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Sap flux–upscaled canopy transpiration, stomatal conductance, and water use efficiency in an old growth forest in the Great Lakes region of the United States

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[1] Combining sap flux and eddy covariance measurements provides a means to study plant stomatal conductance and the relationship between transpiration and photosynthesis. We measured sap flux using Granier-type sensors in a northern hardwood-dominated old growth forest in Michigan, upscaled to canopy transpiration, and calculated canopy conductance. We also measured carbon and water fluxes with the eddy covariance method and derived daytime gross primary production (GPP). The diurnal patterns of sap flux and canopy transpiration were mainly controlled by vapor pressure deficit (D) and photosynthetically active radiation (PAR). Daily sums of sap flux and canopy transpiration had exponential relationships to D that saturated at higher D and had linear relationships to PAR. Sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniesis*) had higher sap flux per unit of sapwood area than eastern hemlock (*Tsuga canadensis*), while sugar maple and hemlock had higher canopy transpiration per unit of leaf area than yellow birch. Sugar maple dominated canopy transpiration per ground area. Canopy transpiration averaged 1.57 mm d^{-1}, accounting for 65% of total evapotranspiration in the growing season. Canopy conductance was controlled by both D and PAR, but the day-to-day variation in canopy conductance mainly followed a negatively logarithmic relationship with D. By removing the influences of PAR, half-hourly canopy conductance was also negatively logarithmically correlated with D. Water use efficiency (WUE) had a strong exponential relationship with D on a daily basis and approached a minimum of 4.4 mg g^{-1}. WUE provides an alternative to estimate GPP from measurements of sap flux.

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1. Introduction

[2] Ecosystem and atmospheric models are increasingly coupled to incorporate carbon, water, and energy exchanges between the atmosphere and ecosystems [*Foley et al.*, 2000; *Sellers et al.*, 1997]. Carbon and water fluxes are not only closely linked in large-scale atmospheric processes that influence climate systems and climate change, but also coupled at small scales, from forest stands to leaf levels. Carbon uptake through photosynthesis and water loss through transpiration are finely regulated by stomatal conductance and optimized for maximum photosynthesis at the cost of minimum transpiration [*Cowan*, 1977; *Farquhar et al.*, 2002; *Hari et al.*, 1986]. These physiological processes are responsive to environmental conditions such as humidity, light, temperature, and soil water content.

[3] The eddy covariance method provides continuous and simultaneous measurements of carbon, water and energy exchange between ecosystems and the atmosphere on sub-daily timescales [*Aubinet et al.*, 2000; *Baldocchi*, 2003]. However, water flux measurements from eddy covariance combine transpiration and evaporation on an ecosystem level and thus cannot provide information on transpiration by species. Transpiration rates per unit of ground area may vary with species and leaf area. For example, conifers and deciduous trees may differ in transpiration rates because of differences in xylem anatomy, leaf longevity, leaf area, and length of growing season [*Ewers et al.*, 2002]. Stem sap flux measurements from individual trees provide a method to estimate canopy transpiration [*Granier*, 1987; *Granier and Loustau*, 1994]. This method also allows estimation of canopy stomatal conductance and its response to environmental factors on an hourly timescale [*Ewers and Oren*, 2000; *Kostner et al.*, 1992; *Phillips and Oren*, 1998]. Combining sap flux measurements and eddy covariance

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measurements provide a means to study stomatal conductance in response to environmental drivers and the relationship between photosynthesis and transpiration.

[4] Stomatal regulation of water vapor loss and carbon dioxide gain and stomatal responses to environmental conditions have been long and extensively studied [e.g., *Jarvis*, 1976; *Lange et al.*, 1971]. The multiple controls of humidity, light, temperature and soil moisture on stomatal conductance vary spatially with ecosystem types and temporally with different timescales. Stomatal conductance may respond to changes of leaf water potential resulting from transpiration, rather than directly to environmental conditions [*Mott and Parkhurst*, 1991]. However, the mechanism of this regulation is not fully understood [*Franks*, 2004; *Oren et al.*, 1999]. It has been reported that the proportionality between the sensitivity of canopy stomatal conductance (G_S) to ln$D$ and the G_S at vapor pressure deficit (D) = 1 kPa averages ~0.6 [*Oren et al.*, 1999]. However, a series of filters for removing other factors have to be often used to obtain this relationship [*Ewers et al.*, 2005]. This makes modeling G_S on the basis of environmental conditions difficult.

[5] Water use efficiency (WUE), defined in this paper as photosynthesis divided by transpiration, describes the linkage between water and carbon flux. We may connect water and carbon flux measurements and determine one flux from another companion flux on the basis of the close relationship between plant hydraulic and biochemical properties [*Katul et al.*, 2003]. Because it is relatively easier to continuously measure water flux of individual trees, particularly through sap flux measurements, than carbon flux from individual trees or from the stand level, and because water use efficiency is a relatively conservative plant property responding to the environment [*Tanner and Sinclair*, 1983], deriving canopy carbon assimilation from water flux provides a new approach for carbon studies [*Moren et al.*, 2001]. It has been reported that WUE is inversely proportional to vapor pressure deficit (D) [*Berbigier et al.*, 2001; *Dewar*, 1997; *Lindroth and Cienciala*, 1996]. However, studies on WUE by combining simultaneous eddy covariance measurements and scaled sap flux measurements are limited.

[6] Old growth forests provide a successional end-member and a future trend for current second-growth forests. It has been proposed that photosynthesis decreases while respiration increases as forests age, resulting in the decline in forest growth and a neutral NEE for old growth forests [*Kira and Shidei*, 1967; *Odum*, 1969]. However, there are few empirical data to support this explanation for decrease in growth [*Ryan et al.*, 2004]. Hydraulic resistance-induced stomatal constraint may be an important reason for observed decrease in growth [*Gower et al.*, 1996]. While carbon flux in old growth forests has been intensively studied [e.g., *Desai et al.*, 2005; *Goulden et al.*, 1998; *Harmon et al.*, 2004; *Saleska et al.*, 2003; *Tang et al.*, 2006], studies on transpiration and the relationship between transpiration and photosynthesis from old trees and old growth forests are relatively limited. *Kostner et al.* [2002] studied transpiration in mature stands of Norway spruce (*Picea abies*) varying in age from 40–140 years in Germany, and found water use efficiency, derived from upscaled sap flux and stem growth, declined with stand age. On the basis of sap flux measurements, *Phillips et al.* [2002] found that old (450 years) Douglas fir (*Pseudotsuga menziesii*) trees in the Pacific Northwest, USA had less crown-averaged stomatal conductance than younger trees because of hydraulic resistance related to tree height. *Irvine et al.* [2004] reported that old (~250 years) ponderosa pine (*Pinus ponderosa*) stands in the Pacific West, USA had similar site-averaged transpiration but much less transpiration per unit leaf area than younger stands, similar to the findings of *Ewers et al.* [2005] for 150-year-old boreal black spruce (*Picea mariana*) forests. *Ewers et al.* [2006] compared transpiration from a single species, sugar maple (*Acer saccharum*), in an old growth, second-growth, and thinned second-growth stands in the Great Lakes region. However, we have not seen studies focused on transpiration in old growth forests in the Great Lakes region.

[7] The objectives of this research were (1) to measure sap flux in an old growth hemlock–northern hardwood forest in the Great Lakes region; (2) to upscale sap flux to canopy transpiration, estimate canopy stomatal conductance, and examine transpiration and stomatal responses to environmental conditions; (3) to calculate water use efficiency and its responses to environmental conditions by combining sap flux measurements and eddy covariance measurements; and (4) to discuss the possibility to use the response of water use efficiency to environmental conditions to predict daily carbon assimilation on the basis of transpiration.

2. Materials and Methods

2.1. Site Description

[8] The study area is located on the boundary of the Sylvania Wilderness and Recreation Area of the Ottawa National Forest in the upper peninsula of Michigan, USA (46°14′31″N, 89°20′52″W). Average elevation is 542 m. The climate is northern continental, characterized by short growing seasons and long, cold winters. Annual average precipitation and air temperature measured in a nearby weather station over 1961–1990 is 896 mm and 3.9°C, respectively. Precipitation is evenly distributed in all seasons. Dominant upland soils are moderately well-drained, coarse or sandy loam spodosols [*Pastor and Broschart*, 1990].

[9] The 8500 ha Sylvania Wildness is one of only two large tracts of old growth forest remaining in the Great Lakes region. The Sylvania Wilderness is a hemlock–northern hardwood forest comprising 3–30 ha patches dominated by either eastern hemlock (*Tsuga canadensis*) or sugar maple (*Acer saccharum*), with yellow birch (*Betula alleghaniesis*), basswood (*Tilia americana*), and ironwood (*Ostrya virginiana*) also present in the overstory [*Frelich et al.*, 1993; *Pastor and Broschart*, 1990]. The forest is a representative of late successional forests and has long-term compositional stability.

[10] The study site, about a hectare in area and within the typical footprint area of an eddy covariance flux tower [*Desai et al.*, 2005], was a hardwood-dominated old growth stand. Sugar maple comprised 71% of trees, in addition to hemlock (14%), yellow birch (7%), and basswood and ironwood (8%). Trees ranged from 0–350 years old, but old trees dominated the canopy. Average canopy height was

approximately 22 m. Stand density was 439 trees/hectare for all trees greater than 7 cm in diameter at breast height (DBH), with an average DBH of 25.9 cm and basal area of 33.1 m^2 ha^{-1} measured in 2002. Maximum leaf area index (LAI) averaged 4.1 m^2 m^{-2} measured with an LAI-2000 (LI-COR, Inc., Lincoln, NE) in 2002 across the site. Leaf debris and coarse woody debris covered the ground. Tree seedlings and saplings, maidenhair fern (*Adiantum spp.*), jack in the pulpit (*Arisaema triphyllum*), and *Lycopodiaceae spp.* were scattered under the closed tree canopy.

2.2. Sap Flux Measurements

[11] We measured sap flux per unit of conducting xylem area (J_S) in stem xylem of 48 trees including 19 sugar maple trees, 14 yellow birch, and 15 hemlock in the growing season of 2002 (days 160–261) and 2003 (days 152–264). Stem sap flux measurements were made at 1.4 m above the ground at two positions toward the north and south of each tree using Granier-type sensors [*Granier*, 1987]. The sensors were inserted into the xylem at 20 mm depth. J_S (g H_2O m^{-2} s^{-1}) was calculated on the basis of the empirical relationship of *Granier* [1987]:

$$J_S = 119\left(\frac{\Delta T_M - \Delta T}{\Delta T}\right)^{1.231}, \tag{1}$$

where ΔT_M (°C) is the maximum temperature difference between heated and unheated reference sensors occurring at night during the course of a day, and ΔT (°C) is the temperature difference between the heated and unheated sensors at any given time. J_S is zero when ΔT_M is measured.

[12] Equation (1) assumes that natural temperature gradients between sensors are small [*Lundblad et al.*, 2001]. Fifteen-minute averages of temperature difference data were computed and stored in data loggers (CR-10x, Campbell Scientific Inc., Logan, UT, USA). The average of J_S in the north and south position represented the mean of the azimuthal pattern. We did not measure J_S across the stem section, but we assumed that J_S in the sapwood deeper than 20 mm from the cambium was 50% of J_S in the outer 20 mm that we measured, following the sharp radial decline pattern in J_S in inner 20 mm of the xylem reported by *Pausch et al.* [2000], *Ewers and Oren* [2000] and *Schäfer et al.* [2000]. Thus we computed mean J_S on the basis of the above radial pattern for each tree and then mean J_S for each of the three species.

[13] Canopy transpiration (E_C) was upscaled from mean J_S by multiplying it with sapwood area per unit ground area [*Ewers et al.*, 1999; *Oren et al.*, 1998]:

$$E_C = J_S \frac{A_S}{A_G}, \tag{2}$$

where A_S is the total sapwood area of the study site, and A_G is the total area of the site.

[14] We used an exponential saturation equation to analyze the relationship between J_S (or E_C) and D [*Ewers et al.*, 2001]:

$$J_S = a\left(1 - e^{-bD}\right), \tag{3}$$

where a and b are fitted coefficients. J_S saturates at a when D approaches $+\infty$.

2.3. Stand Measurements

[15] Tree diameter at breast height (DBH) was read from band dendrometers. Sapwood depth and bark thickness were measured from tree cores taken from all 48 trees with sap flux sensors. Sapwood depth was determined visually from tree cores. The total sapwood area from the site was estimated from the relationship between measured sapwood area and DBH, combined with a 100% inventory of DBH at the site.

[16] Site-averaged LAI was measured using LAI-2000 (LI-COR Inc, Lincoln, NE, USA). LAI for each species was estimated from litterfall measurements. We placed 10 baskets, each with an area of 1969 cm^2, to collect litterfall. Litterfall was sorted by species. Subsamples were taken for individual leaf area measured with an optical scanner and digital summation (SigmaScan, SPSS, Chicago, IL, USA), and dry biomass was weighed to calculate specific leaf area (SLA = leaf area/dry mass). LAI for each species in the stand was estimated on the basis of SLA and total dry biomass from litterfall. Litterfall-based LAI is a measure of maximum LAI for deciduous trees during the growing season. We assumed a constant leaf area during all seasons for hemlock, guided by the lack of seasonality in litterfall. Therefore hemlock LAI was calculated from litterfall data multiplied by 3 years of leaf longevity [*Barnes and Wagner*, 1981].

2.4. Ecosystem Carbon, Water, and Meteorological Measurements

[17] Fluxes of CO_2 and water vapor were measured from a tower at 36 m aboveground at the center of the study site, described in detail by *Desai et al.* [2005]. High-frequency (10 Hz) three-dimensional wind speed was measured by a sonic anemometer (CSAT-3, Campbell Scientific Inc., Logan, UT, USA). CO_2 and water at 10 Hz were measured by an infrared gas analyzer (LI-6262, LI-COR, Lincoln, NE, USA). Gases were drawn by a diaphragm pump (model UN89, KNF Neuberger Inc., Trenton, NJ, USA). Storage flux calculations and calibration of high-frequency CO_2 were obtained by measuring low-frequency (3 min average, 21 min interval), high-precision (±0.5 ppm) CO_2 mixing ratios at seven levels between the ground and flux measurement height [*Desai et al.*, 2005].

[18] Turbulent fluxes of CO_2 and water were calculated at half-hourly intervals as the covariance of vertical wind velocity and the scalar factors, while considering the lag and spectral corrections [*Berger et al.*, 2001]. Net ecosystem exchange (NEE) at the surface was calculated as the sum of the turbulent flux at sensor height and the storage term below sensor height. NEE data were screened for weak turbulence friction velocity ($\sim$0.05 m s^{-1}) at night and nonrepresentative footprints contaminated by lakes and wetlands [*Desai et al.*, 2005]. Nighttime NEE was assumed to be a measurement of ecosystem respiration, and was extrapolated to all times by using a moving-window temperature response function as described by *Cook et al.* [2004] and *Desai et al.* [2005]. Daytime gross primary production (GPP) was then calculated as a sum of ecosystem respiration and NEE.

[19] In addition to flux measurements, a full suite of micrometeorological measurements were made at this site, including total photosynthetically active radiation (PAR; model PAR-LITE, Kipp and Zonen Inc., Saskatoon, SK, Canada), air temperature and humidity (model HMP45C platinum resistance temperature and capacitive polymer humidity probe, Campbell Scientific Inc., Logan, UT, USA), total precipitation (model TE525WS tipping bucket rain gauge and CS705 snowfall adapter, Campbell Scientific Inc., Logan, UT, USA), and soil water contents at 5, 10, 20, 50, and 100 cm using time domain reflectometers (CS615, Campbell Scientific, Inc., Logan, UT, USA). Vapor pressure deficit (D) in the canopy was calculated from humidity and air temperature at 20 m height [*Buck*, 1981]. Half-hourly averages of these micrometeorological measurements were computed and stored on a computer to coincide with the flux measurements. Daytime mean D was calculated from the length with daylight hours determined by measurements of PAR (PAR > 0).

2.5. Canopy Conductance

[20] Assuming an aerodynamically well mixed canopy and similar leaf and air temperature, mean canopy stomatal conductance (G_S) can be calculated as a simplified form of the Penman-Monteith equation as suggested by *Monteith and Unsworth* [1990]:

$$G_S = \frac{\gamma(T) \cdot \lambda(T) \cdot E_L}{C_p \cdot \rho(T) \cdot D}, \tag{4}$$

where γ is the psychrometric constant, λ is the latent heat of vaporization of water, C_p is the specific heat of air, ρ is the density of liquid water, T is the temperature, D is the vapor pressure deficit of the canopy air, and E_L is the canopy transpiration per unit of leaf area (= E_C/LAI) upscaled from sap flux measurements by assuming there are negligible time lags between dynamics of sap flux and environmental variables.

[21] The four temperature-dependent terms in equation (4), γ, λ, C_p, and ρ, can be aggregated into a single parameter, K_G (kPa m^2 kg^{-1}):

$$\begin{aligned} G_S &= K_G \frac{E_L}{D} \\ K_G &= 115.8 + 0.4226T, \end{aligned} \tag{5}$$

where G_S is the canopy stomatal conductance (mm s^{-1}), E_L is canopy transpiration per leaf area (g m^{-2} s^{-1}), and D (kPa) is vapor pressure deficit in the canopy. *Phillips and Oren* [1998] showed that the errors for this aggregation are negligible.

[22] G_S responds to multiple environmental variables. The responses of G_S have been formulated by *Jarvis* [1976] using a series of multiplicative functions:

$$G_S = G_{S\max} f(PAR) f(D) f(T_A) f(\Psi_L), \tag{6}$$

where G_{smax} is the maximum G_S, T_A is the air temperature, and ψ_L is the leaf water potential. Within a range of solar radiation and air temperature and with unlimited soil moisture conditions, the response of G_S to D can be isolated and analytically expressed as a logarithmic equation [*Oren et al.*, 1999]:

$$G_S = G_{Sref} - m \ln D, \tag{7}$$

where G_{Sref} is a reference conductance at D = 1 kPa, and m is the stomatal sensitivity of G_S in response to ln$D$.

2.6. Water Use Efficiency

[23] The ratio of daily sum of GPP to E_C was defined as water use efficiency (WUE). We used an exponential decay equation to analyze the relationship between WUE and D (or PAR):

$$WUE = a_0 + a_1 e^{-a_2 D}, \tag{8}$$

where a_0, a_1 and a_2 are fitted coefficients and WUE minimizes at a_0 when D approaches $+\infty$.

[24] Statistical analyses and regressions were conducted in S-PLUS (version 6.0, Insightful Corp., Seattle, WA, USA) and Sigmaplot (version 8.0, SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Sap Flux per Unit of Sapwood Area

[25] We randomly chose 2 days to show the typical diurnal patterns of sap flux within our time series data in two growing seasons. Figure 1 shows the diurnal patterns of vapor pressure deficit (D), photosynthetically active radiation (PAR), and mean sap flux per unit of sapwood area (J_S) for three species in two representative sunny days in the summers of 2002 and 2003. J_S peaked between 13 h (local standard time) and 15 h on day 192 of 2002 with peak values of 28.9, 24.7, 20.8 g m^{-2} s^{-1} in sugar maple, yellow birch, and hemlock, respectively. J_S peaked between 12.5 h and 14.5 h on day 152 of 2003 with peak values of 27.3, 36.4, 21.7 g m^{-2} s^{-1} in sugar maple, yellow birch, and hemlock, respectively. J_S peaked approximately 1–3 hours later than PAR, but 2–4 hours earlier than the peak of D.

[26] Exponential saturation equations fitted daily sums of J_S against daytime mean D (Figure 2a). The parameters for exponential saturation equations (equation (3)) for sugar maple, yellow birch and hemlock are shown in Table 1. The difference in r^2 suggested that the correlations between J_S and D for sugar maple and yellow birch are higher than for hemlock. The coefficient a suggests the maximum J_S that a species may have. Overall, sugar maple and yellow birch had higher J_S than hemlock. Sugar maple had slightly lower J_S than yellow birch.

[27] Daily sums of J_S were also controlled by daily sums of PAR with a linear relationship fitting the data (Figure 2b). The parameters of the linear equations for three species are shown in Table 1. The sensitivity (slope of response) of J_S to PAR was the lowest for hemlock while J_S responded similarly to PAR for sugar maple and yellow birch.

3.2. Scaling Sap Flux to Canopy Transpiration

[28] We found that measurements of sapwood area of a tree were linearly correlated with DBH. The intercepts are −292.2, −236.1, −188.7 cm^2, slopes are 29.3, 22.3, 22.1 cm, and r^2 are 0.92, 0.75, 0.73 (p all less than 0.001)

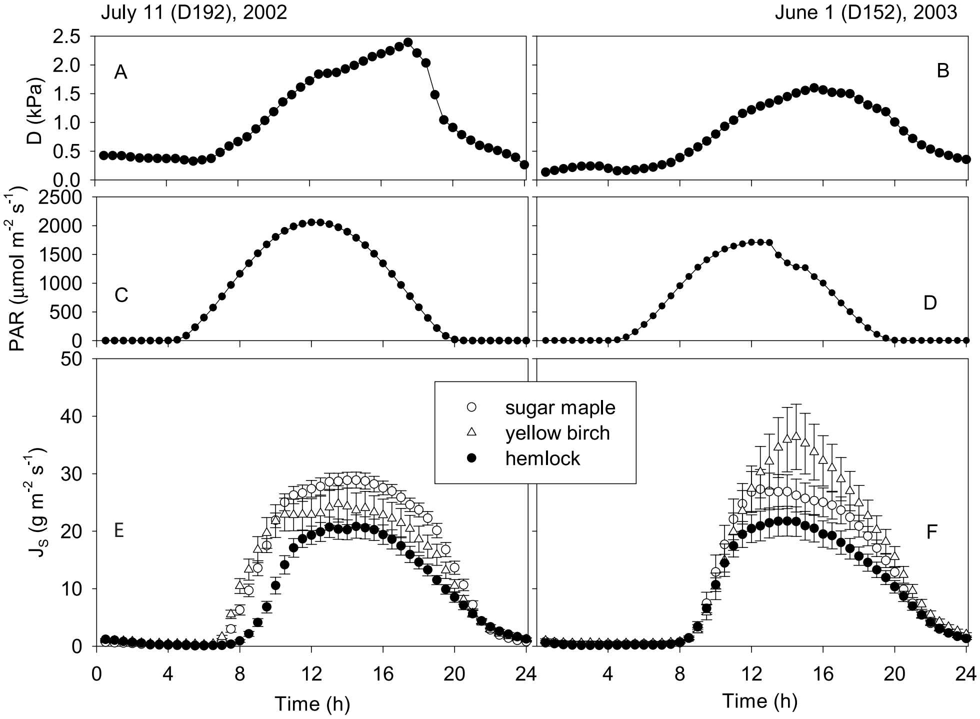

Figure 1. Diurnal patterns of (a and b) D, (c and d) PAR, and (e and f) Js for three species in 2 typical days in the summers of 2002 and 2003. The error bars in Figures 1e and 1f are standard errors.

for sugar maple, yellow birch, and hemlock, respectively. This linear relationship was used to estimate total sapwood area over the site on the basis of DBH measurements. If DBH < 12 cm, sapwood area of a tree was assumed to be the stem area excluding the bark. Sapwood area and leaf biomass and area for three dominant species are shown in Table 2. The total sapwood area was 19.65 cm^2 m^{-2}, or 59% of basal area. Sugar maple accounted for 70% of total sapwood area. Among the three species, the sapwood to leaf area ratio was the largest for hemlock and smallest for yellow birch.

[29] Table 2 also shows dry leaf biomass, leaf area index (LAI), and specific leaf area (SLA) for sugar maple, yellow birch, and hemlock, on the basis of litterfall data averaged from years 2002 and 2003. The total surface LAI measurement based on litterfall data was larger than the optical site-average measurement based on the instrument LAI-2000 (4.1 m^2 m^{-2}). Because of the dominant stem numbers, sugar maple had the largest leaf biomass and LAI. Yellow birch had higher SLA than sugar maple. Hemlock had the lowest value of SLA because of its small and relatively thick leaves.

[30] Canopy transpiration per unit of leaf area (E_L) on the daily basis varied substantially in the growing season, with minimums of 15.8, 14.2, and 13.7 g m^{-2} d^{-1} and maximums of 363.4, 262.3, 422.8 g m^{-2} d^{-1} for sugar maple, yellow birch, and hemlock, respectively (Figures 3a and 3b). The averages of E_L over the growing season of 2002 and 2003 were 220.6, 161.5, 226.8 g m^{-2} d^{-1} for sugar maple, yellow birch, and hemlock, respectively. Opposite to the order of Js, hemlock had the highest E_L, followed by sugar maple and yellow birch, because both Js and the sapwood to leaf area ratio determined E_L. Hemlock had a low sapwood to leaf area ratio compared with sugar maple and yellow birch.

[31] Total daily canopy transpiration per ground area (E_C) also varied substantially from a minimum of 0.13 mm d^{-1} to a maximum of 2.43 mm d^{-1} in the growing season (Figures 3c and 3d). The averages of E_C for sugar maple, yellow birch, and hemlock were 1.15, 0.26, 0.16 mm d^{-1}, respectively. The average of total E_C was 1.58 mm d^{-1} in 2002 and 1.56 mm d^{-1} in 2003 with 1.57 mm d^{-1} averaged over the growing seasons of 2002 and 2003.

[32] We plotted daily sums of E_C against daytime mean D and daily sums of PAR (Figure 4). As the upscaled J_S (Figure 2) and aggregation of three species, E_C responded to D by an exponential saturation curve with $r^2 = 0.81$ and the coefficients $a = 2.17$, $b = 2.27$ (Figure 4a). Similar to the relationship between J_S for each species and PAR, upscaled and aggregated E_C also showed a linear relationship with PAR (Figure 4b) with $r^2 = 0.75$, slope = 0.034, and intercept = 0.16.

[33] We did not find the control of soil moisture on E_C since an average of 896 mm precipitation was almost evenly distributed in all seasons at this site. The average of volumetric soil water content at 10 cm was 0.19 m^3 m^{-3} with standard deviation of 0.03 m^3 m^{-3} in the growing season of 2002 and 2003. As a result of the favorable soil moisture level to plants, the correlation between soil moisture and E_C was not significant ($r^2 < 0.1$).

[34] Canopy transpiration at the site upscaled from sap flux was compared to evapotranspiration measured by the water flux between the canopy and the atmosphere using eddy covariance measurements. The average evapotranspiration was 2.43 mm d^{-1} over the growing season of 2002 and 2003. If these two methods are comparable, transpira-

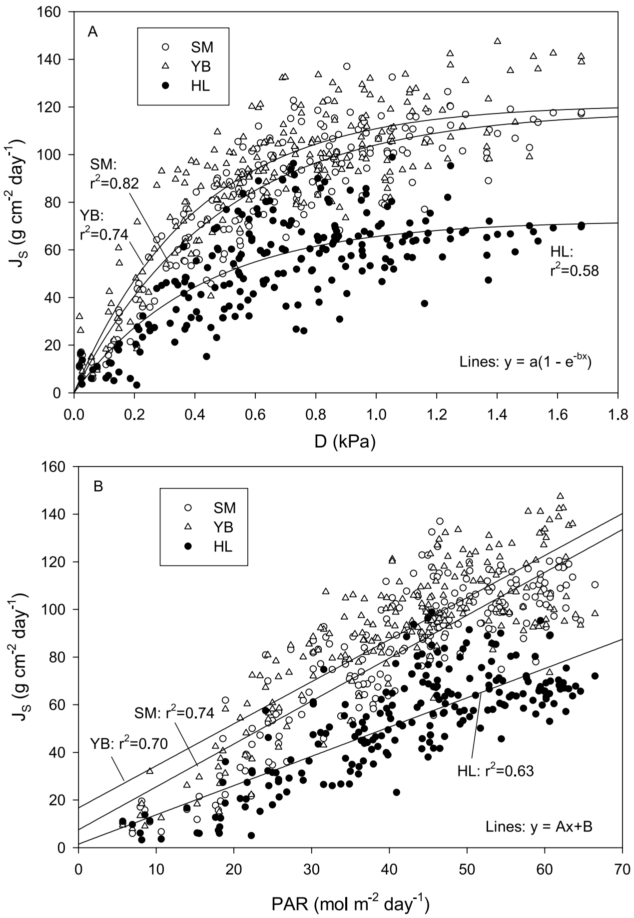

Figure 2. Daily sum of *Js* as a function of (a) daytime mean *D* and (b) daily sum of PAR for sugar maple (SM), yellow birch (YB), and hemlock (HL). Lines are exponential saturation curves ($y = a(1 - \exp(-bx))$ (Figure 2a) and linear curves (Figure 2b).

tion accounted for 65% of total evapotranspiration. The difference between evapotranspiration and transpiration was from soil and tree evaporation, which averaged 0.86 mm d^{-1}, accounting for 35% of total evapotranspiration in the growing season. The average precipitation during these periods was 2.59 mm d^{-1}. The surplus of water at 0.16 mm d^{-1} either permeated into groundwater, stored in the soil, or transported as surface runoff.

Table 1. Parameters for the Exponential Saturation Equation $J_S = a(1 - \exp(-bD))$ and the Linear Equation $J_S = A \times \text{PAR} + B$ for Sugar Maple, Yellow Birch, and Hemlock

Species	Sugar Maple	Yellow Birch	Hemlock
	J_S Versus D		
a	118.6	121.0	72.3
b	2.1	2.5	2.4
r^2	0.82	0.74	0.58
p	<0.001	<0.001	<0.001
	J_S Versus PAR		
A	1.8	1.8	1.2
B	7.5	16.7	1.5
r^2	0.74	0.70	0.63
p	<0.001	<0.001	<0.001

Table 2. Sapwood Area per Unit Ground Area, Sapwood to Leaf Area Ratio, Dry Leaf Biomass per Unit Ground Area, Leaf Area Index (LAI), and Specific Leaf Area (SLA) for Sugar Maple, Yellow Birch, and Hemlock

Species	Sugar Maple	Yellow Birch	Hemlock	Sum
Sapwood area per unit ground area, cm^2 m^{-2}	13.82	2.90	2.93	19.65
Sapwood to leaf area ratio, cm^2 m^{-2}	2.65	1.78	4.26	–
Leaf biomass, g m^{-2}	186.19	48.14	66.65	300.98
LAI, m^2 m^{-2}	5.21	1.63	0.69	7.53
SLA, cm^2 g^{-1}	279.80	338.85	102.92	–

[35] We compared daily sums of transpiration (E_C) upscaled from sap flux measurements and total evapotranspiration (E_T) measured with the eddy covariance method on days with and without rain (Figure 5). Days with rain were separated from without rain because evaporation occurred from leaves and stems in addition to the soil during the rainy days. On days without rain, a power function fitted to the data. On rainy days, E_C and E_T were linearly correlated.

3.3. Canopy Stomatal Conductance

[36] Figure 6 shows two groups of diurnal patterns of stomatal conductance (G_S), D and PAR over five typical sunny days in 2002 and 2003. Daily peak G_S increased from 0.57 mm s^{-1} on day 192 to 0.82 mm s^{-1} on days 195 and 196 of 2002, and decreased from 0.70 mm s^{-1} on day 152 to 0.48 mm s^{-1} on days 154, 155 and 156 of 2003. The peak G_S generally occurred between 10–12 h except day on 156 of 2003. These diurnal patterns of G_S correlated well with PAR with a similar peak time.

[37] Because of multiple controls on G_S, particularly the strong control of PAR at midday, the diurnal patterns of G_S did not show a negative correlation with *D* during the course of a day. However, daytime mean values of G_S negatively correlated with daytime mean *D*. Within the representative 5 days, we found that daytime mean G_S increased from 0.35 mm s^{-1} on day 192 to 0.52 mm s^{-1} on day 195 and decreased to 0.50 mm s^{-1} on day 196 in 2002. Correspondingly, daytime mean *D* decreased from 1.37 kPa on day 192 to 0.94 kPa on day 195 and then increased to 1.05 kPa on day 196 in 2002. A similar correlation pattern also occurred in 2003. Daytime mean G_S decreased from 0.39 mm s^{-1} on day 152 to 0.29 mm s^{-1} on days 155 and 156. At the same time, *D* increased from 0.97 kPa on day 152 to 1.51 kPa on day 156 in 2003.

[38] We plotted daytime mean G_S against *D* over two growing seasons (Figure 7). We selected G_S for the days when $D > 0.1$ kPa for any 15-min daytime period to exclude errors associated in the calculation of G_S using equation (5). G_S was strongly correlated with *D*, indicating the control of *D* on the day-to-day variation of G_S. A logarithmic function, $G_S = 0.48–0.37\ln D$, fitted the data with $r^2 = 0.74$, $p < 0.0001$. Although G_S was correlated with PAR during the course of a day, we did not find a significant relationship between mean G_S and PAR on the daily scale.

[39] To examine the response of G_S to *D* on a half-hour basis, we used a filter of $D = 0.6$ kPa to exclude G_S data for $D < 0.6$ kPa and thus decreased errors associated in computing half-hourly G_S, as suggested by *Ewers and Oren* [2000]. Figure 8 shows the responses of G_S to *D* separated by three

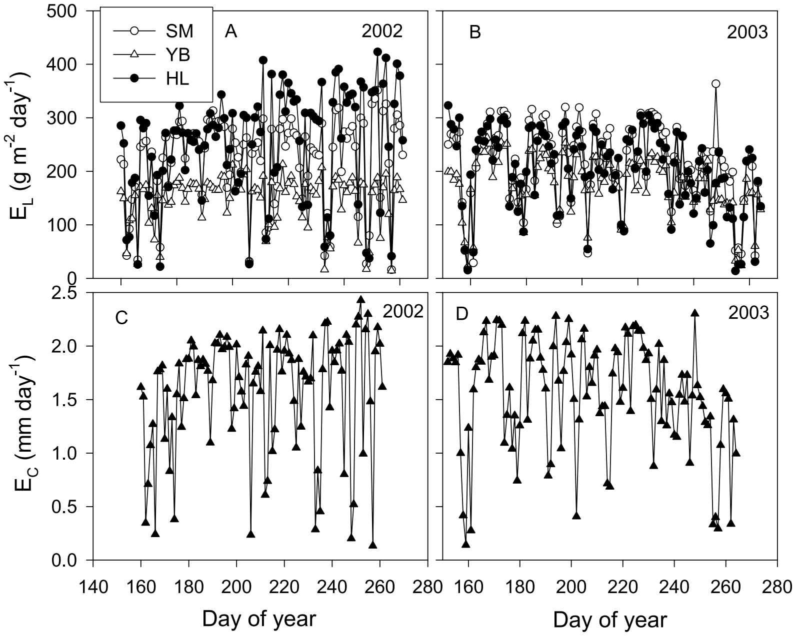

Figure 3. (a and b) Daily sum of E_L for sugar maple (SM), yellow birch (YB), and hemlock (HL) and (c and d) total E_C per unit of ground area between June and September of 2002 and 2003.

PAR groups, PAR (1) > 1000 μmol m^{-2} s^{-1}, PAR (2) = 500–1000 μmol m^{-2} s^{-1}, and PAR (3) <500 μmol m^{-2} s^{-1}. Three negatively logarithmic lines fitted the data with r^2 = 0.51, 0.76, 0.53 for group (1), group (2) and group (3), respectively. The coefficients of the three lines indicate that the correlation was the highest and G_S was the most sensitive to D for the range of PAR at 500–1000 μmol m^{-2} s^{-1}. The sensitivity of G_S to D decreased when PAR was greater than 1000 μmol m^{-2} s^{-1} or less than 500 μmol m^{-2} s^{-1}.

3.4. Water Use Efficiency

[40] We did not find a strong correlation between GPP and D (r^2 = 0.29). However, water use efficiency (WUE) on the daily basis shows a strong relationship with daytime mean D (Figure 9a). An exponential decay function with r^2 = 0.72 fitted this relationship. WUE dramatically increased when D < 0.3 kPa, with a peak measured value of 25.8 mg g^{-1}. WUE was stable when D was larger than 0.6 kPa and approached a minimum of 4.4 mg g^{-1}, indicating conservative WUE when D was high.

[41] WUE also had an exponential decay relationship with PAR with r^2 = 0.52 (Figure 9b). Either PAR or D may be used to predict WUE, but D was a better indicator. PAR and D on the daily basis also correlated with r^2 = 0.61.

4. Discussion

4.1. Controls of Sap Flux and Transpiration

[42] Diurnal patterns and day-to-day variations of J_S and E_C were both controlled by D and PAR. During the course of a day, the peak time of J_S and E_C, falling midway between that of D and PAR, suggests a simultaneous control of D and PAR on J_S and E_C. The saturation of daily sums of J_S and E_C at high D (>1.2 kPa) suggests that at the lower range of D, D is a major control on J_S and E_C because the gradient of water vapor between inside the stomata and ambient air drives transpiration. When D was high, J_S and

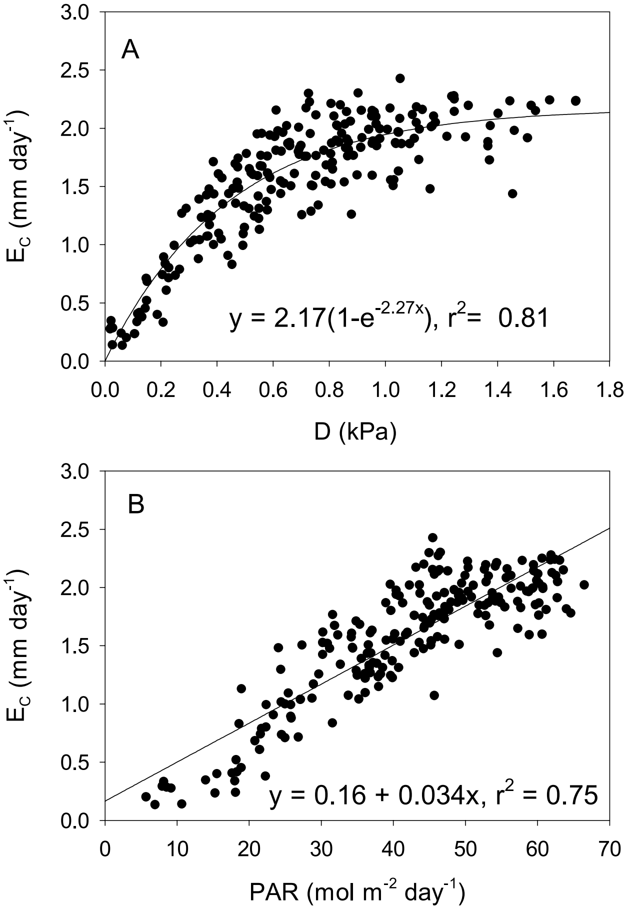

Figure 4. Daily sum of E_C as a function of (a) daytime mean D and (b) daily sum of PAR. An exponential saturation curve fits the data of E_C versus D, and a linear curve fits the data of E_C versus PAR.

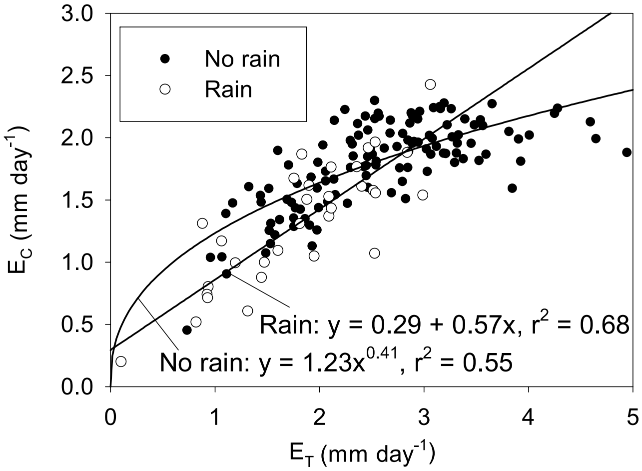

Figure 5. Comparison of daily sum of transpiration (E_C) upscaled from sap flux measurements and total evapotranspiration (E_T) measured with the eddy covariance method on days with and without rain. A power curve fits the data without rain, and a linear curve fits the data with rain.

E_C saturated because of decreased stomatal conductance, despite the favorable water vapor gradient for transpiration. J_S and E_C did not saturate at high PAR on the daily basis, consistent with many other studies [e.g., *Ewers et al.*, 2005]. Within our observation range of PAR between 5 and 70 mol m^{-2} d^{-1}, J_S responded linearly to PAR.

4.2. Transpiration Versus Evapotranspiration

[43] Our result of 65% of E_C/E_T in the growing season is consistent with a recent study that reported 66% of E_C/E_T in a northern hardwood forest in northern lower Michigan [*Bovard et al.*, 2005] and less than a result of 75% when E_T was high in the summer in a temperate forest in North Carolina [*Schäfer et al.*, 2002]. Our E_C/E_T in this old growth forest with ample moisture is less than that in a Mediterranean-type old growth forest in Washington with E_C/E_T of 90% derived from overstory and understory eddy covariance measurements of water flux in dry summer due to low soil moisture and evaporation [*Unsworth et al.*, 2004].

[44] The ratio of E_C/E_T in this paper is derived from two independent methods, both of which suffer from errors during measurements and upscaling processes. Errors associated with eddy covariance measurements have been widely discussed [e.g., *Baldocchi*, 2003]. In addition to measurement errors in J_S, errors of E_C are from upscaling processes, namely, the weighted mean J_S and estimation of sapwood area (equation (2)). Among these error sources, the average of J_S from measurements is a critical one because of the radial pattern of J_S across the stem section. There is no consensus of the radial pattern of J_S for each species because of difficulties in measuring J_S across the stem. This paper used a simple bisection method to average J_S of each tree. Detailed description of J_S as a function of radial tree depth is subject to further investigation.

[45] The power function between E_C and E_T on days without rain (Figure 5) suggests that when E_C was high (>1.5 mm d^{-1}) associated with high D and low G_S, E_T (including evaporation and transpiration) increased faster than E_C, indicating that evaporation from soil is not constrained at high D while E_C is constrained by stomatal closure. The departure of E_C from E_T at high values is in agreement with *Bovard et al.* [2005], *Schäfer et al.* [2002], and *MacKay et al.* [2002], but in disagreement with a simple linear relationship reported by *Oren et al.* [1998]. On rainy days with very low D, E_C was linearly correlated with E_T, indicating little physiological regulation of E_C.

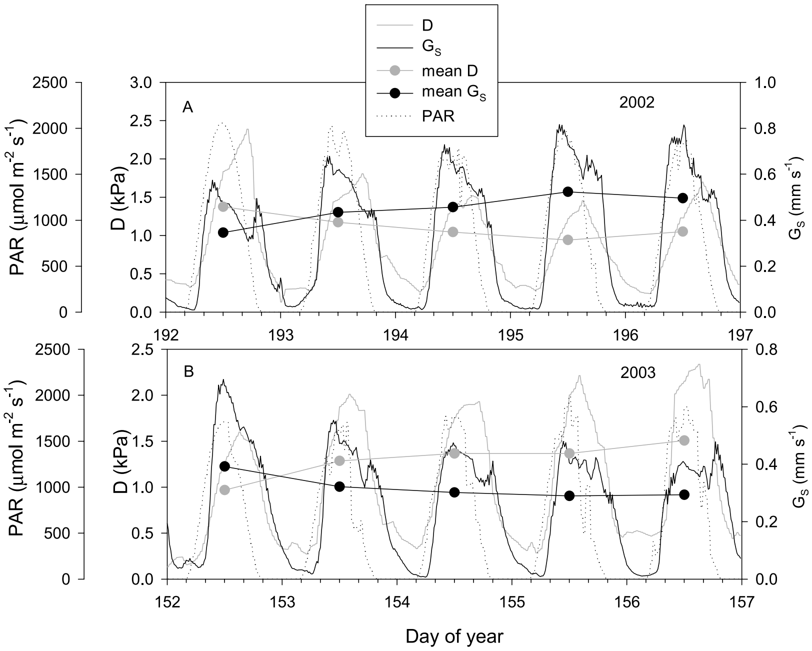

Figure 6. Diurnal patterns of G_S, PAR, and D over 5 typical sunny days between (a) days 192 and 196 in 2002 and (b) days 152 and 156 in 2003 and daytime mean D and G_S over these days.

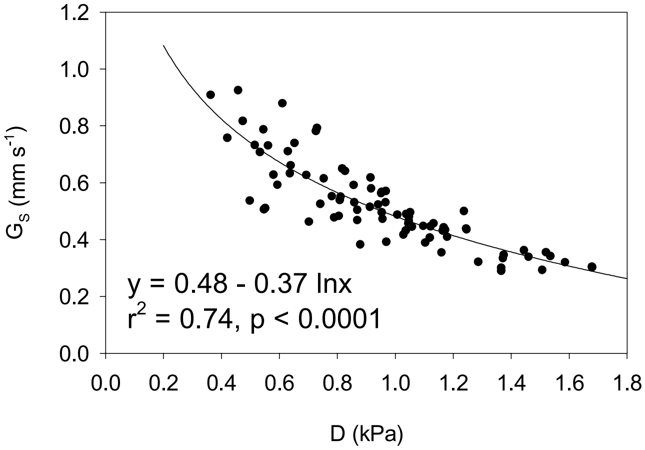

Figure 7. Daytime mean G_S responding to daytime mean D. A negatively logarithmic curve fits the data.

[46] E_C and E_L for sugar maple in this old growth forest (~350 years old) were lower than those in a mature (~70 years old) second-growth northern hardwood (the Willow Creek site) [*Ewers et al.*, 2006] and in a mature aspen stand [*Ewers et al.*, 2002] both in northern Wisconsin with a similar climate, indicating lower stomatal conductance and hydraulic conductance in old growth forests than those in mature forests. Our E_C from sugar maple was also much lower than that observed in a 30–60-years-old sugar maple stand in New York (5.89 mm d^{-1} in the growing season) [*Dawson*, 1996]. Lower transpiration in old growth forests is consistent with potentially lower GPP in old growth forests [*Ryan et al.*, 2004; *Tang et al.*, 2006]. Inconsistently, averaged daily E_C in this old growth forest was larger than that in another mature (~70 years old) northern hardwood (0.8 mm d^{-1}; the Hay Creek site) in northern Wisconsin [*Ewers et al.*, 2002]. E_C in this old growth forest was slightly larger than averaged E_C of 1.47 mm d^{-1} using sap flux measurements while smaller than E_C of 2.08 mm d^{-1} computed from overstory and understory eddy covariance measurements in June and July in an old growth forest in Washington [*Unsworth et al.*, 2004].

4.3. Controls of Stomatal Conductance

[47] G_S was controlled both by D and PAR. During the course of a day, G_S peaked simultaneously with PAR following the peak of PAR despite high D at midday. However, G_S often showed a second lower peak in late afternoons (Figure 6). This midday depression in G_S may be caused by peak D at midday, which correlates with high E_C, low leaf water potential and thus low G_S. The control of D on G_S was more substantial on the daily scale. The daily mean G_S negatively responded to an increase in mean D with a logarithmic form. By removing the influence of PAR by grouping G_S on the basis of PAR, we also found negatively logarithmic relationship between D and G_S on the half-hour basis.

[48] The mechanism of stomatal regulation is not fully understood, but evidence shows that stomatal conductance responds to leaf water potential as a result of transpiration rates, which are correlated with D [*Mott and Parkhurst*, 1991]. When D increases, stomata close in response to decreasing leaf water potential and increasing transpiration. Thus G_S and D are negatively correlated.

[49] The diurnal pattern of G_S, calculated from E_C, indicated that G_S was not immediately close to 0 after sunset (Figure 6). This may suggest a time lag in stomatal response to light. Stomata may not immediately close after sunset with transpiration processes occurring at dark [*Oren et al.*, 2001]. Alternatively, calculated positive G_S at night may reflect extended sap flow to replace water loss from storage in the stem. E_C was upscaled from measurements of J_S at 1.4 m above the ground while the average canopy height was 22 m. It may take a few hours for water transported from lower stems to the canopy, which results in a time lag between J_S and real E_C. Even though E_C may not occur at early night, there is still water flow at 1.4 m

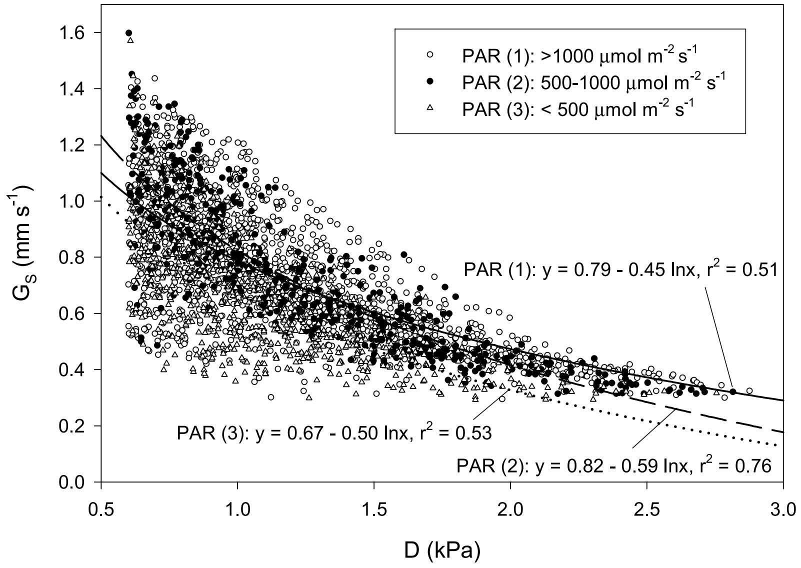

Figure 8. Responses of G_S to D on a half-hour basis separated by three PAR groups. Three negatively logarithmic curves fit the data.

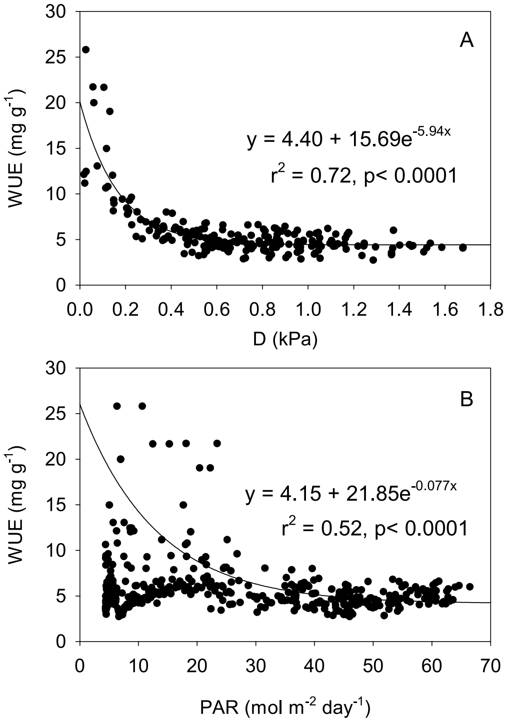

Figure 9. Water use efficiency (WUE) on a daily basis responding to (a) daytime mean D and (b) daily sum of PAR. Fitted lines are exponential decay curves ($y = a_0 + a_1 \exp(-a_2 x)$).

measured as J_S for compensating the water loss from the canopy [*Granier and Loustau*, 1994; *Phillips et al.*, 1997]. Finally, nonzero G_S at night may be due to errors associated with the measurements of J_S and E_L. The small error in measuring ΔT_M for calculating J_S (equation (1)) may be amplified when we calculate G_S at low E_L and low D (equation (5)) at night [*Ewers and Oren*, 2000].

[50] We have found that an exponential saturation equation may be used to describe the relationship between J_S, E_L or E_C with D on the daily basis (equation (3)). Combining equation (3) and equation (5) we have

$$G_S = K_G \frac{a}{D}\left(1 - e^{-bD}\right). \tag{9}$$

[51] We used nonlinear regression to fit our daily data, which resulted in parameters $a = 0.0044$, $b = 2.64$, $r^2 = 0.78$. Equation (9) may be used to estimate the day-to-day variation of canopy stomatal conductance without measurements of transpiration. We also found that the logarithmic function can directly describe the relationship between G_S and D (equation (7)). Within our measurement range of daytime mean D between 0.2 and 1.8 kPa, two fitted lines using the forms of equation (7) and equation (9) were almost identical while equation (7) is a simpler expression for describing the response of G_S to D.

[52] We may ignore the effect of PAR on G_S when we investigate the relationship between G_S and D on the daily timescale (Figure 7), but we have to take into account the effect of PAR for the instantaneous response of G_S to D on the half-hourly basis since the diurnal variation of PAR is more significant in affecting G_S than daily mean PAR. Three groups of PAR data result in three logarithmic lines fitting G_S vs. D (Figure 8). The proportions of m/G_{Sref} are 0.57, 0.72 and 0.74 for PAR greater than 1000, between 500–1000, and less than 500 μmol m^{-2} s^{-1}, respectively. Across a large range of ecosystem types and environmental conditions, m/G_{Sref} is approximately 0.6, indicating the stomatal regulation of water potential to prevent xylem cavitation [*Ewers et al.*, 2005; *Oren et al.*, 1999]. Our results indicated that m/G_{Sref} increased with the decrease in PAR. During the maximum PAR, m/G_{Sref} was the closest to 0.6 among three PAR groups. The stomatal sensitivity of G_S response to ln$D$, m, is the highest for the PAR between 500–1000 μmol m^{-2} s^{-1}, and the lowest for the PAR greater than 1000 μmol m^{-2} s^{-1}. G_{Sref} increased from 0.67 mm s^{-1} at PAR < 500 μmol m^{-2} s^{-1} to 0.82 mm s^{-1} at PAR = 500–1000 μmol m^{-2} s^{-1}, and slightly down to 0.79 mm s^{-1} at PAR > 1000 μmol m^{-2} s^{-1}. This is in agreement with *Schäfer et al.* [2000] that reported a saturation of G_{Sref} at PAR = 600 μmol m^{-2} s^{-1}.

4.4. Modeling GPP Using WUE

[53] Sap flux measurements provide an alternative to directly estimate photosynthesis on the basis of calculation of water use efficiency (WUE) and the correlation between WUE and D. The correlation can be expressed as an exponential decay function (Figure 9 and equation (8)). Therefore GPP can be modeled on the daily scale as

$$GPP = E_C\left(a_0 + a_1 e^{-a_2 D}\right). \tag{10}$$

[54] We found that this model explained 24% of variation in GPP derived from eddy covariance measurements, when we plotted modeled GPP against measured GPP. Although WUE had a high correlation with D, WUE-derived GPP had a relatively low correlation with measured GPP. The reason was probably due to the influence of WUE at high D on GPP. When D was high, the small variation in WUE was amplified by high E_C, resulting in a relatively high error in modeling GPP.

[55] WUE also had a good relationship with PAR. However, since D and PAR were positively correlated at our site ($r^2 = 0.61$), it is possible for us to derive water use efficiency or GPP solely from D that may have confounded effect of PAR.

[56] It is advantageous to use E_C and WUE to estimate GPP given the difficulty in continuously measuring photosynthesis at the leaf level and then upscaling to the canopy level compared with sap flux measurements. Studies on WUE and its control and variation have been conducted since 1950s for crop yield and water supply analyses [e.g., *Bierhuizen and Slatyer*, 1965]. Recently, it has been attempted to use WUE to model carbon exchange in forests [*Dewar*, 1997; *Moren et al.*, 2001]. Although the conservative nature of WUE was found in this forest with ample moisture, WUE may be stable regardless of water supply [*Dewar*, 1997; *Monteith*, 1986]. More studies on WUE and its mechanism in different stages of forest development are suggested.

[57] Although WUE has been defined using various combinations of numerator and denominator at either the

leaf or canopy level, for example, photosynthesis, net production, or aboveground production for numerator, and transpiration or evapotranspiration for denominator, WUE reflects carbon uptake at the cost of water loss. *Tanner and Sinclair* [1983] has summarized that WUE is a conservative plant property on the basis of a synthesis of crop yield and evaporation. It has been reported that WUE correlates with D as an inverse equation (WUE $\sim 1/D$) [*Baldocchi et al.*, 1987; *Berbigier et al.*, 2001; *Dewar*, 1997; *Moren et al.*, 2001]. *Bierhuizen and Slatyer* [1965] and *Monteith* [1986] have theoretically derived this equation at the leaf scale. Both photosynthesis and transpiration can be expressed as a general diffusion equation, that is, multiplication of the difference between ambient and intercellular concentration ($c_a - c_i$) and stomatal conductance to CO_2 (g_c) or to water vapor (g_w). Because of a relatively conservative nature of ($c_a - c_i$) or c_i/c_a for CO_2 and the g_c/g_w ratio, WUE is proportional to $1/(c_a - c_i)$ for water vapor or approximated to be proportional to $1/D$ if D is approximated to be ($c_a - c_i$) for water vapor [*Bierhuizen and Slatyer*, 1965].

[58] However, these approximations may not hold because of stomatal behavior in response to D. First, the c_i/c_a ratio may not be strictly constant as D varies [*Dewar*, 1997]. Second, g_c/g_w may not be constant in response to D. At the leaf scale, stomatal resistance is the sum of boundary layer resistance (r_b), stomatal (pore) resistance (r_s), and intercellular space and wall resistance (r_i). Each component resistance to CO_2 is larger than that to water with different ratios; particularly, r_i to CO_2 is much larger than r_i to water [*Jones*, 1992; *Tanner and Sinclair*, 1983]. The different ratios of each component conductance may explain the variation in the aggregated g_c/g_w in response to D.

[59] We found that an exponential decay function fitted our data better than an inverse equation ($r^2 = 0.42$). The exponential decay function reflects the asymmetric pattern of WUE in lower D and higher D. In the range of higher D (daytime mean $D > 0.6$ kPa), WUE had a small variation and approached a constant. The mechanistic explanation of this exponential decay function is subject to further investigation.

5. Conclusions

[60] Sap flux measurements provide a useful tool to continuously estimate canopy transpiration and stomatal conductance. Combining sap flux and eddy covariance measurements of carbon and water fluxes enables estimation of the relationship between transpiration and photosynthesis from tree to stand levels. We found that the diurnal patterns of sap flux and canopy transpiration were mainly controlled by vapor pressure deficit (D) and photosynthetically active radiation (PAR). Daily sums of sap flux and canopy transpiration had exponential relationships with D that saturated at higher D, and had linear relationships with PAR. Canopy transpiration in this old growth forest was lower than that from a few reported mature northern hardwood forests [*Dawson*, 1996; *Ewers et al.*, 2006], suggesting lower stomatal conductance and hydraulic conductance in old growth forests than those in mature forests.

[61] Canopy conductance was controlled both by D and PAR, but the day-to-day variation in canopy conductance was negatively logarithmically correlated with D. Canopy conductance on the half-hourly basis was also logarithmically correlated with D after grouping canopy conductance on the basis of PAR.

[62] Water use efficiency (WUE), calculated as GPP divided by transpiration, had a strong exponential relationship with D on the daily basis, indicating a conservative nature when D is high. The strong correlation between WUE and environmental conditions indicates that we may potentially estimate GPP from transpiration and environmental variables.

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