Environmental controls on sap flow in a northern hardwood forest

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Summary   Our objective was to gain a detailed understanding of how photosynthetically active radiation (PAR), vapor pressure deficit (D) and soil water interact to control transpiration in the dominant canopy species of a mixed hardwood forest in northern Lower Michigan. An improved understanding of how these environmental factors affect whole-tree water use in unmanaged ecosystems is necessary in assessing the consequences of climate change on the terrestrial water cycle. We used continuously heated sap flow sensors to measure transpiration in mature trees of four species during two successive drought events. The measurements were scaled to the stand level for comparison with eddy covariance estimates of ecosystem water flux (F_w). Photosynthetically active radiation and D together explained 82% of the daytime hourly variation in plot-level transpiration, and low soil water content generally resulted in increased stomatal sensitivity to increasing D. There were also species-specific responses to drought. *Quercus rubra* L. showed low water use during both dry and wet conditions, and during periods of high D. Among the study species, *Acer rubrum* L. showed the greatest degree of stomatal closure in response to low soil water availability. Moderate increases in stomatal sensitivity to D during dry periods were observed in *Populus grandidentata* Michx. and *Betula papyrifera* Marsh. Sap flow scaled to the plot level and F_w demonstrated similar temporal patterns of water loss suggesting that the mechanisms controlling sap flow of an individual tree also control ecosystem evapotranspiration. However, the absolute magnitude of scaled sap flow estimates was consistently lower than F_w. We conclude that species-specific responses to PAR, D and soil water content are key elements to understanding current and future water fluxes in this ecosystem.

Keywords: Acer rubrum, Betula papyrifera, drought, eddy covariance, PAR, Populus grandidentata, Quercus rubra, soil water, transpiration, vapor pressure deficit.

Introduction

Anthropogenic greenhouse gases are important contributors to increased temperatures in the northern hemisphere (Crowley and Lowery 2000). This warming is expected to continue as atmospheric CO_2 and other greenhouse gas concentrations continue to rise. In temperate regions, a 3 °C temperature increase could lead to an increase in transpiration and a decrease in available soil water by as much as 20% relative to current conditions (Schneider and Rosenberg 1989, Mitchell et al. 1990). However, the effects of changing atmospheric and soil water conditions on water use by mature trees in unmanaged forest ecosystems is poorly documented (Oren et al. 1996, 1998). Historically, transpiration in trees has most commonly been measured at either the leaf scale (Hogg et al. 2000) or the ecosystem scale (Granier et al. 1996*a*). Measurements of whole-ecosystem water flux (F_w) can provide important information on forest responses to variations in atmospheric water vapor pressure deficit (D) and soil water (Wofsey et al. 1993, Greco and Baldocchi 1996), but are limited in the information they provide on the biological mechanisms controlling these fluxes. A better understanding of the mechanisms by which trees respond to these factors will be necessary if we are to accurately assess and manage local, regional and global water budgets as the climate changes.

In recent years, measurements of water flux at the scale of individual mature trees have become more widespread with the development of reliable sap flow techniques (e.g., Granier 1985, Köstner et al. 1998). However, few studies have employed these techniques to investigate whole-tree responses to drought (Lu et al. 1995, Ewers et al. 2001, Phillips et al. 2001). This is particularly true in forests of mixed-species composition where, for example, shallow-rooted species may show large reductions in sap flux in response to increasing D when upper soil layers are depleted of water, whereas deep-rooted species may show more gradual reductions in water loss as the soil dries (Granier and Loustau 1994, Pataki et al. 2000, Oren and Pataki 2001). Other species demonstrate moderate water use regardless of soil water content (Goulden and Field 1995) or show highly species-specific sap flow responses to changing photosynthetically active radiation (PAR) and D (Oren and Pataki 2001). Developing a mechanistic basis for predictions

of forest water use as climate changes, or as successional dynamics or land-use demands alter forest composition will require expanded application of sap flow and eddy covariance methods.

We investigated how PAR, D and soil water interact to control transpiration in the dominant canopy species of a mixed hardwood forest in northern Lower Michigan. Because this forest grows on sandy soils derived from glacial outwash (Pearsall 1995), episodic droughts are common, making it an ideal site to investigate the impact of changes in soil water content on forest water use at the tree, stand and ecosystem levels. We predicted that reductions in soil water content would decrease water fluxes at all three scales (tree, stand and ecosystem). Additionally, we hypothesized that the early successional species in our system (i.e., *Populus grandidentata* Michx. and *Betula papyrifera* Marsh.) would have the largest fluxes because of the greater resource requirements of early successional species (Bazzaz 1979). *Quercus rubra* L. is likely the most deeply rooted of the species studied, and therefore, we expected it to be the least responsive to short-term drought (Stone and Kalisz 1991). Lastly, we compared eddy-covariance-based estimates of F_w to multi-species sap-flow measurements scaled to the stand level. This comparison allowed us to assess agreement between the two techniques, in terms of both the absolute magnitude of and the dynamic patterns in ecosystem water fluxes. Our results provide insight into the biological and environmental controls on the water cycle at the scales of the tree and forest canopy.

Methods

Study site

The study site is a mixed-hardwood forest in northern Lower Michigan at the University of Michigan Biological Station (UMBS) in Pellston, MI (45°33′ N, 84°42′ W). We measured height and diameter at breast height (DBH) of all trees with DBH > 3 cm within a 1.1-ha plot surrounding a 46-m meteorological tower as part of a broader effort to quantify climatic effects on forest–atmosphere exchanges of mass and energy (Curtis et al. 2002, Schmid et al. 2003). Dominant canopy species were *Populus grandidentata* Michx. (bigtooth aspen; 44.5% of total basal area), *Quercus rubra* L. (red oak; 13% of total basal area), *Acer rubrum* L. (red maple, 12% of total basal area) and *Betula papyrifera* Marsh. (paper birch; 8% of total basal area). *Pinus strobus* L. (white pine) and *Fagus grandifolia* Ehrh. (American beech) comprised the remaining 22% of total basal area and had generally not reached the upper canopy (Table 1). Most canopy trees were ~90 years old and the stand-level projected leaf area index determined from litterfall was 3.8. Soils are well-drained spodosols (92.9% sand, 6.5% silt, 0.6% clay). Total annual precipitation in 1999 was 774 mm, typical for the region.

Meteorological measurements

We report measurements made over a 61-day period in July and August 1999. All meteorological measurements were made at 34 m from the tower at the center of the study plot, un-less otherwise noted. Photosynthetically active radiation was measured with a quantum sensor (LI-190SZ, Li-Cor, Lincoln, NE), air temperature with a shaded, ventilated thermocouple, water vapor partial pressure with an infrared gas analyzer (LI-6262, Li-Cor) and precipitation with a tipping bucket rain gauge at 46 m (TR-525-M, Texas Electronics, Dallas, TX). Wind speed and direction were measured with a 3-dimensional sonic anemometer-thermometer (CSAT-3, Campbell Scientific, Logan, UT). Water vapor and wind speed and direction were sampled at 10 Hz and 30-s means were stored for subsequent analyses. We report hourly (60-min), daytime (PAR > 10 μmol m^{-2} s^{-1}) and daily (24-h) means. Volumetric soil water in the upper 30 cm was measured twice a week at various locations in the study plot by time domain reflectometry (TDR; Environmental Sensors, Victoria, BC, Canada). We also continuously monitored soil water at a single location with a water content reflectometer (CS-615, Campbell Scientific) calibrated against the TDR probes. Aerodynamic conductance (G_A), a measure of atmospheric coupling with the canopy, was estimated by the method of Thom and Oliver (1977):

$$G_A = \frac{0.212\,(1\,+\,0.54\,U)}{(\ln((z\,-\,d)\,/\,z_0))^2} \qquad (1)$$

where U is windspeed (m s^{-1}) at height z (34 m), d is the zero plane displacement (2/3 canopy height (22 m), or 14.7 m) and z_0 is the roughness length (defined as 10% of canopy height or 2.2 m).

Sap flow and plot-level transpiration

Xylem sap flux (J_s) was measured with 3.0-cm-long continuously heated thermal dissipation probes (TDP-30, Dynamax, Houston, TX; Granier 1985). Each probe consisted of a heated and an unheated reference thermocouple. The bark layer was removed to the edge of the phloem and probes were inserted 3.0 cm into the xylem tissue with the reference thermocouple 2.0 cm below the heated thermocouple. Temperature differentials were measured continuously between the heated and reference thermocouple junctions on each probe and 30-min means recorded. Probes were installed on the north-facing sides of four trees each of *P. grandidentata*, *Q. rubra*, *A. rubrum* and *B. papyrifera*, all of which were of canopy height. Species-specific sap flux (J_{si}) was calculated according to Granier (1985) by the following equations:

$$J_{sj} = 0.0119\,K^{1.23} \qquad (2)$$

$$J_{si} = \frac{\sum_{j=1}^{4} J_{sj}}{n} \qquad (3)$$

$$K = \frac{\Delta T_0\,-\,\Delta T_t}{\Delta T_t} \qquad (4)$$

where ΔT_0 is the maximum temperature differential, ΔT_t is the

Table 1. Number of stems, basal area (A_b), leaf area index (LAI) and mean height of tree species in the study plot. The sapwood area of individual trees (A_s; cm^2) was determined from species-specific allometric equations based on diameter at breast height (DBH; cm) and then summed to give the sapwood area for each species within the study plot (A_{si}). The mean ($\pm$ 1 SE) midday (1030–1300 h) sap flux (J_{si}) of each species is presented for Day 186 to illustrate typical within-species variation in sap flux (n = 4 trees per species).

Species	Stems (No. ha^{-1})	A_b (m^2 ha^{-1})	LAI (m^2 m^{-2})	Height (m)	Allometry (n, r^2)	A_{si} (m^2 ha^{-1})	J_{si} (g cm^{-2} h^{-1})
P. grandidentata	295	12.17	1.13	18.9	$A_s = 0.77 \times DBH^{1.868}$ (16, 0.97)	7.74	10.0 ± 1.6
A. rubrum	302	3.35	0.59	11.3	$A_s = 17.04 \times DBH - 110.66$ (13, 0.98)	2.18	8.0 ± 1.9
B. papyrifera	114	2.13	0.30	12.8	$A_s = 17.17 \times DBH - 112.21$ (12, 0.98)	1.44	9.1 ± 2.6
Q. rubra	110	3.60	0.87	11.8	$A_s = 3.24 \times DBH - 10.24$ (11, 0.90)	0.46	5.6 ± 2.0
P. strobus	1301	5.81	0.78	5.7	–	–	–
F. grandifolia	36	0.27	0.21	7.3	–	–	–

temperature differential at time t, K is the dimensionless index of sap flux, J_{sj} (g cm^{-2} s^{-1}) is sap flux of the jth individual tree of the ith species and n is sample size (= 4) for each species. Data are expressed either as mean half-hourly or mean day-time sap fluxes. Data were aggregated to hourly means for comparison with eddy-covariance-based estimates of F_w.

For all species, xylem sap flux was scaled to plot-level transpiration (E_p) by the following equations:

$$E_i = J_{si} A_{si} \tag{5}$$

$$E_p = \sum_{i=1}^{4} E_i \tag{6}$$

where J_{si} is mean half-hourly sap flux of the ith species, A_{si} is sapwood area of the ith species within the 1.1-ha study plot and E_i is plot-level transpiration for the ith species. Sapwood area was determined from on-site allometric relationships between DBH and sapwood depth (Table 1). To develop these relationships, sapwood depths were determined by staining tree cores taken at a height of 1.3 m with 2% tetrazolium trimethylchloride. This compound stains the active portion of the xylem red, making the determination of sapwood depth less ambiguous. Because radial profile information was lacking for our site, sap flow was assumed to be constant over the radial sapwood profile for all species (Phillips et al. 1996). Plot-level transpiration is expressed either as mean hourly rates (g m^{-2} h^{-1}) or as cumulative daily totals (kg m^{-2} day^{-1}).

Ecosystem water vapor flux

Ecosystem water vapor flux (F_w) was measured from the meteorological tower at 34 m by eddy covariance techniques (Schmid et al. 2000). Turbulent statistics and eddy covariance fluxes were calculated by Reynolds decomposition from hourly, raw 10-Hz data from the sonic anemometer and an infrared gas analyzer. Three rotation angles as defined in Kaimal and Finnigan (1994) were calculated for each hour. Hourly aggregates of E_p were then compared with hourly F_w for days without rain events and for periods with good turbulent mixing to assess the degree of agreement between the two techniques. For this study, adequate turbulent mixing was defined as periods when the friction velocity (u^*) was > 0.3 m s^{-1}, a typical lower limit for eddy covariance measurements.

Statistical analyses

Effects of PAR, D and soil water on daily J_{si} and E_p were investigated by linear regression and analysis of covariance (AN-COVA). The degree to which PAR, D and soil water controlled half-hourly estimates of E_p was determined by stepwise linear regression. The effect of soil water on mean midday J_{si} was tested by two-way analysis of variance (ANOVA) and a Scheffe post-hoc multiple comparisons test.

Results

Daily time scale

Over the 61-day study, two pronounced drought events occurred during which soil water fell from near field capacity (~20% v/v) to < 5% (v/v) (Figure 1A). Cumulative daily PAR was variable, with a high of over 50 mol m^{-2} day^{-1} on clear days, but reaching less than half that amount on cloudy days (Figure 1B). Declining day length led to a ~20% reduction in cumulative daily PAR over the 61-day study. Variation in mean daytime D ($\overline{D}$) was broadly associated with variation in cumulative daily PAR, occasionally exceeding 1 kPa on clear days (Figure 1B). Aerodynamic conductance (G_A) remained high for the entire study period, ranging between 45 and 205 mm s^{-1} (data not shown), indicating strong coupling between the canopy and atmosphere (Hogg et al. 1997, Phillips and Oren 1998).

Daily E_i varied more than tenfold among the study species, with *P. grandidentata* transpiring more than 1 kg H$_2$O m^{-2} day^{-1} compared with less than 50 g H$_2$O m^{-2} day^{-1} lost by *Q. rubra* (Figure 1C). These large species-specific differences in daily E_i reflect comparable differences in A_{si} (Equation 1, Table 1). The species all responded similarly to major climatic events, with marked declines in daily E_i when cumulative daily PAR and $\overline{D}$ were low (e.g., Days 190, 222 and 226) and a gradual decline in maximum daily E_i coincident with declining day length. There was no response in daily E_i to changes in soil water content in any of the species at the daily timescale.

The underlying causes of E_i sensitivity to cumulative daily PAR and $\overline{D}$ were examined. We found a linear relationship between daily J_{si} and cumulative PAR, but with variation among species in the closeness of the correlation (Figure 2A). Daily J_{si} in *P. grandidentata* and *B. papyrifera* was significantly
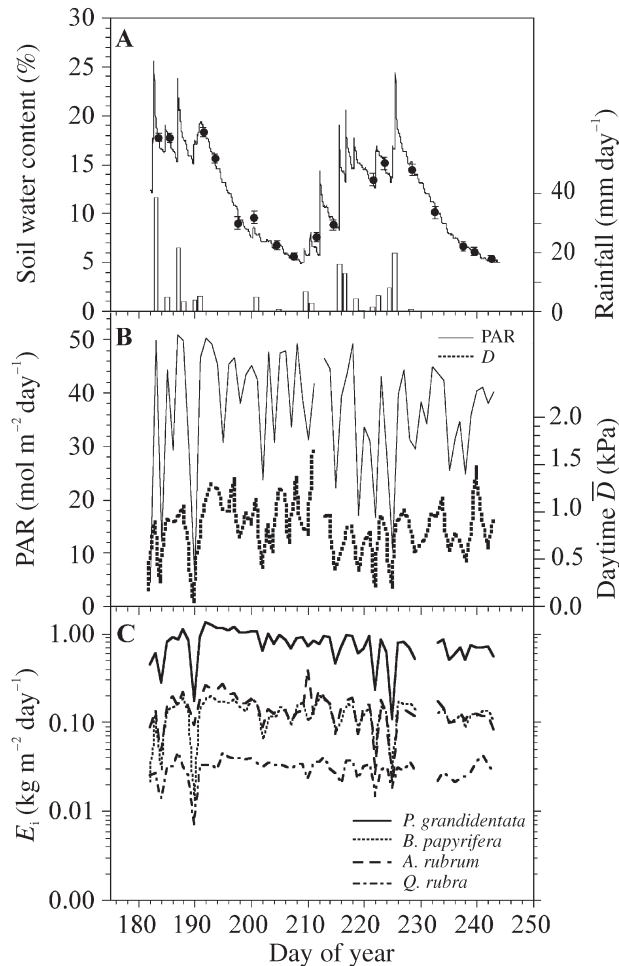
Figure 1. Variation in environmental parameters and plot-level transpiration during the 61-day study. (A) Soil water and precipitation. Closed symbols are from point measurements (mean ± SE, $n = 8$) and the solid line is a continuous recording from one location. Bars are rain events. (B) Daily cumulative photosynthetically active radiation (PAR) and mean daytime vapor pressure deficit ($\overline{D}$). (C) Plot-level transpiration (E_i) for *Populus grandidentata*, *Betula papyrifera*, *Acer rubrum* and *Quercus rubra*.

There were no soil water effects on E_p responses to cumulative PAR, but daily E_p at high $\overline{D}$ was significantly lower at low soil water content than at high soil water content ($P < 0.05$, AN-COVA).

Hourly time scale

At the hourly time scale, variation in E_p was most closely related to changes in D and PAR (Figure 3). Hourly E_p increased during the morning, peaked near solar noon and declined to a minimum shortly following sunset. However, changes in hourly E_p were not always in phase with changes in D (e.g., Day 197) and often showed a closer relationship to changes in PAR. During an extended period without rain (Days 193–199), when soil water content declined from ~16 to ~7% (Figure 1), PAR, D and their interaction explained 82% of the variation in hourly E_p ($P < 0.05$, ANOVA). Soil water had no significant effect on hourly E_p.

We found soil water effects on hourly J_{si}, but only at high D and only in certain species (Figure 4, Table 2). For this analysis, we considered data only for the midday period (1030–1330 h) and from days when soil water content was either > 15% (wet) or < 10% (dry). In general, at low D, J_{si} increased log-linearly with increasing D in all species and this increase was independent of soil water content (Figure 4). Above 1 kPa D, however, both mean J_{si} and the slope of the J_{si} versus D relationship were sensitive to soil water content (Table 2). Above 1 kPa D, mean J_{si} declined in dry soil compared with wet soil in all species except *Q. rubra*. As D increased above 1 kPa, all species except *Q. rubra* showed increasing J_{si} when soils were wet, but showed either no response in J_{si} to increasing D (*P. grandidentata*, *B. papyrifera*) or a decline in J_{si} with increasing D (*A. rubrum*) when soils were dry. *Quercus rubra* had significantly lower mean J_{si} at high D than the other species, and J_{si} did not change as D increased above 1 kPa in either wet or dry soil (Table 2).

Ecosystem water use

We compared hourly F_w and E_p for days without rain events and for periods with $u^* > 0.3$ m s^{-1}. Hourly F_w showed a power function-type relationship with E_p (Figure 5) and became asymptotic when E_p approached 0.1 kg m^{-2} h^{-1}. During periods of low fluxes, the two methods were in closer agreement. When F_w was above 0.2 kg m^{-2} h^{-1}, E_p increased very little, and the differences between the two estimates was greatest. On average, E_p was 34% lower than F_w.

Discussion

We found substantial differences in the relative contributions of individual species to E_p as well as species-specific responses to changing atmospheric and soil water conditions in this mixed-species hardwood forest. Much of the variation in E_p at the species-level (E_i) was due to large differences in stand-level sapwood area, but there were also significant differences in maximum sap flux (J_{si}) that contributed to this variation. For example, J_{si} in *P. grandidentata* and *B. papyrifera*
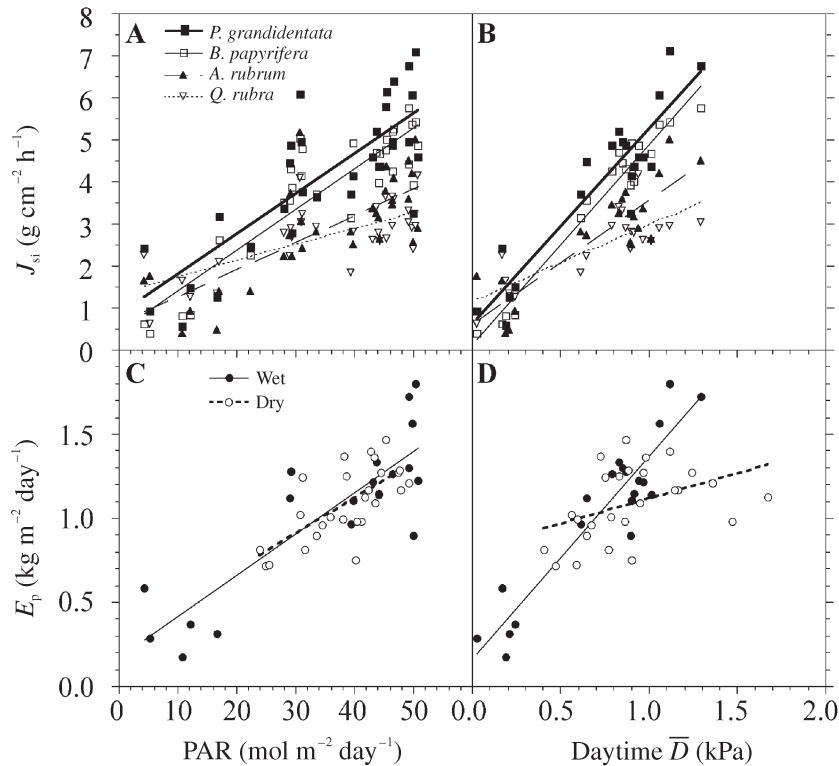
more closely correlated with cumulative PAR than in *A. rubrum* and *Q. rubra* ($P < 0.05$, ANCOVA). Daily J_{si} responses to changing $\overline{D}$ were linear, but there were interspecific differences (Figure 2B). The correlations in *P. grandidentata* and *B. papyrifera* were statistically indistinguishable and had the steepest slopes (i.e., J_{si} was most responsive to changes in $\overline{D}$ in these species) at high soil water contents compared with the other species. *Quercus rubra* had the lowest slope and *A. rubrum* had an intermediate slope relative to the other species. For clarity, only J_{si} data for days with soil water content >15% are shown in Figure 2. Soil water content had no effect on J_{si} responses to cumulative daily PAR in any species. However, in all species, low soil water content (< 10%) significantly reduced the sensitivity of J_{si} to $\overline{D}$. This soil water effect is reflected in daily E_p responses to PAR and $\overline{D}$, which are shown at both low and high soil water contents in Figures 2C and 2D.

Figure 2. Effects of daily cumulative photosynthetically active radiation (PAR) and mean daytime (PAR > 10 μmol m^{-2} s^{-1}) and mean daytime vapor pressure deficit ($\overline{D}$) on mean daily sap flux (J_{si}) of *Populus grandidentata*, *Betula papyrifera*, *Acer rubrum* and *Quercus rubra* (A, B) and on plot-level transpiration (E_p) summed across all species (C, D). Soil water was > 15% for periods when J_{si} was reported, but E_p data are separated according to periods when soil water content was either < 10% (dry) or > 15% (wet).

was about twice that of *Q. rubra*. *Populus grandidentata*, *B. papyrifera* and *A. rubrum*, all diffuse-porous xylem species, had higher J_{si} than the ring-porous species *Q. rubra*.

We examined sap flow across two pronounced soil-drying events, and contrary to our original hypothesis, found little evidence for soil water controls over E_i in any species. Rather, the dominant controls over E_i, and hence E_p, were daily cumulative PAR and $\overline{D}$. We also found differences among species, with mean daily J_{si} and E_i being significantly less responsive to
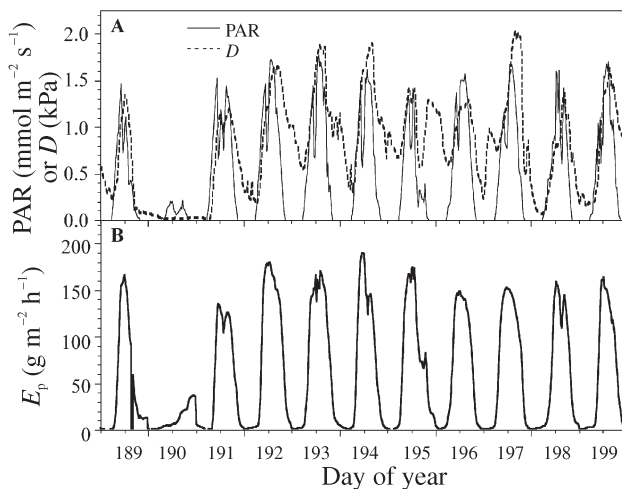

Figure 3. (A) Typical patterns in mean half-hourly photosynthetically active radiation (PAR) and vapor pressure deficit (*D*), and (B) hourly plot-level transpiration (E_p) during an 11-day period in July 1999.

increases in PAR and $\overline{D}$ in *Q. rubra* and *A. rubrum* than in *P. grandidentata* or *B. papyrifera*. Oren and Pataki (2001) observed similar magnitudes of sap flux and patterns of stomatal closure in response to high $\overline{D}$ in an oak–hickory forest. They found that J_{si} in *A. rubrum*, the only species in common to the two studies, was more responsive to high $\overline{D}$ and PAR than several *Quercus* species.

Although soil water had little effect on daily variation in E_p, J_s was sensitive to drought in all species except *Q. rubra* when *D* exceeded ~1 kPa. In general, we found that J_s increased exponentially with increasing *D* < 1 kPa. This response was independent of soil water content. At *D* > 1 kPa, however, J_{si} reached an asymptote, as has been reported for other forest ecosystems (Meinzer et al. 1993, Goulden and Field 1995, Granier et al. 1996*b*, Hogg et al. 1997, Oren and Pataki 2001), and its response to *D* became sensitive to soil water content. If forest canopies are well coupled to the atmosphere, as indicated by the high aerodynamic conductances (G_A) observed in this study, the response of J_{si} to *D* above 1 kPa should reflect changes in leaf-level g_s (Hogg et al. 1997). For example, a positive slope indicates little change in g_s with increasing *D*, whereas a flat or negative slope indicates stomatal closure (declining g_s) as *D* increases.

We observed significant interspecific differences in J_{si} responses to changing *D* above 1 kPa at both high and low soil water contents. When soil water content was high, *P. grandidentata*, *B. papyrifera* and *A. rubrum* all had positive slopes, indicating little change in g_s with increasing *D*. When soil water content was low, however, these species all showed declining g_s as *D* increased, with *A. rubrum* being the most extreme
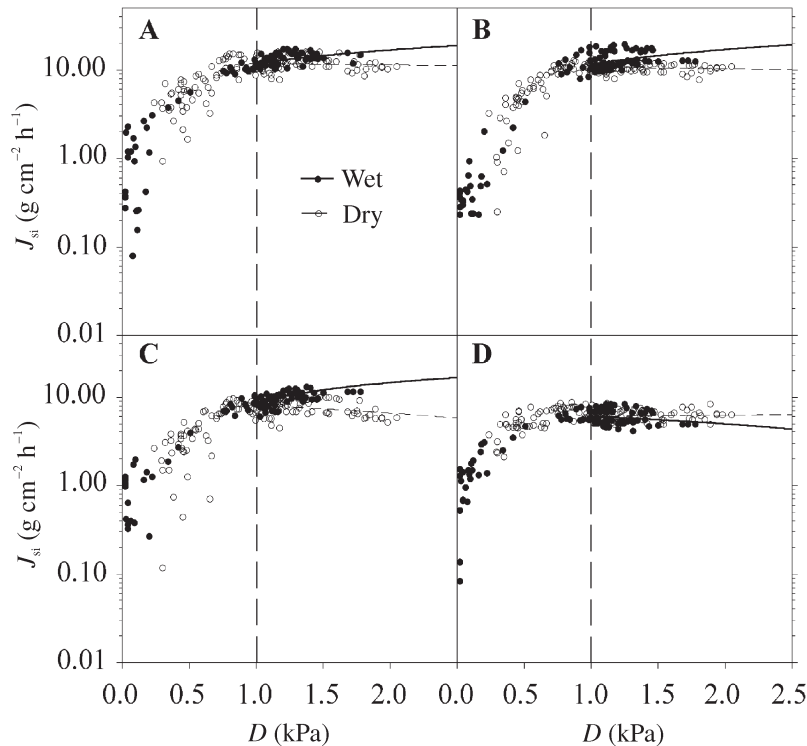
Figure 4. Effect of changing vapor pressure deficit (D) on mean hourly sap flux (J_{si}) in *Populus grandidentata* (A), *Betula papyrifera* (B), *Acer rubrum* (C) and *Quercus rubra* (D) when soil water was either < 10% (dry) or > 15% (wet). Data are restricted to midday hours (1030–1330 h) from the 61-day study period.

(the only species with a negative slope). In contrast, *Q. rubra* reduced g_s with increasing D at both high and low soil water contents. The greater sensitivity of g_s to D in *A. rubrum* under drought conditions may reflect the species' shallow rooting system. Roots of *A. rubrum* are generally located in the upper 25 cm of the soil horizon with a typical maximum rooting depth of 2–3 m (Burns and Honkala 1990, Abrams 1998). This rooting pattern is characteristic of most eastern hardwood species including *Populus* and *Betula* species; however, *Quercus* species are an exception and tend to be more deeply rooted with more pronounced tap roots (Burns and Honkala 1990, Stone and Kalisz 1991). Such differences in rooting depth may explain why J_{si} was reduced in *A. rubrum*, *B. papyrifera* and *P. grandidentata* but not in *Q. rubra* during periods of low soil water availability.

Additionally, *Q. rubra* may be more susceptible to cavitation events at our site given the highly conductive soils and fre-

quent episodic droughts. Ring-porous species have wider vessels than diffuse-porous species resulting in higher xylem conductivity (Pallardy and Rhoads 1993), which is beneficial under high flux conditions. However, when cavitation occurs, the resulting embolisms are much larger (Kozlowski and Pallardy 1997). Furthermore, *Q. rubra* has a leaf area to sapwood area ratio ~7 to 13.5 higher than the other species in our study which, given equal stomatal conductances, would lead to substantially larger water losses per unit of sapwood area at high D and further increase the risk of cavitation.

Our comparison of above-canopy, whole-ecosystem water flux (F_w), with plot-level transpiration (E_p), which was scaled from the product of species-specific sap flux (J_{si}) and plot-level sapwood area per species (A_{si}), revealed several patterns. Broadly, the close correlation between the two measures suggests the dominant environmental controllers of sap flow variation at the individual tree level (PAR and D) were similar to

Table 2. Mean midday (1030–1330 h) sap flux (J_{si}) and slope of the J_{si} versus D relationship for periods when D was > 1 kPa and under dry or wet (< 10% or > 15% soil water content, respectively) conditions. Data are means ± SE. Different letters indicate significant differences ($P < 0.05$) between species and soil water conditions for J_{si}, and between soil water conditions only for slopes. Asterisks indicate that the slope differs significantly from zero.

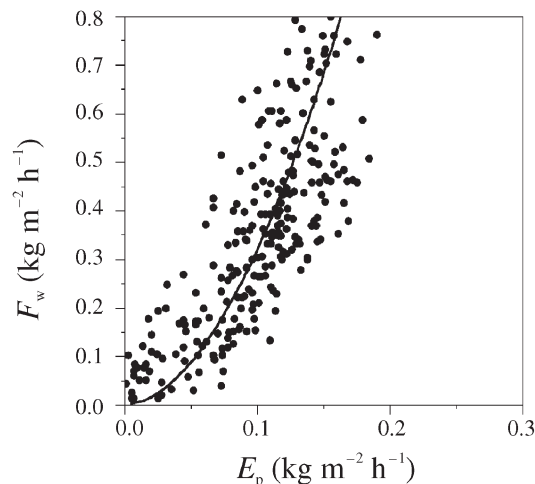| Species	J_{si} (g cm^{-2} h^{-1})		Slope (g cm^{-2} h^{-1} kPa^{-1})	
	Dry	Wet	Dry	Wet
P. grandidentata	11.9 ± 0.2 a	13.6 ± 0.3 b	−0.5 ± 0.8 a	4.0 ± 1.2 b *
A. rubrum	7.8 ± 0.2 c	9.9 ± 0.2 d	−1.7 ± 0.6 a *	5.3 ± 1.0 b *
B. papyrifera	10.5 ± 0.1 d	13.2 ± 0.4	−0.4 ± 0.4 a	4.2 ± 2.1 b *
Q. rubra	6.3 ± 0.1 e	6.1 ± 0.1 e	0.2 ± 0.4 a	−1.3 ± 0.9 a

Figure 5. Comparison of hourly plot-level transpiration (E_p) and hourly ecosystem water vapor flux (F_w) measured at 46 m for days without rain and the friction velocity (u^*) > 0.3 m s^{-1}. A power function is fit to the data of the form $F_w = 0.18 \times E_p^{0.53}$ ($r^2 = 0.66$).

those operating at the ecosystem level. However, the relationship we observed between E_p and F_w was neither linear nor had a slope close to unity. Rather, E_p consistently underestimated F_w, with a closer match between the two measures at low water fluxes than at high water fluxes. In two previous studies in which E_p estimates from tree-level sap flux densities were compared with eddy-covariance-based estimates of F_w, E_p underestimated F_w. The E_p–F_w comparison presented by Granier et al. (1996a) for a *Pinus sylvestris* L. plantation appears to be nonlinear (similar to the relationship in our study) and, at high fluxes, E_p was ~58% of F_w. Oren et al. (1998) studying a *Pinus taeda* L. plantation, found a linear relationship between E_p and F_w, but E_p was ~67% of F_w under high flux conditions.

The slope of an ordinary linear regression between the sum of sensible and latent heat fluxes and available energy during the daytime over the growing season (June through August) of 1999 at the UMBS site is 0.974 (Su et al. 2004). This level of energy balance closure is quite good compared with those from other FLUXNET sites (Wilson et al. 2002) and gives us confidence in our estimates of F_w. Furthermore, it suggests an apparent systematic underestimation of E_p, which could have several causes. First, there are several potential sources of error in scaling sap flow estimates of single-tree transpiration to the stand level, including incorrect assumptions concerning radial sap flow patterns (Granier et al. 1994, Phillips et al. 1996, Čermák and Nadezhdina 1998, Wullschleger and King 2000, Ford et al. 2004) or errors in estimating sapwood area. Because sap flow generally decreases in older or deeper sapwood, if sap flow sensors are at depths where sap flow is below average, E_p would be underestimated. Preliminary data on radial profiles of sap flow velocity in the diffuse-porous species at our site suggest our probes were located in the region of highest sap flow (P.S. Curtis, unpublished data). Therefore, we may have overestimated, rather than underestimated, E_p of *P. grandidentata*, *B. papyrifera* and *A. rubrum*. For *Q. rubra*, however, sap-

wood depth was about 2 cm, which was similar to the measurement junction of our sap flow sensors and likely resulted in an underestimate of E_p in this species. Given the predominance of diffuse-porous species at our site, underestimation of total E_p associated with sensor placement seems unlikely.

Other factors that could contribute to underestimates of F_w by E_p include transpiration by species excluded from our study (e.g., white pine (*Pinus strobus* L.)) or by understory species. These contributions are likely of the same order of magnitude as the contribution from *B. papyrifera* or *A. rubrum*. Although significant, such fluxes could not by themselves explain the discrepancy between the techniques. Evaporative water losses from surfaces (e.g., leaves and soil), which can be substantial following rain events, were not measured as part of E_p. Increasing D should increase surface evaporative losses relative to transpirational losses, which tend to be fairly constant at $D >$ 1 kPa. This would result in a smaller proportion of F_w derived from transpiration when fluxes are large (i.e., when $D >$ 1 kPa), and lead to a nonlinear E_p–F_w relationship. Finally, J_s of the individual trees that we measured might not be representative of the trees in the area of the forest measured by the eddy-covariance technique. Although the trees we selected and the stand characteristics of our study plot are broadly representative of the surrounding landscape, we cannot rule out unsuspected systematic bias, and further work will be needed to resolve this discrepancy.

In conclusion, we found that, although operating at different time scales, PAR, D and soil water are important interacting environmental controls on ecosystem water fluxes in a mixed hardwood forest in northern Lower Michigan. Therefore, climate change that impacts these components of the environment will likely impact ecosystem water use and the hydrologic cycle as a whole. In addition, species-specific differences in responses to PAR, D and soil water suggest that, as the current early successional species are replaced, patterns of ecosystem water use will also change.

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