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Predawn plant water potential does not necessarily equilibrate with soil water potential under well-watered conditions

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Abstract Predawn leaf water potential (Ψ_w) and xylem pressure potential (Ψ_p) are expected to be in equilibrium with the soil water potential (soil Ψ_w) around roots of well-watered plants. We surveyed 21 plant species (desert, chaparral, and coastal salt marsh species, as well as two temperate tree and two crop species) for departures from this expectation and for two potential mechanisms explaining the departures. We measured soil Ψ_w , leaf Ψ_w , and xylem Ψ_p in the glasshouse under well-watered conditions that eliminated soil moisture heterogeneity and ensured good soil-root hydraulic continuity. Most species failed to equilibrate fully with soil Ψ_w , depending on whether leaf Ψ_w or xylem Ψ_p was used as the measure of predawn plant water potential. The contribution of nighttime transpiration to predawn disequilibrium was assessed by comparing plants with bagged canopies (enclosed overnight in plastic bags to eliminate transpiration) to plants with unbagged canopies. Nighttime transpiration significantly reduced predawn xylem Ψ_p for 16 of 21 species and the magnitude of this contribution to predawn disequilibrium was large (0.50–0.87 MPa) in four woody species: *Atriplex confertifolia*, *Batis maritima*, *Larrea tridentata*, and *Sarcobatus vermiculatus*. The contribution of nighttime transpiration to predawn disequilibrium was not more prevalent in mesic compared with xeric or desert phreatophytic compared with non-phreatophytic species. Even with bagging that eliminated nighttime transpiration, plants did not necessarily equilibrate with soil Ψ_w . Plant xylem Ψ_p or leaf Ψ_w were significantly more negative than soil Ψ_w for 15

of 15 species where soil Ψ_w was measured. Predawn disequilibrium based on leaf Ψ_w was of large magnitude (0.50–2.34 MPa) for seven of those 15 species, predominately halophytes and *Larrea tridentata*. A portion of the discrepancy between leaf and soil Ψ_w is consistent with the putative mechanism of high concentrations of leaf apoplastic solutes as previously modeled for a halophyte, but an additional portion remains unexplained. Predawn leaf Ψ_w and xylem Ψ_p may not reflect soil Ψ_w , particularly for woody plants and halophytes, even under well-watered conditions.

Keywords Apoplastic solutes · Desert shrubs · Chaparral shrubs · Halophytes · Leaf water potential

Introduction

Predawn leaf water potential (Ψ_w) and xylem pressure potential (Ψ_p) are often used as surrogates for soil Ψ_w based on the expectation that predawn plant Ψ is in equilibrium with “wettest” soil Ψ_w accessed by roots (Ritchie and Hinckley 1975; Hinckley et al. 1978a; Richter 1997). Predawn leaf Ψ usually corresponds to daily maximum or base Ψ (Ritchie and Hinckley 1975; but see Sellin 1999). Examination of the literature yields a number of empirical studies that directly address the expectation of predawn plant-soil equilibration (Table 1). These studies measured leaf Ψ_w or xylem Ψ_p and measured or estimated soil Ψ_w in known or expected rooting zones. With regard to these studies, we defined predawn plant-soil water potential disequilibrium (hereafter “predawn disequilibrium”) as predawn plant Ψ more negative than the wettest soil Ψ_w . Approximately half of the available studies reported large magnitude (≥ 0.5 MPa) predawn disequilibrium (Table 1). It is possible that false reports of predawn disequilibrium may be included if the “wettest” soil Ψ_w was reported for soil with no roots or inactive roots. This is unlikely, however, because the methods used in these studies included either extensive measurements of soil Ψ_w at many known rooting depths, irrigation treat-

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Table 1 Literature comparing soil Ψ_w and predawn leaf Ψ_w or xylem Ψ_p . Soil Ψ_w was measured with psychrometers, tensiometers, or estimated with gravimetric soil moisture measurements and soil moisture retention curves. Plant Ψ_w and Ψ_p were measured with psychrometers and pressure chambers, respectively. Discrepancies of ≥ 0.5 MPa are interpreted as literature support for large magnitude predawn disequilibrium. (¹Klepper et al. 1973, ²Ritchie and Hinckley 1975, ³Berger et al. 1996, ⁴Le Roux and Bariac 1998, ⁵Hinckley et al. 1978a, ⁶Bréda et al. 1995, ⁷Gallego et al. 1994,

⁸Cermák et al. 1980, ⁹Garnier and Berger 1987, ¹⁰Lu et al. 1995, ¹¹Sellin 1999, ¹²Schmidhalter 1997, ¹³Schmidhalter et al. 1998, ¹⁴Améglio et al. 1999, ¹⁵Donovan et al. 1999, ¹⁶Jordan and Ritchie 1971, ¹⁷Sala et al. 1981, ¹⁸Elfving et al. 1972, ¹⁹Cohen et al. 1983, ²⁰Ourcival et al. 1994, ²¹Sobrado 1986, ²²Maier-Maercker 1998, ²³Fahey and Young 1984, ²⁴Nnyamah et al. 1978, ²⁵Lassoie et al. 1983, ²⁶Meinzer et al. 1988, ²⁷Franco et al. 1994, ²⁸Nilsen et al. 1983, ²⁹Küppers et al. 1987, ³⁰Donovan et al. 1996, ³¹Hinckley et al. 1978b, ³²Ourcival and Berger 1995)

	Difference between predawn plant Ψ_w or Ψ_p and soil Ψ_w	
	<0.5 MPa	≥ 0.5 MPa
Field/descriptive studies	Cotton ¹ , soybean ² , steppe herbaceous species ³ , savanna shrub and grass species ⁴ , conifers and <i>Cornus</i> sp. ² , <i>Quercus</i> sp. ^{6,7,8} , <i>Prunus persica</i> ⁹ , <i>Betula alba</i> ⁸ , <i>Picea abies</i> and <i>Vaccinium myrtillus</i> ^{10,11}	Cotton ¹⁶ , <i>Bouteloua gracilis</i> ¹⁷ , citrus ^{18,19} , Tunisian desert shrubs ²⁰ , tropical dry forest evergreens ²¹ , steppe woody species ³ , <i>Picea abies</i> ²² , <i>Pinus contorta</i> ²³ , <i>Pseudotsuga menziesii</i> ^{5,24} , <i>Juniperus virginiana</i> ²⁵ , <i>Larrea tridentata</i> ^{26,27} , <i>Prosopis glandulosa</i> ²⁸ , <i>Eucalyptus behriana</i> ²⁹ , cold desert shrubs ³⁰
Glasshouse/experimental studies	Crop seedlings (barley, wheat, maize, sunflower) ^{12,13} , <i>Juglans regia</i> saplings ¹⁴ , <i>Chrysothamnus nauseosus</i> ¹⁵	<i>Quercus</i> sp. and <i>Acer</i> sp. saplings ³¹ , Tunisian desert shrubs ³² , <i>Sarcobatus vermiculatus</i> ¹⁵

ments, or precipitation treatments to keep the soil around roots close to field capacity. In addition, the relatively high threshold used (≥ 0.5 MPa) minimizes possible effects of sample size or methodological errors. Some of the studies in the <0.5 MPa column also report well-documented examples of small magnitude predawn disequilibrium (Donovan et al. 1999; Sellin 1999). Overall, documented examples of predawn disequilibrium, whether of large or small magnitude, include a wide range of species and growing conditions. The mechanisms contributing to these examples of predawn disequilibrium are likely varied and not mutually exclusive (Sellin 1996; Richter 1997; Donovan et al. 1999; Sellin 1999).

Conceptually, it is useful to divide the factors that may contribute to predawn disequilibrium into those relevant only when soil moisture conditions are heterogeneous or dry, from those that may contribute even when soil moisture conditions are uniform and wet. When roots are growing in dry soil, discrepancies between predawn plant and soil Ψ_w are likely due to poor soil hydraulic continuity and poor soil-root hydraulic continuity (Passioura 1988; Nobel and Cui 1992; Nobel 1994; Kramer and Boyer 1995; Richter 1997). While dry soils are obviously ecologically important, most of the studies in Table 1 included at least one treatment or soil region where water availability was close to field capacity and predawn disequilibrium was still observed.

Soil moisture heterogeneity may contribute to predawn disequilibrium if only some of the roots are in wet soil and plant hydraulic conductivity is low or capacity is high (e.g. Ourcival et al. 1994). There may not be enough time overnight for a few roots in wet soil to supply enough water for the whole plant to equilibrate (Sellin 1996; see model Améglio et al. 1999). However, split-pot experiments with walnut saplings suggest that plants can equilibrate with the wettest soil accessed by roots even when only 20% of the rooting volume is very

wet (Améglio et al. 1999). A similar study of water uptake for the leaf succulent *Agave deserti* indicated that only 40% of the root system was necessary for equilibration with the wettest soil (Graham and Nobel 1999). For some species, heterogeneous soil moisture conditions can lead to root-mediated hydraulic lift (or hydraulic redistribution) of water among soil layers (Caldwell et al. 1998). Continued overnight water loss from some roots to soil can theoretically contribute to predawn disequilibrium, although this mechanism has not been empirically isolated (Donovan et al. 1996, 1999). Although outside of the scope of this study, mechanisms contributing to predawn disequilibrium under heterogeneous soil conditions deserve further experimental investigation.

Other mechanisms that can contribute to predawn disequilibrium are revealed when uniform well-watered conditions eliminate the effects of dry soil and soil moisture heterogeneity. These mechanisms include hydraulic conductance/capacitance limitations, nighttime transpiration, putative apoplastic solutes in intercellular spaces, and growth (Hinckley et al. 1978a; Boyer 1995; Ourcival and Berger 1995; Richter 1997; Donovan et al. 1999; Sellin 1999). Hydraulic conductance/capacitance contributions to predawn disequilibrium are most prevalent in large trees with long path lengths and large capacitance, particularly conifers with lower xylem conductivities (Hinckley et al. 1978a; Sellin 1999). Nighttime transpiration contributes to predawn disequilibrium in two desert shrubs, *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus*, even when growth and hydraulic conductance/capacitance limitations are not factors (Donovan et al. 1999). Although substantial nighttime transpiration is an unexpected phenomenon for non-CAM plants, it has also been reported or inferred for other species: *Abies* sp., *Betula pendula*, *Eucalyptus grandis*, *Larrea tridentata*, *Picea abies*, *Pseudotsuga menziesii*, *Rosa* sp., and *Vaccinium myrtillus* (Hinckley and Ritchie 1973;

Blake and Ferrell 1977; Hinckley et al. 1978b; Meinzer et al. 1988; Wieser and Havranek 1993; Matyssek et al. 1995; Assaf and Zieslin 1996; Maier-Maercker 1998; Benyon 1999; Sellin 1999). In contrast, nighttime transpiration is not found for *Typha latifolia* or for West African humid savanna plants (Knapp and Yavitt 1995; Le Roux and Bariac 1998). The growing number of reports makes it worthwhile to investigate the occurrence and magnitude of nighttime transpiration in relation to predawn disequilibrium.

Even when all of the above mechanisms are eliminated or minimized, there appear to be additional factors contributing to predawn disequilibrium. Measurements of stem xylem Ψ_p and Ψ_s and leaf symplast Ψ_w and Ψ_p have been incorporated into a model that predicts substantial concentrations of apoplastic solutes in leaf intercellular spaces (Donovan et al. 1999). In this model, xylem Ψ_s is taken into account and the discrepancy is not an error associated with comparison of pressure chamber and psychrometer methods. The model predicts that leaf intercellular solute concentrations at predawn and with zero water flow must be much greater than those found in the xylem. The model is based on measurements of well-watered plants with canopies bagged to prevent nighttime transpiration and both growth and hydraulic conductance/capacitance limitation effects were eliminated. The putative concentrations of apoplastic solutes in leaf intercellular spaces are indicated by substantial differences between stem xylem Ψ_p and leaf Ψ_w and could result in a Ψ_w gradient that does not drive water flow (Stirzaker and Passioura 1996; Donovan et al. 1999). Discrepancies between soil Ψ_w and leaf Ψ_w may also result in predictions of large root intercellular apoplastic solute concentrations or other unknown mechanisms (Donovan et al. 1999). Regardless of whether or not apoplastic solutes in leaf intercellular spaces are confirmed, the apparent lack of equilibration under well-watered conditions where nighttime transpiration has been eliminated warrants further investigation in this study.

The objectives for this current study were to (1) evaluate the occurrence and magnitude of predawn disequilibrium for a broad range of species under well-watered conditions, and (2) determine if nighttime transpiration and putative apoplastic solutes in leaf intercellular spaces contribute to plant-soil predawn disequilibrium for any of these species. In addition, we looked for associations between predawn disequilibrium mechanisms and habitat that might suggest ecological implications of predawn disequilibrium. Is nighttime transpiration more prevalent for phreatophytic species that generally have unlimited access to water? Is the mechanism of putative leaf intercellular apoplastic solutes more prevalent in species from saline habitats?

Materials and methods

The plant species used in this study represent a range of life histories and habitats (Table 2). Experiments were conducted in glasshouses during May–July 2000 at the University of Georgia,

Athens, Ga. (UGA), and June–July 2000 at the University of California, Davis, Calif. (UCD). The UGA glasshouse received natural light supplemented by metal halide lights (14 h/day) and the UCD glasshouse received natural light. Plants were collected from various sources (Table 2) and grown in the glasshouses for 3 months to several years prior to the experiments. Plants were generally grown in a mixture of 75% calcined clay (Turface, PROFILE Products, Buffalo Grove, Ill.) and 25% washed river sand. The exceptions, ARVI, ARMA, CECU, and CEJE (see Table 2 for codes), were grown in 25% calcined clay mixed with native serpentine soil. At the time of the experiments, plants were 20–60 cm tall and reproductively mature (except for QUMA, PIPA, LATR), but reproductive tissue was avoided during sampling.

For all species, watering was increased to daily for at least a week prior to measurements and plants were watered twice daily during the measurements. The plant and soil water relations measurements occurred over several weeks, weather permitting, but predawn measurements for each species (xylem Ψ_p , leaf Ψ_w , and soil Ψ_w) were completed on the same morning. Midday xylem Ψ_p was measured within 24 h, usually the day before, of predawn xylem Ψ_p .

Xylem Ψ_p was measured on stem tissue (leaf tissue for ZEMA and PIPA) using a pressure chamber (PMS, Corvallis, Ore.). Standard precautionary steps were rigorously followed to minimize errors (Turner 1988; Boyer 1995). Leaf Ψ_w and soil Ψ_w were measured in stainless steel chambers with individually calibrated (Brown and Bartos 1982) screen-cage thermocouple psychrometers (74 series, Merrill Specialty Equipment, Logan, Utah) and a CR7 data logger (Campbell Scientific, Logan, Utah). For leaf Ψ_w , leaves were plucked from the plant and sealed in the chamber within 30 s using 10–15 small linear leaves (e.g. CHNA and SAVE) or fewer large leaves or leaf sections when necessary (e.g. IVFR, ZEMA) (Bennett and Cortes 1985). Mature leaf tissue was used to minimize growth effects on leaf Ψ_w (Boyer 1995). For soil Ψ_w , a soil core was extracted from the plant-rooting zone and sealed inside a psychrometer chamber. After chambers were sealed and placed in an isothermal water bath, psychrometer μV values were checked hourly. Psychrometer outputs stabilized within 4–12 h and were used to calculate leaf Ψ_w and soil Ψ_w (Brown and Bartos 1982).

Nighttime transpiration assessments were made on nights that followed sunny days. UGA plants were randomly assigned to bagged and un-bagged treatments ($n=4-6$ per treatment). UCD plants were paired according to size and for ARVI, ARMA, CECU, and CEJE fertilizer history (fertilized or unfertilized) and then one of each pair was randomly assigned to bagged and un-bagged treatments. For the bagged treatment, plant canopies were enclosed in a plastic bag secured around the top of the pot or around the base of the plant stem, approximately 1 h before dark. Condensation on the inside of the bag indicated that relative humidity reached 100% overnight. The bags were opened just prior to excision of tissue for xylem Ψ_p at predawn. Xylem Ψ_p for bagged and un-bagged plants were compared with one-way ANOVA for UGA measurements and with paired t -tests for UCD measurements (SAS 1989).

For assessment of predawn disequilibrium in the absence of nighttime transpiration, plant canopies were bagged overnight and measurements of xylem Ψ_p , leaf Ψ_w , and soil Ψ_w were made at predawn. The values were compared with one-way ANOVA and subsequent Tukey multiple range tests. The data were transformed as necessary to meet ANOVA assumptions.

Results

We found evidence for predawn disequilibrium, although of variable magnitude, in most of the species surveyed. The magnitude and statistical significance of predawn disequilibrium depended upon whether xylem Ψ_p or leaf Ψ_w was used as the measure of predawn plant Ψ and

Table 2 List of the 21 species used in this study with species code, source information, location where experimental measurements were made, description of habitat, life form, photosynthetic pathway, and midday plant Ψ_p values determined within 24 h (usually the day before) of the predawn measurements reported in the figures

Genus, species, attribution	Code	Collection location	Source material	Expt. site	Description	Midday Ψ_p (MPa)
<i>Arachis hypogaea</i> L.; Fabaceae	ARHY	Greenhouse	Seeds	UGA	Perennial crop, C3	-0.17±0.08
<i>Arctostaphylos manzanita</i> C. Parry; Ericaceae	ARMA	N Coast Range, Calif.	Seedlings	UCD	Chaparral shrub, C3	-0.85±0.16
<i>Arctostaphylos viscida</i> C. Parry; Ericaceae	ARVI	N Coast Range, Calif.	Seedlings	UCD	Chaparral serpentine shrub, C3	-0.93±0.19
<i>Artemisia tridentata</i> Nutt. ssp. <i>vaseyana</i> (Rydb.) Beetle; Asteraceae	ARTR	Mono Lake, Calif.	Seedlings	UGA	Cold desert shrub, C3	-0.95±0.09
<i>Atriplex confertifolia</i> (Torrey and Frémont) S. Watson; Chenopodiaceae	ATCO	Mono Lake,	Seedlings	UGA	Cold desert halophytic shrub, C4	-2.37±0.29
<i>Atriplex parryi</i> S. Watson; Chenopodiaceae	ATPA	Owens Lake, Calif.	Seedlings	UCD	Mojave desert halophytic shrub, C4	-1.81±0.11
<i>Batis maritima</i> L.; Bataceae	BAMA	Sapelo Island, Ga.	Cuttings	UGA	Salt marsh halophytic perennial, C3	-2.09±0.17
<i>Borrchia frutescens</i> L.; Asteraceae	BOFR	Sapelo Island, Ga.	Cuttings	UGA	Salt marsh halophytic perennial, C3	-1.42±0.13
<i>Ceanothus cuneatus</i> (Hook.) Nutt.; Rhamnaceae	CECU	N Coast Range, Calif.	Seedlings	UCD	Chaparral shrub, C3	-0.88±0.15
<i>Ceanothus jepsonii</i> E. Greene; Rhamnaceae	CEJE	N Coast Range, Calif.	Seedlings	UCD	Chaparral serpentine shrub, C3	-0.92±0.14
<i>Chrysothamnus nauseosus</i> (Pallas) Britt. ssp. <i>consimilis</i> (E. Greene) H.M. Hall and Clements; Asteraceae	CHNA	Mono Lake, Calif.	Seeds	UGA	Cold desert shrub, some salt tolerance, C3	-1.20±0.14
<i>Helianthus annuus</i> L.; Asteraceae	HEAN	Central Utah	Seeds	UGA	Herbaceous annual, C3	-0.82±0.07
<i>Iva frutescens</i> L.; Asteraceae	IVFR	Sapelo Island, Ga.	Cuttings	UGA	Salt marsh marginal halophytic shrub C3	-1.42±0.18
<i>Larrea tridentata</i> (DC.) Cov.; Zygophyllaceae	LATR	Lemitar, N.M.	Seedlings	UGA	Warm desert shrub, C3	-2.30±0.53
<i>Pinus palustris</i> Miller; Pinaceae	PIPA	Columbus, Ga.	Seeds	UGA	Temperate tree, C3	-1.08±0.15
<i>Purshia tridentata</i> (Pursh) DC.; Rosaceae	PUTR	Mono Lake, Calif.	Seedlings	UGA	Cold desert and mountain shrub, C3	-1.20±0.13
<i>Quercus marilandica</i> Muenchh.; Fagaceae	QUMA	Columbus, Ga.	Seeds	UGA	Temperate tree, C3	-1.90±0.59
<i>Sarcobatus vermiculatus</i> (Hook.) Torrey; Chenopodiaceae	SAVE	Mono Lake, Calif.	Seeds	UGA	Cold desert halophytic shrub, C3	-1.94±0.19
<i>Salicornia virginica</i> L.; Chenopodiaceae	SAVI	Sapelo Island, Ga.	Seedlings	UGA	Salt marsh halophytic perennial, C3	-2.18±0.25
<i>Suaeda moquinii</i> (Torrey) E. Greene; Chenopodiaceae	SUMO	Owens Lake, Calif.	Seedlings	UCD	Desert halophytic shrub	-2.40±0.26
<i>Zea mays</i> L.; Poaceae	ZEMA	commercial	Seeds	UGA	Annual crop, C4	-0.63±0.15

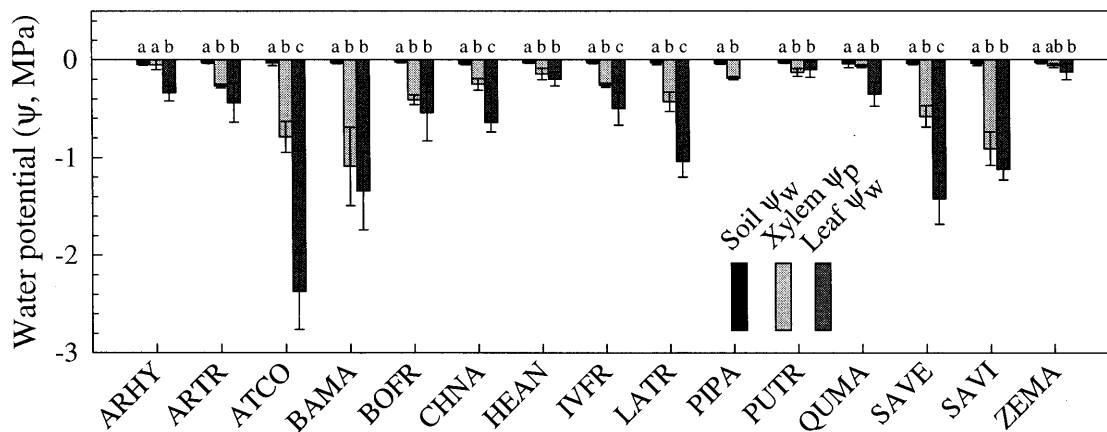
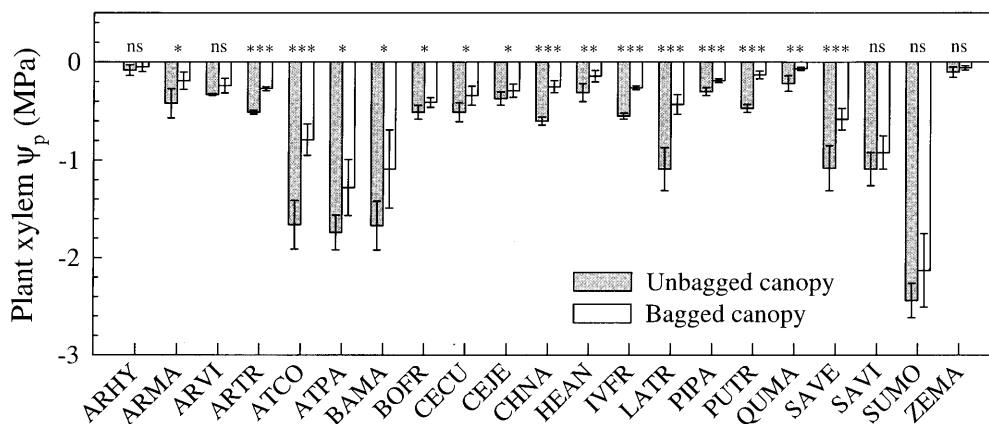


Fig. 1 Predawn soil Ψ_w , xylem Ψ_p and leaf Ψ_w (mean \pm SD) for 15 plant species with canopies bagged overnight to eliminate transpiration. See Table 2 for species codes. For each species $n=4-6$ for

xylem Ψ_p and leaf Ψ_w , and $n = 2-4$ for soil Ψ_w . Significant ($P \leq 0.05$) differences between the three measurements within each species are indicated with different letters

Fig. 2 Predawn xylem Ψ_p (mean \pm SD) for plant canopies bagged overnight and those remaining unbagged for 21 species. See Table 2 for species codes. For each species $n=6$ per treatment, except for IVFR where $n=4$ per treatment. For each species, a significant difference between bagged and unbagged plants is indicated as: * $P \leq 0.05$, ** $P \leq 0.01$, and *** $P \leq 0.001$



whether plants were bagged or unbagged. At least one of the two measures of predawn plant Ψ was significantly more negative than measured soil Ψ_w for 15 of 15 species where all three measurements were taken for plants with bagged canopies (Fig. 1). Both xylem Ψ_p and leaf Ψ_w were significantly more negative than soil Ψ_w for 11 of 15 species. Large magnitude (≥ 0.5 MPa) predawn disequilibrium based on the difference between soil Ψ_w and leaf Ψ_w in bagged plants was found for seven of those 15 species: four desert shrubs (ATCO, CHNA, LATR and SAVE) and three salt marsh perennials (BAMA, BOFR, and SAVI). Predawn disequilibrium for unbagged plants was also suggested for most of the 21 species surveyed (Fig. 2), since measured soil water potential in the well-watered pots was less negative than -0.05 MPa (see Fig. 1). Predawn xylem Ψ_p of unbagged plants was more than 0.5 MPa lower than this estimate of soil Ψ_w (i.e. xylem $\Psi_p \leq -0.55$ MPa) for 9 of 21 species (Fig. 2).

The mechanism of nighttime transpiration contributed to predawn disequilibrium in 16 of 21 species as indicated by significantly less negative predawn xylem Ψ_p in plants that had nighttime transpiration eliminated by canopy bagging compared to unbagged plants (Fig. 2). The

magnitude of this contribution was large (≥ 0.5 MPa) for three desert shrubs (ATCO, LATR, and SAVE) and one salt marsh perennial (BAMA).

Comparing organs within the canopy provides an indication of the mechanism of putative leaf apoplastic solutes. Xylem Ψ_p was significantly less negative than leaf Ψ_w for 7 of 15 species (Fig. 1). The magnitude of this difference was large (≥ 0.5 MPa) for three desert shrubs (ATCO, LATR, and SAVE).

Midday xylem Ψ_p ranged from -0.17 to -2.40 MPa. These values were from 0.12 to 1.87 MPa more negative than predawn xylem Ψ_p for bagged canopies of the respective species (Table 2).

Discussion

For many plant species in this study, predawn plant water potentials were not a reliable estimate of soil water potential around the roots. The plants growing in well-watered homogeneous soils (measured soil Ψ_w of -0.020 to -0.045 MPa) had predawn xylem Ψ_p or leaf Ψ_w values ranging from -0.05 to -2.44 MPa. These data are largely consistent with the few previous reports in the lit-

erature. Predawn disequilibria were either non-existent or of small magnitude for crop species (peanut and corn) and saplings of temperate trees (Klepper et al. 1973; Ritchie and Hinckley 1975; Hinckley et al. 1978a; Bréda et al. 1995; Schmidhalter et al. 1998; Améglio et al. 1999; Sellin 1999), and of large magnitude in some desert shrubs and halophytes (Ourcival and Berger 1995; Donovan et al. 1999).

The maximum extent of predawn disequilibrium differed depending on which potential mechanism was experimentally evaluated. Nighttime transpiration accounted for predawn disequilibrium of up to 0.87 MPa (difference between xylem Ψ_p of bagged and unbagged canopies in Fig. 2) and was of large magnitude (≥ 0.5 MPa) for only 4 of the 21 species surveyed. Nevertheless, nighttime transpiration made a smaller significant contribution to predawn disequilibrium in 12 other species. The mechanism of putative apoplastic solutes in leaf intercellular spaces contributed to soil-leaf predawn disequilibrium of up to 2.34 MPa (difference between soil Ψ_w and leaf Ψ_w in Fig. 1) and was of large magnitude (≥ 0.5 MPa) for 7 of the 15 species surveyed. These predawn disequilibrium mechanisms commonly co-occurred. The relationship between mechanisms and species characteristics may further our understanding of the ecological or evolutionary conditions favoring these mechanisms.

Nighttime transpiration

Because water availability often limits plant productivity, transpirational water loss at night when no carbon gain is possible seems wasteful for C3 and C4 plants. However, in habitats where plants generally have access to water, there may be less of a cost to nighttime transpiration, no cost (e.g. selectively neutral) or maybe even a gain in terms of nutrient uptake or some other aspect of plant growth and survival. We expected the contribution of nighttime transpiration to predawn disequilibrium to be greater for plants that generally have access to more water: e.g. for mesic as compared with xeric species, and for desert phreatophytes compared with non-phreatophytes. Under the well-watered greenhouse conditions in this study, the species patterns did not support this expectation. Species that usually grow under relatively wetter conditions included examples of no nighttime transpiration (ARHY, ZEMA) and small magnitude nighttime transpiration contribution to predawn disequilibrium (HEAN, PIPA, QUMA) (Schwarzbach et al. 2001; R. Addington, unpublished data). For species that routinely grow under water stressed conditions in the field there were examples of no significant contribution (SAVI, SUMO) and large magnitude contribution of nighttime transpiration to predawn disequilibrium (ATCO, BAMA, LATR, SAVE) (Antlfinger and Dunn 1983; Caldwell 1985; Meinzer et al. 1988; Donovan et al. 1996; Dahlgren et al. 1997).

Among the desert plants, the obligate and facultative phreatophytes (SAVE, ARTR, CHNA, SUMO) did not

have a greater contribution of nighttime transpiration to predawn disequilibrium than non-phreatophytes (LATR, ATCO) (Smith et al. 1997). As some might question whether ARTR or SUMO are phreatophytic, a broader comparison of obligate desert riparian phreatophytes, such as *Populus*, *Salix*, and *Prosopis*, and upland desert species would be needed to thoroughly examine this suggestion.

Halophytic species do not appear to be predisposed to nighttime transpiration when grown under the non-saline conditions of our experiments. The contribution of nighttime transpiration to predawn disequilibrium was large for three halophytes (ATCO, BAMA, SAVE), but non-significant for two other halophytes (SAVI, SUMO). However, for halophytes, increasing substrate salinity is likely to affect the magnitude of nighttime transpiration. In SAVE the nighttime transpiration contribution to predawn disequilibrium that was evident with 0 and 100 mM NaCl saturated substrates disappeared in 300 and 600 mM NaCl treatments that reduced plant Ψ_p and increased plant Na (Donovan et al. 1999). Halophytes provide an interesting system for investigating nighttime transpiration because of their tendency to take up large amounts of Na. Altered ion concentrations and K/Na ratios may affect xylem hydraulic conductance and the turgor-mediated regulation of stomatal movement (Donovan et al. 1997; Véry et al. 1998; Zwieniecki et al. 2001).

The soil-leaf hydraulic conductance and the rate of nighttime transpiration can interact to affect the magnitude of predawn disequilibrium, particularly for tall trees (Hinckley et al. 1978a; Ourcival et al. 1994; Richter 1997; Maier-Maercker 1998). In *P. abies* and *V. myrtillus*, where maximal Ψ_p can occur up to 2 h after dawn, nighttime transpiration and low hydraulic conductivity lead to both predawn Ψ_p and base Ψ_p more negative than soil Ψ_w (Sellin 1996, 1999). For two desert shrubs with short but relatively similar hydraulic path lengths, the rate of nighttime transpiration per leaf area is actually higher in CHNA than SAVE, but the magnitude of predawn disequilibrium and the contribution of nighttime transpiration are both greater for SAVE (Donovan et al. 1999; M. Linton and M. Caird, unpublished results), probably due to lower hydraulic conductance in the soil-leaf pathway. Low rates of nighttime transpiration may induce predawn disequilibrium in species with low hydraulic conductance, potentially explaining predawn disequilibrium in the shallow rooted warm desert shrub, *Larrea tridentata* (Meinzer et al. 1988; Franco et al. 1994; Pockman and Sperry 2000).

Investigation of the ecological relevance of nighttime transpiration will be furthered by studies of the proximate mechanisms regulating stomatal control at night, such as leaf abscisic acid levels and vapor pressure deficit (Blake and Ferrell 1977; Sellin 1999), and measurements of nighttime transpiration for a broader array of conditions and species. For example, an experimental soil drought appears to reduce nighttime transpiration in CHNA, similar to *P. menziesii* (Blake and Ferrell 1977),

but not in SAVE (M. Caird, unpublished data), suggesting species specific differences in nighttime stomatal regulation. Studies are also underway to quantify the amount of nighttime water loss in the field, and the impact of eliminating nighttime transpiration on subsequent gas exchange and nutrient relations.

Putative apoplastic solutes

Some plants growing in well-watered uniform soils and with canopies bagged to eliminate nighttime transpiration apparently have an additional mechanism contributing to predawn disequilibrium. Under these conditions, leaf Ψ_w was significantly more negative than soil Ψ_w for 15 species in this study (Fig. 1). It is useful to consider this phenomenon at two scales: (1) differences between xylem Ψ_p measured with the pressure chamber and leaf Ψ_w measured with psychrometers, and (2) differences between soil Ψ_w and leaf Ψ_w , both measured with psychrometers.

When xylem Ψ_p is much less negative than leaf Ψ_w (see Fig. 1), this suggests that apoplastic solutes are concentrated in leaf intercellular spaces, as has been modeled for SAVE by Donovan et al. (1999). Small differences between xylem Ψ_p and leaf Ψ_w may be due to xylem Ψ_s and experimental errors inherent in comparing different techniques. However, four of the species (ATCO, CHNA, LATR, SAVE) had a large difference (>0.5 MPa) between xylem Ψ_p and leaf Ψ_w , predicting large concentrations of apoplastic solutes in the leaf intercellular spaces (see Donovan et al. 1999 for model). The concentrated apoplastic solutes might come from the adjacent symplast or from transpirational flow during the previous day. In either case, the path length from leaf intercellular space to the lumen of stem xylem would prevent diffusional dissipation of the concentration gradient and the concentration gradient would not drive water flow. Studies are underway to test the model with direct measurements of leaf apoplastic solutes in SAVE.

At the whole plant scale, in absence of nighttime transpiration (i.e. bagged plants), there was a large magnitude of predawn disequilibrium (leaf Ψ_w 0.50–2.34 MPa more negative than soil Ψ_w , both measured with psychrometers) for seven of 15 species. Six of these seven species were halophytes, suggesting a relationship between the underlying mechanism(s) and the ion physiology prevalent in halophytes. The leaf-stem portion of the “whole plant” predawn disequilibrium is consistent with the mechanism of concentrated leaf apoplastic solutes as described above. There remains, however, the unexplained stem-soil portion of the predawn disequilibrium. This may be attributed to the concentration of apoplastic solutes in root intercellular spaces or an unknown mechanism (Stirzaker and Passioura 1996; Donovan et al. 1999). An alternative mechanism might be that a very low soil-leaf hydraulic conductance prevented complete recovery to equilibrium overnight, as would be evidenced by plant Ψ_w still recovering in the

early morning hours instead of reaching a plateau. However, continued plant Ψ_w recovery was not found for SAVE and CHNA in a previous experiment (Donovan et al. 1999) and seems unlikely for any of these species under the conditions in our experiments: well-watered soils, small plants and bagged canopies. If high apoplastic solute concentrations are confirmed, then the question remains whether the solutes and resulting predawn disequilibrium provide some water or nutrient benefit for the desert and halophytic plants, or are just a by-product of some aspect of drought tolerant or halophytic metabolism. Proper ecological interpretation of predawn disequilibrium will require further resolution of magnitude and mechanisms under field conditions for a broader array of species.

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