

What the towers don't see at night: nocturnal sap flow in trees and shrubs at two AmeriFlux sites in California

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Summary At the leaf scale, it is a long-held assumption that stomata close at night in the absence of light, causing transpiration to decrease to zero. Energy balance models and evapotranspiration equations often rely on net radiation as an upper bound, and some models reduce evapotranspiration to zero at night when there is no solar radiation. Emerging research is showing, however, that transpiration can occur throughout the night in a variety of vegetation types and biomes. At the ecosystem scale, eddy covariance measurements have provided extensive data on latent heat flux for a multitude of ecosystem types globally. Nighttime eddy covariance measurements, however, are generally unreliable because of low turbulence. If significant nighttime water loss occurs, eddy flux towers may be missing key information on latent heat flux. We installed and measured rates of sap flow by the heat ratio method (Burgess et al. 2001) at two AmeriFlux (part of FLUXNET) sites in California. The heat ratio method allows measurement and quantification of low rates of sap flow, including negative rates (i.e., hydraulic lift). We measured sap flow in five *Pinus ponderosa* Dougl. ex Laws. trees and three *Arctostaphylos manzanita* Parry and two *Ceanothus cordulatus* A. Kellogg shrubs in the Sierra Nevada Mountains, and in five *Quercus douglasii* Hook & Arn. trees at an oak savanna in the Central Valley of California. Nocturnal sap flow was observed in all species, and significant nighttime water loss was observed in both species of trees. Vapor pressure deficit and air temperature were both well correlated with nighttime transpiration; the influence of wind speed on nighttime transpiration was insignificant at both sites. We distinguished between storage-tissue refilling and water loss based on data from Year 2005, and calculated the percentage by which nighttime transpiration was underestimated by eddy covariance measurements at both sites.

Keywords: *Arctostaphylos manzanita*, Blue oak, *Ceanothus cordulatus*, eddy covariance, evapotranspiration, FLUXNET, heat ratio, night, *Pinus ponderosa*, *Quercus douglasii*, transpiration.

Introduction

Energy balance models rely on closure of the equation $R_n = LE + H + G + S$, where net radiation (R_n) is partitioned into evapotranspiration (LE), sensible heat (H), and ground (G) and canopy (S) storage. These models generally reduce LE to zero when R_n goes to zero (and becomes negative at night), though nighttime LE can be induced by large downward H on wet surfaces in an inverted nighttime temperature profile (Monteith 1957, Baldocchi 1994). Without large H and wet surfaces, however, nighttime LE is minimal. Most LE equations rely heavily on R_n , which generally accounts for the bulk of variability in LE (Penman 1948, Monteith 1965, Priestley and Taylor 1972, Shuttleworth and Wallace 1985, Fisher et al. 2005). The widely used Priestley-Taylor (1972) model, for instance, is calculated as $LE = 1.26R_n(\Delta/(\Delta + \gamma))$, where Δ is the rate of change of vapor pressure with temperature, and γ is the psychrometric constant. As R_n goes to zero, the assumption is that there should be no LE according to the Priestley-Taylor calculation. This assumption has been generally accepted because leaf stomata are assumed to open during the day and close at night. Thus, both photosynthesis and transpiration go to zero as radiation diminishes. Nonetheless, several studies of leaf gas exchange have shown nighttime conductance accounting for 5–30% of daily water loss (Rawson and Clarke 1988, Winner et al. 1989, Matyssek et al. 1995, Assaf and Zieslin 1996, Donovan et al. 1999, Snyder et al. 2003).

The eddy covariance method, which is based on micrometeorological theory and the covariance between vertical wind velocity and scalar concentration fluctuations (Baldocchi et al. 1988, Desjardins 1991), allows for measurement of water, carbon and energy exchange between the biosphere and atmosphere on relatively large spatial scales (1–5 km²) at high frequency (10 Hz, averaged to 30 min). Flux measurements can be in error at night, however, when wind turbulence is light and intermittent (Goulden et al. 1996, Cienciala et al. 1998, Lee 1998, Cienciala and Lindroth 1999, Kellomaki and Wang 2000, Baldocchi 2003, Turnipseed et al. 2003). Nighttime flux

is underestimated and energy balance closure is not achieved when there is stable stratification of the air below the sensors as the result of drainage flows near the ground. Fluxes are overestimated at sunrise as the result of short-term venting as convective turbulence resumes (Leuning and King 1992, Grace et al. 1996, Moncrieff et al. 1996, Lindroth et al. 1998, Sun et al. 1998, Yi et al. 2000). Although the sources and sinks for LE, H and CO_2 differ, eddy covariance measurement generally may be underestimated by up to 12% at night (Soegaard et al. 2000, Berger et al. 2001). A comprehensive evaluation of energy balance closure at 22 sites in FLUXNET—a global network of over 200 eddy covariance towers (Wofsy et al. 1993, Schmid 1994, Baldocchi et al. 2001)—showed a mean imbalance of 20% that was greatest during nocturnal periods (Wilson et al. 2002).

Given the possibility of nocturnal transpiration (Marks and Lechowicz 2007, Cavender-Bares et al. 2007, Dawson et al. 2007, Hubbart et al. 2007, Kavanagh et al. 2007, Scholz et al. 2007), the measurement problems associated with nighttime eddy covariance and the limitations of gas exchange measurements, an alternative approach to these methods is required and is provided by the measurement of transpiration by determining sap flow of individual plants by heat transfer—a method that neither alters the surrounding environment of the plant nor includes soil evaporation (Huber 1932, Marshall 1958, Cermak et al. 1973, Cohen et al. 1981, Granier 1985, Swanson 1994, Smith and Allen 1996). Until recently, there has been no reliable method to measure and quantify low rates of sap flow, including zero and negative (i.e., hydraulic lift) rates. Calibration of the widely used Granier method (Granier 1985), for example, assumes zero nighttime sap flow. If this assumption is invalid, the reliability of measurements with this method is open to question, particularly at low sap flow rates (Köstner et al. 1998, Oren et al. 2001). However, a variation of the Granier method, the compensation heat pulse method (Edwards et al. 1996), allows accurate estimates of low flow rates such as may be observed at night (Green et al. 1989, Benyon 1999, Song et al. 1999). Recently, Burgess et al. (2001) developed an improved heat pulse method, the heat ratio method, which is well-suited to the measurement of nighttime transpiration. The heat ratio method corrects for physical and thermal errors, including wound effects, and improves on the measure-

ment range and resolution of the original heat pulse method. Since its development, the heat ratio method has been used widely for sap flow measurement and hydraulic redistribution (Kurpius et al. 2003, Bleby et al. 2004, Bucci et al. 2004, Burgess and Dawson 2004, Hultine et al. 2004, Williams et al. 2004, Oliveira et al. 2005).

We used the heat ratio method at two FLUXNET sites (AmeriFlux) to measure sap flow in five *Pinus ponderosa* Dougl. ex. Laws. trees (ponderosa pine), three *Arctostaphylos manzanita* Parry shrubs and two *Ceanothus cordulatus* A. Kellogg shrubs in the Sierra Nevada Mountains; and, five *Quercus douglasii* Hook & Arn. (Blue oak) trees at an oak savanna in the Central Valley of California. Given that R_n is negative at night and cannot drive LE, we followed the Penman-Monteith model (Monteith 1965) and recent sap flow research (Hogg and Hurdle 1997, Benyon 1999, Oren et al. 2001) to test nocturnal transpiration (H_0) against possible driving forces of vapor pressure deficit (VPD), wind speed and air temperature (T_a). We analyzed the differentiation between xylem water-storage tissue refilling and transpirational water loss, and the sap flow signal associated with each. Finally, we determined the percentage of nighttime transpiration missing in the eddy covariance measurements at our sites and compared these errors to errors reported in the literature.

Materials and methods

Study sites

Data were gathered during year 2005 at Blodgett Forest Research Station (38.8952 °N, 120.6328 °W, 1315 m) in the Sierra Nevada mountains and at Tonzi Ranch (38.4192 °N, 120.9503 °W, 177 m) in the lower foothills of the Sierra Nevada mountains of California (Figures 1A and 1B). The Blodgett Forest study site (Goldstein et al. 2000), owned and managed as a commercial forest by Sierra Pacific Industries, was planted in 1990 at 1275 trees ha^{-1} and is dominated by *Pinus ponderosa* with occasional trees of other species. The major understory shrubs are *Arctostaphylos manzanita* and *Ceanothus cordulatus* (Xu et al. 2001, Misson et al. 2006). Shrubs were cut during spring 1999 and the plantation was thinned in May 2000 (Misson et al. 2005, Tang et al. 2005). Tree density

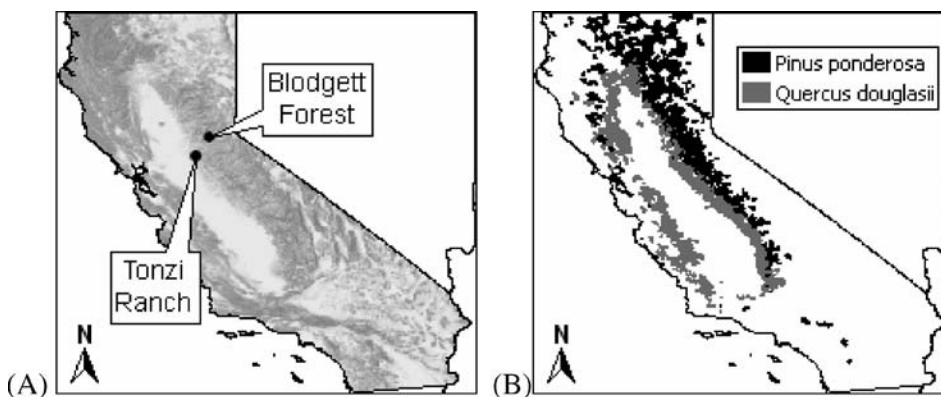


Figure 1. (A) Digital elevation map showing the locations of Blodgett Forest, a *Pinus ponderosa* plantation, in the Sierra Nevada mountains and Tonzi Ranch, an oak savanna, in the lower foothills of the Sierra Nevada mountains of California, USA. (B) Distribution of *Pinus ponderosa* and *Quercus douglasii* in California based on GAP analysis (Scott et al. 1993).

was 510 trees ha⁻¹ in spring 2003, and shrubs were fast developing in the large gaps between tree crowns of the open stand. In spring 2003, total one-sided leaf area index (LAI) was 2.49, comprising 72% *P. ponderosa* in the overstory, and 28% understory shrubs (*A. manzanita* 22% and *C. cordulatus* 6%). Mean tree diameter at breast height (DBH) was 12.0 cm, mean tree height was 4.7 m (mean shrub height was 1.0 m), and basal area was 9.6 m² ha⁻¹. The site is characterized by a Mediterranean climate, with warm dry summers and cold wet winters. Since 1998, annual precipitation has averaged 1290 mm primarily between September and May, and almost no rain in the summer. Mean daily temperature has ranged from 14 to 27 °C during summers and from 0 to 9 °C during winters. The soil is 60% sand, 29% loam and 11% clay (fine-loamy, mixed, mesic, ultic haploxeralf in the Cohasset series) with pH 5.5 ± 0.3 whose parent material was andesitic lahar (Goldstein et al. 2000).

The Tonzi Ranch study site is an oak–grass savanna consisting of scattered blue oak trees (*Quercus douglasii*), with occasional gray pine trees (*Pinus sabiniana* L.), and grazed grassland (*Brachypodium distachyon* L., *Hypochaeris glabra* L., *Bromus madritensis* L. and *Cynosurus echinatus* L.) (Kiang 2002). A demographic survey on stand structure of the oak woodland was conducted with a multi-return laser altimeter system; the survey, which extended for a square kilometer centered on the meteorological tower, found mean tree height was 9.41 m ± 4.33 m, mean trunk height was 1.75 m ± 1.35 m, mean crown radius was 3.18 m ± 1.54 m and mean basal area was 0.074 m² ± 0.0839 m² (Chen et al. 2006). The trees covered 40% of the landscape (Tang and Baldocchi 2005). Leaf out was at the end of March, reaching a maximum LAI for this heterogeneous canopy of 0.706 ± 0.408 as determined by a combination of remote sensing information (CASI, IKONOS, LiDAR) and allometric relationships. This LAI estimate is slightly greater than our previous estimate of 0.6 (Kiang 2002) made with a Li-Cor LAI-2000 along a 200-m transect. The grass grows from November to May, and reaches a maximum LAI of around 1. The climate is Mediterranean with a mean annual temperature of 16.3 °C and precipitation of 560 mm. The soil is an Auburn, extremely rocky silt loam (Lithic haploxerepts) composed of 43% sand, 43% silt and 13% clay. Soil water, as measured at 50 cm depth by time domain reflectometry (TDR), at both the Sierra Nevada and oak-savanna sites peaks at 35–40% in the winters and drops to 15–20% in the summers (Figure 2).

Sap flow

Sap flow probe sets were designed as described by Burgess et al. (2001) and Burgess and Dawson (2004). We built thermocouple temperature probes with copper-constantan wire (36 G) inside a flexible micro-capillary filled with silicone heat transfer compound inserted into a capped steel hypodermic needle. Two thermocouple junctions 1.5 cm apart were soldered to allow for temperature readings at two radial depths (4.0 and 2.5 cm) in the xylem. We built heater probes with coiled nichrome wire (36 G, 85 Ω m⁻¹) inside a flexible mi-

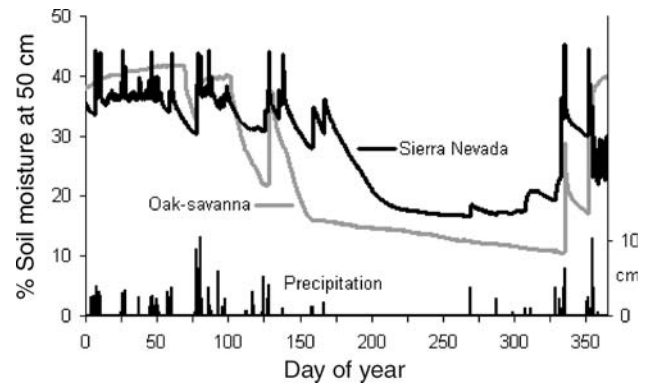


Figure 2. Soil water at 50 cm depth during 2005 at the oak-savanna site and Sierra Nevada site. Because the timing of precipitation is generally similar at both sites, precipitation data are shown for the oak-savanna site only. Precipitation reached a maximum of 14.2 cm at the Sierra Nevada site and 10.4 cm at the oak-savanna site. The Sierra Nevada site, at an elevation that receives snow, retains soil water longer into the summer though still experiences prolonged summer drought as controlled by the Mediterranean climate.

cro-capillary inserted in a capped steel hypodermic needle. Both the thermocouple and heater needle bases were encased in waterproof epoxy resin. Needle lengths were 4.5 cm, with 4.0 cm extruding from the epoxy base.

Probes were connected to centrally placed AM416 multiplexers attached to CR10X data loggers (Campbell Scientific Inc., Logan, UT) with cables ranging from 7 to 17 m depending on the distance from the tree or shrub to the multiplexer. Data were logged every 30 min. We attached a temperature thermistor to each multiplexer for a reference temperature. The heat pulse was controlled by solid-state relays.

Sap flow sensors were installed in each tree at breast height and in each shrub at the base. We stripped the outer bark to ensure xylem contact, and used a steel drill guide to maintain equidistance (1 cm) between probes. The sap flow sensors were encased in protective and reflective insulation. Random data spikes were corrected with a standard deviation threshold calculation. We recorded measurements on a half-hourly time step to align with the eddy flux half-hourly measurements. We calculated heat pulse velocity following Marshall (1958) and converted to sap flow with corrections for probe misalignment, wounding and thermal diffusivity following Burgess et al. (2001). A constant thermal diffusivity of heat through woody tissue was assumed for each species, though it varies with wood water content. We report heat pulse velocities for ease of comparison.

At the Sierra Nevada site, we conducted a forest inventory and selected five *P. ponderosa*, three *A. manzanita* and two *C. cordulatus* shrubs throughout the eddy flux footprint representative of the stand DBH and height structure. The DBHs of the five trees were 18, 20, 21, 24 and 24 cm. The LAI of the shrubs ranged from 1 to 3 (LAI-2000, Li-Cor, Lincoln, NE). At the oak-savanna site, we selected five *Q. douglasii* trees as determined from the sampling scheme of Kiang (2002). The DBHs of the five trees were 16, 18, 22, 23 and 37 cm. Sap flow

was measured from the beginning of spring 2005 through winter 2006.

Eddy covariance

Ongoing eddy covariance flux measurements at the Sierra Nevada and oak-savanna sites have been described extensively (Goldstein et al. 2000, Baldocchi et al. 2004, Misson et al. 2005). Meteorological measurements included in this analysis were R_n , VPD, T_a , wind speed, precipitation and soil water at 50 cm depth. Micrometeorological instruments were attached to towers 12.5 m from the ground for the Sierra Nevada site, and 23 m (overstory) and 2 m (understory) for the oak-savanna site. We measured wind velocity and air temperature at 10 Hz with three-dimensional sonic anemometers (ATI Electronics Inc., Boulder, CO for Blodgett Forest; Windmaster Pro, Gill Instruments, Lymington, UK for Tonzi Ranch). Water vapor mixing ratios were measured with infrared gas analyzers (Li-Cor Model 6262 for Blodgett Forest, Li-Cor Model 7500 for Tonzi Ranch). The output of the water vapor channel was referenced to a dew point hygrometer (LI-610, Li-Cor) at the oak-savanna site. We used the eddy covariance method to measure fluxes of water and carbon dioxide between the biosphere and atmosphere (Goldstein et al. 2000, Baldocchi et al. 2004). This method quantifies vertical fluxes of scalars from the covariance between vertical wind velocity and scalar fluctuations averaged over 30-min periods, which matched the temporal resolution of the sap flow data loggers (Shuttleworth et al. 1984, Baldocchi et al. 1988, Wofsy et al. 1993). Data were processed and analyzed in Microsoft Excel, JMP IN (SAS Institute, Cary, NC) and ArcGIS 9.0 (ESRI, Redlands, CA).

Results

Daytime (daily) and nighttime (nightly) mean sap flow rises into the summer and decreases into the winter for both *Q. douglasii* (Figure 3A) and *P. ponderosa* (Figure 3B). Data shown are for the 16-cm DBH *Q. douglasii* tree and the 20-cm DBH *P. ponderosa* tree. The annual pattern is similar for the other size classes. A polynomial fit is overlaid for visualization of the general pattern. The starting date of the sap flow measurements was 16 days earlier for the *P. ponderosa* than for the *Q. douglasii*. Although both daytime and nighttime sap flow peaked in the summer, daytime sap flow peaked earlier than nighttime sap flow. Daytime and nighttime sap flows differed during the summer, and converged near zero in the winter. Daytime sap flow peaked earliest for *Q. douglasii* around Days 160–170, and nighttime sap flow peaked around Days 210–220. For *P. ponderosa*, daytime sap flow peaked around Days 190–200, and nighttime sap flow peaked around Days 210–220. All species exhibited small amounts of negative sap flow likely associated with settling or root efflux as described in other studies (Burgess et al. 2000a, Burgess et al. 2000b).

For plants that have exhibited nocturnal transpiration, VPD is a primary driving force (Hogg and Hurdle 1997, Benyon 1999, Oren et al. 2001), consistent with theoretical considerations (Monteith 1965). Vapor pressure deficit will not be influential, however, if it reaches zero every night. Both of our

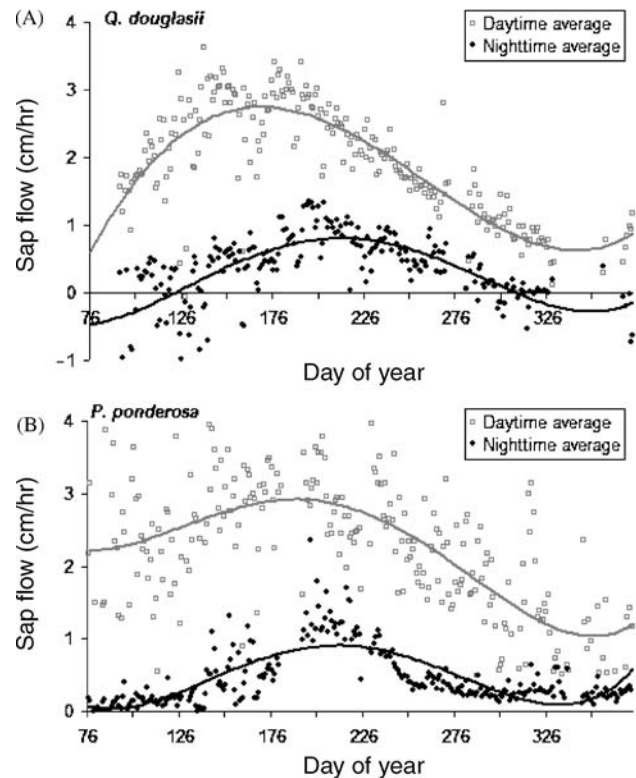


Figure 3. Daytime and nighttime mean sap flow rates during 2005 for (A) 16-cm DBH *Quercus douglasii* and (B) 20-cm DBH *Pinus ponderosa*. Polynomial fits are overlaid for visualization of the general pattern.

sites are dry, so VPD remained positive throughout the night, particularly in the summer (Figure 4A). Mean nighttime VPD corresponded closely with mean nighttime sap flow at both sites (Figure 4B). Linear regression fits (Figures 4C and 4D) showed good and similar agreements for both *Q. douglasii* ($r^2 = 0.79$, $P < 0.0001$, RMSE = 0.18) and *P. ponderosa* ($r^2 = 0.71$, $P < 0.0001$, RMSE = 0.17). For *P. ponderosa*, the slope of the regression is steeper and the fit less good than that for *Q. douglasii* because of the vertical asymptote of negative sap flow rates at low VPD.

The Penman-Monteith (1965) equation includes T_a as a driver for LE. At both sites, T_a and VPD showed a tight exponential correlation because the hottest period of the year is during the summer drought (Figure 5A). At the Sierra Nevada site, as nighttime T_a increased into the summer, nighttime sap flow increased more rapidly (Figure 5B). The linear regression fit ($r^2 = 0.70$, $P < 0.0001$, RMSE = 0.24) is similar to that with VPD for *P. ponderosa* (Figure 5C), though an exponential curve improved the fit slightly ($r^2 = 0.72$). The linear regression fit for *Q. douglasii* ($r^2 = 0.66$, $P < 0.0001$, RMSE = 0.25) is less close than for VPD, however (Figure 5D). The slopes of the linear regression between sap flow and T_a for both species were equivalent ($m = 0.06$ for *P. ponderosa*, and 0.05 for *Q. douglasii*). A multiple regression of T_a and VPD (which are auto-correlated and thus not expected to improve fits) against nighttime sap flow yielded a slight improvement for

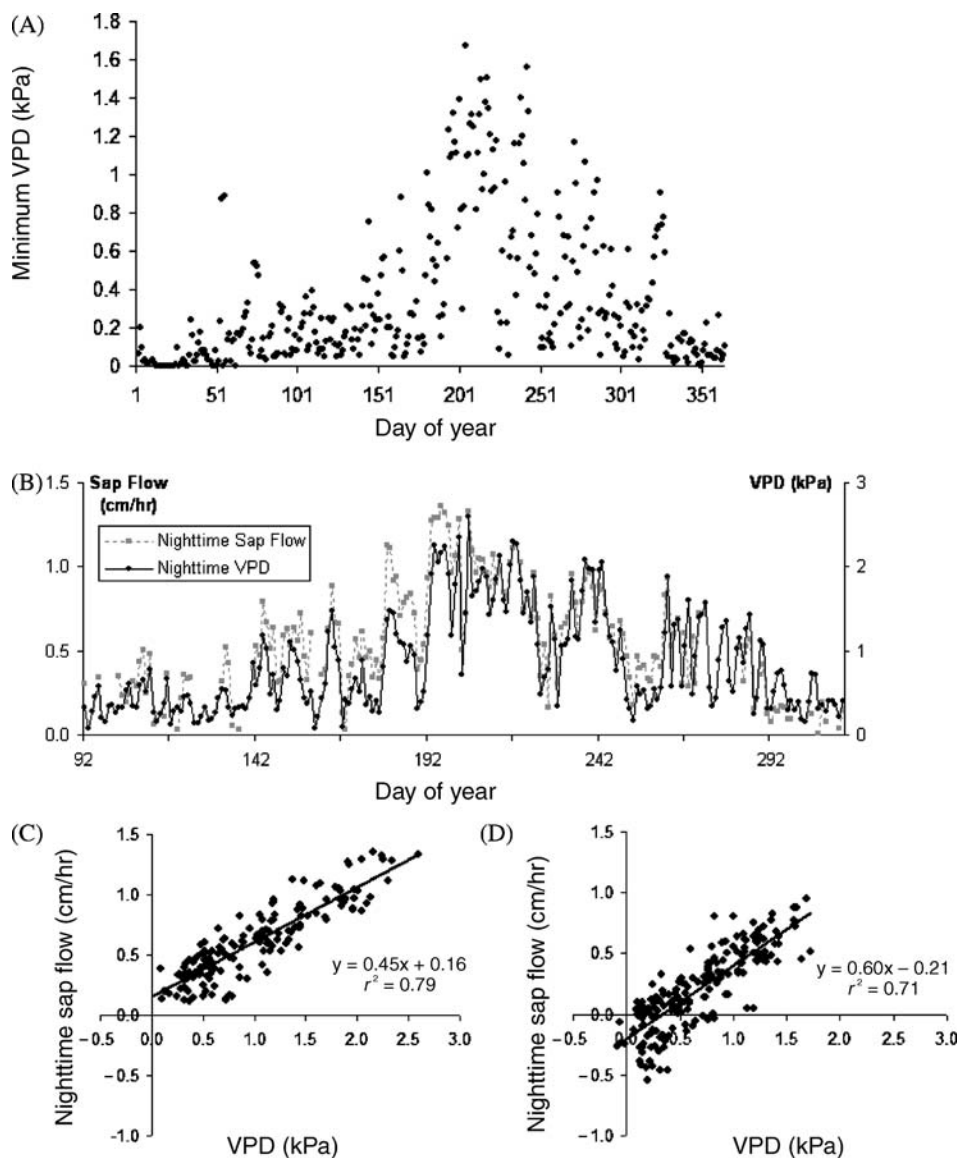


Figure 4. (A) Minimum vapor pressure deficit (VPD) for 2005 at the oak-savanna site. (B) Mean nighttime VPD and sap flow for a *Quercus douglasii* (16-cm DBH) tree. (C) Linear regression of the data in Figure 4B. (D) Linear regression for mean daily nighttime VPD and sap flow for 2005 at the Sierra Nevada site for a *Pinus ponderosa* (18-cm DBH) tree.

P. ponderosa ($r^2 = 0.80$, $P < 0.0001$, RMSE = 0.15), but not for *Q. douglasii* ($r^2 = 0.75$, $P < 0.0001$, RMSE = 0.17), which was better predicted by VPD alone. Wind speed was a poor predictor (insignificant correlations) for nighttime transpiration at both sites (Table 1).

To differentiate nighttime xylem refilling (alleviation of xylem pressure from daytime-decreased water potentials) from water loss (actual transpiration or conductance), we assessed the pattern of nocturnal sap flow during two periods: (1) when the nighttime driving force, VPD, was minimized, as generally occurred during the winter as a result of moist cold air; and (2) when the nighttime driving force was maximized (generally during the summer). Under the first condition, any sap flow occurring at night should be limited to refilling (no water loss). The diurnal pattern of sap flow was marked by a rise soon after solar radiation became positive, declining with decreasing solar radiation in the evening and tailing off to zero within a couple of hours after sunset (Figure 6A). Under the second condi-

tion, when VPD remained positive and high throughout the night, nocturnal sap flow followed the same slope and temporal pattern following sunset as in Figure 6A, but remained positive throughout the night as well (Figure 6B). The integral of sap flow from the end of the refilling period to sunrise marks the amount of nighttime water loss. Refilling constituted 70% and water loss 30% of the integral of nocturnal sap flow in Figure 6B.

As two alternatives to the time-separation approach to refilling and transpiration, we can estimate the partitioning if the refilling period crosses into the transpiration period (Figure 6C) or if the transpiration period crosses into the refilling period (Figure 6D). In both cases, refilling and transpiration occur at the same time. In the first approach, we forecast the initial steep slope of the sap flow curve forward into the refilling zone. In the latter approach, we back-extrapolate the line above the refilling phase as was first calculated. Refilling from the forecasted, extended refilling approach constitutes 85%

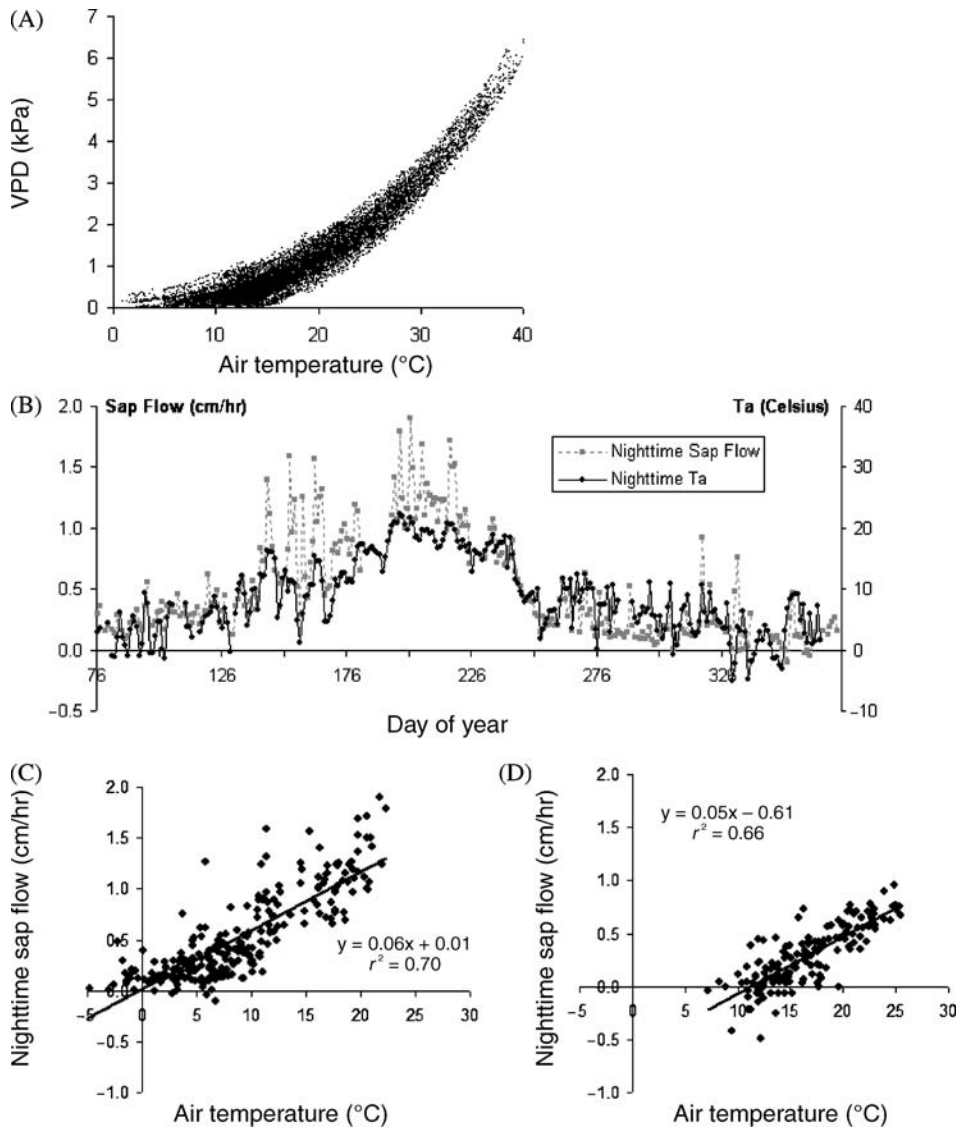


Figure 5. (A) Vapor pressure deficit (VPD) versus air temperature (T_a) follows an exponential curve for 2005 at both sites; data shown here are for the oak-savanna site. (B) As T_a increases at the Sierra Nevada site, nighttime sap flow (20-cm DBH tree) increases much more rapidly. The exponential relationship holds for nighttime sap flow versus T_a during the summer at the (C) Sierra Nevada site, but not at the (D) oak-savanna site (16-cm DBH tree).

and water loss 15% of the integral in Figure 6C. Refilling from the back-extrapolated, extended transpiration approach constitutes 40% and water loss 60% of the integral in Figure 6D.

At sunrise, when VPD and T_a dropped briefly in the inversion, sap flow also dropped to zero before ramping back up in the typical diurnal pattern. Also evident in Figures 6A and 6B

is a small peak then a dip immediately after sunrise. This sub-peak represents the depletion of stored water for transpiration (Tatarinov and Čermák 1999, Steppe and Lemeur 2004). The subsequent replenishment of this source is indicated by the steeper slope in sap flow following the sub-peak. The sub-peak was not always evident in the sap flow measurements, however, depending on how fast the trees were able to replenish stored water reserves.

After differentiating nocturnal refilling from water loss, our next step was to link nighttime transpiration from the sap flow measurements to measurements of LE from eddy covariance at the towers. First, to assess this link during reliable measurement periods, we evaluated daytime sap flow with daytime LE. At the Sierra Nevada site, mean daytime sap flow followed mean daytime LE throughout the year, though with scatter because of the disconnect between the individual tree response and the mean response of all trees in the footprint (Figures 7A and 7B). The fit between sap flow and LE was similar for every tree at the Sierra Nevada site ($r^2 = 0.62$, $P < 0.0001$, RMSE =

Table 1. Correlation coefficients for nighttime sap flow predictors (VPD, T_a , and wind speed) versus nighttime sap flow for *Quercus douglasii* ($n = 203$) and *Pinus ponderosa* ($n = 268$). All correlations were significant ($P < 0.0001$) for VPD and T_a , none of the correlations was for wind speed.

	VPD	T_a	Wind speed
<i>Q. douglasii</i>	0.79	0.70	0.01
<i>P. ponderosa</i>	0.71	0.66	0.03

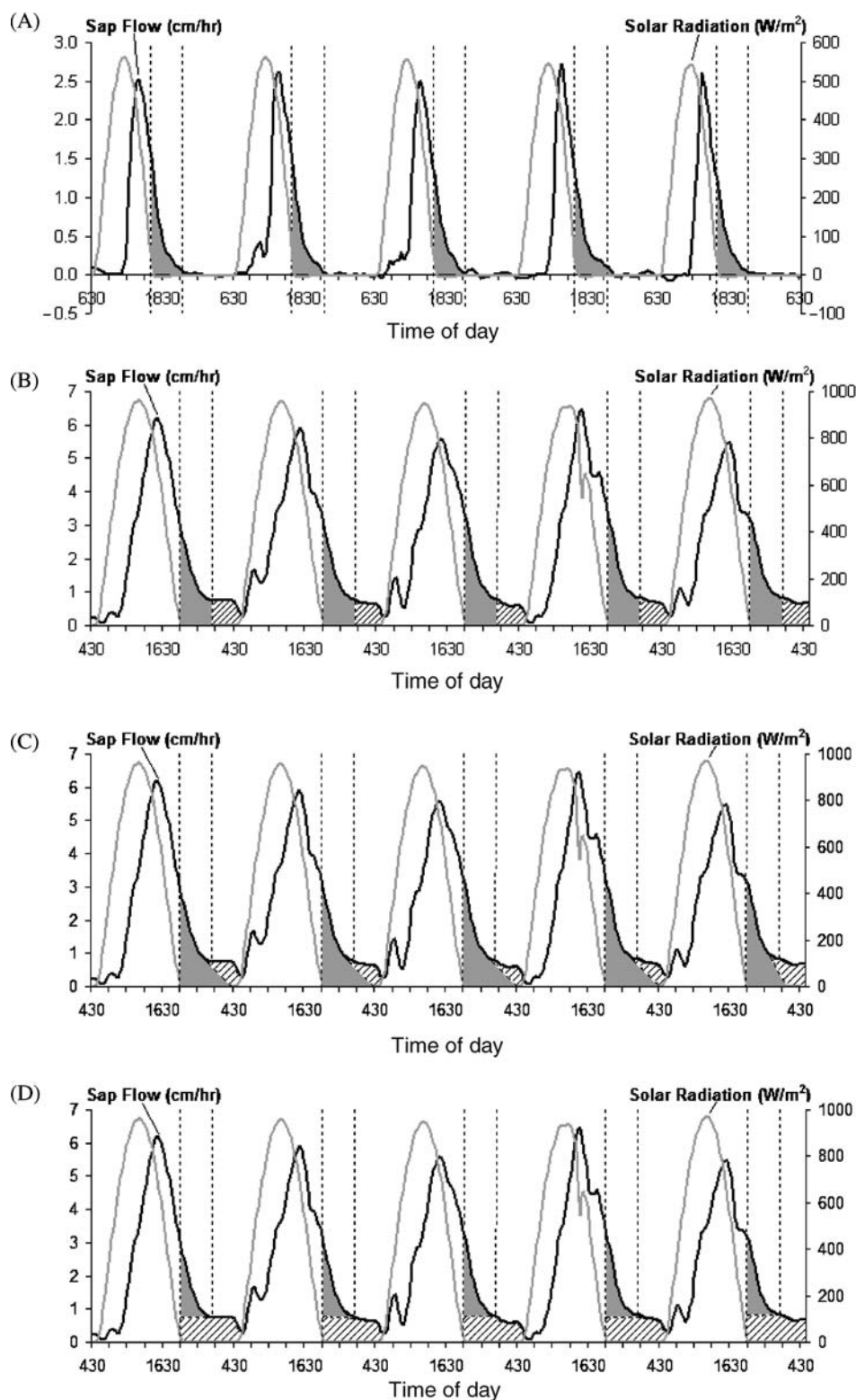


Figure 6. Five-day period for sap flow and solar radiation for a *Quercus douglasii* (16-cm DBH) tree (A) late in the year when VPD and T_a are low, so that only refilling occurs (filled area ~3-h periods between dashed vertical lines) and (B) and in midsummer when water loss (diagonal hatching) follows the refilling period. The diurnal patterns of VPD and T_a match the diurnal pattern of sap flow. Two approaches to analyzing the refilling-transpiration partitioning: (C) forecasted refilling into the transpiration period and (D) back-extrapolated transpiration into the refilling period.

0.51). At the oak-savanna site, where the life cycle of the grassland contributes to ecosystem LE in this open canopy, we separated the two sources of LE with an above-canopy eddy flux tower and a below-canopy eddy flux tower (Figure 8A). The grasses and near-surface soil dried out and stopped con-

tributing significantly to overall LE before Day 200, but the trees continued to transpire further into the summer (Day 250).

The sap flow measurements, however, indicate a lag between sap flow and eddy covariance whereby the trees con-

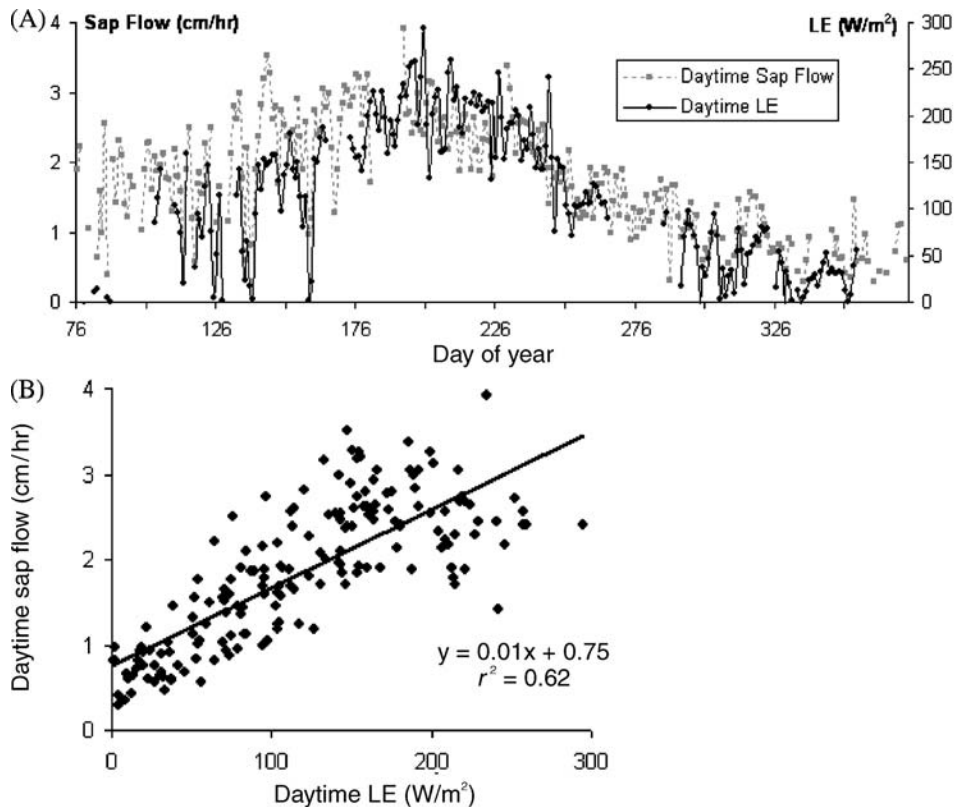


Figure 7. (A) Mean daytime sap flow (20-cm DBH tree) and LE from eddy covariance at the Sierra Nevada site. (B) Linear regression of the data in Figure 7A.

tinue to transpire at high rates much later into the summer, finally decreasing to near zero around Day 340 (Figure 8B). Furthermore, the fit between daytime sap flow and daytime LE was poor ($r^2 = 0.44$, $P < 0.0001$, RMSE = 0.55), although a logarithmic relationship improved the fit ($r^2 = 0.54$) for the data shown and for the other *Q. douglasii* trees. A logarithmic fit indicates that trees tapped a deeper source of soil water and thus continued to transpire later into the season. Given high rates of LE as measured by eddy covariance, the sap flow measurements were not recording such high rates and may have reached a mean daytime limit of 4 cm h^{-1} (individual measurements at 30-min reached 10 cm h^{-1}) as a result of the creation of early wood, high-flow xylem vessels (Tyree and Zimmerman 1983, Granier et al. 1994) during periods of high water availability that the stationary-depth sap flow sensors did not detect. Stand structure is much more heterogeneous at the oak-savanna site than at the Sierra Nevada site (which is a relatively uniform plantation). Nonetheless, the objective here is not to scale up individual tree sap flow measurements to footprint measurements, but to assess whether daytime sap flow follows daytime eddy covariance LE. Daytime sap flow approximately follows daytime eddy covariance LE albeit with scatter at both sites and with a time lag at the oak-savanna site.

Given the approximation of daytime sap flow to daytime eddy covariance LE, we next compared nighttime sap flow to nighttime eddy covariance LE. As predicted from the known limitations of nighttime eddy covariance measurements, nighttime LE did not correspond well to nighttime sap flow. At the Sierra Nevada site, summer nighttime transpiration was

significantly underestimated (Figure 9A). At the oak-savanna site, nighttime LE sometimes matched nighttime sap flow, but for the most part it underestimated nighttime transpiration as well (Figure 9B). Nighttime sap flow as a percent of daily total was 18% versus 6% for eddy covariance at the oak-savanna site, and 21% (sap flow) versus 1% (eddy covariance) at the Sierra Nevada site (Figure 9C). The number of nights with valid measurements was also greater for sap flow than for eddy covariance—185 versus 153 at the oak-savanna site, and 241 versus 208 at the Sierra Nevada site during the 2005 measurement period (Figure 9D). The number of days with valid measurements were equivalent for sap flow and eddy covariance at the oak-savanna site (Figure 8B), but for the Sierra Nevada site sap flow maintained higher reliability partly because of a 3-week gap in eddy covariance measurements around Day 276 (Figure 7A). For valid data, nighttime eddy covariance measurements depend on adequate wind speed and equipment reliability, whereas nighttime sap flow measurements depend only on equipment reliability.

Discussion

Nighttime transpiration was well coupled (low Ω) with VPD but was not well coupled with wind speed (McNaughton and Jarvis 1991). There was a strong response with T_a as well, but VPD and T_a are so well correlated that it is difficult to separate the two influences. With nighttime T_a as high as $> 30^\circ \text{C}$, nighttime transpiration may be an adaptive response that cools the leaves (Montero et al. 2001). Wind was not well coupled

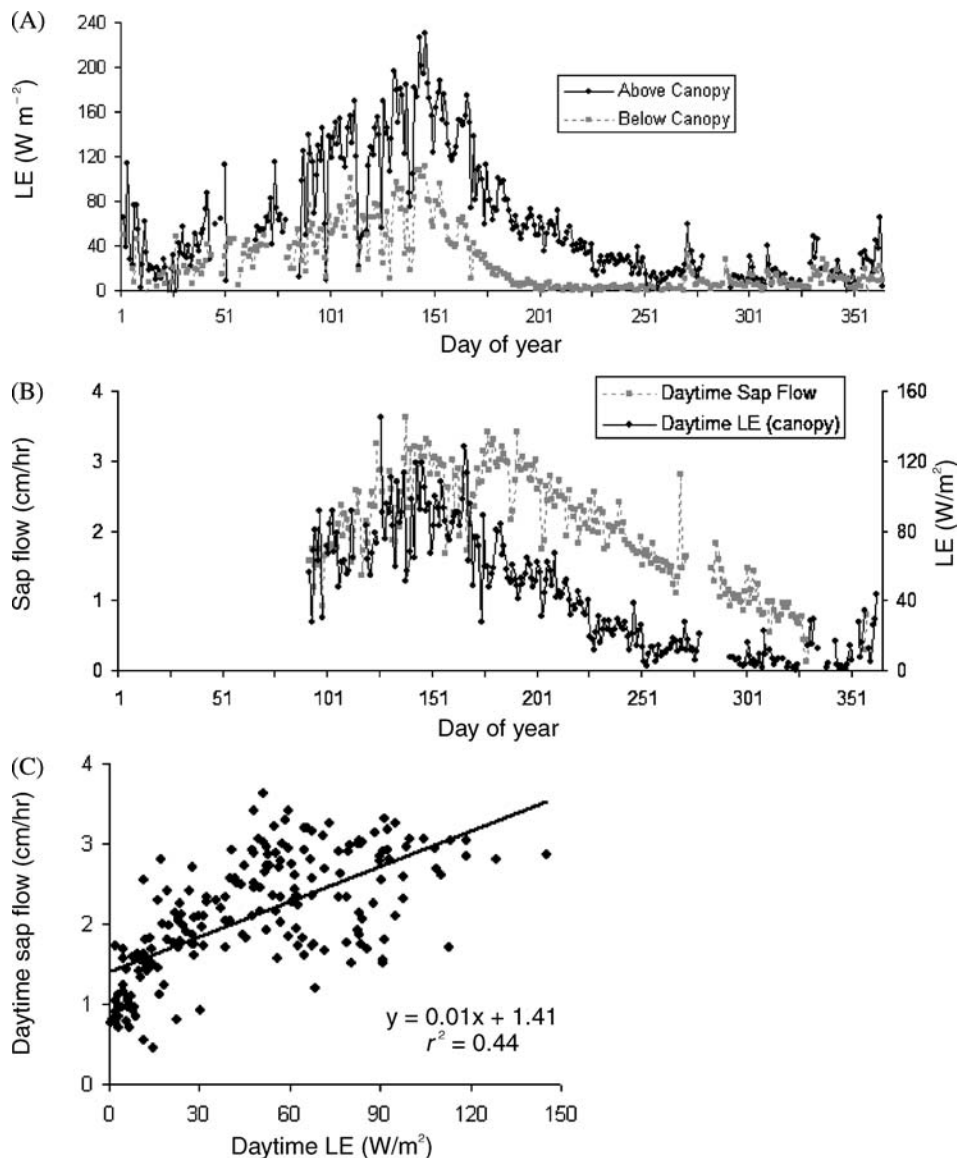


Figure 8. (A) Mean daytime LE for above-canopy and below-canopy towers at the oak-savanna site. (B) The difference between the LE above- and below-canopy towers equals the LE from the trees only, which is compared to the sap flow from a 16-cm DBH tree. (C) The correlation between eddy covariance and sap flow is reduced because of the temporal lag as shown in Figure 8B.

(high Ω) with sap flow because our sites were dry (hence, low Ω with VPD). Wind is more closely coupled with transpiration in a humid environment, where it can act as a physical mechanism to break up the stable boundary layer above the leaf and canopy, removing recently transpired water vapor and replacing the air immediately above the leaf with dry air (Meinzer et al. 1995). Vapor pressure deficit is a well-known driver of transpiration owing to the water potential gradient and the ability of dry air to pull in water from a source of higher water potential (Monteith 1965). In a moist environment, however, VPD may not be as well coupled to sap flow as it is at our sites. At the root, however, soil water is perhaps the most important input at our sites, without which transpiration cannot occur, regardless of the values of VPD, T_a or any other driver. Sap flow was minimized when soil water content was at its lowest—at 10.5% around Day 330 for the oak-savanna site and at 16.8% around Day 260 for the Sierra Nevada site (Figure 2).

Nighttime sap flow peaked later than daytime sap flow in

the summer season. At these water-limited sites, it would be expected that daytime LE would peak early in the season with leaf-flush when water is available, but that later, transpiration would be down-regulated when soil water becomes limited. Nocturnal transpiration is an unregulated and passive process that would scale with VPD, which peaks in the mid- to late-summer because there is less daily LE to humidify the atmosphere. This differentiation was more pronounced in the oaks than in the pines because the oak trees are better adapted at down-regulating photosynthesis to minimize water loss during severe drought (Xu and Baldocchi 2003, David et al. 2004). Soil water was generally lower and atmospheric humidity higher at the oak-savanna site relative to the Sierra Nevada site.

There were many peculiarities in the shrub sap flow data that are difficult to explain; hence, we omitted them from the primary results, but show the data here for discussion. For *A. manzanita* and *C. cordulatus*, daytime sap flow followed

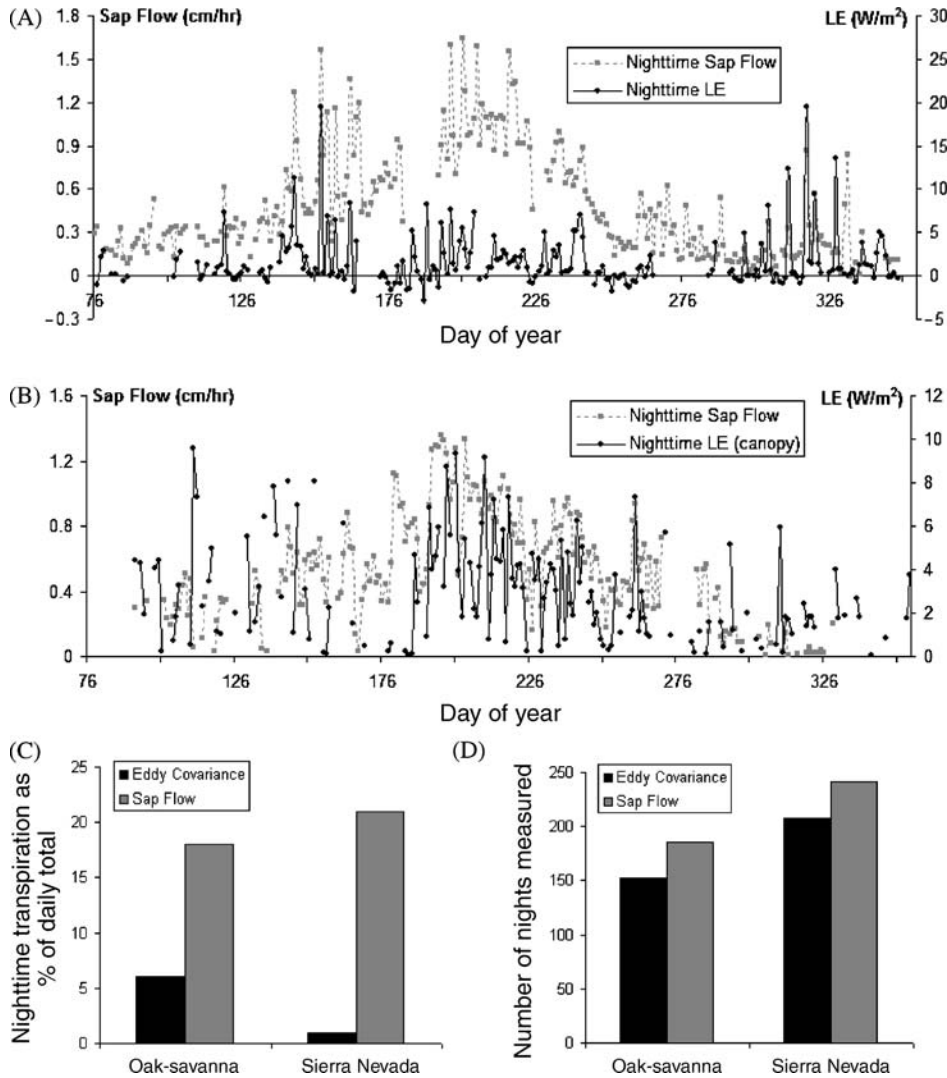


Figure 9. (A) Mean nighttime sap flow for the same tree as in Figure 7 (20-cm DBH) compared with mean nighttime LE from eddy covariance at the Sierra Nevada site. (B) Mean nighttime sap flow for the same tree as in Figure 8 (16-cm DBH) compared with mean nighttime LE calculated as the difference between the above- and below-canopy eddy covariance towers at the oak-savanna site. (C) Measured nighttime transpiration was much larger for sap flow than for eddy covariance at both sites. (D) The number of nights with valid measurements was larger for sap flow than for eddy covariance.

that of the overstory trees with peaks around Days 190–200 (*A. manzanita*) and 200–210 (*C. cordulatus*), but the nighttime sap flow of the shrubs showed a different pattern from that of the trees, remaining close to zero in the summer but in-

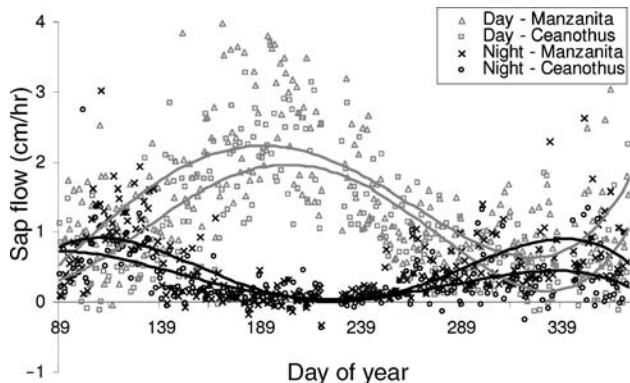


Figure 10. Mean daytime and nighttime sap flows during 2005 for *Arctostaphylos manzanita* and *Ceanothus cordulatus*.

creasing in the winter (Figure 10). Any summer water loss at night by the shrubs was relatively insignificant compared with daytime transpiration. During the day, sap flow values were highly variable, likely because of the differing responses to variations in sunlight and diffuse light caused by shading by the adjacent trees (Norman et al. 1971, Abrams and Mostoller 1995). During the night, however, the sap flow measurements were stable, although there was some variation in the data possibly in response to refilling, redistribution of water, or leaky stomata coupled with an atmospheric driver. Unfortunately, we could not determine the causes of this variation, because nighttime sap flow was minimal and difficult to correlate with environmental drivers.

The shrubs likely are exposed and limited to a different source of soil water—possibly more shallow—than the trees, though we excavated some shrubs and found they had tap roots in addition to shallow fine roots. The shallow soils are dry during the summer, however (Figure 2). Thus, it is likely that the shrubs are well adapted to drought and do not lose water at night unless it is freely available (Hinckley et al. 1983, Condit et al. 1995, Reynolds et al. 1999).

A key question about nocturnal sap flow is how to differentiate between storage tissue refilling and water loss. Nighttime refilling occurs because leaf water potential declines as a result of daytime transpiration, so that at night the water potential gradient between soil and plant drives nocturnal sap flow (Burgess and Dawson 2004). Refilling, in other words, is the alleviation of a build-up of negative xylem pressure potential. Stomata control the slope of the diurnal sap flow curve in three ways: (1) when stomata are wide open, photosynthesis and water loss are maximized; (2) when stomata are closed, sap flow continues as desiccated tissues refill and water potential gradients diminish; and (3) when stomata close imperfectly (van Hove et al. 1992), sap flow continues at a limited, rate which is dependant on atmospheric demand. The three phases or slopes can be seen in Figure 6B. During the day, we observed a few distinct sub-slopes to the first phase—the depletion of stored water, the subsequent replenishment of that water the slope of which depends on how quickly the stored water was depleted, and the continuation of sap flow as dictated by solar radiation. As soon as solar radiation goes to zero, the negative slope of sap flow rate become less negative during the refilling phase, which can be seen in both Figures 6A and 6B. The nocturnal refilling phase is marked by the short period between the dashed vertical lines from when solar radiation goes to zero until the slope of the decline shifts to a steady, near-zero slope. Water loss from nighttime transpiration is assumed to occur during the period following the refilling phase until solar radiation becomes positive, based on water potential gradients, though we present two alternate approaches as well. The three approaches to viewing the sap flow data give rather different partitioning results. It is possible that some combination of the approaches or another mechanism is involved in the refilling–transpiration process. It may be possible to evaluate the sub-peak of stored water depletion–replenishment as an indicator of water storage, though the sub-peak is not consistently detectable. Here, we present ideas, not evidence, on the process. Further research should validate what combination of the approaches is correct.

Nighttime VPD was highly correlated with daytime VPD ($r^2 = 0.87$, both sites) so that more refilling is required at night as a result of high water loss during the day. It is possible that refilling takes the entire night or may be incomplete at dawn, in which case nighttime transpiration will be minimal. Based on the water potential gradients, however, if more refilling is needed (more negative water potentials), then nighttime sap flow will be faster. Refilling may only slowly eliminate the plant–soil water potential gradient during a night with high VPD. Nevertheless, the sap flow curve should gradually decline as the pull decreases (water potential gradient becomes less steep). Our data show, however, that sap flow curve remains steady throughout the night, only dropping when VPD dropped at the sunrise inversion (Figure 6B).

Gas exchange measurements have shown nighttime transpiration to be 5–30% of daily water loss (Rawson and Clarke 1988, Winner et al. 1989, Matyssek et al. 1995, Assaf and Zieslin 1996, Donovan et al. 1999, Snyder et al. 2003), and nighttime eddy covariance errors of around 12–20% have

been reported (Soegaard et al. 2000, Berger et al. 2001, Wilson et al. 2002). We report nighttime transpiration as a percent of daily water loss at 18% (oak-savanna site) and 21% (Sierra Nevada site) from sap flow, which is within the range of published values from gas exchange measurements (5–30%). The nighttime eddy covariance LE as a percent of daily water loss was 12% underestimated (oak-savanna site) and 20% underestimated (Sierra Nevada site) relative to sap flow measurements—also within the range of published error (12–20%). Much of the eddy covariance error analysis has focused on CO₂ with the assumption that LE errors match, and we confirmed those assumptions at our sites. The relative ranges of our measurements show congruence with the literature and provide amounts of transpiration on a 30-min interval. We recommend VPD as a proxy with which to estimate and gap-fill uncertain nighttime eddy covariance measurements at our sites and other sites with similar climate and vegetation.

In conclusion, to quantify nocturnal transpiration at our sites we relied on several methods of measurement and analysis. To measure sap flow, we used the heat ratio method, which is especially useful for measuring low flow rates that are critical to nighttime flows. We found that nocturnal sap flow occurred in both tree species (*P. ponderosa* and *Q. douglasii*) and two species of shrubs (*A. manzanita* and *C. cordulata*) investigated, though significant nighttime water loss occurred only in the trees. When testing possible nighttime drivers, VPD, T_a and wind speed, we found that, at our sites, VPD did not go to zero every day and was strongly coupled with nighttime sap flow ($r^2 = 0.79$ and 0.71 at the oak-savanna and Sierra Nevada sites, respectively), T_a was also associated with nighttime sap flow but autocorrelated with VPD, and wind speed was not significantly associated with nighttime sap flow. Because VPD was well coupled with nighttime sap flow, we were able to assess nocturnal sap flows when VPD was low and high to determine patterns of refilling versus water loss. Individual sap flow measurements generally followed daytime eddy covariance LE measurements for large-scale footprints, but diverged considerably at night. Finally, we were able to quantify the underestimation of nighttime water loss by eddy covariance, or what the “towers don’t see at night.” We suggest that new models of evapotranspiration, water balance, net primary productivity and climate change reflect this proportion of nighttime LE.

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