

Tree species effects on stand transpiration in northern Wisconsin

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[1] We quantified canopy transpiration (E_C) using sap flux measurements representing the four major forest types (northern hardwoods, conifer, aspen/fir, and forested wetland) around the WLEF-TV tall tower in northern Wisconsin. In order to scale individual sap flux measurements to E_C , we quantified the amount of sapwood area per unit ground area and the spatial distribution of sap flux within trees. Contrary to our hypothesis that all tree species would have the same positive relationship between tree diameter and sapwood depth, white cedar and speckled alder, both wetland species, showed no relationship. We also hypothesized that the conifer trees would have a lower whole tree hydraulic conductance than deciduous trees. We actually discovered that white cedar had the highest hydraulic conductance. Our third hypothesis, that sapwood area per unit ground area would determine stand E_C , was not rejected. The resulting average daily E_C values over 53 days (23 June to 16 August 2000) from combining sap flux and sapwood area per unit ground area were 1.4, 0.8, 2.1, and 1.4 mm d⁻¹ for conifer, northern hardwoods, aspen/fir, and forested wetland cover types, respectively. Average daily E_C was only explained by an exponential saturation with daily average vapor pressure deficit. **INDEX TERMS:** 1818 Hydrology: Evapotranspiration; 1851 Hydrology: Plant ecology; 1890 Hydrology: Wetlands; 1655 Global Change: Water cycles (1836); **KEYWORDS:** water transport, whole-tree water use, wetlands, sapwood

1. Introduction

[2] The role of terrestrial vegetation in atmospheric processes has received increasing scrutiny. Recent developments in global climate modeling have linked dynamic vegetation models to global circulation models through exchanges of energy, water, carbon dioxide, and momentum between the land surface and the atmosphere [Foley *et al.*, 2000]. Anthropogenic carbon dioxide has altered the radiation regime of the globe, but the effect on global temperature is uncertain because feedback processes such as the hydrologic cycle are poorly quantified [Harries *et al.*, 2001]. Most biosphere models only consider potential vegetation and the dynamics within a certain vegetation type, such as relating water fluxes from vegetation to gross characteristics of deciduous versus conifer and leaf area index [Running and Coughlan, 1988; Foley *et al.*, 1996; Schimel *et al.*, 1997]. Changes in vegetation cover due to natural or human-induced succession alter the partitioning of energy to latent and sensible heat [Pielke and Avissar, 1990]. Changes in the successional status of forests may appear subtle across the landscape if the species do not switch from deciduous to coniferous trees. The actual trajectory of successional change is often heavily influenced by soil properties such as texture and fertility. However, models have generally been used to investigate large changes in vegetation such as forest to pasture conversion.

[3] Canopy transpiration (E_C) is often thought to increase asymptotically with leaf area index (L) for a species [Meinzer and Grantz, 1991; Hatton *et al.*, 1995; Vertessy *et al.*, 1995; Arneth *et al.*, 1996; Oren *et al.*, 1996; Sala *et al.*, 1996]. Among species, annual evapotranspiration by forests may be relatively stable due to a number of feedbacks, such as understorey vegetation and climate coupling [Roberts, 1983]. On the other hand, long-term records of streamflow following the conversion of hardwood stands to conifers show reduced water yield [Hornbeck *et al.*, 1997]. The differences between conifers and deciduous trees are often incorporated into large-scale models because of differences in xylem anatomy (vessels versus tracheids), leaf longevity, leaf area index, and growing season. In addition, intensive forest management with fertilization and irrigation can change the relationship between E_C and L within a species [Ewers *et al.*, 1999, 2001a]. Given such exceptions to the relationship between L and E_C , it appears plausible that even within a forest type large differences in species characteristics may lead to significant differences in E_C . Such changes in E_C with species could lead to large errors in regional hydrologic models that do not account for species effects within a forest type.

[4] At a given leaf area index, the morphological and physiological effects of species may affect vapor phase conductance through the stomata and liquid phase conductance to the stomata. The following equation, modified from Whitehead and Jarvis [1981], encapsulates this idea:

$$E_C = K A_S \left(\frac{n \rho_w \Delta \Psi}{l \eta} \right), \quad (1)$$

where E_C is canopy transpiration, K is the hydraulic conductivity of the whole tree (m² MPa⁻¹ s⁻¹), A_S is sapwood area (m²), n is the number of stems, ρ_w is the density

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Table 1. Stand Parameters for the Four Measurement Stands^a

Cover Type	Species	Density	dbh	dbh range	H	H	A_B	A_S	L
Conifer	red pine	5140	14.0	6.7–32.5	15.1	9.6–17.6	51.6	39.3	3.6 (0.5)a
Northern hardwoods	sugar maple	370	22.4	4.0–36.1	18.6	11.5–25.3	18.8	12.6	3.8 (0.7)a
	basswood	145	25.4	6.3–43.4	18.2	6.0–22.7	9.7	4.2	
Aspen	aspen	2930	11.0	5.2–18.2	14.7	9.0–17.8	30.0	15.8	3.5 (0.8)a
	balsam fir	890	6.6	5.1–9.2	4.2	2.9–5.9	3.7	2.5	
Forested wetland	white cedar	796	19.3	9.8–26.1	10.1	8.8–11.8	24.4	6.1	4.1 (0.5)a
	speckled alder	42500		0.6–4.4	5.6	3.5–8.5		16.1	
	balsam fir	286	6.8	5.0–10.0	2.1	1.4–3.1	1.1	0.6	

^aDensity is the number of trees per hectare, dbh is mean stem diameter at 1.3 m height (centimeters), dbh range is the minimum and maximum dbh (centimeters), H is mean tree height (meters), H range is the minimum and maximum H (meters), A_B is basal area per unit ground area ($\text{m}^2 \text{ha}^{-1}$), A_S is sapwood area per unit ground area ($\text{m}^2 \text{ha}^{-1}$), and L is leaf area index ($\text{m}^2 \text{m}^{-2}$). Letters indicate significant difference ($\alpha = 0.05$), and values in parentheses are 1 standard error ($n = 16$).

of water (kg m^{-3}), $\Delta\Psi$ is the water potential gradient between leaves and soil (MPa), l is the path length (m), and η is the viscosity of water ($\text{N s}^{-1} \text{m}^{-2}$). The physiological parameters $\Delta\Psi$, K , and l are species-specific [Sperry *et al.*, 1998]. Current theory and a large pool of data indicate that stomata regulate species-specific leaf water potential (Ψ_L) to prevent runaway cavitation [Sperry *et al.*, 1998; Oren *et al.*, 1999a; Ewers *et al.*, 2000]. A_S and n determine the magnitude of E_C based on the number and size of trees. The effect of stand stocking and A_S has been shown to have a large impact on E_C [Oren *et al.*, 1998; Wullschleger *et al.*, 1998; Wullschleger *et al.*, 2000]. In addition, even within a species, site fertility and water availability can alter K and thus E_C irrespective of changes in leaf area [Ewers *et al.*, 1999, 2001a]. Species level information may be necessary to estimate E_C , but such detailed information is generally only available for plant functional groups. Meinzer *et al.* [2001] showed that A_S and the flow of water per unit xylem area (J_S) in the outer xylem can be predicted based on stem diameter for 30 tropical tree species. Other studies across a wide range of species and environmental conditions found that species with a high stomatal conductance are more sensitive to vapor pressure deficit than species with a low stomatal conductance [Oren *et al.*, 1999a; Ewers *et al.*, 2000, 2001b]. Several studies have investigated hydraulic conductance mechanisms as a means to converge species in water transport [Meinzer *et al.*, 2001; Sperry *et al.*, 1998; Oren *et al.*, 1999a; Wullschleger *et al.*, 1998]. However, Meinzer *et al.* [2001] discussed the necessity of appropriate scaling when investigating converging whole plant water transport, and Wullschleger *et al.* [1998] reviewed studies that showed hydraulic conductance per unit leaf area was almost 5 times as variable as hydraulic conductance per unit sapwood area (K). Because only four studies reported K in that review, it is unclear whether broad functional groups such as conifers with smaller conduits for water transport will have a lower K than deciduous trees. All of these general relationships point to the possibility of using broad relationships between species to incorporate species level information on E_C into landscape level E_C estimates.

[5] Northern Wisconsin provides an ideal location to study the effects of species on E_C . The forested vegetation reflects the combined effects of landform, glaciation, and soil type interacting with management activities such as thinning, selective harvests, and clear-cut harvests on forest structure and function [Fassnacht *et al.*, 1997]. To investigate the

relationships quantified in equation (1), we selected stands representing the four major forest types in northern Wisconsin while still maintaining a similar L (Table 1). The main objective of this study was to determine the effect of the four major forest types on the quantitative and temporal distribution of E_C . Because there is limited information available on some species in northern Wisconsin, the following hypotheses are based on broad generalizations across the species in northern Wisconsin: (1) All species share a positive relationship between A_S and stem diameter; (2) hardwoods will have higher K than conifers; and (3) E_C will be best predicted by A_S .

2. Materials and Methods

2.1. Site Description

[6] The study was conducted in northern Wisconsin, near Park Falls (46.15°N, 90.27°W). The study sites were located between 3 and 10 km north of a 396-m-tall eddy covariance tower instrumented to measure energy, water, and carbon exchange between the land surface and the atmosphere [Bakwin *et al.*, 1998]. The tower is located in the Chequamegon-Nicolet National Forest, and four forest types (Table 1) were instrumented for transpiration studies within the adjacent Hay Creek Wildlife Management Area. The area is situated in the Northern Highlands physiographic province, a southern extension of the Canadian Shield. The bedrock is composed of Precambrian metamorphic and igneous rock, overlain by 8 to 90 m of glacial and glaciofluvial material. Topography is slightly rolling, varying by at most 45 m between highest and lowest elevations in the entire study area. Outwash, pitted outwash, and moraines are the dominant geomorphic features. The growing season is short and the winters are long and cold, with mean July and January temperatures of 19°C and −12°C, respectively. The soils are loamy sands with sandy loams below 30 cm. We verified the soil textures using standard laboratory texture analysis on soil samples from the three upland cover types. The forested wetland site had continuously saturated peat soils. The water table was at the soil surface in the forested wetlands and was greater than 2 m in depth in the other forest types.

[7] Four forest types make up over 80% of the land surface [Burrows *et al.*, 2002]: (1) Upland conifers consisting of red pine (*Pinus resinosa* Ait.) and Jack pine (*Pinus banksiana* Lamb.) occur on excessively drained glacial outwash; (2) northern hardwood forests dominated by sugar

maple (*Acer sacharum* Marsh), with many other deciduous broad-leaved species, occur on finer-textured moraines and drumlins; (3) aspen/fir forests occur primarily on intermediate sites dominated by trembling aspen (*Populus tremuloides* Michx) and balsam fir (*Abies balsamea* (L.) Mill); and (4) forested wetlands occur on poorly drained lowland sites dominated by white cedar (*Thuja occidentalis* L.), balsam fir (*Abies balsamea* (L.) Mill), and speckled alder (*Alnus regosa*).

[8] The four forest types were identified through local land classification [Burrows *et al.*, 2002; Mackay *et al.*, 2002]. We chose our sample sites such that they had the same soil texture and similar basal area to the forest types measured by Burrows *et al.* [2002]. Our sample species, trembling aspen, balsam fir, sugar maple, red pine, speckled alder, and white cedar, represented 24, 13, 12, 12, 8, and 8% of the total basal area around the tall tower (~300 plots in a 2.5-km radius), respectively [Burrows *et al.*, 2002]. We chose a northern hardwoods stand with a component of basswood (*Tilia americana* L., 3% basal area) as a contrast to maple and to determine how different basswood's water use was from sugar maple. Trees on the three upland sites were established in 1930 after clear-cutting. The age of the white cedars in the forested wetland is approximately the same.

2.2. Stand Parameter Measurements

[9] We measured L optically using a Li-Cor LAI-2000 plant canopy analyzer (Li-Cor Inc., Lincoln, Nebraska). In each forest type, 16 measurements were made in a 16-m radius of a canopy access tower at the center of each plot. The location of each measurement was recorded in order to analyze the means and standard errors spatially using the spatial statistics of Burrows *et al.* [2001]. Standard field measurement methods were used to quantify L [Gower and Norman, 1991; Fassnacht *et al.*, 1994; Chen *et al.*, 1997; Gower *et al.*, 1999]. Tree diameters were determined with a diameter tape, and heights were measured with a clinometer and measuring tape to obtain angles and distances.

[10] Sapwood depth and bark thickness were determined from tree cores taken from the north and south side of 14 trees of each species in each stand outside of the sap flux measurement plot. Sapwood depth was determined visually from either coloration changes or staining with bromocresol green [Schäfer *et al.*, 2000].

2.3. J_s Measurements and Calculation of E_c

[11] We measured sap flux per unit conducting xylem area (J_s) in stem xylem of eight trees of each dominant species in the four forest types. Stem sap flux measurements (1.4 m above ground) were made with Granier-type sensors [Granier, 1987] at three stem locations: (1) the outer 20 mm of the xylem ($J_{S\text{north}}$, 23 June to 16 August 2000; 53 days), (2) the next 20 mm of the xylem ($J_{S\text{in}}$, 18–25 July 2000) from the cambium to 40 mm for radial patterns in J_s , and (3) the outer 20 mm of xylem on the south side ($J_{S\text{south}}$, 28 July to 4 August 2000) to account for circumferential trends. When the depth of sapwood was less than 20 mm for $J_{S\text{north}}$ or $J_{S\text{south}}$ or less than 40 mm for $J_{S\text{in}}$ we used the corrections described by Clearwater *et al.* [1999] to determine the appropriate J_s . The three measurement positions could not be measured simultaneously due to power limitations, so only $J_{S\text{north}}$ was measured continuously. J_s ($\text{m}^3 \text{H}_2\text{O}$

$\text{m}^{-2} \text{s}^{-1}$) is calculated based on the relationship of Granier [1987]:

$$J_s = 119 \times 10^{-6} \left(\frac{\Delta T_M - \Delta T}{\Delta T} \right)^{1.231} \quad (2)$$

where ΔT_M is the maximum temperature difference (which varied between 10° and 13°C) between heated and unheated reference hypodermic needles occurring at night, and ΔT (°C) is the difference between the heated and unheated hypodermic needles at any given time. Equation (2) assumes that zero sap flow occurs at night and that natural temperature gradients are small [Lundblad *et al.*, 2001].

[12] We calculated a stem mean J_s [Oren *et al.*, 1998; Ewers *et al.*, 1999; Ewers and Oren, 2000] using the following:

$$J_s = \sum_{i=1}^3 W_i J_{Si} / \sum_{i=1}^3 W_i \quad (3)$$

where i equals each of the J_s ($\text{g m}^{-2} \text{s}^{-1}$) measurement positions, northern, southern, and inner, and W (nondimensional) is the weight of each J_{Si} measurement position. Equation (3) assumes that $J_{S\text{in}}$ represents the flux inside of 40 mm from the cambium. Equation (3) also assumes that the proportions measured when $J_{S\text{in}}$, or $J_{S\text{south}}$ measurements overlap with the continuous $J_{S\text{north}}$ measurements area and thus the W_i among $J_{S\text{north}}$, $J_{S\text{in}}$, and $J_{S\text{south}}$ are constant throughout the entire $J_{S\text{north}}$ measurement period.

[13] Alder trees were too small for Granier-type measurements, so we used Kucera-type sensors (baby sap flux sensors, EMS, Brno, CZ [Cienciala *et al.*, 1994; Ewers and Oren, 2000]). These sensors quantify sap flux by maintaining a constant 4°C difference between heated and unheated sections of the stem. The amount of heat required to maintain the temperature difference is proportional to the sap flux. The Kucera-type sensors measure the entire sap flow of the stem (for diameters between 12 and 18 mm) and do not need additional scaling measurements. To avoid thermal gradients from direct radiation, all sensors were shielded with mylar. Analyses of daily water use for both Granier- and Kucera-type sensors were performed on daily sums of J_s from 0500 to 0430 LT, which approximately corresponded to the time of zero flow, and therefore includes nighttime recharge [Phillips and Oren, 1998]. To calculate E_c (mm d^{-1}), J_s ($\text{mm}^3 \text{mm}^{-2} \text{d}^{-1}$) is combined with sapwood area per unit ground area ($A_s/A_g \text{mm}^2 \text{mm}^{-2}$) as follows [Oren *et al.*, 1998; Ewers *et al.*, 1999]:

$$E_c = J_s \frac{A_s}{A_g} \quad (4)$$

[14] The sap flux measurement plot sizes were 5-, 10-, and 6-m radius for aspen/fir, forested wetland, and red pine, respectively, and the northern hardwoods plot was 20 × 40 m. The plot sizes were selected to include at least 30 trees and a range of sizes of trees for detailed measurements.

2.4. Ψ_L Measurements and Calculation of K

[15] To quantify Ψ_L , midcanopy, shaded leaves were sampled from three trees of each species and immediately

placed in a sealed and moistened plastic bag on 18 June, 13 July, and 1 and 13 August 2000. Ψ_L measurements were made on the leaves within 30 min using a pressurized chamber (PMS Instruments, Corvallis, Oregon). We calculated K from the following [Pataki *et al.*, 1998]:

$$K = \frac{J_S}{(\Psi_S - \Psi_L)} \quad (5)$$

where Ψ_S is soil water potential (MPa) and Ψ_L is the leaf water potential taken at midday (MPa) and J_S is $\text{mol m}^{-2} \text{s}^{-1}$. We assumed that predawn Ψ_L was equal to Ψ_S .

2.5. Environmental Measurements

[16] Vapor pressure deficit (D) was calculated from relative humidity (R_H) and air temperature (T_A) measurements based on equations adapted from Goff and Gratch [1946]. We measured R_H and T_A (Vaisala HMP 35C, Campbell Scientific, Logan, Utah) at two thirds the average tree height using a scaffolding tower (Table 1, sensor height/stand height, $z/h = 0.79-0.83$) for all stands except red pine where no scaffolding was available. To “fill in” for D at the red pine stand, we measured R_H and T_A on a cloudy and a sunny day for several hours and related the measurements to R_H and T_A from the forested wetland and found no difference (slope = 1.01, intercept = 0.03, $R^2 = 0.98$). Photosynthetic photon flux density (Q) above the canopy was monitored with a quantum sensor (LI-190s, Li-Cor, Lincoln, Nebraska) attached to the scaffolding in the forested wetland. Soil volumetric water content was monitored with continuous TDR measurements (CS 615, Campbell Scientific, Logan, Utah) in all stands except the forested wetland because of continuous soil saturation. Soil temperature was measured in each stand at 5 cm with a thermistor (107 probe, Campbell Scientific, Logan, Utah). Xylem flux and all environmental sensors were sampled every 30 s (CR10X, Campbell Scientific, Logan, Utah) and 30-min means were recorded.

[17] In order to quantify the daily time pattern in J_S and E_C , we used the following exponential saturation model to predict E_C from D_Z (daily average vapor pressure deficit over daylight hours [Oren *et al.*, 1996]) adapted from Ewers *et al.* [2001a]:

$$E_C = a(1 - e^{-bD_Z}), \quad (6)$$

where a and b are fitting parameters and E_C is in mm d^{-1} and D_Z is in kPa.

2.6. Statistics

[18] Statistical analyses were done in SAS (version 8.0, SAS Institute, Cary, North Carolina). Because sap flux measurements are collected in a serial fashion, they often violate the assumption of independent errors. Thus we used the mixed procedure to account for the effect of time series data on analysis of variance (ANOVA) calculations. We also used the mixed procedure to perform ANOVA using the L data collected spatially. We used the range (117 m), sill (1.78), and nugget (0.55) from the forest cover dependent semivariogram from Burrows *et al.* [2002]. The effect of species on daily sums of J_S was analyzed using two methods. One was to use repeated measures analyses and then test for means effects based on species. We determined

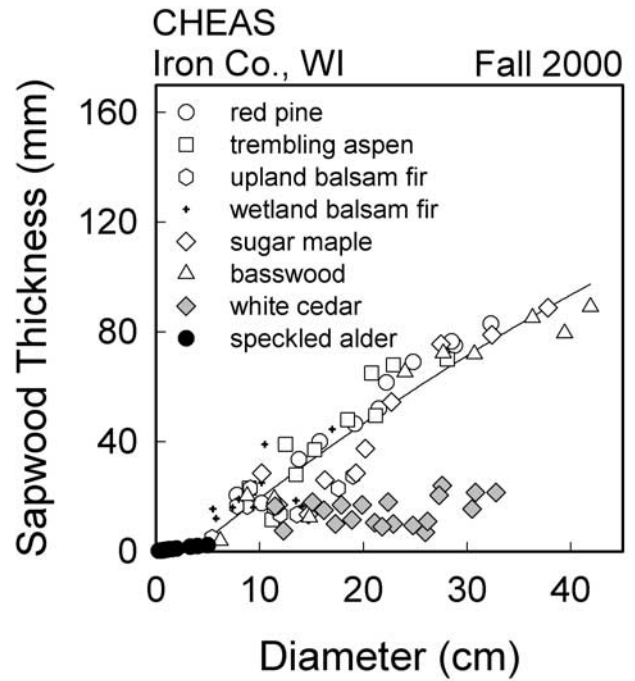


Figure 1. Relationship between diameter at 1.3 m above ground and depth of sapwood from the cambium.

the appropriate number of parameters and variance structure in repeated measures analysis that minimized the Akaike's information criterion (AIC) and Bayesian information criterion (SBC) [Littel *et al.*, 1996]. Both of these criteria are log likelihood values penalized for the number of parameters used. Analyses of Ψ_L and K measurements were conducted on the four days of measurements using repeated measures analysis. Separation of daily sapflux means by tree species means was performed using the LSMEANS statement in the MIXED procedure of SAS. Analyses of time lags and correlation were done using the ARIMA procedure in SAS. Nonlinear fits were performed using the NLMIXED procedure in SAS and Sigmaplot (version 6.0, SPSS Inc., Chicago Illinois).

3. Results

3.1. Scaling Point Measurements of J_S to the Whole Tree

[19] Sapwood depth was positively related to diameter at breast height (dbh) for all species (Figure 1) except white cedar. For white cedar the mean sapwood depth of 14.5 mm was used. Speckled alder did not share the same relationship as the rest of the species ($P < 0.001$). We calculated sapwood area per unit ground area using the regressions from Figure 1 or the mean values for white cedar and tree diameters in each plot (Table 1).

[20] There was no difference in $J_{S\text{north}}$ and $J_{S\text{south}}$ in any species except white cedar. The $J_{S\text{south}}$ in white cedar was 1.17 that of the $J_{S\text{north}}$ ($P < 0.05$), and there was no effect of tree size on the ratio. For white cedar the sapwood depth was less than 20 mm (Figure 1), and we measured zero $J_{S\text{inner}}$. Thus we scaled the 20-mm $J_{S\text{north}}$ measurements back to the appropriate sapwood depth based on that of Clearwater *et al.* [1999]. We also found zero $J_{S\text{inner}}$ in

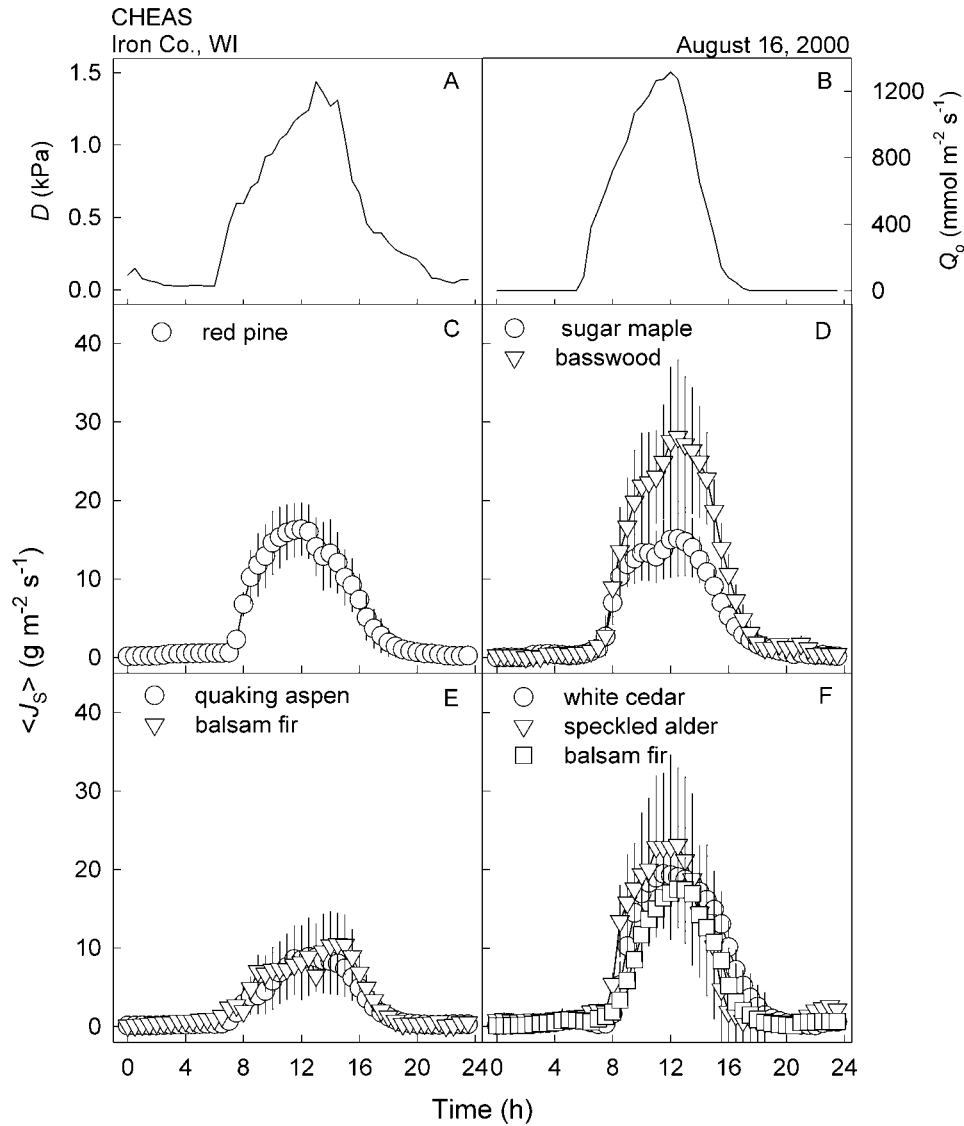


Figure 2. Representative diel pattern of (a) vapor pressure deficit D , (b) photosynthetically active radiation (Q_o), and stem sap flux (J_S) in (c) red pine, (d) sugar maple/basswood, (e) quaking aspen balsam fir, and (f) white cedar/balsam fir/speckled alder. Each point represents the mean of eight trees, and bars are 1 standard error.

balsam fir where the sapwood depth was less than 20 mm (Figure 1), confirming our method for determining sapwood. Sapwood thickness was always greater than 20 mm in red pine, and we found no daily or diurnal difference in $J_{S\text{north}}$ and $J_{S\text{inner}}$ ($P > 0.3$ for both). In contrast, the inner J_S was lower in trembling aspen, sugar maple, and basswood on both a diurnal and daily basis ($P < 0.01$ for all). The $J_{S\text{north}}$ was higher than the $J_{S\text{inner}}$ by 1.5, 1.5, and 1.2 in trembling aspen, sugar maple, and basswood, respectively. The ratio of $J_{S\text{north}}$ to $J_{S\text{inner}}$ was extremely variable once D was less than 0.6 kPa because of measurement uncertainties at low sap flux values, resulting in high signal-to-noise ratios [Ewers and Oren, 2000]. These measurement uncertainties may be reduced when additional temperature measurements are taken to correct for vertical gradients in stem temperature [Lundblad et al., 2001]. There was no effect of tree diameter or height on the ratio of $J_{S\text{inner}}$ to J_{north} in any

species. We calculated a weighted average J_S for basswood, trembling aspen, and sugar maple assuming that all the sapwood inside of 20 mm had the same $J_{S\text{in}}$ (equation (3)). This assumption is reasonable given the trends shown by Schäfer et al. [2000] where there was a sharp decline in J_S between 0–20 and 20–40 mm from the cambium in beech and oak but no subsequent decline from 40 mm inward to the heartwood boundary. Sapwood thickness did not exceed 40 mm (Figure 1), except in sugar maple and basswood. In sugar maple the sapwood was as deep as 80 mm, and so our assumption of constant J_S beyond 40 mm provides an upper bound to the total water flux. From this point forward, any discussion of J_S refers to J_S calculated from equation (3) to appropriately scale the point measurements to the whole tree.

[21] The highest peak J_S on a representative, partially sunny day was $30 \text{ g m}^{-2} \text{s}^{-1}$ in basswood, and the lowest was upland balsam fir at $9 \text{ g m}^{-2} \text{s}^{-1}$ (Figure 2). The peak

Table 2. Hydraulic Parameters for the Four Forest Types by Species^a

Forest Type	Species	Predawn Ψ_L (-MPa)	Midday Ψ_L (-MPa)	K , mol m ⁻² MPa ⁻¹ s ⁻¹
Conifer	red pine	0.5 (0.3)a	1.7 (0.5)a	0.6 (0.1)ab
Northern hardwoods	sugar maple	0.3 (0.1)b	1.2 (0.4)bc	0.9 (0.2)cd
	basswood	0.3 (0.2)b	1.2 (0.3)bc	1.3 (0.3)d
Aspen/fir	trembling aspen	0.2 (0.2)bc	1.6 (0.3)a	2.0 (0.1)e
	balsam fir	0.3 (0.1)b	1.2 (0.2)b	0.9 (0.1)bc
Forested wetland	white cedar	0.4 (0.1)b	1.1 (0.1)bc	2.2 (0.4)e
	speckled alder	0.1 (0.1)c	1.0 (0.1)c	1.5 (0.4)ce
	balsam fir	0.4 (0.2)b	1.2 (0.1)b	0.3 (0.2)a

^a Ψ_L is leaf water potential, and K is hydraulic conductivity per unit sapwood area. Values in parenthesis are 1 standard error ($n = 3$), and letters indicate significant differences at the $\alpha = 0.05$ level.

value of J_S occurred at different time periods, with the earliest in red pine at 1200 LT and the latest at 1300 LT in basswood. On all days the conifers had a peak flux earlier than the hardwoods. The lag between D and J_S varied between 0 in the conifer trees to 1.5 hours in alder trees.

3.2. Species Effects on Hydraulic Parameters

[22] Using repeated measures analysis with the four days as repeated measures, predawn Ψ_L was lowest (more negative) in red pine and highest in speckled alder (Table 2), and there was no effect of species, measurement day, or their interaction on Ψ_L ($P > 0.2$). All of the other species had intermediate values of predawn Ψ_L . Midday Ψ_L (approximately noon, within 10% of peak sap flux) was lowest in red pine but not significantly different from trembling aspen, while midday Ψ_L was highest in speckled alder. All of the other species had intermediate values of midday Ψ_L (Table 2). Using repeated measures analysis with the four days as repeated measures, the measurement day affected midday Ψ_L ($P < 0.001$) and there was an interaction with species ($P < 0.001$). On the basis of mean separation analysis, red pine and trembling aspen both had a lower Ψ_L by -0.3 MPa on one day when D_Z was 0.9 kPa compared with their means reported in Table 2. The other three days had D_Z less than 0.6 kPa.

[23] The effect of species on tree hydraulics was calculated using equation (5) and the value of J_S at the time of midday Ψ_L measurement for each species. In contrast to midday Ψ_L , there were no significant differences in K between the four measurement days. K was highest in white cedar and trembling aspen, slightly lower values were found in speckled alder and basswood, with lowest values in sugar maple, upland balsam fir and red pine (Table 2).

3.3. Impact of Species and Environmental Conditions on Daily J_S

[24] Using day as a repeated measure (all 53 measurement days were used in the analysis to calculate daily averages), the variance estimates of J_S were not homogeneous and varied with time across all species. To account for this, we evaluated different models of heterogeneous variability. We found that the lowest AIC and BIC occurred when a repeated measures model included an autoregressive heterogeneous variance term that included an additional term to account for between tree variability. This type of analysis was required

because the variance was dependent on time, and increased with increasing D_Z (Figure 3). The highest average daily J_S was found in basswood, with slightly lower values in aspen, white cedar, and speckled alder. The lowest values were found in red pine, and balsam fir at both the upland and lowland sites (Table 3). Using equation (6), the average daily sum of J_S was explained by D_Z in all species ($P < 0.05$), except upland balsam fir, for which daily sums of Q were the only significant variable ($P < 0.01$). There was a linear pattern in the residuals of the relationship shown in Figure 3 for the individual J_S of red pine, trembling aspen, and white cedar. In red pine the residuals increased with day of year from the beginning to the end of the data set, and in aspen and white cedar they decreased with day of year. The residuals patterns could not be explained by any environmental variable including D_Z , daily Q , T_A , R_H , soil temperature, or soil moisture ($P > 0.2$ for all). Instrumentation problems can also be ruled out because there were no corresponding patterns in upland balsam fir measured on the same power supplies as aspen, and wetland balsam fir measured on the same power supply as white cedar.

3.4. Impact of Species and Environmental Conditions on E_c

[25] In the same manner as J_S , the variance of average daily E_c was heterogeneous with time and increasing D_Z and was adjusted using an autoregressive heterogeneous variance term that included an additional term to account for between tree variability. Aspen had the highest average daily E_c followed by red pine (Table 3). Intermediate values of average daily E_c were found in speckled alder and sugar maple (Table 3). The lowest values were found in basswood and both balsam firs, with wetland balsam fir having the lowest E_c (Table 3). Only D_Z significantly explained the variability in average daily E_c in each forest type (Figure 4).

4. Discussion

[26] Canopy transpiration is expected to follow leaf area index, which is determined by site quality variables [Fassnacht and Gower, 1997]. Our results show that despite having the same soil type and the same L (Table 1), there was a twofold difference in transpiration among the different forests (Figure 4 and Table 3). We utilized three hypotheses to determine why E_c varied by forest type. Our first hypothesis, species have no effect on the relationship between A_S and stem diameter, was invalid for both wetland species, white cedar and speckled alder. Our second hypothesis, that deciduous trees have a higher K than conifers, was rejected because white cedar had the highest values of K . Our third hypothesis, E_c will be best predicted by A_S and n (equation (1)), was not rejected.

4.1. Scaling Point Measurements of J_S to Trees and Stands

[27] To scale from point measurements of J_S to E_c , radial and circumferential measurements of J_S must be weighted to whole tree J_S and multiplied by $A_S:A_G$ [Oren et al., 1998, equations (3) and (4)]. Recently, attempts have been made to find universal relationships between J_S , sapwood area, and diameter based on the hypothesis that allometric scaling of plant vascular systems is universal [Enquist et al., 1998; West et al., 1999; Enquist and Niklas, 2001]. Meinzer et al. [2001]

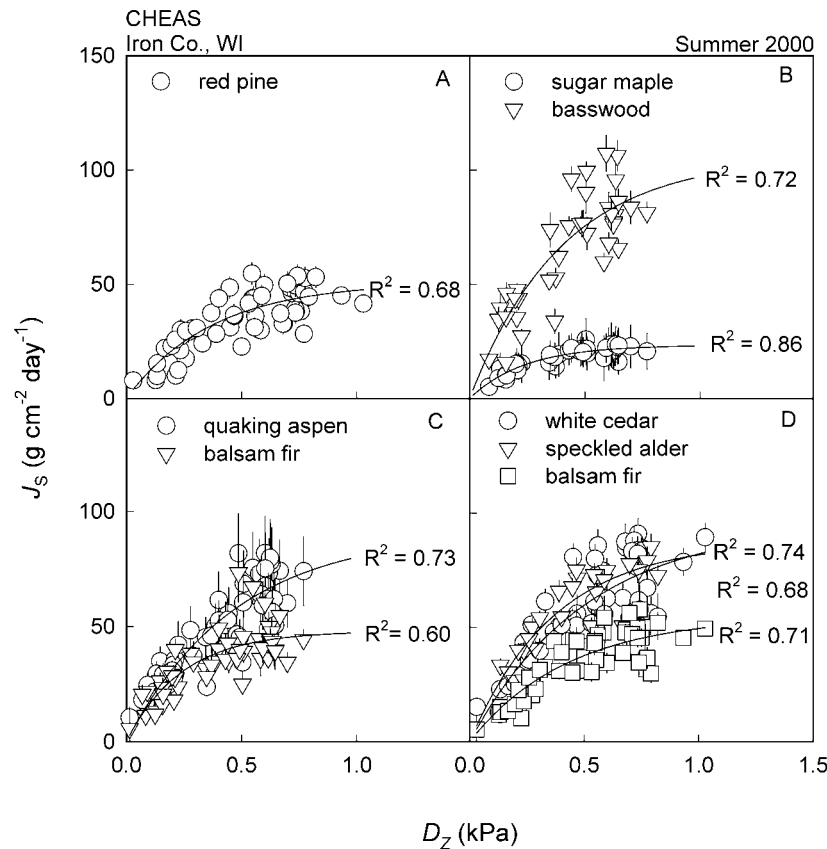


Figure 3. Relationship between daily average vapor pressure deficit over light hours (D_z) versus daily sums of stem sap flux (J_s) in (a) red pine, (b) sugar maple/basswood, (c) quaking aspen balsam fir, and (d) white cedar/balsam fir/speckled alder. Each point represents the mean of eight trees, and bars are 1 standard error. Line are exponential saturation curves of the form ($Y = a(1 - \exp(-bX))$).

tested this hypothesis across 30 tropical canopy trees and found good relationships between sapwood depth or area and diameter and outer J_s and diameter. The relationship between diameter and sapwood depth in most of the species from this study (Figure 1) agrees with the results of Meinzer *et al.* [2001]. However, as Meinzer *et al.* [2001] point out, such relationships can be confounded by spatial patterns in sap flux when only a point measurement of sap flux is made. In addition, the sap flux measurements used in this study and in that of Meinzer *et al.* [2001] must be corrected for sapwood

depth when the depth of sapwood is less than the length of the sensor (20 mm in this study [Clearwater *et al.*, 1999]). Our results combined with the other study point to a universal scaling approach to E_C based on diameter. Perhaps more important than the universal findings are instances when the relationship does not work. In both of the obligate wetland species (white cedar and speckled alder), there was no relationship between diameter and sapwood area (Figure 1). These two exceptions may actually provide more evidence for the approach of Meinzer *et al.* [2001] because they suggest water limitation as the cause of the universal relationship, which is certainly relieved in obligate wetland species.

[28] The second piece of information necessary to determine stand E_C is weighted average J_s (equation (3)). We determined weighted average J_s by measuring sap flux circumferentially and radially. In balsam fir, white cedar, and red pine, there was no radial trend in sap flux. This was because the hydroactive sapwood was usually 20 mm or less in balsam fir and white cedar (Figure 1). J_s was measured from 20 to 40 mm and found to be zero in white cedar and balsam fir, lending further support to our estimation of sapwood thickness. The lack of radial trend in red pine contrasts with other pine sap flux studies. Ewers *et al.* [1999] and Ewers and Oren [2000] showed a 60–40% reduction in *Pinus taeda* (loblolly pine) depending on growth rate, which is similar to the 50% shown by Phillips *et al.* [1996]. In both of these studies the decline in J_s

Table 3. Average Daily Values of Sap Flux (J_s) and Canopy Transpiration (E_C) From 23 June to 16 August 2000 for Each Species^a

Forest Type	Species	J_s , $\text{g cm}^{-2} \text{ d}^{-1}$	E_C , mm d^{-1}
Conifer	red pine	34.8 (0.9)a	1.4 (0.02)a
	sugar maple	17.5 (1.5)b	0.6 (0.03)b
Northern hardwoods	basswood	67.2 (1.1)c	0.2 (0.03)c
	aspen	51.5 (0.9)d	2.0 (0.02)d
Aspen	balsam fir	38.1 (1.0)a	0.1 (0.03)ce
	white cedar	57.7 (1.9)e	0.5 (0.02)f
Forested wetland	speckled alder	62.5 (1.5)ce	0.9 (0.04)g
	balsam fir	34.7 (0.9)a	0.03 (0.02)e

^aValues in parentheses are 1 standard error ($n = 8$), and letters indicate significant differences.

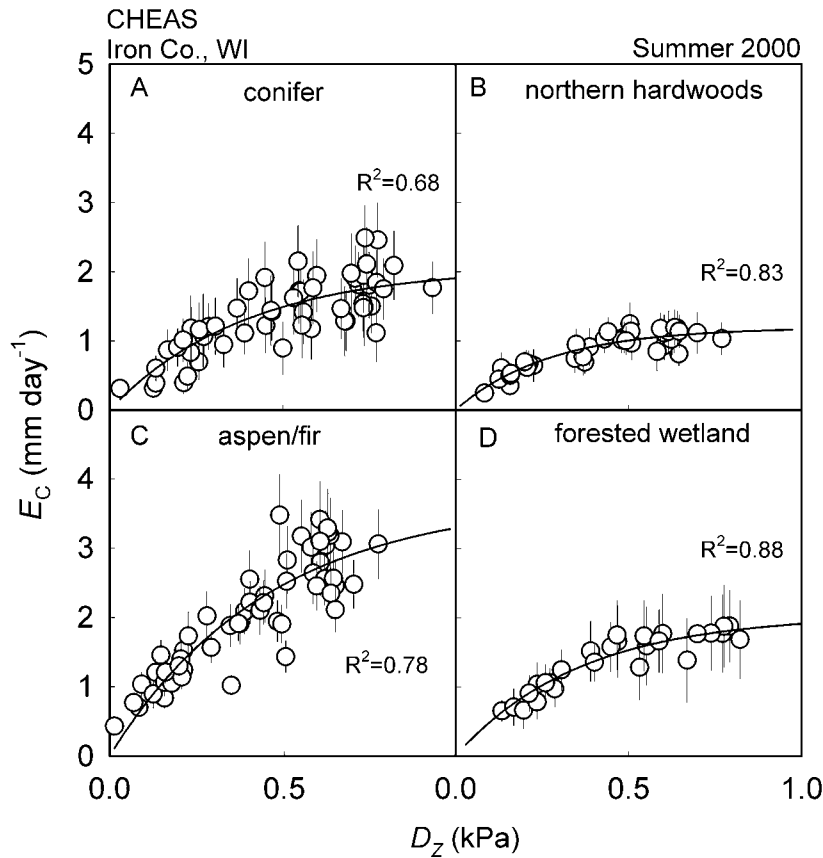


Figure 4. Relationship between daily average vapor pressure deficit over light hours (D_z) versus daily sums of canopy transpiration (E_c) in (a) red pine, (b) sugar maple/basswood, (c) quaking aspen balsam fir, and (d) white cedar/balsam fir/speckled alder. Each point represents the mean of eight trees, and bars are 1 standard error. Lines are exponential saturation curves of the form ($Y = a(1 - \exp(-bX))$).

radially was attributed to juvenile wood. Because of the lack of decline in J_s of red pine, we hypothesize that red pine has little change in the properties of its juvenile wood due to its much slower growth than loblolly pine.

[29] We found the largest radial decline in J_s (50%) in sugar maple and aspen. The 15% reduction in basswood was much lower than the other two diffuse porous species, sugar maple and aspen. Previous work on diffuse porous species has generally shown either an even distribution [Phillips *et al.*, 1996; Edwards and Booker, 1984] or a decline in J_s with depth [Cohen *et al.*, 1981; Pausch *et al.*, 2000]. While there is no information available for basswood or trembling aspen radial trends, Pausch *et al.* [2000] showed a similar trend to this study between 0–20 and 20–40 mm in sugar maple, and they showed a further decline beyond 40 mm.

[30] In our calculation of whole stem J_s (equation (3)), we assumed that in the species where sapwood was deeper than 40 mm (Figure 1), all J_s at depths greater than 40 mm was the same as at 20–40 mm. Our assumption is supported by measurements in beech by Schäfer *et al.* [2000] that showed a sharp decline from 0–20 to 20–40 and no change in J_s to the heartwood boundary at 100 mm. On the other hand, Pausch *et al.* [2000] showed the same radial trend in sugar maple as found here, but showed an additional decline beyond 40 mm. Thus our assumption provides an upper limit to whole stem J_s . The lack of relation (or an unstable

proportion) between $J_{s\text{in}}$ and $J_{s\text{north}}$ below D of 0.6 kPa is remarkably similar to *Pinus taeda* under varying water and nutrient supplies [Ewers and Oren, 2000]. The 0.6-kPa D value was shown by Ewers and Oren [2000] to be the point at which the relative errors in Granier-type sap flux and the relative humidity/temperature measurements go below 15%. Additional variability in J_s radial trends can be imposed by soil drought [Oren *et al.*, 1998]. However, since soil moisture did not decline enough to impact average daily J_s , it is likely that soil moisture did not impact the radial J_s patterns. Even though radial trends are increasingly studied [Mark and Crews, 1973; Edwards and Booker, 1984; Granier *et al.*, 1994; Phillips *et al.*, 1996; Lu *et al.*, 2000; Ewers and Oren, 2000; Jimenez *et al.*, 2000], no unifying anatomical or physiological explanation has been established. Thus detailed knowledge of radial trends will be required for every species in which the goal is to determine whole tree sap flux when Granier-type sap flux sensors are used.

[31] Similar to the unexplained variation shown in radial patterns of J_s , literature is mixed on circumferential trends in J_s , with some studies showing no circumferential trend [Ewers and Oren, 2000; Loustau *et al.*, 1998] and other studies showing higher J_s on the southern sides of stems [Daum, 1967; Čermák *et al.*, 1984; Oren *et al.*, 1999b]. We found no circumferential trend in J_s in any of our measured species except white cedar. White cedar and bald

cypress are similar conifer species that both grow in flooded areas, and Oren *et al.* [1999b] showed almost a doubling of J_S on the southern side of bald cypress compared with the north side. All of the studies that have found a higher J_S to the south have attributed the increase to more radiation on the southern side of trees. Oren *et al.* [1999b] notes that bald cypress had a low L and relatively open crowns. The white cedar that we measured also had relatively open crowns but a higher total L than the previous study. However, the low leaf area index stands of *Pinus taeda* ($1.8 \text{ m}^2 \text{ m}^{-2}$) reported by Ewers and Oren [2000] did not show a circumferential trend. Thus there seems to be no discernable mechanism behind the similarity of bald cypress and white cedar. However, even when the circumferential differences in sap flux are not systematic, there still seems to be a stable relationship between sap flux measurements at one point circumferentially compared with another point on the stem [Lu *et al.*, 2000]. While the Kucera-type sap flux measurements in alder were not subject to the same sort of scaling errors, either radially or circumferentially, as Granier-type sap flux in the other tree species, the Kucera-type sap flux only provides a whole tree estimate of sap flux. Thus, until a mechanism is found, both circumferential and radial trends in J_S must be measured for each new species in which Granier-type sap flux sensors are used.

4.2. Effect of Species on Hydraulic Properties

[32] Current theory states that stomata limit transpiration to prevent water potentials from going below threshold values that cause runaway cavitation [Sperry *et al.*, 1998]. Once the minimum or critical leaf water potential is reached, stomata close to maintain the value [Saliendra *et al.*, 1995]. The minimum leaf water potential does not appear to vary within a species [Sperry *et al.*, 1998] even under drastic changes in tree hydraulics and environmental conditions [Ewers *et al.*, 2000], but K can be limited by xylem morphology or soil texture and result in a lower stomatal conductance to maintain the same minimum leaf water potential [Sperry *et al.*, 1998; Hacke *et al.*, 2000; Ewers *et al.*, 2000]. No change in predawn water potential during the growing season in all species indicates that soil water was not limiting transpiration. The change in midday water potential with time in red pine and aspen indicates that on low D_Z days, there was not enough driving force to cause water potentials to reach their minimums.

[33] Contrary to our hypothesis, K was not higher in hardwoods; in fact, white cedar had the highest K . Generally, a species that is more vulnerable to cavitation will have a higher K because of trade-offs between efficiency and safety. Our values of K were about half the range in the literature representing only five species [Wullschleger *et al.*, 1998]. White cedar may have a higher K than the hardwoods (sugar maple and basswood) because it is a wetland species that is not soil moisture limited. This suggests that white cedar can have a higher supply of water to the leaves under good conditions, but white cedar cannot withstand drought conditions, characteristics that are common to wetland conifers [Oren *et al.*, 1999b]. White cedar also showed a different behavior in the relationship between diameter and sapwood depth (Figure 1). These two pieces of evidence point to the need to distinguish between obligate wetland species and the other species in northern Wisconsin.

sin. Such a result is all the more important in northern Wisconsin because forested wetland represents 40% of the land area [Mackay *et al.*, 2002].

4.3. Effect of Species and Environmental Conditions on Daily J_S

[34] Recent studies have looked at daily J_S from the standpoint of tree size [Schäfer *et al.*, 2000; Oren *et al.*, 1999b], tree allometrics [Meinzer *et al.*, 2001], and environmental conditions [Ewers *et al.*, 1999; Oren *et al.*, 1999b; Wullschleger *et al.*, 2000]. We found no effect of tree size on J_S of any species group. When tree sap flow is standardized by conducting or transpiring area, differences in sap flow among different trees decrease [Oren *et al.*, 1998]. However, in bald cypress [Oren *et al.*, 1999b], *Nothofagus fusca* [Kelliher *et al.*, 1992], and European beech [Schäfer *et al.*, 2000], larger trees had higher J_S , possibly in response to microclimate or sapwood-to-leaf area ratio. We found no effect of tree size on J_S , and the species effects were not related to size (Table 1 and Table 3). Tree allometrics can have a strong effect on J_S . Across 30 tropical tree species in Panama, J_S in the outer xylem was inversely related to sapwood thickness and area [Meinzer *et al.*, 2001]. We found no correlation between sapwood thickness and J_S , suggesting that our J_S values may be more related to sapwood-to-leaf area ratio than intrinsic qualities of the species we studied. However, such an investigation is beyond the scope of this study.

[35] We found that daily J_S was only explained by D_Z in all species except upland balsam fir (Figure 4). The relationship between J_S and D_Z was best described by an exponential saturation. This type of response can indicate that (1) stomata are closing to maintain Ψ_L above the runaway cavitation threshold, and (2) at high water flux the soil moisture near roots may decrease [Pataki *et al.*, 1998; 2000]. The second scenario may not be as likely since we saw no effect of soil moisture on J_S or Ψ_L in any species, indicating that soil moisture was never low enough to cause stomatal closure. The first scenario appears more plausible since Ψ_L was higher in red pine and trembling aspen on days in which D_Z was low. However, the limited Ψ_L data shown here, combined with the high amount of precipitation during the growing season, suggest more study is needed to determine the contribution of soil moisture to J_S in northern Wisconsin.

4.4. Effect of Species on E_C

[36] For species where E_C information is available, our estimates (Table 3) were generally close to reported values. Our estimates of E_C from trembling aspen (peak values $\sim 3.0 \text{ mm d}^{-1}$) were very similar to pure trembling aspen plots in the Rocky Mountains of Wyoming (peak values $\sim 3.0 \text{ mm d}^{-1}$) [Pataki *et al.*, 2000]. Our estimates of forested wetland were similar to a pure *Taxodium distichum* wetland in North Carolina (1.2 mm d^{-1}) [Oren *et al.*, 1999b] and lower than a forested wetland in Florida [Brown, 1981], the latter perhaps due to lower D at our site. Our estimates of daily E_C from the northern hardwoods were as little as 20% of sugar maple from New York [Dawson, 1996], but our values were only half that of mature beech stand [Magnani *et al.*, 1998] or upland hardwood forest in Tennessee [Wullschleger *et al.*, 2000]. The low values of E_C in the northern hardwoods of northern Wisconsin may reflect the thinning of these stands to half

the maximum L of $8 \text{ m}^2 \text{ m}^{-2}$ [Burrows *et al.*, 2002; Fassnacht *et al.*, 1997] or the low values of stomatal conductance of sugar maple [Kruger and Reich, 1997].

[37] The exponential saturation found in E_C with increasing D_Z (equation (6) and Figure 4) indicates stomatal closure at high D as found in other studies of both conifers and deciduous trees [Ewers *et al.*, 2001a; Pataki *et al.*, 2000; Oren *et al.*, 1999b; Martin *et al.*, 1997; Jarvis, 1980]. Both predawn Ψ_L and regression analysis agree that soil moisture was never low enough to cause stomata to close and thus limit daily E_C . The net result of the individual species effects on whole tree hydraulic conductance (Table 2) and A_S (Table 1) on E_C (Table 3) show that E_C cannot be predicted by L (Table 1) or soil properties alone. Such results indicate a need for robust whole tree hydraulic mechanisms that operate across a range of environmental conditions and species. Oren *et al.* [1999a] showed that the sensitivity of stomatal conductance to vapor pressure deficit can be predicted across a wide range of species by quantifying stomatal conductance at low vapor pressure deficit. That work is supported by water relations theory that says that the hydraulic pathways of trees are regulated by the stomata so as to maintain a minimum leaf water potential [Sperry *et al.*, 1998]. These types of broad studies are further supported by the idea that allometric relations and water relations are universally linked [Enquist *et al.*, 1998; West *et al.*, 1999; Enquist and Niklas, 2001]. However, the sapwood area relationships and the K values from this study suggest that the species effects may not be easily explained using current theory, especially with regard to wetland species. Thus future research on these sites as well as other studies that seek to address species effects on transpiration should focus on whole tree hydraulics and stomatal control of transpiration that can be broadly applied. We thank Kemp Natural Resources Station for the use of their personnel and facilities.

5. Conclusions

[38] In northern Wisconsin, canopy transpiration cannot be predicted from leaf area index alone. Canopy transpiration varied by a factor of 2 while leaf area index varied by less than 15%. The variability in transpiration can be attributed to species effects on sap flux, sapwood area, leaf water potential, and hydraulic conductance. The hypotheses put forth in this study failed to adequately address the species effects because of the wetland species. The wetland species did not share the same relationship between sapwood area and diameter as the upland species, and the hydraulic conductance of white cedar, a wetland species and a conifer, was higher than all of the other species including the deciduous species. Even though the absolute amount of canopy transpiration varied among the species, the response of transpiration to environmental variables such as vapor pressure deficit was very similar. The results of this study show that when trying to determine the amount of canopy transpiration across a forested landscape, classification of plant functional types such as coniferous and deciduous may not be sufficient and that forested wetlands require greater scrutiny.

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