

## Night-time transpiration can decrease hydraulic redistribution

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### ABSTRACT

**C<sub>3</sub> plants dominate many landscapes and are critically important for ecosystem water cycling. At night, plant water losses can include transpiration ( $E_{\text{night}}$ ) from the canopy and hydraulic redistribution (HR) from roots. We tested whether  $E_{\text{night}}$  limits the magnitude of HR in a greenhouse study using *Artemisia tridentata*, *Helianthus anomalous* and *Quercus laevis*. Plants were grown with their roots split between two compartments. HR was initiated by briefly withholding all water, followed by watering only one rooting compartment. Under study conditions, all species showed substantial  $E_{\text{night}}$  and HR (highest minus lowest soil water potential [ $\Psi_s$ ] during a specified diel period). Suppressing  $E_{\text{night}}$  by canopy bagging increased HR during the nightly bagging period ( $HR_N$ ) for *A. tridentata* and *H. anomalous* by 73 and 33% respectively, but did not affect  $HR_N$  by *Q. laevis*. Total daily HR ( $HR_T$ ) was positively correlated with the  $\Psi_s$  gradient between the rooting compartments, which was correlated with light and/or atmospheric vapour pressure deficit (VPD<sub>a</sub>) the prior day. For *A. tridentata*,  $HR_T$  was negatively correlated with night-time VPD<sub>a</sub>. Ecological implications of the impact of  $E_{\text{night}}$  on HR may include decreased plant productivity during dry seasons, altered ecosystem water flux patterns and reduced nutrient cycling in drying soils.**

**Key-words:** *Artemisia*; *Helianthus*; hydraulic lift; nighttime; nocturnal; *Quercus*.

### INTRODUCTION

Plants move water through two major pathways at night: (1) movement from the roots to the canopy and subsequent loss to air [night-time transpiration ( $E_{\text{night}}$ )]; and (2) movement from one part of the root system to another and subsequent loss to the soil [hydraulic redistribution (HR)]. Separately, the processes of  $E_{\text{night}}$  and HR have been documented for a wide range of plant species across many ecosystems (Caldwell, Dawson & Richards 1998; Caird, Richards & Donovan

2007a; Dawson *et al.* 2007). Several authors have suggested that these two processes could be competitive, with naturally occurring  $E_{\text{night}}$  limiting HR (Hultine *et al.* 2003; Caird *et al.* 2007a; Dawson *et al.* 2007; Scholz *et al.* 2008). Consistent with this, previous studies have shown that when ' $E_{\text{night}}$ ' is experimentally increased by night-time lighting, HR is diminished (Caldwell & Richards 1989; Caldwell 1990; Bauerle *et al.* 2008). However, there are no studies quantifying the effect of naturally occurring  $E_{\text{night}}$  on HR, and night-time lighting likely has unintended impacts, such as interrupting diurnal fluctuations of water potentials, or changing growth processes because of hydraulic, photoperiod or temperature effects. We provide the first controlled test of the impact of  $E_{\text{night}}$  on the magnitude of HR.

HR is the passive movement of water from areas of higher to lower (more negative) soil water potential ( $\Psi_s$ ), using roots as a conduit. Water flow in the root xylem can occur in an upward, downward or lateral direction (Richards & Caldwell 1987; Brooks *et al.* 2002; Scott, Cable & Hultine 2008). Traditionally, it was thought that HR occurred only when transpiration was minimal, such as at night or when the canopy was bagged. However, there is now evidence that HR can occur at the same time as substantial transpiration both during the day and night as long as the necessary environmental conditions are present to drive each process (Scholz *et al.* 2002; Donovan, Richards & Linton 2003).

Substantial  $E_{\text{night}}$  occurs when stomata remain partially open at night and a vapour pressure difference between the leaf and air (VPD<sub>l</sub>) drives water loss. Recent studies demonstrate that  $E_{\text{night}}$  can be a large fraction of daytime transpiration (5–30%; Benyon 1999; Fisher *et al.* 2007; Snyder, Richards & Donovan 2003; Bucci *et al.* 2004, 2005; Daley & Phillips 2006; Caird, Richards & Hsiao 2007b; Cavender-Bares, Sack & Savage 2007; Dawson *et al.* 2007; Howard & Donovan, 2007; Scholz *et al.* 2007). Such substantial  $E_{\text{night}}$  can decrease predawn leaf water potential (Donovan, Linton & Richards 2001; Donovan *et al.* 2003; Bucci *et al.* 2005; Kavanagh, Pangle & Schotzko 2007). As HR is a passive process driven by water potential gradients, reduced canopy water potential – because of  $E_{\text{night}}$  – may increase the portion of water moving towards the canopy and decrease flow towards areas of dry soil.

Several consequences of HR and  $E_{\text{night}}$  to plants have been proposed. Evidence suggests that HR reduces surface

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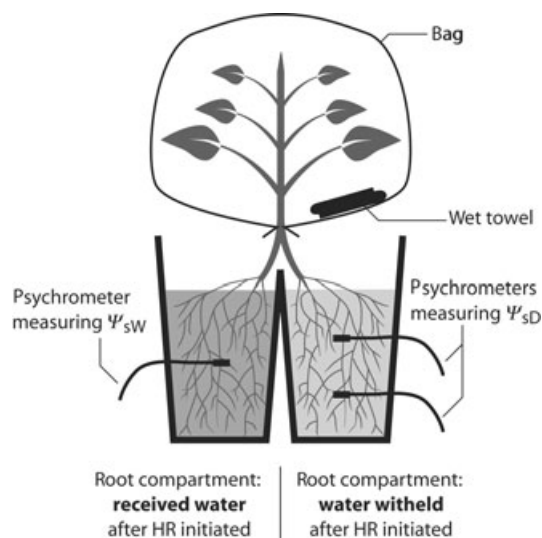
soil evaporative loss (when redistribution is downward), increases next-day transpiration and photosynthesis, prolongs fine root lifespan, increases microbial and mycorrhizal activity in the rhizosphere, and overall improves carbon, water and nutrient acquisition (Caldwell *et al.* 1998; Querejeta, Egerton-Warburton & Allen 2003; Domec *et al.* 2004; Lee *et al.* 2005; Bauerle *et al.* 2008; Scott *et al.* 2008). The consequences of  $E_{\text{night}}$  for plants remain less clear. Canopy water loss at night without concomitant carbon gain could decrease productivity in water-limited environments, where HR often occurs, but a fitness cost of  $E_{\text{night}}$  has not yet been documented. A proposed benefit of  $E_{\text{night}}$  is delivery of soil-mobile nutrients to roots for uptake (McDonald, Erickson & Kruger 2002; Snyder *et al.* 2008; but see also Christman, Donovan & Richards 2009). It seems likely that interactions between  $E_{\text{night}}$  and HR could impact plant productivity, plant water use and nutrient cycling.

Our study species, *Artemisia tridentata*, *Quercus laevis* and *Helianthus anomalous*, were chosen because substantial  $E_{\text{night}}$  and/or HR have been documented for each (Caldwell *et al.* 1998; Espeleta, West & Donovan 2004; Caird *et al.* 2007a), and they represent a diversity of growth forms. The species are native to habitats in which the necessary environmental conditions for  $E_{\text{night}}$  (substantial night-time VPD) and HR (substantial  $\Psi_s$  gradient) often exist concurrently. In the Western United States, *A. tridentata* is the dominant shrub within much of the Great Basin whereas *H. anomalous* is a large annual endemic to desert sand dunes in Utah and Arizona. *Q. laevis* is a tree native to the sandhills of the Southeastern United States. Our objective was to use controlled manipulations to test the effect of  $E_{\text{night}}$  on the magnitude of HR of soil water by plant roots. Additionally, we assessed the impact of environmental variables on the magnitude of HR. These included the magnitude of the  $\Psi_s$  gradient, photosynthetically active radiation (PAR) and atmospheric vapour pressure deficit (VPD<sub>a</sub>) during the day preceding HR and VPD<sub>a</sub> during the night of HR.

## MATERIALS AND METHODS

*Artemisia tridentata* ssp. *tridentata* seedlings were collected near Eureka in Juab County, UT, USA and grown for 1.5 years at the University of Georgia greenhouse facilities, Athens GA, USA prior to this study. *Q. laevis* acorns were obtained from Sheffield Seeds (Sheffield Seed Co. Inc., Locke, NY, USA) and grown for 2 years prior to study. *H. anomalous* seeds were collected from Little Sahara Dunes Recreational Area in Juab County, UT, germinated in Petri dishes, and seedlings transferred to pots 4 months prior to experimentation.

All plants were grown in a soil mix consisting of 3/4 Turface (fritted clay, Profile Products LLC., Buffalo Grove, IL, USA) and 1/4 sand. After initial root development, plants were removed from original pots and soil was carefully washed away from roots. Two tree pots ('Tall-one' Treepot, Stuewe and Sons Inc., Corvallis, OR, USA)



**Figure 1.** Experimental set-up of plants with two separate rooting compartments. Plant is shown 'bagged' with a wet paper towel included in the bag to assure minimal night-time transpiration ( $E_{\text{night}}$ ). The single psychrometer in the left-hand compartment confirmed that the water potential of the soil stayed near 0 MPa in this compartment throughout the period of  $E_{\text{night}}$  manipulation (measures of  $\Psi_{\text{sw}}$ ). The two psychrometers in the right-hand compartment measured  $\Psi_{\text{sd}}$  and were used to calculate hydraulic redistribution (HR).

measuring 35 × 10 × 10 cm were placed side-by-side and a notch approximately 6 cm deep was cut in the top of the adjoining sides. Roots were split approximately 50:50 between the two pots with the central stem resting above the notch (Fig. 1). Soil was filled up to the base of the stem and 15 g of a slow release fertilizer (Osmocote Plus, The Scotts Co., Marysville, OH, USA) containing micronutrients was applied to each rooting compartment. Prior to experimentation, both rooting compartments were watered daily and fertilized weekly with 20:8.8:16.6 NPK water-soluble fertilizer (20-10-20 Peter's Peat-Lite Special, The Scotts Co.). Upon initiation of HR, the height of soil in each rooting compartment was checked and surface soil was removed as needed to ensure that the soil volumes in the two compartments were not in contact with each other.

Experiments were conducted in a heated and lighted greenhouse during April 2006 (*A. tridentata*), June 2006 (*Q. laevis*) and May–June 2007 (*H. anomalous*). PAR, air temperature and air humidity in the greenhouse were logged hourly with an LI-190 PAR sensor (Li-Cor Inc., Lincoln NE, USA) and a Vaisala humidity and temperature sensor (Vantaa, Finland), both interfaced with a CR23X data logger (Campbell Scientific, Logan, UT, USA). Light conditions and VPD<sub>a</sub> in the greenhouse (calculated from temperature and humidity measures) during the period of study for each species are given in Table 1. During the study periods, night-time temperature in the greenhouse was maintained above 20 °C and daytime temperature was maintained below 33 °C.

**Table 1.** Light conditions and atmospheric vapour pressure deficit (VPDa) in the greenhouse for date and time periods used for measurement of total hydraulic redistribution (HR<sub>T</sub>) and hydraulic redistribution during E<sub>night</sub> treatments (HR<sub>N</sub>)

Species	Mean VPDa (kPa)			Sunrise	Lights on	Sunset	Lights off	HR <sub>N</sub> time constraints	HR <sub>N</sub> dates	HR <sub>T</sub> time constraints	HR <sub>T</sub> dates
	Day	Night	Day								
<i>A. tridentata</i>	2.14 ± 0.05	0.99 ± 0.02	0.700–0.710 h	~0700 h	1959–2005 h	~1930 h	2000–0600 h	8–16 April	1000–0900 h next day	8 April–4 May	
<i>H. anomalous</i>	2.19 ± 0.04	0.76 ± 0.03	0623–0628 h	~0540 h	2032–2039 h	~1930 h	2000–0500 h	21 May–1 June	1000–0900 h next day	20 May–10 June	
<i>Q. laevis</i>	1.54 ± 0.03	0.91 ± 0.03	0622–0624 h	~0700 h	2046–2048 h	~2000 h	2030–0530 h	14–25 June	1000–0900 h next day	7–25 June	

VPDa is a mean of hourly logs from 2000 to 0600 h (night) and from 0700 to 1900 h (day) ± 1 SE during the HR<sub>N</sub> date range.

Approximate times are indicated by '~'. Sunrise and sunset times are for Athens, GA during the HR<sub>N</sub> date range according to the US Naval Observatory, Astronomical Applications Department, Washington DC, USA.

## Instrumentation

$\Psi_s$  was assessed with individually calibrated (Brown & Bartos 1982) screen-cage psychrometers (Merrill Specialty Equipment, Logan, UT, USA). Every plant was instrumented with three psychrometers (Fig. 1). The single psychrometer in the centre of the rooting compartment that was watered prior to and during experimentation (wet compartment; readings of  $\Psi_{sw}$ ) confirmed that soil in this rooting compartment stayed near 0 MPa during HR measurements. The other two psychrometers were placed one-third and two-thirds up from the base of the rooting compartment from which water was withheld during experimentation (unwatered, drier compartment; readings of  $\Psi_{sd}$ ) and were used to assess HR. Psychrometers were inserted into the soil through holes drilled in the side of each pot. After insertion, holes were sealed around the insulated psychrometer wire using silicone glue. Plants were given a minimum of 1 week for roots to re-colonize the disturbed soil before initiation of HR. To minimize the effect of temperature fluctuations on measurements, plant pots and psychrometers were placed in a 0.6 × 1.2 × 2.4 meter styrofoam box and surrounded with foam packing chips. Psychrometers were interfaced with CR7 data loggers (Campbell Scientific) and  $\Psi_s$  was logged every half hour for *A. tridentata* and *Q. laevis*, and every hour for *H. anomalous*. To further minimize the effect of temperature fluctuation on measurements, psychrometer wires running between pots and the data loggers were bundled into pipe insulation and coated with reflective silver tape and the data loggers were kept under a canopy that allowed air circulation but blocked direct sunlight. These precautions allowed water potential measurements with minimal zero offset values (within 10  $\mu$ V of zero). Water potentials were corrected for both temperature and zero offset following Brown & Bartos (1982).

## HR and E<sub>night</sub> treatments

To initiate HR, water was withheld from plants until  $\Psi_{sw}$  and  $\Psi_{sd}$  (i.e. both root compartments) declined to approximately -1.0 MPa (2–4 d). When this was achieved, HR was initiated by applying water to the rooting compartment with a single psychrometer until field capacity was reached ( $\Psi_{sw}$  raised to approximately 0 MPa). From this time on, no water was applied to the rooting compartment with the two psychrometers. Watering of the compartment with the single psychrometer continued one to three times daily to maintain the soil near field capacity and provide a  $\Psi_s$  gradient between the two rooting compartments to drive HR. Mean  $\Psi_{sw}$  ( $\pm 1$  SE), logged every half-hour or hour during the 9 to 12 days/nights of E<sub>night</sub> manipulation (HR<sub>N</sub> dates, Table 1), were -0.028 ( $\pm 0.0003$ ), -0.025 ( $\pm 0.001$ ) and -0.023 ( $\pm 0.002$ ) MPa for *A. tridentata*, *H. anomalous* and *Q. laevis*, respectively.

E<sub>night</sub> treatments occurred in 9–12 consecutive nights (HR<sub>N</sub> dates; Table 1). For each species, plants were randomly divided into two groups. On each night one group

had  $E_{\text{night}}$  suppressed and the other group was a control. Groups alternated daily between control and suppression treatments.  $E_{\text{night}}$  suppression consisted of enclosing a plant canopy and a wet paper towel in a plastic bag and securing the bag around the plant stem. Bagging minimizes  $E_{\text{night}}$  by trapping water vapour transpired from leaves and evaporated from the wet towel. The trapped water vapour causes air humidity in the bag to rise, thereby minimizing the gradient needed to drive transpiration. Bags were secured up to 1 h before lights-off in the evening and were removed during the half-hour before lights came on in the morning. The  $E_{\text{night}}$  treatment period was 9–10.5 h long.

The criteria for identifying diel fluctuations of  $\Psi_{\text{SD}}$  as HR were that they did not mirror temperature fluctuations and included a pattern of increasing  $\Psi_{\text{SD}}$  in the evening and night but decreasing  $\Psi_{\text{SD}}$  in the morning (Espeleta *et al.* 2004). HR was calculated in two different ways: total daily HR ( $HR_{\text{T}}$ ) and HR during  $E_{\text{night}}$  treatments ( $HR_{\text{N}}$ ).  $HR_{\text{T}}$  was calculated as the highest diel  $\Psi_{\text{SD}}$  – the lowest diel  $\Psi_{\text{SD}}$  occurring with offsets  $\pm 10 \mu\text{V}$  during the 24 h period from 1000 to 0900 h the following day (Table 1). The broad time interval allowed us to find the 24 h highest and lowest  $\Psi_{\text{SD}}$  and the offset allowance was narrow enough to exclude clearly incorrect data, although not so narrow as to omit a large amount of daytime data.  $HR_{\text{T}}$  was calculated for all nights of the experiment ( $HR_{\text{T}}$  dates; Table 1) and included only control (unbagged) plants during the subset of nights used for  $E_{\text{night}}$  manipulation. Daily  $HR_{\text{T}}$  was compared to daily PAR and VPDa (mean of hourly logs from 0700 to 1900 h) and nightly VPDa (mean of hourly logs from 2000 to 0600 h).

$HR_{\text{N}}$  was calculated as the highest  $\Psi_{\text{SD}}$  minus the lowest  $\Psi_{\text{SD}}$  occurring with offsets of  $\pm 5 \mu\text{V}$  (Brown & Bartos 1982).  $HR_{\text{N}}$  only included measures of  $\Psi_{\text{SD}}$  during the  $E_{\text{night}}$  treatment period (i.e. after all bags used to minimize  $E_{\text{night}}$  were secured and before any bags were removed) ( $HR_{\text{N}}$  time constraints; Table 1). Ambient greenhouse temperature at night was relatively constant allowing a more stringent zero offset cut-off for  $HR_{\text{N}}$  than for  $HR_{\text{T}}$ .

## Gas exchange procedures

Leaf-level measurements of daytime and night-time gas exchange were made with a portable photosynthesis system (LI-6400, Li-Cor Inc.) as described in Howard & Donovan (2007). Night-time measures were taken between 0000 and 0300 h North America Eastern Standard Time (EST) and daytime measures were taken between 1200 and 1500 h EST. Measurements were made on a mature leaf of each *H. anomalus* and *Q. laevis* and on a branch of each *A. tridentata*.

For *A. tridentata*, night-time gas exchange measures were taken on control plants nightly from 9 to 17 April 2006 (the nine nights of  $E_{\text{night}}$  treatments). Daytime measures were taken on 13 April 2006. For *H. anomalus* daytime and night-time measures were taken on all plants on 8 June 2007 (six nights after completion of  $E_{\text{night}}$  treatments). For *Q. laevis* night-time measures were taken on all plants on 1 July 2006

(four nights after completion of  $E_{\text{night}}$  treatments). Daytime measures for *Q. laevis* were also taken after completion of  $E_{\text{night}}$  treatments but they have been omitted because of an irrigation failure the morning of measurements.

Leaves of *H. anomalus* did not fill the standard LI-6400 chamber (2 by 3 cm) and were marked and scanned (Winfolia, Regent Instruments Inc., Quebec, Canada) to obtain leaf area within the chamber. Leaves on the branches of *A. tridentata* were detached, spread out and scanned to obtain total area within the chamber. This provided a very conservative estimate of gas exchange measures for this species since the natural bunching of leaves on branches increases boundary resistance and results in shading of many leaves during daytime measurements. The chamber red/blue LED (6400-02B, Li-Cor Inc.) light source was turned off at night and was set to  $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$  during the day, except when measures were taken on *H. anomalus* when light was set to  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Airflow was  $100\text{--}200 \mu\text{mol s}^{-1}$  at night and  $500\text{--}700 \mu\text{mol s}^{-1}$  during the day. The block temperature surrounding the infrared gas analysers in the chamber head was set to match ambient and  $\text{CO}_2$  was supplied at  $400 \mu\text{mol mol}^{-1}$ . Chamber relative humidity was manually manipulated to a target 5–10% above ambient. Instrument error was assessed after every three to four leaf measurements with the chamber empty or clamped onto dry paper. Instrument error at night for transpiration was  $0.04 \pm 0.01$ ,  $0.03 \pm 0.01$  and  $0.10 \pm 0.03 \text{ mmol m}^{-2} \text{s}^{-1}$  during collection of *A. tridentata*, *H. anomalus* and *Q. laevis* data, respectively, and was always substantially lower than plant measures.

## Biomass

Above- and below-ground biomass were collected for all *H. anomalus* and *Q. laevis* within 2 weeks and 3 months, respectively, of completion of the extended study. *A. tridentata* were reserved for use in a future study. Biomass was dried at  $60^\circ\text{C}$ , weighed and used to calculate root mass ratio (root mass/total plant mass).

## Statistics

To test the effect of  $E_{\text{night}}$  treatments on  $HR_{\text{N}}$ , for each species we used a repeated-measures, cross-over design (Neter, Wasserman & Kutner 1990) in which plants alternated (crossed-over) between control  $E_{\text{night}}$  and suppressed  $E_{\text{night}}$  treatments from day to day. The *A. tridentata* study contained 12 plants, the *H. anomalus* study seven plants and the *Q. laevis* study eight plants. By applying the  $E_{\text{night}}$  suppression treatment to half of the set of plants, we assessed the impact of  $E_{\text{night}}$  on  $HR_{\text{N}}$  within a night, which eliminated potentially confounding environmental variables that differ across nights. And by alternating which plants are bagged across many nights we accounted for inherent differences in the magnitude of  $HR_{\text{N}}$  by individual plants and any carry-over effects.

Magnitude of  $HR_{\text{N}}$  and highest and lowest  $\Psi_{\text{SD}}$  during the period of  $E_{\text{night}}$  treatments were analysed in a repeated-

measures mixed model analysis of variance with compound symmetric covariance structure (PROC MIXED; 2004, version 9.1, SAS Institute, Cary NC, USA).  $E_{\text{night}}$  treatment (suppressed or control) and psychrometer position (bottom or top psychrometer measuring  $\Psi_{\text{SD}}$ ; Fig. 1) were fixed effects, and the plant was the subject in which repeated measures occurred. An interaction between psychrometer position and  $E_{\text{night}}$  treatment was also tested but was never significant and was subsequently dropped from the analysis. The effect of environmental variables including daytime VPDa and PAR and night-time VPDa on mean daily  $HR_T$  was analysed for each species using a linear regression (PROC REG; SAS Institute, 2004, version 9.1).

## RESULTS

Substantial HR occurred in all species, irrespective of  $E_{\text{night}}$  manipulation. For all species,  $\Psi_{\text{SD}}$  declined through the morning and into the afternoon, then began to increase mid- to late afternoon and continued increasing through the night (Fig. 2).  $HR_T$  averaged across all control nights was similar for all species ( $0.43 \pm 0.02$  MPa in *A. tridentata*,  $0.45 \pm 0.02$  MPa in *H. anomalus*,  $0.42 \pm 0.06$  MPa in *Q. laevis*). For all species, the magnitude of  $HR_T$  was much larger than  $HR_N$  since rapid increase in  $\Psi_{\text{SD}}$  often occurred during late afternoon (Fig. 2).

All species exhibited significant  $E_{\text{night}}$  and night-time stomatal conductance ( $g_{\text{night}}$ ) when plant canopies were not bagged to suppress  $E_{\text{night}}$  (Table 2).  $E_{\text{night}}$  and  $g_{\text{night}}$  were highest for *H. anomalus* and lowest for *A. tridentata*. Experimental suppression of  $E_{\text{night}}$  by canopy bagging resulted in a significant increase in  $HR_N$  in *A. tridentata* (73% increase) and *H. anomalus* (33% increase), but not in *Q. laevis* (Table 3, Fig. 3).  $E_{\text{night}}$  suppression affected the highest, but not the lowest  $\Psi_{\text{SD}}$  recorded overnight for each species and used to calculate  $HR_N$ . In other words, suppressing  $E_{\text{night}}$  did not affect the  $\Psi_s$  gradient at the start of the dark period but resulted in a larger overnight increase in  $\Psi_{\text{SD}}$ . For *A. tridentata*, measures of daytime transpiration were made directly following a night of  $E_{\text{night}}$  treatments.  $E_{\text{night}}$  treatments had no effect on instantaneous measures of daytime transpiration of *A. tridentata* ( $t_{10} = 0.03$ ,  $P > 0.9$ ).

For *Q. laevis*,  $HR_N$  was not affected by  $E_{\text{night}}$  treatments (Fig. 3). Although there was a significant effect of  $E_{\text{night}}$  suppression on highest  $\Psi_{\text{SD}}$  during the  $HR_N$  time period, this was paralleled by a non-significant effect on the nightly low for  $\Psi_{\text{SD}}$  (Table 3). Thus, the result was that  $HR_N$  (highest  $\Psi_{\text{SD}}$  – lowest  $\Psi_{\text{SD}}$  between 2030 and 0530 h) by *Q. laevis* was not different between nights when plants transpired naturally and nights when  $E_{\text{night}}$  was suppressed (Table 3). Considering each species,  $\Psi_{\text{SD}}$  only differed between the psychrometer positions in the unwatered rooting compartment for *Q. laevis*. For *Q. laevis*, mean  $\Psi_{\text{SD}}$  ( $\pm 1$  SE) was lower in the upper portion of the rooting compartment ( $-0.55 \pm 0.09$  MPa) than in the lower portion ( $-0.42 \pm 0.09$  MPa) (Table 3). The root mass ratio for *Q. laevis* was 0.563, for *H. anomalus* was 0.181, and biomass was not collected for *A. tridentata*.

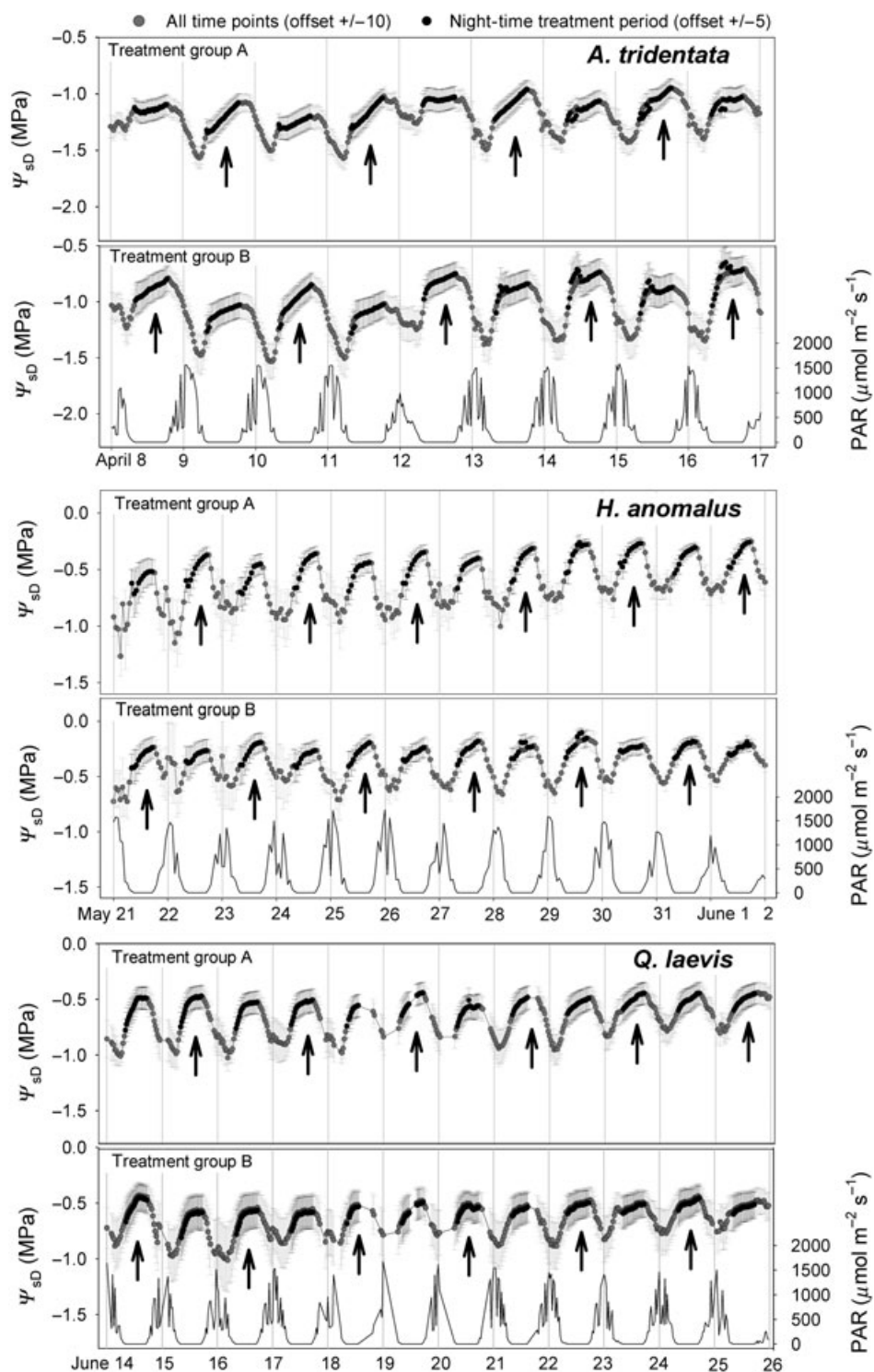
$HR_T$  in control (unbagged) plants was correlated with several environmental parameters.  $HR_T$  for all species was positively correlated with the  $\Psi_s$  gradient ( $\Psi_{\text{sw}} - \Psi_{\text{SD}}$ ) between the watered and unwatered rooting compartments at the start of  $HR_T$  (Fig. 4).  $\Psi_{\text{sw}} - \Psi_{\text{SD}}$  was in turn significantly correlated with same day mean PAR and/or mean daytime VPDa (Table 4).  $\Psi_{\text{sw}} - \Psi_{\text{SD}}$  was generally larger for *A. tridentata* compared with the other two species. However, a lower slope for the correlation between  $HR_T$  and  $\Psi_{\text{sw}} - \Psi_{\text{SD}}$  for *A. tridentata* compared with the other species resulted in a similar magnitude of  $HR_T$  observed across all species (Fig. 4).

For *H. anomalus* and *Q. laevis*, mean night-time VPDa was positively correlated with  $\Psi_{\text{sw}} - \Psi_{\text{SD}}$  ( $P < 0.01$ ). Therefore an independent effect of VPDa at night on  $HR_T$  could not be tested. However, in *A. tridentata*, removal of two data points from cloudy days/nights, where the  $\Psi_{\text{sw}} - \Psi_{\text{SD}}$  was lower than 0.8 MPa allowed for VPDa at night to vary independently ( $P = 0.22$ ) of the  $\Psi_{\text{sw}} - \Psi_{\text{SD}}$  gradient. On the remaining 25 nights of  $HR_T$  measurement,  $HR_T$  in *A. tridentata* was negatively correlated to mean night-time VPDa (Fig. 5).

## DISCUSSION

Substantial naturally occurring  $E_{\text{night}}$  can reduce overnight water potential recovery by plant canopies (Donovan *et al.* 2001, 2003; Bucci *et al.* 2005; Kavanagh *et al.* 2007), but its affect on the magnitude of HR was not well understood. Given the passive nature of HR, in which water movement is driven along water potential gradients, we hypothesized and confirmed that  $E_{\text{night}}$  reduced the magnitude of HR. For *A. tridentata* and *H. anomalus*, the impact of  $E_{\text{night}}$  on the magnitude of HR was large and suppression of  $E_{\text{night}}$  resulted in a 73 and 33% increase in  $HR_N$ , respectively. Scholz *et al.* (2002) noted that reverse sap flow in a lateral root (HR) during the daytime increased linearly as the soil-to-leaf water potential difference decreased. More recently, Scholz *et al.* (2008) bagged a tree canopy for 24 h and recorded increased HR during this time period. They noted in these studies, that the plant shoot and soil seemed to act as competing sinks for hydraulically redistributed water. We provide new correlative data and the first controlled, manipulative test showing that naturally occurring  $E_{\text{night}}$  can decrease the magnitude of HR.

An effect of reducing  $E_{\text{night}}$  on  $HR_N$  was not seen in *Q. laevis*. This was not caused by the differences in the ability of the species to conduct HR because, in the absence of  $E_{\text{night}}$  manipulation, the magnitude of  $HR_T$  was similar among all species. It was also not caused by the lack of transpiration at night as *Q. laevis* neither exhibited the lowest  $E_{\text{night}}$  nor did the study occur during a period of particularly low night-time VPD (Tables 1 & 2). Among the three species, a significant effect of psychrometer position on  $\Psi_{\text{SD}}$  was only found in *Q. laevis*. Lower  $\Psi_{\text{SD}}$  was recorded in the soil close to the top of the unwatered rooting compartment, possibly because of the evaporation of water from the soil surface or high root density resulting in large



**Figure 2.** Mean soil water potential ( $\pm 1$  SE) for all species in the unwatered rooting compartment ( $\Psi_{sd}$ ) during the dates of  $\text{HR}_N$  measurement. For each species, data for the two  $E_{\text{night}}$  treatment groups (A and B) are presented in separate panels. Arrows indicate nights where transpiration for the indicated treatment group was minimized by canopy bagging. Vertical lines indicate midday. Note that the  $\Psi_{sd}$  axis shifts range among species but scale is constant. Missing data for *Q. laevis* was caused by a logger malfunction. Photosynthetically active radiation (PAR) is presented below the  $\Psi_{sd}$  data in the lower panel for each species.

**Table 2.** Instantaneous gas exchange measures during the day and night for control (unbagged) plants allowed to transpire without manipulation

Species	Night-time		Daytime		
	Conductance (mol m <sup>-2</sup> s <sup>-1</sup> )	Transpiration (mmol m <sup>-2</sup> s <sup>-1</sup> )	Conductance (mol m <sup>-2</sup> s <sup>-1</sup> )	Transpiration (mmol m <sup>-2</sup> s <sup>-1</sup> )	Photosynthesis (μmol m <sup>-2</sup> s <sup>-1</sup> )
<i>A. tridentata</i>	0.014 ± 0.001	0.18 ± 0.01	0.088 ± 0.010	3.12 ± 0.30	5.87 ± 0.39
<i>H. anomalus</i>	0.131 ± 0.023	1.01 ± 0.14	1.60 ± 0.00	18.14 ± 0.69	34.8 ± 2.7
<i>Q. laevis</i>	0.051 ± 0.008	0.39 ± 0.05			

Values are means ± 1 SE. Readings were taken on a single day or night and averaged ( $n = 7-12$ ), except for night-time measures on *A. tridentata*. For *A. tridentata* at night, the mean is an average of measures taken on control (unbagged) plants on each night of the  $E_{\text{night}}$  manipulation study ( $n = 54$ ).

daily decline in  $\Psi_{\text{SD}}$  in this region. These explanations do not involve competing water sinks at night, and therefore the significant effect of psychrometer position does not explain the lack of effect of  $E_{\text{night}}$  suppression on  $\text{HR}_{\text{N}}$  for *Q. laevis*.

The lack of an effect of reducing  $E_{\text{night}}$  on  $\text{HR}_{\text{N}}$  could have been caused by a relatively low canopy biomass (and leaf area) compared with root biomass in the young *Q. laevis* used in this study. The root mass ratio of *Q. laevis* was three times greater than that of *H. anomalus*, which minimized the impact of whole canopy  $E_{\text{night}}$  on  $\text{HR}_{\text{N}}$ . Stem and taproot water storage and the amount of water required at night for phloem sap flux might also have acted as competing water sinks, additionally minimizing the impact of  $E_{\text{night}}$  on HR (Windt *et al.* 2006; Scholz *et al.* 2008). Although biomass measures were not collected on *A. tridentata*, branches were densely covered in leaves (personal observation) and these plants likely had a relatively low root mass ratio compared to the young *Q. laevis* used here. We think it unlikely that the lack of treatment effect for *Q. laevis* is because it is a tree as compared to the shrubby *A. tridentata* and the annual *H. anomalus*. Further controlled tests are needed to quantify the competitive effect of plant water storage and phloem flux on HR and  $E_{\text{night}}$  and rule out any effects of life form.

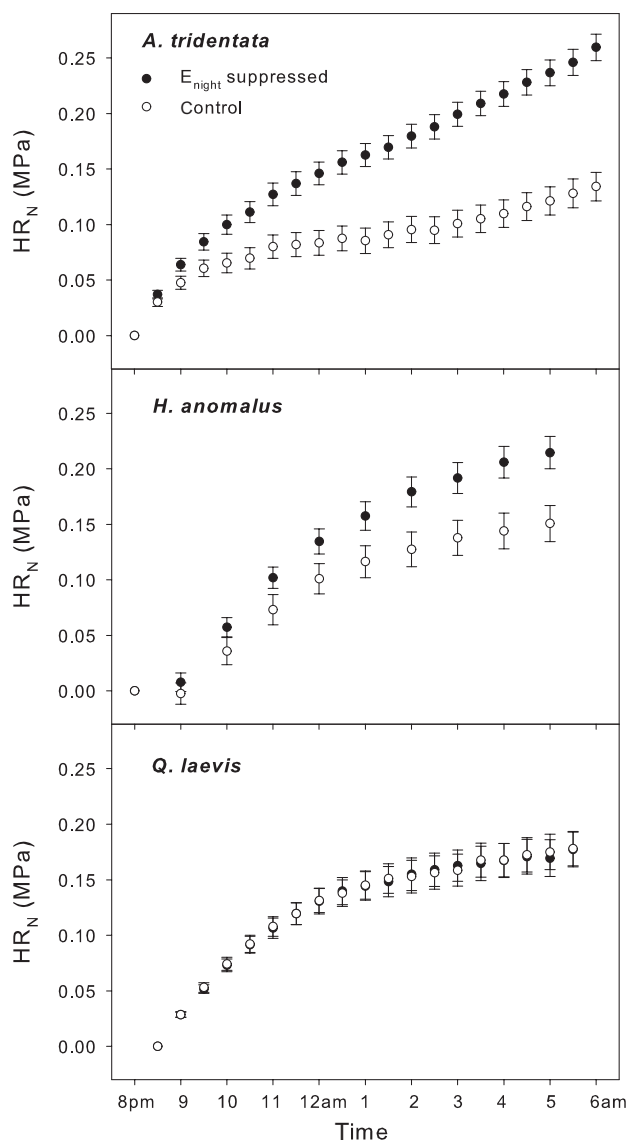
We expect our measured effects of  $E_{\text{night}}$  on  $\text{HR}_{\text{N}}$  in a greenhouse experiment to be comparable to, or even underestimate, what might happen in natural plant populations. Plants in this study exhibited  $g_{\text{night}}$  rates comparable to previously published estimates for these species (*A. tridentata*, *H. anomalus*) or closely related species (*Q. rubra*) (Caird *et al.* 2007a and references therein). The range of  $\Psi_{\text{s}}$  and magnitude of  $\text{HR}_{\text{T}}$  in this study were within the range reported in field studies for *A. tridentata* (Richards & Caldwell 1987; Caldwell & Richards 1989; Caldwell *et al.* 1998) and represent the drier and larger end of what has been seen for *Q. laevis* (Espeleta *et al.* 2004). To our knowledge this is the first study of HR in *H. anomalus*. Environmental conditions in natural plant populations might promote even greater effects because higher night-time VPDa and increased wind speed possible in the field have both been correlated with increased  $E_{\text{night}}$  in natural populations (Benyon 1999; Oren *et al.* 2001; Daley & Phillips 2006; Dawson *et al.* 2007; Kavanagh *et al.* 2007), which could result in a larger reduction in HR.

The magnitude of  $\text{HR}_{\text{T}}$  was positively correlated with the  $\Psi_{\text{s}}$  gradient between the watered and unwatered rooting compartments ( $\Psi_{\text{sw}} - \Psi_{\text{sd}}$ ), explaining from 42 to 82% of the variation in  $\text{HR}_{\text{T}}$  (Fig. 4). Differences in the slope of

**Table 3.** Effect of minimizing night-time transpiration ( $E_{\text{night}}$ ) on soil water potential ( $\Psi_{\text{SD}}$ ) and magnitude of hydraulic redistribution ( $\text{HR}_{\text{N}}$ ) between a rooting compartment maintained near field capacity and an unwatered compartment in which  $\Psi_{\text{SD}}$  readings were taken

Species	Treatment	Lowest $\Psi_{\text{SD}}$ (MPa)	Highest $\Psi_{\text{SD}}$ (MPa)	$\text{HR}_{\text{N}}$ (MPa)
<i>A. tridentata</i>	Suppressed $E_{\text{night}}$	-1.12 ± 0.09	-0.86 ± 0.08	0.26 ± 0.02
	Control $E_{\text{night}}$	-1.13 ± 0.09	-0.97 ± 0.08	0.15 ± 0.02
	$E_{\text{night}}$ treatment	$F_{1,11} = 0.07$	<b><math>F_{1,11} = 14.43^{**}</math></b>	<b><math>F_{1,11} = 80.23^{***}</math></b>
	Psychrometer position	$F_{1,7} = 2.00$	$F_{1,7} = 0.87$	$F_{1,7} = 1.73$
<i>H. anomalus</i>	Suppressed $E_{\text{night}}$	-0.43 ± 0.09	-0.23 ± 0.06	0.21 ± 0.04
	Control $E_{\text{night}}$	-0.44 ± 0.09	-0.28 ± 0.06	0.16 ± 0.04
	$E_{\text{night}}$ treatment	$F_{1,6} = 0.05$	<b><math>F_{1,6} = 10.00^{*}</math></b>	<b><math>F_{1,6} = 18.98^{**}</math></b>
	Psychrometer position	$F_{1,5} = 1.49$	$F_{1,5} = 0.92$	$F_{1,5} = 2.53$
<i>Q. laevis</i>	Suppressed $E_{\text{night}}$	-0.64 ± 0.12	-0.47 ± 0.09	0.17 ± 0.03
	Control $E_{\text{night}}$	-0.67 ± 0.12	-0.50 ± 0.09	0.17 ± 0.03
	$E_{\text{night}}$ treatment	$F_{1,7} = 3.58$	<b><math>F_{1,7} = 13.13^{**}</math></b>	$F_{1,7} = 0.01$
	Psychrometer position	$F_{1,3} = 2.98$	<b><math>F_{1,3} = 104.26^{**}</math></b>	<b><math>F_{1,3} = 29.62^{*}</math></b>

Data are for the 9–12 days during the period of  $E_{\text{night}}$  treatments for each species ( $\text{HR}_{\text{N}}$  dates). Measures of  $\Psi_{\text{SD}}$  are based on psychrometer offsets of ± 5 μV and shown as lsmeans ± 1 SE.  $F$  values and degrees of freedom are presented for each model effect (PROC MIXED repeated measures, subject = plant). Bold indicates statistical significance (\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ).

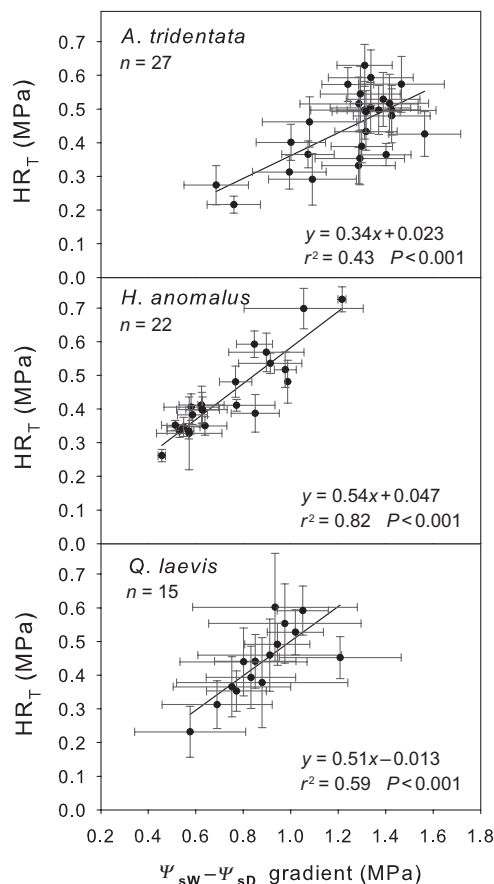


**Figure 3.** Mean hydraulic redistribution ( $HR_N$ ) for each species during the period of  $E_{night}$  treatments. Plants were either allowed to transpire naturally (control) or bagged to suppress transpiration ( $E_{night}$  suppressed).  $HR_N$  was calculated as  $\Psi_{SD}$  at each time-point minus the first  $\Psi_{SD}$  recorded during the period of  $E_{night}$  treatment for that plant each night. This removes variation caused by daily initial  $\Psi_{SD}$ , psychrometer position and plant. Values are means averaged across 42–95 plants \* psychrometers \* days  $\pm$  1 SE.

the correlation among species (Fig. 4) could be caused by the differences in xylem conductivity, production and maintenance of fine roots in drying soil, differences in abundance and regulation of aquaporins, and effects of root architecture (combined with xylem anatomy) on branch conductance (Caldwell *et al.* 1998; Hultine *et al.* 2003; Domec *et al.* 2004; Espeleta *et al.* 2004; Vandeleur *et al.* 2005; Valenzuela-Estrada *et al.* 2009).  $\Psi_{sw} - \Psi_{SD}$  on a particular day was correlated, often quite strongly, with mean PAR and/or mean VPDa during that day (Table 4). As one

rooting compartment ( $\Psi_{sw}$ ) was kept near field capacity,  $\Psi_{sw} - \Psi_{SD}$  was driven by changes in  $\Psi_{SD}$ . Under conditions of high PAR (and concomitant high VPDa) open stomata contribute to both high photosynthesis and high transpiration. Our findings agree with data from a natural population showing that shading by clouds, which minimizes daytime  $\Psi_{sw} - \Psi_{SD}$  gradients, limits HR the following night (Williams, Caldwell & Richards 1993).

A relationship between  $E_{night}$  and HR additionally can be examined using VPDa as a surrogate for  $E_{night}$ , because stomatal regulation does not fully compensate for changes in VPDa (Barbour & Buckley 2007; Christman *et al.* 2009; Howard, unpublished results) For *A. tridentata*, we found that as night-time VPDa increased, the magnitude of  $HR_T$  decreased, above a  $\Psi_{sw} - \Psi_{SD}$  threshold of 0.8 MPa (Fig. 5). We were able to test for this relationship only above this threshold and only for *A. tridentata*, because these data fulfilled the necessary condition that VPDa at night and  $\Psi_{sw} - \Psi_{SD}$  not be significantly correlated. Our result is consistent with that of Hultine *et al.* (2003) who found that HR, measured as reverse sap flux in a lateral root of *Fraxinus*



**Figure 4.** Relationship for each species, between total hydraulic redistribution ( $HR_T$ ) and the soil water potential gradient from watered to unwatered rooting compartments. The gradient was measured at the time when  $HR_T$  began ( $\Psi_{sw} - \Psi_{SD}$  at time of lowest  $\Psi_{SD}$  daily). Data points are means of  $HR_T$  and ( $\Psi_{sw} - \Psi_{SD}$ ) ( $\pm$  1 SE) averaged across all psychrometers ( $n=3-17$ ) in the unwatered rooting compartment each day.

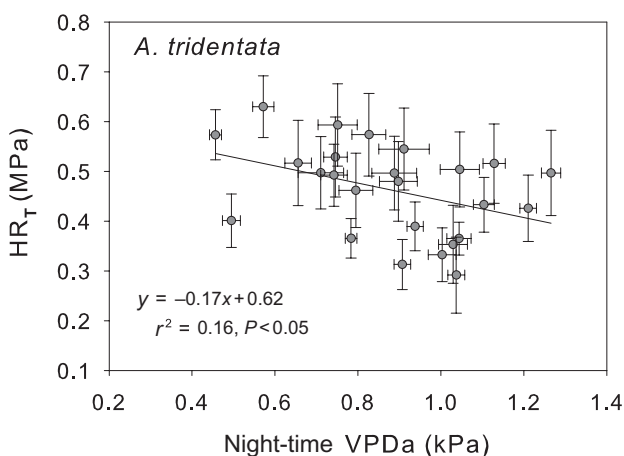
**Table 4.** Pearson correlation of photosynthetically active radiation (PAR) and daytime atmospheric vapour pressure deficit (VPDa) with soil water potential gradient ( $\Psi_{sw} - \Psi_{sd}$ ) for each species during the dates of HR<sub>T</sub> measurement

Species and variable	$\Psi_{sw} - \Psi_{sd}$		
	<i>n</i>	<i>r</i>	<i>P</i>
<i>A. tridentata</i>			
Daytime VPDa	27	<b>0.595</b>	<b>0.001</b>
PAR	27	<b>0.651</b>	<b>&lt;0.001</b>
<i>H. anomalous</i>			
Daytime VPDa	22	<b>0.743</b>	<b>&lt;0.001</b>
PAR	22	0.328	>0.1
<i>Q. laevis</i>			
Daytime VPDa	15	0.459	0.085
PAR	15	<b>0.632</b>	<b>0.012</b>

Data analysed were daily means of  $\Psi_{sw} - \Psi_{sd}$  based on psychrometer offsets of  $\pm 10 \mu\text{V}$  for control plants at time of lowest  $\Psi_{sd}$  (start of HR<sub>T</sub>) and daily means of VPDa and PAR logged hourly between 0700 and 1900 h. Bold indicates statistical significance.

*velutina*, declined strongly with increasing VPDa at night. Our result demonstrates this relationship for more than one individual and confirms that the correlation is not simply the result of HR and VPDa both being correlated with the daily  $\Psi_s$  gradient. Our correlative evidence and that of Hultine *et al.* (2003) suggests that to fully understand the degree  $E_{\text{night}}$  limits HR, further study of the relationship between  $E_{\text{night}}$  and VPD is needed.

The impact of  $E_{\text{night}}$  on HR<sub>N</sub> was large for two of our three study species and this may have substantial impacts on both



**Figure 5.** Relationship between total hydraulic redistribution (HR<sub>T</sub>) and atmospheric vapour pressure deficit (VPDa) at night for *Artemisia tridentata*. Data points (*n* = 25) are daily means of HR<sub>T</sub> ( $\pm 1$  SE) across all psychrometers in the unwatered rooting compartment (*n* = 8–17 psychrometers) and for VPDa measured hourly between 2000 and 0600 h (*n* = 11 VPD logs daily). Two cloudy days (night of 19 April and 4 May 2006) with the lowest  $\Psi_{sw} - \Psi_{sd}$  gradients (less than 0.8 MPa) and small HR<sub>T</sub> have been omitted (see two points in lower left quarter of the *A. tridentata* panel in Fig. 4).

plant water-use and ecosystem hydrology where HR is common. Many studies have demonstrated that HR benefits plants by increasing next-day transpiration, prolonging the growing season and improving growth (Caldwell & Richards 1989; Emerman & Dawson 1996; Caldwell *et al.* 1998; Lee *et al.* 2005; Scott *et al.* 2008). Although we did not find an impact of  $E_{\text{night}}$  manipulation, and thereby magnitude of HR, on following day transpiration in *A. tridentata*, this is likely because of fairly high root density in a relatively small pot volume. Much of the gain in daytime transpiration of plants in natural populations is expected to be caused by water moving from deep soils with relatively low root density, to shallower soils where root density is high, and water can be more rapidly extracted to meet daytime transpirational demand (Caldwell & Richards 1989). Thus, in natural populations,  $E_{\text{night}}$  not only represents water lost without concomitant carbon gain in C<sub>3</sub> plants, but may also reduce total carbon gain by reducing following day transpiration and shortening the growing season. Models that incorporate HR generally do not consider  $E_{\text{night}}$  and may overestimate the impact of HR on ecosystem hydrology (Jackson, Sperry & Dawson 2000) and seasonal air temperatures cycles (Lee *et al.* 2005).

Another suggested benefit of HR is to improve nutrient acquisition by wetting the rhizosphere and increasing activity of mycorrhizae and microbes (Caldwell *et al.* 1998; Querejeta *et al.* 2003). Thus, substantial  $E_{\text{night}}$  may decrease nutrient uptake in drying soils by decreasing HR. However,  $E_{\text{night}}$  has itself been proposed as a mechanism to enhance uptake of mobile soil nutrients (McDonald *et al.* 2002; Howard & Donovan 2007; Scholz *et al.* 2007; Snyder *et al.* 2008). The relative nutrient benefit or cost of each process may depend on soil moisture level and nutrient form.  $E_{\text{night}}$  may enhance uptake of nitrate when it is readily available in the soil and soil moisture is abundant, but likely reduces the beneficial effects of HR on decomposition, microbe activity and nutrient mobilization and uptake in drying soils.

Here we provide results from a controlled manipulative experiment, and supporting correlative data, to demonstrate that naturally occurring  $E_{\text{night}}$  can substantially reduce the magnitude of HR. This relationship may have important consequences for plant productivity, ecosystem hydrology and nutrient cycling. However, the size of the impact of  $E_{\text{night}}$  on HR differed among the species investigated here, and further exploration of the relationship among multiple, potentially competitive water sinks and flows at night is still needed.

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