Interspecific variation in nighttime transpiration and stomatal conductance in a mixed New England deciduous forest

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Summary   Transpiration is generally assumed to be insignificant at night when stomata close in response to the lack of photosynthetically active radiation. However, there is increasing evidence that the stomata of some species remain open at night, which would allow for nighttime transpiration if there were a sufficient environmental driving force. We examined nighttime water use in co-occurring species in a mixed deciduous stand at Harvard Forest, MA, using whole-tree and leaf-level measurements. Diurnal whole-tree water use was monitored continuously with Granier-style sap flux sensors in paper birch (*Betula papyrifera* Marsh.), red oak (*Quercus rubra* L.) and red maple (*Acer rubrum* L.). An analysis was conducted in which nighttime water flux could be partitioned between refilling of internal water stores and transpiration. Substantial nighttime sap flux was observed in all species and much of this flux was attributed to the refilling of depleted water stores. However, in paper birch, nighttime sap flux frequently exceeded recharge estimates. Over 10% of the total daily sap flux during the growing season was due to transpiration at night in paper birch. Nighttime sap flux was over 8% of the total daily flux in red oak and 2% in red maple; however, this flux was mainly associated with recharge. On nights with elevated vapor pressure deficit, sap flux continued through the night in paper birch, whereas it reached zero during the night in red oak and red maple. Measurements of leaf-level gas exchange on a night with elevated vapor pressure deficit showed stomatal conductance dropping by only 25% in paper birch, while approaching zero in red oak and red maple. The study highlighted differences in ecophysiological controls on sap flux exerted by co-occurring species. Paper birch is a fast-growing, shade-intolerant species with an earlier successional status than red oak and red maple. Risking water loss through nighttime transpiration may provide paper birch with an ecological advantage by enabling the species to maximize photosynthesis and support rapid growth. Nighttime transpiration may also be a mechanism for delivering oxygen to respiring cells in the deep sapwood of paper birch.

Keywords: Acer rubrum, Betula papyrifera, nighttime water use, Quercus rubra, recharge, sap flux, water storage.

Introduction

According to the optimization theory, stomatal aperture varies over time to minimize water loss for a required amount of carbon gain (Cowan 1977). In C_3 and C_4 plants, there is no opportunity for carbon gain at night because of the lack of photosynthetically active radiation necessary for the light reactions of photosynthesis. Based on the optimization theory, stomata will close at night to prevent water loss when there is no opportunity for carbon gain. Although it is generally assumed that stomata close at night, several studies have documented nighttime stomatal opening in many species and in a range of habitats (reviewed in Musselman and Minnick 2000).

Nighttime stomatal conductance has significant implications for many physiological processes in trees. In many hydrologic models, stomatal conductance at night is assumed to approach zero with solar radiation (e.g., Jarvis 1976, Bevin 1997). Many sap flow measurement systems assume zero flow at night (e.g., Catovsky and Bazzaz 2000, Phillips et al. 2003) and the validity of this assumption can substantially impact estimates of daytime sap flux. Nighttime water loss creates disequilibrium between leaf and soil water potentials and thus limits the use of predawn leaf water potential to determine soil water potential in soil–plant–atmosphere continuum models (Bucci et al. 2004). Plants with nighttime stomatal conductance are more susceptible to ozone damage because the detoxification of oxidants is more efficient in light, when the photosynthetic electron transport is active (Matyssek et al. 1995, Musselman and Minnick 2000, Grulke et al. 2004). Finally, isotope models used to partition ecosystem respiration are highly sensitive to nocturnal stomatal conductance because canopy conductance is a critical regulator of the stable carbon isotope signature of ecosystem respiration ($\delta^{13}C_R$) (Cernusak et al. 2004, McDowell et al. 2004).

Observations of nighttime water vapor exchange between plants and the atmosphere have been made through whole-tree sap flux measurements (Green et al. 1989, Hogg and Hurdle 1997, Benyon 1999), stomatal conductance measurements (Matyssek et al. 1995, Snyder et al. 2003) and through energy balance/Bowen ratio methods (Iritz and Lindroth 1994) in a range of habitats and species. Leaf-level gas exchange measurements are useful because they can easily detect the pres-

ence of nighttime stomatal conductance and reveal directly whether exchange of water between leaves and the atmosphere is occurring. However, scaling and sampling limitations make it difficult to assess the magnitude and timing of water exchange for the whole tree. The use of sap flux sensors allows for reliable estimates of daily whole-tree water use. Green et al. (1989) found that, on average, about one-fifth of the daily sap flux in kiwifruit occurred at night. Nighttime sap flux was found to be 5% of the total water use in a *Eucalyptus grandis* W. Hill ex Maiden plantation (Benyon 1999).

Measurements of nighttime sap flux do not necessarily indicate nighttime transpiration. The refilling of depleted water storage in the bole is a significant component of daily sap flux (Phillips et al. 2003). Based on measurements made with the heat pulse technique, Lopushinsky (1986) and Casparie et al. (1993) attributed nighttime sap flux to recharging depleted water in the xylem. However, the positive correlation between nighttime sap flow and vapor pressure deficit (D) suggests flow can be attributed to nighttime transpiration (Green et al. 1989, Hogg and Hurdle 1997). Oren et al. 2001 found that nighttime canopy conductance in *Taxodium distichum* L. is highly sensitive to D. Benyon (1999) concluded that measurements of nighttime sap flux in *Eucalyptus* could not have been the result of refilling of water stores because sap flux rates increased during the night after several hours of zero flow rates. Further, high rates of recharge would be expected following days with high cumulative sap flux, but observations of night flux occurred on nights following days with low sap flux.

The objective of this study was to examine nighttime sap flux in three species in a mixed deciduous forest through the use of whole-tree sap flux sensors as well as measurements of leaf-level stomatal conductance.

Methods

Study site and species

The study was conducted in the Prospect Hill tract of Harvard Forest, Petersham, MA, USA (42°32′ N, 72°10′ W, 340 m a.s.l.). The study site is a mixed deciduous stand dominated by paper birch (*Betula papyrifera* Marsh.), northern red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), black birch (*Betula lenta* L.), eastern hemlock (*Tsuga canadensis* L.) and eastern white pine (*Pinus strobus* L.). The site burned 50 years ago resulting in an even-aged hardwood forest today. The forest is about 20 m tall and during the growing season has a leaf area index between 2.8 and 3.3 (J. Hadley, Harvard Forest, MA, personal communication). Soils in this portion of the Prospect Hill tract are classified as Typic Dystrochrepts, well-drained, sandy loams derived from glacial till, with average mineral soil depth and rooting zone of 0.75 m (Alison Magill, University of New Hampshire, NH, personal communication). Mean annual temperature is 8.5 °C and the site receives 105 cm of rain and 150 cm of snow annually.

The trees selected for monitoring were located on Little Prospect Hill. The site is 1.0 km from the Fisher Meteorological Station. The station is equipped with environmental monitoring equipment to measure air temperature (T_a), relative humidity, precipitation and solar radiation. Air temperature and relative humidity were measured with CS500 temperature and relative humidity probes (Campbell Scientific, Logan, UT). Photosynthetically active radiation was measured with a LI-COR 190 SA quantum sensor (LI-COR, Lincoln, NE). The meteorological data were sampled at 10-s intervals and averaged and recorded at 60-min intervals. Meteorological data for use in this study were interpolated into 30-min intervals so as to match sap flux measurements.

Three representative trees of each of the dominant species, paper birch, red oak and red maple, were selected for study (Table 1). The selected trees were located within 10 m of a small access road. This allowed for canopy access using a mobile canopy access vehicle. The trees chosen were typical of the stand size class. Table 1 presents biometric data on the study trees.

Instrumentation and sampling

Constant-heat, sap flux sensors (Granier 1985) were installed in each tree at breast height and at the base of the live crown in accessible trees. Both the heated and reference probes were 20 mm long and contained a copper-constantan thermocouple junction. At breast height, a set of sensors was installed on opposite sides of each tree. One set of sensors was installed at the base of the live crown in the bole just below the live branches in all paper birch and red oak trees but only in one red maple

Table 1. Diameter at breast height (DBH), height, sapwood area and sapwood depth of the trees selected for study at Harvard Forest, MA.

Tree number	Species	DBH (cm)	Height (m)	Sapwood area (cm^2)	Sapwood depth (cm)
1	Paper birch	21.6	19.3	290.1	6.3
2	Paper birch	6.3	8.5	27.3	3.0
3	Paper birch	15.7	16.4	130.1	3.7
4	Red oak	15.0	14.3	38.1	0.9
5	Red oak	18.4	15.0	66.5	1.3
6	Red oak	21.2	18.4	78.0	1.3
7	Red maple	18.7	16.5	208.6	5.4
8	Red maple	8.6	9.7	49.7	3.6
9	Red maple	4.3	8.4	12.6	2.0

tree because of limited canopy access. The sensors were sealed in plastic containers with silicone caulk to protect them from precipitation and moisture. The sensors were also surrounded with reflective bubble wrap to prevent direct solar heating and minimize environmentally induced temperature variations.

As a measure of water exchange, sap flux (g H_2O m^{-2} sapwood area s^{-1}) was calculated based on an empirical calibration equation (Granier 1985). Granier found that:

$$u = 1.19 \times 10^{-6}(K^{1.23}) \tag{1}$$

where u is sap flux (m^3 m^{-2} s^{-1}) and K is related to the temperature difference between the two probes:

$$K = \frac{(\Delta T_m - \Delta T)}{\Delta T} \tag{2}$$

where K is sap flux index, ΔT is the temperature difference between heated and reference probe and ΔT_m is the temperature when there is no sap flux ($u = 0$).

Data were sampled every 10 s, averaged and recorded at 30-min intervals. Measurements of sap flux density were made from May to September in 2003 and 2004.

Partitioning into recharge and nighttime transpiration

Some proportion of the nighttime sap flux measured may be attributed to the recharge of depleted water stores. To assess the depletion and recharge of stored water, the 24-h sum of flux at the base of the live crown in each tree was normalized so that it equaled the 24-h sum of the flux at breast height. Assuming the quantity of stored water in the crown is small compared with stem storage (Waring et al. 1979), the normalized flux at the base of the live crown represented transpiration. The sums of instantaneous differences between flux at breast height and transpiration represented changes in stored water. Transpiration that exceeded flux at breast height represented water storage withdrawal. When flux at breast height exceeded transpiration, the excess water was refilling depleted water stores. Night was defined as hours during which solar radiation was less than 5.0 W m^{-2}. The sums of instantaneous changes in stored water were calculated for daytime and nighttime on each date during the 2003 growing season. Nighttime transpiration and recharge were calculated as percentages of the total 24-h sap flux.

This analysis assumes that 24-h sums of flux at the base of the live crown equal flux at breast height (Shulze et al. 1985, Pallardy et al. 1995, Loustau et al. 1996, Martin et al. 1997, Phillips et al. 1997, Goldstein et al. 1998, Maherali and Delucia 2001). This method does not account for the possibility of long-term depletion of tree water content. The implications of this assumption are discussed by Phillips et al. (2003). If net daily water content is decreasing, nighttime transpiration estimates may be greater than we estimated.

Nighttime gas exchange measurements

Leaf-level stomatal conductance and transpiration were mea-

sured with a LI-COR LI-6400 gas exchange system (LI-COR, Lincoln, NE) on a clear late-summer night beginning at 1500 h on September 1, 2004 and ending at 0800 h the following morning. Leaf-level measurements in the upper canopy of each species were made with a mobile canopy access vehicle. Three leaves from three branches in the upper canopy of each species were sampled every 3 h. The system was set up to closely match ambient environmental light, temperature and humidity conditions. At night, the measurement chamber was unilluminated (2100–0500 h).

Results

Sap flux remained elevated in paper birch on the night of September 1, 2004 when leaf gas exchange was measured (Figure 1), whereas sap flux ceased shortly after sundown in red oak and red maple. In the 24-h period beginning at 0500 h, 13% of the total daily sap flux at breast height occurred at night in paper birch compared with only 6.6% in red oak and 2.4% in red maple (Figure 2). Sap flux in paper birch on this night was slightly greater than the 2003 growing season mean and less than the seasonal mean in red oak and red maple (Table 2). Leaf-level measurements showed that transpiration re-
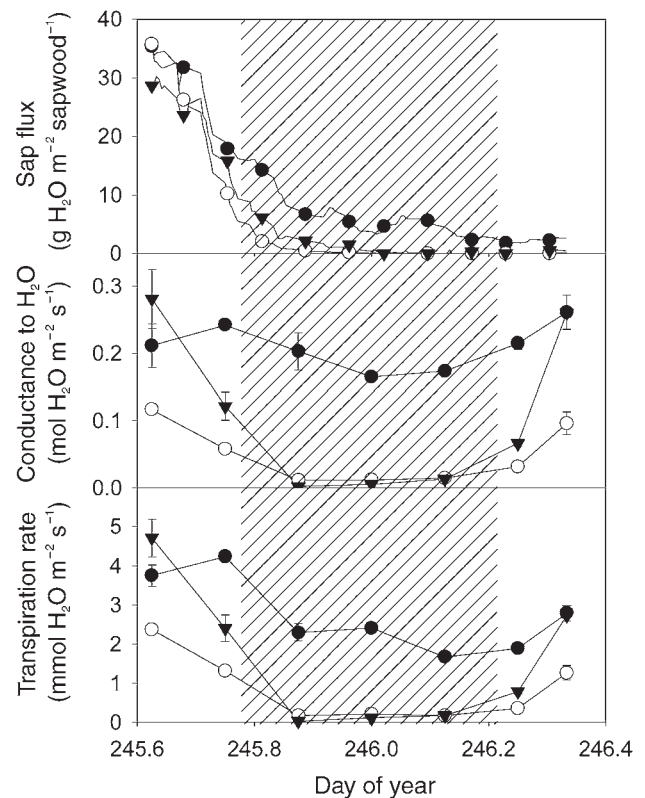

Figure 1. Sap flux at breast height, stomatal conductance and transpiration during the night of September 1, 2004 in paper birch (●), red oak (▲) and red maple (○). The shaded area represents nighttime. The sap flux values reported for each species are the means of three trees. Stomatal conductance and transpiration were measured at the leaf level.
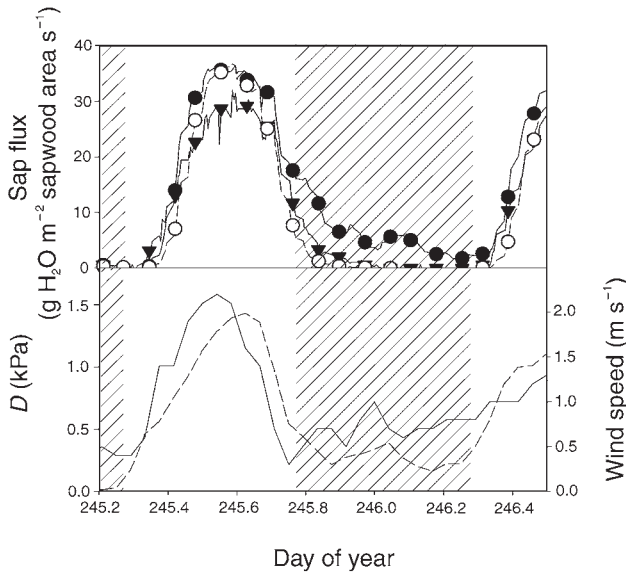
Figure 2. Diurnal sap flux at breast height in paper birch (●), red oak (▲) and red maple (○) for the dates when leaf gas exchange was measured (September 1–2, 2004). The sap flux values reported for each species are the means of three trees. Shaded areas represent night. Vapor pressure deficit (D) (dashed line) and wind speed (solid line) for these dates are also shown.

mained elevated in paper birch through the night and was about 50% of daytime rates (Figure 1). High nighttime stomatal conductance values were observed through the night in paper birch but not in red oak or red maple. Stomatal conductance dropped only 25% in paper birch after sunset, reaching a minimum of 0.17 mol H_2O m^{-2} s^{-1}. Stomatal conductance quickly dropped below 0.05 mol H_2O m^{-2} s^{-1} after sunset in red oak and red maple.

Sap flux at the location of upper sensors was greater than sap flux at breast height, indicating that all species utilized water stored in the bole for transpiration in the early hours of September 1, 2004 (Figure 3). Recharge in paper birch occurred during daytime and water stores were again depleted at night

Table 2. Summary of nighttime transpiration and recharge during the 2003 growing season. Night transpiration and recharge are calculated as the mean percent of total daily flux for the growing season. Abbreviation: ND = not detectable.

Tree number	Species	Night transpiration (%)	Recharge (%)
1	Paper birch	8.8	0.22
2	Paper birch	8.6	0.54
3	Paper birch	13.5	0.43
4	Red oak	ND	10.1
5	Red oak	ND	7.6
6	Red oak	ND	8.9
7	Red maple	ND	3.1
8	Red maple	ND	2.4
9	Red maple	ND	2.5

during nighttime transpiration. Recharge did not occur at night in paper birch, whereas the bole was recharged during the night in red oak and red maple. In paper birch, the nighttime flux at the base of the live crown, which represents nighttime transpiration, was 23% of the total 24-h flux, whereas nighttime flux at breast height amounted to only 13% of total 24-h flux.

On two consecutive nights (August 23 and August 24) during the 2003 growing season, paper birch trees had unusually high nighttime sap fluxes (Figure 4). The raw sap flux signal in red oak and red maple showed a stable baseline on the nights of August 23 and 24; however, in paper birch, the baseline was depressed on the nights of August 23 and August 24. This depressed baseline indicates nighttime sap flux, whereas the stable baselines of red oak and red maple indicate sap flow reached zero during the night. The environmental variables that drive nighttime transpiration are also shown in Figure 4. Vapor pressure deficit (D) remained elevated on August 23 and 24. Nighttime sap flux was highly correlated with D dur-
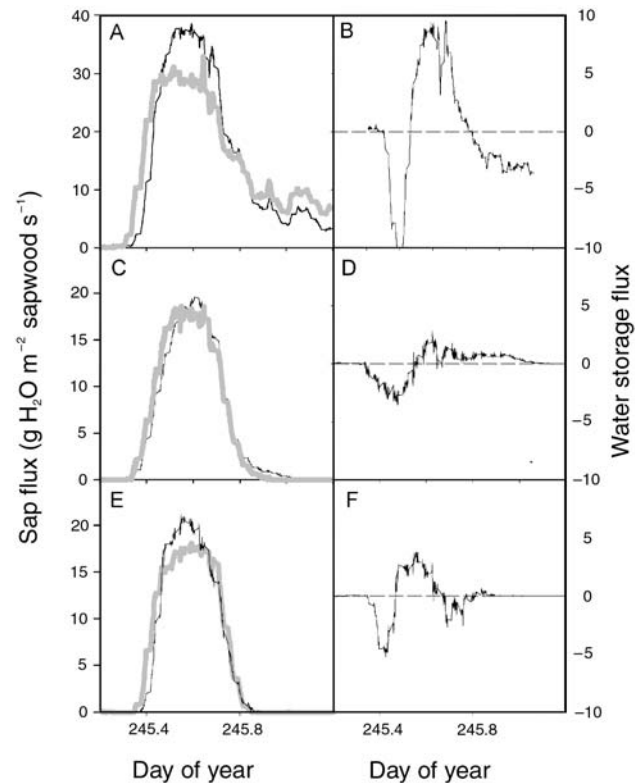

Figure 3. Time course of sap flux in a sample tree of paper birch (A), red oak (C) and red maple (E) on September 1, 2004. Gray lines represent the normalized flux at the base of the live crown and black lines represent sap flux at breast height. The flux at the base of the live crown was normalized to equal the 24-h sum of sap flux at breast height. The depletion and recharge of stored water in the bole is shown for the paper birch (B), red oak (D) and red maple (F) trees. The water storage flux is calculated as the difference between sap flux at the base of the live crown and sap flux at breast height. Values greater than zero indicate periods of recharge and negative values indicate periods of water withdrawal.
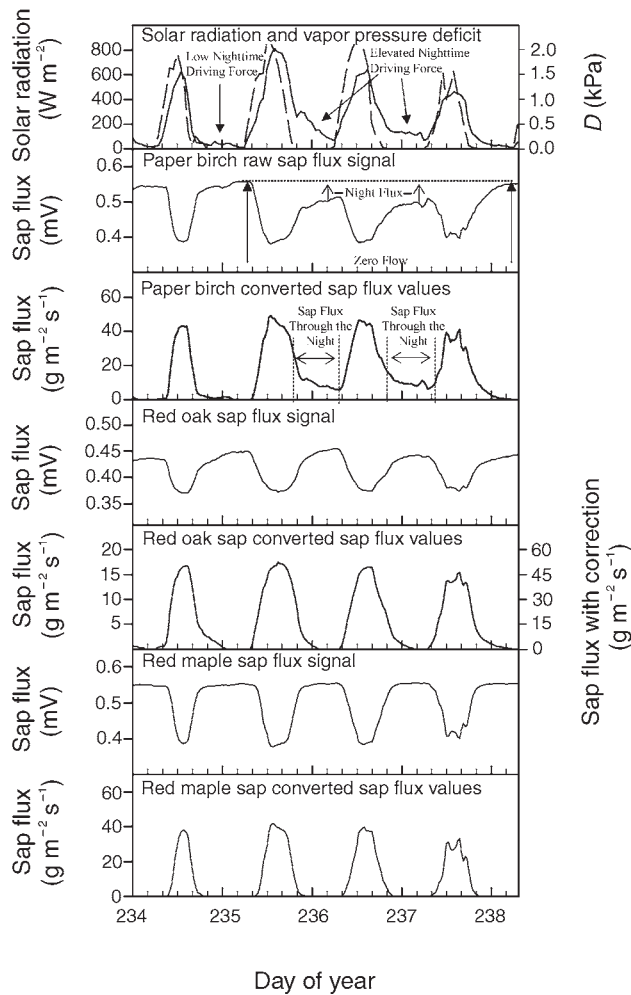
Figure 4. Daily patterns of solar irradiance, vapor pressure deficit (*D*) and sap flux at breast height in paper birch, red oak and red maple from Day 234 to Day 238 (August 22–26, 2003). The sap flux values reported for each species are means for three trees. Throughout the night on Days 235 and 236, sap flux remained elevated in paper birch. Also shown are patterns in the raw sap flux signal. The corrected values in red oak account for the proportion of sensors not located in conducting sapwood (Clearwater et al. 1999).

ing the month of August in paper birch (Figure 5). The relationship between sap flux and *D* at night did not appear to differ from the relationship during the day. The relationship between nighttime sap flux and *D* in red oak and red maple differed significantly from the daytime relationship.

Direct evidence of nighttime transpiration was obtained from leaf gas exchange measurements made on the night of September 1 only. However, other indicators suggest that nighttime transpiration occurred in paper birch throughout the growing season. For example, immediately after sunset on August 16, sap flux in paper birch had almost stopped (Figure 6). Several hours after sunset, there was a rise in *D* and, thereafter, sap flux in paper birch increased during the night in response to the increase in *D*. The nighttime increase in *D* had no effect on sap flux in red oak or red maple, which remained at zero. Another indicator of nighttime transpiration is in the pattern of
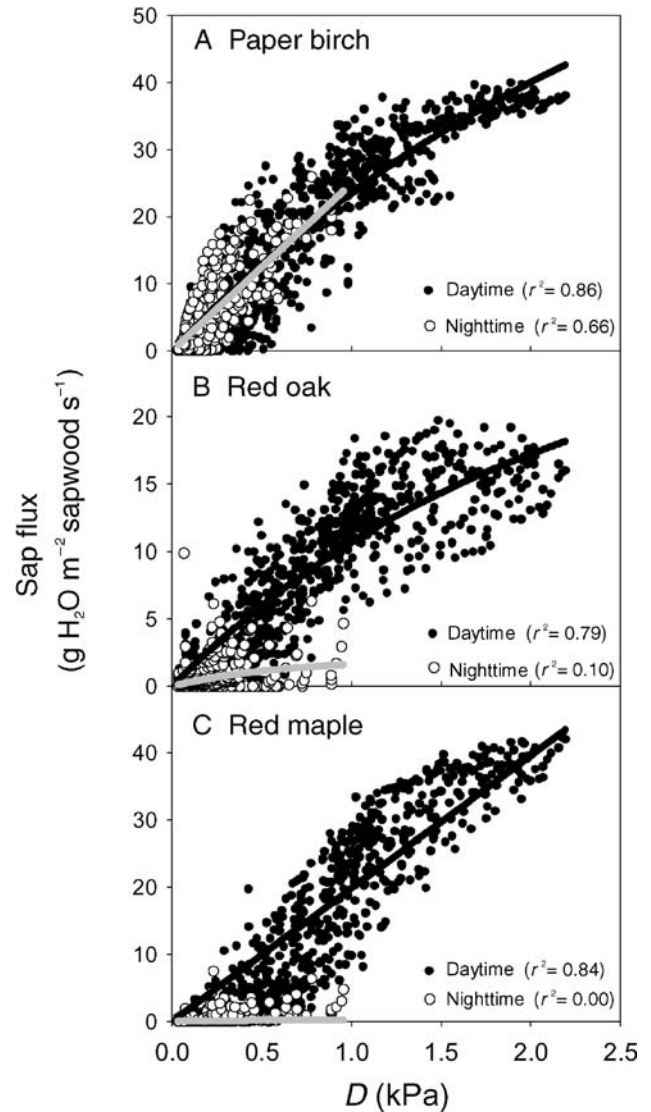

Figure 5. Sensitivity of sap flux to vapor pressure deficit (*D*) measured at the base of the live crown in paper birch (A), red oak (B) and red maple (C) during August 2003. Sensitivity at night ($\bigcirc$) and during the day ($\bullet$) are shown. The best fit exponential relationship ($y = a(1 - e^{-bx})$) is shown for both daytime (black line) and nighttime (gray line).

recharge. Recharge would be expected to be greatest on nights following high daytime sap flux. The cumulative sap flux on the night of September 1 was much greater than on nights following days with greater cumulative sap fluxes during daylight hours. The correlation between *D* and nighttime transpiration during the month of August strongly suggests nighttime transpiration occurs (Figure 5).

Nighttime sap flux was common in all species during the growing season (Table 2), but the magnitude of nighttime sap flux varied among species. Over the course of the growing season, nighttime sap flux, averaged across trees, represented 10.7% of the total sap flux at breast height in paper birch, 8.7% in red oak and 2.7% in red maple. Partitioning sap flux into
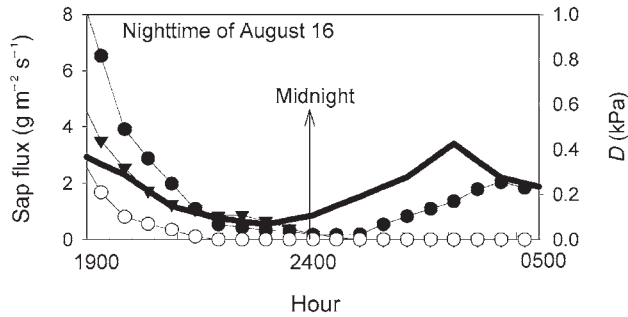
Figure 6. Mean sap flux at breast height in paper birch (●), red oak (▲) and red maple (○) during the night of August 16. Paper birch responded to the increase in vapor pressure deficit (D) (thick line), whereas red oak and red maple did not.

nighttime recharge and transpiration resulted in 10.3% of the total daily flux in paper birch being attributed to nighttime transpiration. The high percentage of nighttime flux attributed to transpiration is itself a function of the use of stored water to supply nighttime transpiration (Figure 3). Although the partitioning method indicated nighttime transpiration occurs in red oak and red maple, the flux was attributed to recharge because negligible nighttime transpiration was detected when leaf-level measurements were taken on a night with high evaporative demand.

Discussion

This study is one of few to quantify interspecific changes in nighttime stomatal conductance in co-occurring tree species. Substantial nighttime stomatal conductance has been observed in another species of *Betula*, namely *Betula pendula* Roth (Günthardt-Goerg et al. 1993, Matyssek et al. 1995). In this study, average nighttime transpiration in paper birch as a proportion of daily water flux (10.3%) is comparable with values published for other species. Nighttime water use was 5% of total daily water use in *Eucalyptus grandis* (Benyon 1999), 12.8% in *Populus trichocarpa* Torr. & Gray × *P. deltoids* Bartr ex. Marsh (Kim 2000), 6% in *Malus sylvestris* L. and 19% in *Actinidia deliciosa* Chev. (Green et al. 1989). On nights with extremely high wind speeds or D, or both, the percent of daily water use occurring at night was 53% in *Populus* (Kim 2000), 15% in *Malus* and 30% in *Actinidia* (Green et al. 1989).

In previous studies, measurements of nighttime sap flux were made with similar Granier-style sensors, but nighttime sap flux was not partitioned between recharge and transpiration. The discharge and recharge of stored water may represent a substantial component of the daily sap flux in plants (Goldstein et al. 1998, Phillips et al. 2003). Incorporating an estimate of nighttime sap flux associated with recharge, as we have done in this study, provides a more reliable estimate of the proportion of daily water use attributable to nighttime transpiration. There are some limitations to our partitioning method, however, because sap flux in terminal branches was not measured. In red oak and red maple, the low stomatal con-

ductance on a night with elevated D (Figure 1) and the low sensitivity of sap flux to D at night (Figures 5 and 6), suggest that nighttime transpiration is negligible in these species. The nighttime sap flux measured in the sensors positioned at the base of the live crown thus likely represented the recharge of depleted water stores in the terminal branches and leaves of the canopy. In paper birch, however, our partitioning method provides a reliable estimate of nighttime transpiration because sap fluxes at the base of the live crown exceeded sap fluxes at breast height, indicating a withdrawal of stored water (Figure 3).

Environmental variables, such as D and wind speed, affected the timing and magnitude of nighttime transpiration in paper birch (Figure 2). Iritz and Lindroth (1994) used an energy balance/Bowen ration method to measure evaporation in a *Salix viminalis* L. stand and found nighttime evaporation is controlled mainly by D and ventilation. Hogg and Hurdle (1997) found that nighttime sap flux was correlated with D in *Populus tremuloides* Michx. Nighttime D and wind speed explained the variation in nighttime sap flux in *Eucalyptus* (Benyon 1999), *Malus*, and *Actinidia* (Green et al. 1989). Contrary to these results and our results for paper birch, D did not adequately explain the variation in nighttime sap flux in red oak and red maple (Figure 5). This is consistent with greater allocation of nighttime sap flux to refilling of depleted stores in these species.

Although we found clear evidence of substantial nighttime transpiration in paper birch, we also obtained evidence suggesting that some nighttime transpiration is itself dependent on the use of stored water. Paper birch had a greater proportional decrease in sap flux than in stomatal conductance and transpiration on the night of September 1 (Figure 1). The discrepancy between sap flux and leaf-level measurements was probably not associated with the enhanced mixing of air in the measurement chamber, because estimates of bulk aerodynamic conductance at night were 10–20 times greater than stomatal conductance (data not shown), indicating the canopy was well coupled to the air. Instead, the smaller proportional decrease in water flux at the leaf level from day to night is consistent with the pattern in the bole where sap flux was greater at night in sensors positioned at the base of the live crown than at the base of the tree (Figure 3). This indicates that nighttime transpiration is to some degree supported by stored water in woody tissues. If nighttime use of stored water is also derived from the crown itself, this would represent a stored water reservoir that we have neglected and may reconcile the difference between our leaf-level and sap flux measurements. Additionally, the discrepancy may be associated with our sampling method because only leaves in the upper canopy were measured.

Hydrologic significance of nighttime transpiration

The sensitivity of nighttime transpiration and stomatal conductance in paper birch to D and wind speed raises a question of hydrologic significance—how often do environmental conditions occur that can drive nighttime sap flux? Evaluating the

relationship of nighttime transpiration to D in paper birch (Figure 5) shows that a low D may be sufficient to drive transpiration. Vapor pressure deficits are typically low at night in New England forests; nevertheless, elevated D occurs on many nights. Additionally, on any typical night, D is substantial in the hours following sundown. Sap flux during this time is often assumed to be recharge; however, our analysis indicates substantial nighttime transpiration occurs during these hours in paper birch.

Paper birch is significant on a continental scale because it is one of the most widely distributed species in North America (Burns and Honkala 1990). The species is at the southern limit of its range in Massachusetts and one of many species found in New England deciduous forests, so nighttime transpiration in paper birch is unlikely to have a drastic impact on ecohydrological function. However, the species is a significant component of Canadian forests, particularly in British Columbia where there are about 250,000 ha of birch forests (Massie et al. 1994). Given the species composition of Canadian forests, further examination of paper birch and nighttime environmental conditions in Canada is warranted. Additionally, global climate change has led to a shift in nighttime versus daytime temperatures. In northern latitudes, night temperatures increased more than day temperatures in the 20th century (Folland et al. 2001) and unless atmospheric humidity increases, this may lead to elevated evaporative demand at night. Thus, in species like paper birch, increased evaporation demand during the night may alter the diurnal balance of forest water use.

If climate change leads to an increased nighttime D, the data in Figure 5A indicate that nighttime sap flux in paper birch may increase with increasing D as it does during the daytime. However, care must be taken in extrapolating the sensitivity of sap flux to D at night to the higher values currently observed only during the day, because analysis of nighttime sensitivity of maximum canopy stomatal conductance in paper birch to D does not support this simple interpretation. When we used a boundary line analysis to isolate maximum canopy stomatal conductance (expressed as the exactly proportional quantity J_s/D) versus D (Oren et al. 2001), we found that the sensitivity of maximum canopy stomatal conductance to D is heightened at night. For example, at a D of 0.15 kPa, canopy stomatal conductance is the same at night as during daytime with optimal light conditions. However, at a D of 1.0 kPA, canopy stomatal conductance at night is only 16% of daytime values. The increase in nighttime sensitivity in paper birch is consistent with observations in other species found to transpire at night including *Salix viminalis* (Iritz and Lindroth 1994), *Populus tremuloides* (Hogg and Hurdle 1997) and *Taxodium distichum* (Oren et al. 2001).

Ecophysiological differences

Our results highlight the presence of ecophysiological differences among species and further illustrate how species composition can impact ecosystem function. Nighttime transpiration is often considered an unnecessary cost to a plant. With no prospect for carbon assimilation through photosynthesis, water lost at night is often considered wasted. Nighttime transpi-

ration counters the notion that plants maximize carbon gain and minimize water loss (Cowan 1977). The differences we observed among species raise the ecophysiological question: why does paper birch have greater nighttime transpiration than red oak and red maple under the same environmental conditions?

Incomplete closure of stomata at night may provide an ecological advantage. Trees in the northeast typically grow in environments with low D at night and low drought risk (Paulson et al. 1991). Under such conditions, partial stomatal closure may confer an advantage by enabling trees to continue photosynthesis up until sundown and resume higher photosynthetic rates earlier in the morning than competitors. This may allow trees to maximize the ratio of photosynthesis to transpiration and avoid lags between assimilation and increased stomatal conductance (Oren et al. 2001). However, this strategy has risks during periods of drought. It has been found that red maple (Oren and Pataki 2001) and red oak (Abrams 1990, Pataki and Oren 2003) are relatively drought tolerant in southeastern deciduous forests. Our results are consistent with these findings because the lack of nighttime transpiration in red oak and red maple would contribute to drought tolerance in these species.

Based on measurements of only three species, we speculate that the water use characteristics of paper birch may be a function of its successional status. Paper birch is an early successional species and may preferentially accommodate high growth rates over water conservation. Paper birch is shade intolerant, whereas red oak is intermediate and red maple is shade tolerant (Burns and Honkala 1990). Tobiessen (1982) observed dark stomatal opening in shade-intolerant trees but not in shade-tolerant trees and concluded that dark opening of stomata is a function of relative shade tolerance. The results of our study are consistent with this conclusion: we found the highest nighttime transpiration and stomatal conductance in paper birch, the most shade intolerant of the species studied, whereas red maple, the most shade tolerant of the three species, had the lowest nighttime transpiration and stomatal conductance.

Functional sapwood contains living parenchyma cells that require oxygen for respiration. Gansert et al. (2001) speculated that respiration in wood parenchyma is limited by insufficient oxygen supply. Diffusion through intercellular gas spaces may be insufficient to supply oxygen to deep parenchyma cells, particularly in trees with deep sapwood. Substantial oxygen can be delivered to xylem parenchyma cells in the aqueous state through sap flux (Mancuso and Marras 2003). Gansert (2003) found that 60% of the oxygen delivered to the inner depths of sapwood in *Betula pubescens* Ehrh. was through dissolved oxygen in the xylem rather than through a gaseous pathway. The study also revealed that oxygen concentrations in the xylem reached minimum values after sundown. Nighttime transpiration may play a vital role in delivering oxygen during this period of the diurnal cycle when oxygen concentrations can be critically low. By delivering oxygen for parenchyma respiration in the deep sapwood of paper birch trees, nighttime transpiration indirectly enhances nutrient transport

because parenchyma cells function in nutrient transport in trees. Nighttime transpiration may also directly provide a benefit to paper birch by allowing greater mass flow nutrient uptake by roots compared with other species.

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