P = 0.315$, $df = 8$).

Chrysothamnus xylem Ψ_s values were -0.15 ± 0.02 and -0.16 ± 0.03 MPa for 0 mM ($n=6$) and 100 mM ($n=3$) NaCl, respectively. *Sarcobatus* xylem Ψ_s was -0.19 ± 0.05 , -0.17 ± 0.01 , and -0.21 ± 0.01 for 0 mM ($n=2$), 100 mM ($n=2$), and 300 mM ($n=4$) NaCl, respectively.

Chrysothamnus 0 mM NaCl and *Sarcobatus* 0, 100, and 300 mM NaCl had nighttime conductances (g_s) which were significantly greater than zero as determined by comparison with values from empty chambers (Table 1). *Chrysothamnus* in the 100 mM NaCl treatment and *Nicotiana* and *Coleus* growing on fresh water had nighttime conductances that were not significantly different from zero. At night, significant leaf respiration was indicated by CO_2 release for *Chrysothamnus* and *Sarcobatus* in all treatments (data not presented). Daytime stomatal conductances and photosynthetic rates were high for both *Chrysothamnus* and *Sarcobatus* (Table 1).

Discussion

We found statistically significant predawn disequilibria of large magnitude for both *C. nauseosus* and *S. vermiculatus* in all salinity treatments, including controls grown without salt. For plants with bagged canopies and minimal nighttime canopy water loss, *Chrysothamnus* predawn leaf Ψ_w was 1.0–1.2 MPa more

Table 1 Nighttime and midmorning stomatal conductances (g_s , mol H₂O m⁻² s⁻¹) and photosynthesis (A , μmol CO₂ m⁻² s⁻¹) (means ± SD) for *Chrysothamnus nauseosus* ($n = 3-6$), *Sarcobatus vermiculatus* ($n = 2-5$), *Coleus* sp. ($n = 4$), and *Nicotiana ta-*

bacum ($n = 4$) growing in different salinity treatments. Within the column for nighttime g_s , letters different from empty chamber ($n = 17$) indicate a statistical difference ($\alpha = 0.05$)

| Species | Treatment (mM NaCl) | Nighttime g_s | Midmorning g_s | Midmorning A |
|----------------------|---------------------|-----------------|------------------|----------------|
| <i>Chrysothamnus</i> | 0 | 0.45 ± 0.04 b | 1.22 ± 0.18 | 26.8 ± 1.7 |
| | 100 | 0.12 ± 0.05 a | 0.63 ± 0.28 | 15.5 ± 5.1 |
| <i>Sarcobatus</i> | 0 | 0.39 ± 0.09 b | 0.52 ± 0.11 | 16.4 ± 6.6 |
| | 100 | 0.27 ± 0.17 b | 0.51 ± 0.14 | 18.5 ± 2.9 |
| | 300 | 0.22 ± 0.13 b | 0.44 ± 0.18 | 18.5 ± 4.7 |
| <i>Coleus</i> | 0 | 0.01 ± 0.01 a | 0.37 ± 0.07 | 17.4 ± 1.4 |
| <i>Nicotiana</i> | 0 | 0.06 ± 0.01 a | 0.37 ± 0.05 | 21.6 ± 0.7 |
| Empty chamber | | -0.01 ± 0.01 a | 0.01 ± 0.01 | -0.1 ± 0.1 |

negative than soil Ψ_w , and *Sarcobatus* predawn leaf Ψ_w was 1.4–1.8 MPa more negative than soil Ψ_w (Fig. 1). An additional contribution to predawn disequilibrium resulted from nighttime transpiration. With nighttime transpiration, the disequilibria were up to 0.2 MPa greater for *Chrysothamnus* and 0.7 MPa greater for *Sarcobatus*, based on comparison of predawn xylem Ψ_p values for bagged versus unbagged plant canopies (Fig. 2). These findings confirm the existence and large magnitude of predawn disequilibria in these two species, as suggested by field experiments (Donovan et al. 1996). The glasshouse results are more reliable, however, because substrate water potential was controlled and homogeneous, and any root-soil hydraulic barrier was minimized by the experimental protocol. The phenomenon of large predawn disequilibrium has been previously observed in two Tunisian shrubs (Ourcival and Berger 1995). Predawn plant Ψ_w was more negative than soil Ψ_w by 2 MPa in *Artemisia herba-alba* and by 1 MPa in *Anthyllis henoniana*, even when soil Ψ_w was near 0 MPa. This is the only prior study we are aware of that documented discrepancies between predawn plant and soil Ψ_w under controlled soil Ψ_w conditions designed to eliminate poor soil-root hydraulic continuity as a liming factor. Both our current results and those of Ourcival and Berger (1995) indicate the potential for large-magnitude predawn disequilibria in some plants. Our work further demonstrates that predawn disequilibria occurred when substrate water potentials were reduced osmotically and when nighttime canopy water loss was eliminated.

What mechanisms are operating in these plants to result in such large predawn soil-plant Ψ_w disequilibria under conditions where soil-root hydraulic continuity is not a limiting factor? These mechanisms, which are not mutually exclusive, could include (1) nighttime water losses either from the plant canopy (nighttime transpiration; as shown in this study) or from portions of the root system (hydraulic lift), (2) lack of time to reach equilibrium overnight due to low plant hydraulic conductance or high capacitance, (3) nighttime growth-induced reduction in Ψ_w , and (4) apoplastic space considerations such as solute accumulation in leaf apoplast and the composite model of root hydraulic flow. Some

of these mechanisms would only be active under specific field conditions and were eliminated in the glasshouse studies. Each of these possibilities is discussed below.

Nighttime transpiration made a significant contribution to predawn disequilibrium in several treatments for *Chrysothamnus* and *Sarcobatus*. Measured nighttime stomatal conductances were remarkably high, up to 0.45 mol m⁻² s⁻¹ for *Chrysothamnus* and 0.39 mol m⁻² s⁻¹ for *Sarcobatus* (Table 1). These high conductances were confirmed by interspersed measurements of empty chambers, *Coleus* and *Nicotiana*, and repeated calibrations of the LI-6400, and measurements with a different type of photosynthesis system (LiCor LI-6200). The high nighttime conductances for *Chrysothamnus* and *Sarcobatus* were in accordance with lower predawn stem xylem Ψ_p of the unbagged plants (Fig. 2) and whole-plant water loss measurements (based on weighing of plants with sealed pots) of *Sarcobatus* shrubs at University of California, Davis (N. Alder and J. Richards, unpublished data). Although significant nighttime transpiration and water loss seems counterintuitive for desert C₃ species, there is precedent in the literature for open stomata at night in some C₃ plants (Hinckley and Ritchie 1973; Matyssek et al. 1995; Assaf and Zieslin 1996) but not all (Elfving and Kaufman 1972; Knapp and Yavitt 1995). In addition, because *Chrysothamnus* and *Sarcobatus* are at least somewhat phreatophytic, they may not be as constrained by water availability as more shallowly rooted desert shrubs or species that do not gain access to the capillary groundwater fringe. The extent and significance of *Chrysothamnus* and *Sarcobatus* nighttime canopy water loss under field conditions remains to be documented.

A process comparable to nighttime canopy water loss is nighttime root water loss. Although our experimental conditions of uniform soil moisture in the pots eliminated the soil Ψ_w gradient necessary to drive this process, it deserves mention because it could be a contributor to the apparent predawn disequilibrium observed in field studies (Donovan et al. 1996). Hydraulic lift is a process in which water moves from deep to shallow soil at night, via plant roots, down a gradient in water potential (Richards and Caldwell 1987; Caldwell et al. 1998). The water “leaked” during the night

into the shallow soils is then taken up during the day as the stomata open and shoot water potential drops. Nighttime water loss into dry soil layers could prevent the canopy from equilibrating with the wettest soil layer. Hydraulic lift has been documented for an increasing number of species, including *Sarcobatus* in natural populations (Muller et al. 1995; Caldwell et al. 1998). Hydraulic lift is not likely to play a role in natural *Chrysothamnus* populations because the shallow roots of this species are not functional for water uptake in mid to late summer (Flanagan et al. 1992; Donovan and Ehleringer 1994a). The magnitude of the contribution of hydraulic lift to predawn disequilibrium is unknown and remains to be assessed in field studies.

Another mechanism that could contribute to predawn disequilibrium is inadequate time for overnight equilibration, due to low hydraulic conductance or high capacitance in the plants. We did not expect these mechanisms to be important because the literature generally reports plant recovery to least negative water potentials soon after nightfall (Klepper 1968; Elfving and Kaufmann 1972; Griffin 1973; but see Hinckley and Ritchie 1973), and because our study species have the capacity for high rates of water transport and water loss under both field and glasshouse conditions (Davis et al. 1985; Donovan and Ehleringer 1991, 1994b; Donovan et al. 1996; this study). In addition, *Artemisia tridentata*, another desert shrub with architecture similar to our study species, has been shown to have little capacitance or storage capacity (Caldwell et al. 1991). We confirmed that inadequate time for overnight recovery to equilibration was not a primary mechanism contributing to predawn disequilibrium in our study by showing that most of our plants reached a plateau in xylem Ψ_p several hours before dawn. However, *Sarcobatus* in the 300 mM NaCl treatment did have a significant (0.2 MPa) continued recovery in xylem Ψ_p between 0300 and 0530 h, indicating that hydraulic conductance or capacitance may contribute under some conditions. These factors may also play a larger role in natural populations where mature plant root and stem volumes are larger and flow path lengths much longer. Again, field assessment of this mechanism is needed.

Nighttime growth-induced reduction in Ψ_w is another mechanism that could contribute to predawn disequilibrium. The Ψ_w of growing tissue can be lower than that of nearby mature tissue by as much as 0.4 MPa (Westgate and Boyer 1984; Boyer 1995). In growing tissue, equilibrium is not reached because water transport continues to the expanding volume of symplast. This mechanism is unlikely to account for the large predawn disequilibria in our experiments, because our measurements of leaf Ψ_w were bulk averages of predominately mature tissue. However, the magnitude of this mechanism under varying conditions remains to be quantified.

Significant predawn disequilibria between leaf Ψ_w and soil Ψ_w were observed for *Chrysothamnus* and *Sarcobatus*, even under experimental conditions that eliminated or minimized all of these potential mecha-

nisms of predawn disequilibrium (Fig. 1). Thus, we propose an additional potential mechanism for predawn disequilibrium that considers several aspects of apoplastic solutes. First, the suggestion that solutes in the stem xylem could explain the discrepancy can be eliminated. Our measurements indicated that Ψ_s of the stem xylem lumen contents (xylem Ψ_s) averaged -0.15 MPa for *Chrysothamnus* and -0.19 MPa for *Sarcobatus*. These values are slightly more negative than the -0.10 MPa predicted for these species based on stem xylem ion content analyses which included both Na^+ and K^+ as major components (Donovan et al. 1996), and the -0.01 MPa estimated for most plants on the basis of comparisons between psychrometers and pressure chamber measurements (Ritchie and Hinckley 1975; Baughn and Tanner 1976; Passioura 1991; Boyer 1995). However, the measured stem xylem Ψ_s values account for only a small portion of the differences between xylem Ψ_p and soil Ψ_w , and cannot explain the large differences between soil Ψ_w and leaf Ψ_w (Fig. 1).

We propose that solute accumulation in leaf apoplast (intercellular and cell wall spaces) could account for more negative Ψ_w in leaves compared to stems. Solute can accumulate in leaf or root apoplast, creating a substantial apoplast Ψ_s that would contribute to a reduced apoplast Ψ_w (Passioura 1991; Flowers et al. 1991). For non-transpiring leaves, high leaf apoplastic solute concentrations could result from residual buildup from daytime transpiration, or from ion transport from symplast to apoplast. Although we observed predawn disequilibrium in salt treatments where Na^+ might be expected to be a significant leaf apoplastic solute, disequilibria were also observed in the control treatments and in the species studied by Ourcival and Berger (1995), suggesting that other ions, perhaps K^+ , may also be involved. This mechanism might be expected to be more prevalent in Na-accumulating halophytes such as *Sarcobatus*, but the mechanism could also explain smaller stem xylem Ψ_p to leaf Ψ_w , differences in glycophytes or under non-saline conditions, as observed for *Chrysothamnus* and in the control treatments. The proposed solute concentration gradient between leaf apoplast and stem xylem lumen would not be expected to dissipate overnight by diffusion, due to the large diffusional distance ($\gg 2$ cm in our species) (Jungk 1991).

In Table 2, we present, as a testable prediction, our hypothesis that solute accumulation in leaf apoplast spaces (leaf apoplast Ψ_s) could account for the leaf Ψ_w and stem xylem Ψ_p discrepancy. The data in parentheses are from this study for *Sarcobatus* in the 100 mM NaCl treatment: Ψ_p in the stem xylem and leaf apoplastic (measured with the pressure chamber), and leaf Ψ_w and soil Ψ_w (measured with psychrometers). Recall that during these measurements, experimental conditions prevented canopy water loss, hydraulic lift, and poor soil-root hydraulic continuity. The leaf cell Ψ_p values, averaging $+0.4$ MPa, were measured with a cell pressure probe under low transpiration conditions for epidermal and mesophyll cells of *Sarcobatus*, grown under

Table 2 Prediction of significant leaf apoplast Ψ_s , in *italics*, calculated from greenhouse experiment data for non-transpiring (i.e., predawn, bagged plants) *S. vermiculatus* in the 100 mM NaCl

treatment. Experimental measurements are shown in *parentheses*, === indicates equilibration (see text)

| | Leaf symplast | | Leaf apoplast | Stem xylem (root xylem??) | | Root symplast | | Cortex apoplast | | Bulk soil |
|----------|-----------------------|-----|---------------|---------------------------|-----|---------------|-------|-----------------|-----|--------------------|
| Ψ_w | (-2.26) | === | -2.26 | -1.21 | === | -1.21 | ?=?=? | -0.46 | | (-0.43) |
| Ψ_s | -2.66 | | <i>-1.22</i> | (-0.17) | | ??? | | -0.46 | | -0.46 ^b |
| Ψ_p | (+0.40 ^a) | | -1.04 | <i>-1.04</i> | | ??? | | -0.00 | === | -0.00 ^b |

^a Value measured on other plants in similar treatment (see text)

^b Soil Ψ_s is nominal value for 100 mM NaCl treatment and is within error of measurement for Ψ_w , making soil Ψ_p zero, as expected in the saturated pots

100 mM NaCl treatment conditions at UC Davis (N. Alder, K. Shackel, J. Richards, unpublished data). The prediction of substantial leaf apoplast solutes in Table 2 assumes equilibration (indicated by ===) of Ψ_w for leaf cell symplast and adjacent apoplast, and equilibration of Ψ_p for leaf apoplast and somewhat distant stem xylem not separated by a cell membrane. The statistically significant discrepancy between stem xylem Ψ_p and leaf Ψ_w (see also Fig. 1) predicts the presence of substantial solutes in the leaf apoplast (leaf apoplast Ψ_s ; Table 2). The predicted contribution of leaf apoplastic solutes can be further investigated by direct measurements of ion accumulations with X-ray microanalysis (e.g., Canny and Huang 1993; Flowers et al. 1991; Mostaert et al. 1996) or by indirect measurements of other water potential components allowing calculation of leaf apoplast Ψ_s (Murphy and Smith 1994).

Accounting for the entire difference between soil Ψ_w and predawn leaf Ψ_w still requires that a remaining "root portion" be explained (i.e., the soil-stem xylem Ψ_w discrepancy; Table 2), and the question marks in Table 2 indicate that this is still unresolved. In Table 2, root cortex apoplast and bulk soil Ψ_w are shown as identical because both Ψ_p and Ψ_s should be equilibrated under the non-transpiring conditions of these measurements. Root apoplastic solute accumulation (a more negative root cortex apoplast Ψ_s) was one possibility that we considered and rejected as unlikely. For transpiring plants, solute accumulation in the root apoplast (or just outside the root) creating a large apoplast Ψ_s has been proposed to account for apparent interfacial resistances between soil and root (Stirzaker and Passioura 1996). Indeed, this mechanism could then account for the "threshold" pressure differential often required to induce sap flow (Nulsen and Thurtell 1980; Passioura and Munns 1984; Rieger and Motisi 1990; Stirzaker and Passioura 1996). In our non-transpiring plants, however, the predicted ion accumulation in the apoplast outside the endodermis is not likely because the ion concentration gradient between the root apoplast and bulk soil would quickly dissipate due to diffusion down the relatively short path length (approximately equivalent to a root radius). An alternative explanation for our soil-xylem Ψ_w discrepancy may be provided by the composite root transport model that incorporates apoplastic pathways from stele to root exterior, and metabolically driven solute accumulation in the root xylem (Rüding

et al. 1994; Steudle 1994; Steudle and Frensch 1996). This model suggests that in the absence of transpiration, expected net flow from soil to xylem in response to a Ψ_w gradient can be obscured by apoplastic "back-flow," resulting in apparent disequilibrium. However, this apoplastic "back-flow" scenario is not consistent with our data, if we assume that xylem Ψ_p and Ψ_s are the same for stem and root, because the required Ψ_p gradient for moving water from xylem back to soil via an apoplastic pathway was not found in any of our treatments. More data on root water potential components (e.g., root Ψ_w , root xylem Ψ_p , and Ψ_s) are needed before we can account for the soil-root Ψ_w discrepancy.

In summary, the glasshouse experiments conclusively document substantial predawn disequilibrium under conditions of uniform soil Ψ_w and non-limiting soil-root hydraulic conductance. Predawn disequilibria were shown for both *Chrysothamnus*, a marginally salt tolerant non-Na-accumulator, and for *Sarcobatus*, a very salt tolerant Na-accumulator. In addition to demonstrating that nighttime transpiration is a mechanism contributing to predawn disequilibria, these experiments indicate that there must be other mechanism(s) since the disequilibria were present in these species when nighttime transpiration was eliminated. These findings, along with those for the non-salt-tolerant, non-phreatophytic Tunisian desert shrubs (Ourcival et al. 1994; Ourcival and Berger 1995) indicate that predawn disequilibrium may be a feature of many desert shrubs. More research is needed to determine which species or functional species types exhibit predawn disequilibrium, the range of plant-related mechanisms contributing to the disequilibrium, the magnitude of the disequilibrium in natural populations, and the ecological consequences of this phenomenon.

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