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Transpiration in response to variation in microclimate and soil moisture in southeastern deciduous forests

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Abstract Responses of forests to changes in environmental conditions reflect the integrated behavior of their constituent species. We investigated sap flux-scaled transpiration responses of two species prevalent in upland eastern hardwood forests, *Quercus alba* in the upper canopy and *Acer rubrum* in the low to mid canopy, to changes in photosynthetically active radiation above the canopy (Q_o), vapor pressure deficit within the canopy (D), and soil moisture depletion during an entire growing season. Water loss before bud break (presumably through the bark) increased linearly with D , reaching 8% of daily stand transpiration (E_C) as measured when leaf area index was at maximum, and accounting for 5% of annual water loss. After leaves were completely expanded and when soil moisture was high, sap flux-scaled daily E_C increased linearly with the daily sum of Q_o . Species differences in this response were observed. *Q. alba* reached a maximum transpiration at low Q_o , while *A. rubrum* showed increasing transpiration with Q_o at all light levels. Daily E_C increased in response to daily average D , with an asymptotic response due to the behavior of *Q. alba*. Transpiration of *A. rubrum* showed a greater response to soil moisture depletion than did that of *Q. alba*. When evaluated at a half-hourly scale under high Q_o , mean canopy stomatal conductance (G_S) of individuals decreased with D . The sensitivity of G_S to D was greater in species with higher intrinsic G_S . Regardless of position in the canopy, diffuse-porous species in this and an additional, more mesic stand showed higher G_S and greater stomatal sensitivity to environmental variation than do ring-porous species.

Keywords *Acer rubrum* · *Quercus alba* · Sap flux · Seasonal pattern of water use · Vapor pressure deficit · Photosynthetically active radiation · Soil moisture · Bark water vapor loss

Introduction

Transpiration of long-lived, co-occurring species can be similar when integrated over long periods. However, transpiration often varies greatly among species at any point of a single wet-dry cycle due to differences in sensitivity to soil moisture variations (Hinckley et al. 1978; Oren et al. 1996; Pataki et al. 1998, 2000). Thus, measurements of whole-canopy water vapor flux provide necessary information on the responses of complex natural forests to variations in atmospheric and soil moisture conditions (Shuttleworth 1988; Wofsey et al. 1993; Greco and Baldocchi 1996), but are of limited use in assessing variation in responses among species. Species differences in response to fluctuations in resource availability and driving forces complicate attempts to quantify and predict mass and energy exchanges over mixed-species forests in response to changing climate.

Where the root zone is limited, decreasing soil moisture strongly reduces sap flux (J_S) and its response to vapor pressure deficit (D ; Oren et al. 1996, 1998a). Similarly, species that are inherently shallow-rooted may show large reductions of J_S in response to D upon drying of the upper soil layer, while deeply rooted species typically show gradual reductions in transpiration as the soil dries (Crombie et al. 1988; Bréda et al. 1993; Granier and Loustau 1994; Pataki et al. 2000). Thus, some species assimilate a large proportion of their annual carbon while soil moisture is available, but show a large reduction in conductance, and thus photosynthesis, as the soil dries. Other co-occurring species may maintain moderate rates of conductance and photosynthesis regardless of soil moisture (Goulden 1996). In addition to soil moisture, species-specific responses to light and D may cause species to shift ranks in terms of mean stomatal conduc-

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tance (G_S) diurnally and seasonally. However, limited access to crowns of large trees has restricted studies on G_S and transpiration responses to environmental variation to only a few mature mixed-species forests.

We investigated the seasonal pattern of daily J_S in an upland eastern deciduous forest composed predominantly of four ring- and two diffuse-porous species. The purpose of the study was to evaluate the effect of seasonal variability in leaf area index (L), above-canopy photosynthetically active radiation (Q_o), within-canopy D , and soil moisture depletion (SMD) on transpiration by the entire canopy (E_C), and by its component species as reflected in their J_S and G_S , at temporal scales ranging from half an hour to a season. We primarily focused on the responses of one species in the upper canopy (*Quercus alba* L.) and one in the low to mid canopy (*Acer rubrum* L.). The responses of one to two individuals of four additional species were monitored to assess the generality of responses of the more intensively studied species.

Materials and methods

Site

The site in the Eno Division of Duke Forest, North Carolina (35°52'00" N, 79°59'45" W), is a transitional zone between the coastal plain and the Piedmont plateau, on a Georgeville silt loam, at an elevation of about 130 m above sea level. Mean annual temperature is 15.5°C. Mean annual precipitation is 1,140 mm, with rainfall generally well distributed throughout the year, but a moisture deficit may develop during the growing season in rainless periods (Ruffner and Bair 1985).

The 800-m² experimental plot was located on a hillside (2–10% slope) in an 80-year-old oak-hickory forest community. The plot contained 106 trees [67 *A. rubrum* L. (red maple), 4 *Carya tomentosa* [Poir.] Nutt (mockernut hickory), 17 *Cornus florida* L. (flowering dogwood), 6 *Liquidambar styraciflua* L. (sweetgum), 9 *Q. alba* L. (white oak), 1 *Q. velutina* Lam. (black oak), 1 *Q. falcata* Michx. Var. *falcata* (southern red oak), and 1 *Juniperus virginiana* L. (eastern red cedar)], with a stand basal area of 23.0 m² ha⁻¹.

Microclimate and sap flux

Photosynthetically active radiation (Q_o , $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was measured with a spherical quantum sensor (LI200SA; LI-COR, Lincoln, Neb.) placed in an adjacent clearing, while temperature

and relative humidity were recorded at two-thirds canopy height (Vaisala HMP35C, Finland) to calculate vapor pressure deficit (D , kPa). Five standard rain gauges and two tipping buckets (Texas Electronics, Dallas, Tex.) were distributed randomly in the understory to estimate throughfall (P_T , mm).

Stem flux was monitored with 20-mm-long constant heat flow Granier-type radial flow meters (Granier 1987). The temperature difference between the heated and reference probes was recorded, and by comparing the difference to the maximum occurring at pre-dawn when there is no flow, sap flux density J_S ($\text{g H}_2\text{O m}^{-2}$ sapwood s^{-1}) was calculated according to Granier (1987). In cases where sapwood depth was less than the 20-mm sensor length, the measured temperature difference was corrected (Clearwater et al. 1999). Where sapwood depth exceeded the sensor depth, J_S measured with the sensor was assumed uniform over the entire depth, based on the findings in the same stand by Phillips et al. (1996) for *Q. alba* and *L. styraciflua*. Six individuals each of *A. rubrum* and *Q. alba*, two of *L. styraciflua*, and one each of *C. tomentosa*, *Q. falcata*, and *Q. velutina* were chosen to approximate the frequency of individuals of each species in the stand (Table 1), and were monitored from March to October 1993.

Microclimate and sap flux data were sampled every 30 s, and 30-min averages were recorded (DL2; Delta-T Devices, Cambridge, UK).

Leaf area index and dynamics

In 1993, a canopy area analyzer (LAI2000; LI-COR) was used to evaluate the relative dynamics of stand leaf area index (L), and the maximum values at the peak of the growing season were set to equal the values obtained after complete senescence with the line intercept method. This approach does not reproduce the dynamics in L for each species (L_j). Thus, in 1994, the year following the study, L_j was estimated by catching leaves in five 1×1 m litter traps placed above the forest floor. We assumed that while the maximum value of L_j changes annually, the general dynamics of L_j and L_j/L change greatly only in years with unusual weather. Weather conditions were similar to the long-term average in both years. Thus the dynamics in absolute values of L_j in 1993 were estimated by combining the relative dynamics in 1994 with the peak value of L in 1993. In 1994, senesced leaves were collected weekly and identified. A subsample of leaves was measured optically for projected leaf area (DIAS Digital Image Analysis System; Decagon Devices, Pullman, Wash.), dried for 48 h at 70°C, and weighed to obtain the specific leaf area ($A_L:M_L$, $\text{cm}^2\text{ g}^{-1}$). The leaf area index of each species L_j is its $A_L:M_L$ multiplied by its dry leaf weight, summed over the season and divided by the collection area.

Stand transpiration and mean canopy stomatal conductance

Sap flux density estimates were scaled to the stand level as follows:

$$E_{Cj} = A_{Sj} : A_G \cdot \frac{1}{n} \sum_{i=1}^n J_{Sj} \quad (1)$$

Table 1 Means for each species of tree basal area for the whole plot (A_{bp}) and of the sampled trees (A_{bs}), percentage of stand basal area in the plot (A_{Bp}) and of the trees monitored for sap flux (A_{Bs}), specific leaf area ($A_L:M_L$), sapwood-to-ground area ratio ($A_{Sj}:A_G$),

leaf-to-sapwood area ratio ($A_L:A_S$), and leaf area index of each species in 1993 (L_j) based on percent of stand L obtained in 1994 (L in 1993=0.8 L in 1994)

Species	A_{bp} (cm ²)	A_{bs} (cm ²)	A_{Bp} (%)	A_{Bs} (%)	$A_L:M_L$ (cm ² g ⁻¹)	$A_{Sj}:A_G$ (cm ² m ⁻²)	$A_L:A_S$ (m ² cm ⁻²)	L_j (m ² m ⁻²)
<i>Acer rubrum</i>	54 (SD=8)	78 (SD=37)	18	4	168	5.1	0.04	0.1 (3%)
<i>Carya tomentosa</i>	531 (SD=238)	765	6	7	135	1.0	1.33	1.3 (26%)
<i>Liquidambar styraciflua</i>	208 (SD=85)	392 (SD=120)	8	11	135	1.4	0.21	0.4 (6%)
<i>Quercus alba</i>	1,001 (SD=182)	1,152 (SD=238)	49	64	88	3.2	0.96	3.1 (61%)
<i>Quercus velutina</i> and <i>Quercus falcata</i>	1,568 (SD=836)	1,568 (SD=836)	17	25	91	1.0	0.13	0.1 (2%)

where E_{Cj} ($\text{mm}\cdot\text{day}^{-1}$) is transpiration by species j , and $A_{Sj}:A_G$ ($\text{m}^2\text{ m}^{-2}$) and $\frac{1}{n} \sum_{i=1}^n J_{Sij}$ ($\text{g H}_2\text{O m}^{-2}$ sapwood day^{-1}) are the sapwood-to-ground area ratio, and the mean sap flux density for species j , respectively. Stand transpiration for trees >30 mm in diameter (E_C) was calculated by summing E_{Cj} .

The sapwood area of each tree was estimated from a set of species-specific relationships between A_S and diameter at 1.3 m aboveground. These relationships covered the entire range in tree size and originated from trees from ridge tops, hill slopes, and bottomlands. To construct the relationships, stem diameter to 1-mm precision, and bark thickness and heartwood diameter in four radial directions to 0.1 mm were measured in each sample tree. Sapwood area for each individual in the experimental plot was estimated using the relationships between sapwood area and diameter. $A_{Sj}:A_G$ was estimated by summing sapwood area for each species, and dividing by the plot area.

Using half-hour values of J_{Sij} from individual sensors, where i represents individually monitored xylem patches, and a species mean sapwood-to-leaf area ratio ($A_{Sj}:A_L$, $\text{m}^2\text{ m}^{-2}$), estimated from $A_{Sj}:A_G$ and L_j , mean leaf transpiration rate ($\text{g H}_2\text{O m}^{-2}$ leaf area s^{-1}) was estimated for individuals (Oren et al. 1998b). Then, mean stomatal conductance for individual crown patches, G_{Sij} (m s^{-1}), was calculated from the transpiration rate and D , according to Landsberg (1986), and assuming a high boundary layer relative to stomatal conductance (Oren et al. 1999). This assumption was validated in a nearby stand of similar structure, height, and species composition. We note that where this assumption is greatly violated, the estimate of conductance is in error, but the analysis of the response of conductance to environmental variables is hardly affected (Oren et al. 1999). Conductance values were converted to molar units (Pearcy et al. 1989).

Results

Seasonal sap flux and transpiration

Values for daily J_{Sj} are shown in Fig. 1. Missing J_{Sj} data are due to lightning-induced equipment failure. Data collected on some individuals during the first 15 days, before bud break, show low values of daily J_{Sj} even when D was high. After bud break, J_{Sj} increased rapidly. During the leaf senescence period, J_{Sj} was available only for the period just before the beginning of rapid senescence (days 140–150, in Fig. 1, corresponding to days 85–75 before full senescence in Fig. 2), followed by a 50-day gap in the J_{Sj} data, and a second period when senescence had already reached an advanced stage. Declines in J_{Sj} did not correspond well to declines in L_j , as is clearly apparent in the high values of late-season J_{Sj} of *Q. alba* (days 198–220) corresponding to a time of rapidly declining L_j .

Effects of environmental factors on daily stand transpiration

Sap flux was scaled to stand transpiration using estimates of sapwood area from diameter (r^2 ranged from 0.86 to 0.92) and Eq. 1. The effects of environmental factors on stand transpiration were then evaluated using three methods.

First, the effect of Q_o or D on daily E_C was assessed using a least-square regression analysis during the mid-season period of stable L . To account for changes in daylength over the study period, we used daylength-normal-

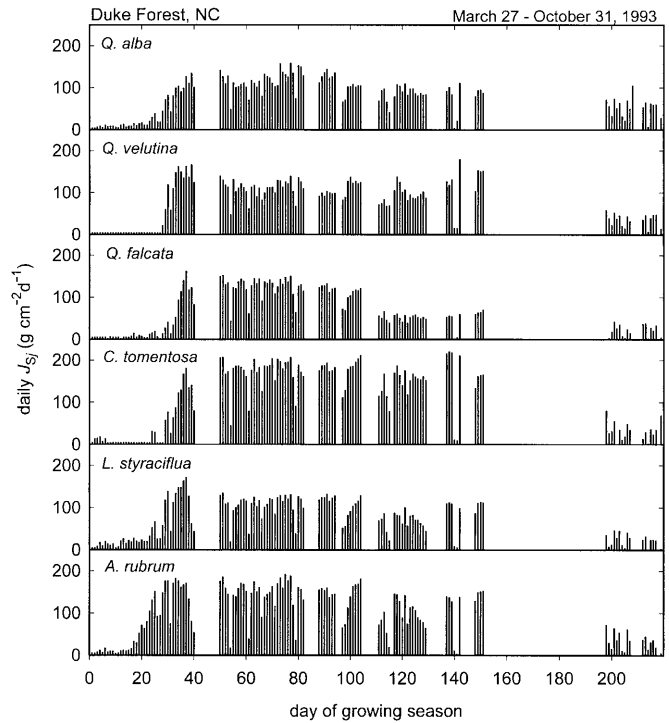


Fig. 1 Daily sap flux density (J_{Sj}) for each species during the growing season. Missing data represent days in which equipment failed, mostly as a result of lightning strikes

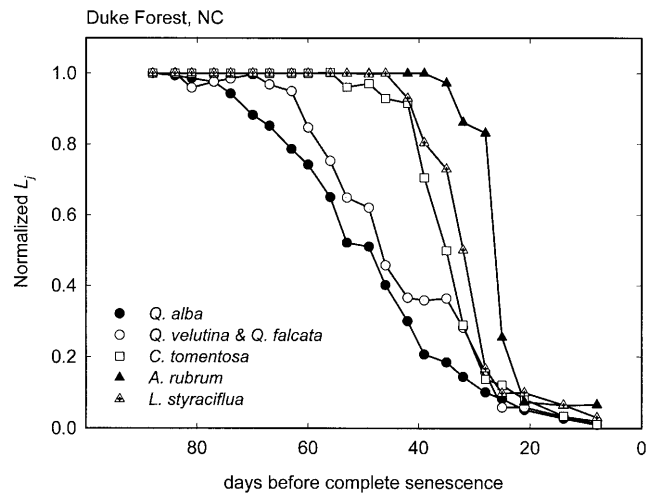
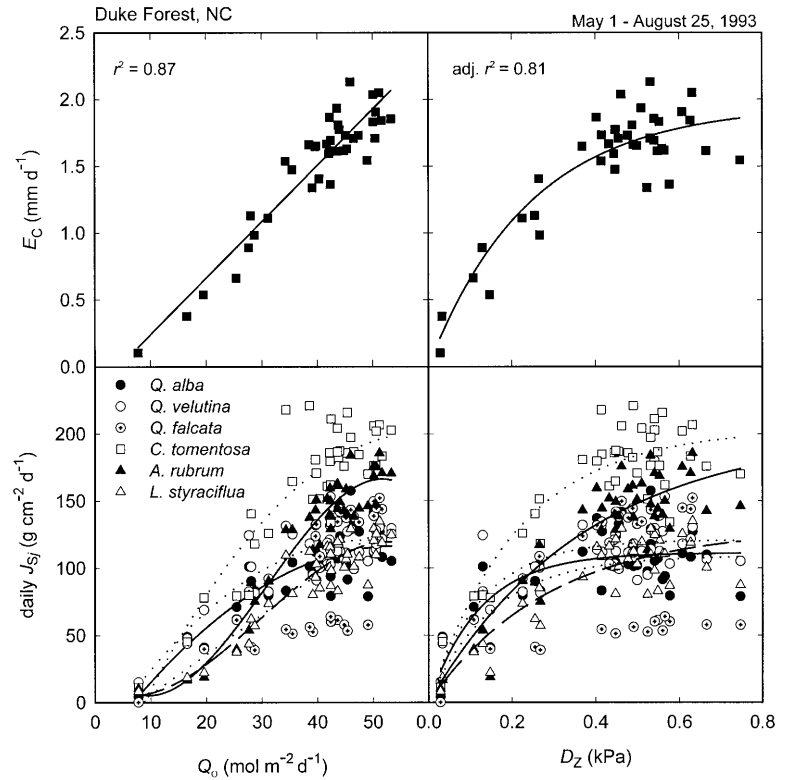


Fig. 2 Relative leaf area index (L_j) of each species during senescence as estimated by litter collection in fall 1994 (maximum L was $4\text{ m}^2\text{ m}^{-2}$). Values for each species are normalized by the maximum value obtained (see Table 1)

ized daytime mean D , or D_Z . With a second-order polynomial fit, Q_o explained 59% of the variation in daily stand E_C , while D_Z explained 22% ($P < 0.01$ for both; relationships not shown). Variations in soil moisture, and lag responses to changes in soil moisture, may obscure the relationship between microclimate and E_C . Thus, we incorporated the effect of SMD as an additional independent variable. An index of SMD was derived as follows.

Fig. 3 Daily stand transpiration (E_C) and mean sap flux of each species (J_{Sj}) in relation to incident photosynthetically active radiation (Q_0) and day-length-normalized daytime mean vapor pressure deficit (D_Z). Values are given for well-watered conditions (soil moisture depletion, SMD < 10 mm). No differences were found among species within the *Quercus* genus and between them and *Liquidambar styraciflua* ($P > 0.05$), forming one group. *Carya tomentosa* and *Acer rubrum* were different from each other and from the first group. All models were significant at $P < 0.05$



After the first large rain event of the growing season (28.3 mm on 28 March) added moisture to an already moist soil, SMD was set to zero. Thereafter, SMD was calculated as cumulative E_C reduced by P_T , with SMD < 0 set to zero. For mid-season days in which data were missing, E_C was estimated for the purpose of calculating SMD using the regression coefficients with Q_0 .

SMD did not explain variations in measured E_C when included in a multivariate regression with Q_0 and D_Z ($P > 0.1$). However, analyzing only days on which SMD < 10 mm (approximately half the data during the stable L period), a strong linear relationship emerged between E_C and Q_0 , and the second-order polynomial model between E_C and D_Z was greatly improved (Fig. 3; both $P < 0.001$). For days of SMD ≥ 10 mm, Q_0 explained only 31% of the variation in E_C ($P < 0.01$), while D_Z did not account for the variability in E_C ($P = 0.13$).

To evaluate the effects of Q_0 , D_Z , L , and SMD on E_C throughout the entire growing season, a statistical method based on principal component analysis (proc princomp; SAS Institute, Cary, N.C.) removed the confounding effects of multicollinearity expected among some of the variables (Weisberg 1985). During the leaf expansion period, L was estimated by fitting an exponential curve from day 15 ($L=0$) to day 40 ($L_{\max}=5.0$), the period of rapid increase in daily J_S during leaf expansion, and interpolating changes in L during this period according to:

$$L = L_{\max} \times e^{-0.2d} \quad (2)$$

where d is the number of days before full expansion. Changes in L during senescence were estimated using

leaf fall data obtained by litter collection in the fall of 1994 ($L=4.0 \text{ m}^2 \text{ m}^{-2}$; Fig. 3). Assuming the temporal distribution of litter fall was similar in 1993 ($L=5.0 \text{ m}^2 \text{ m}^{-2}$), L was estimated backward in time from the first day of full senescence in 1993. Daily $E_C < 0.1 \text{ mm}$ data ($n=6$) were excluded, as such values are subject to a large relative measurement error. The principal component analysis showed that the four components (Q_0 , D_Z , L , and SMD) can explain 75% of the variation in E_C over the entire growing season ($P < 0.01$; residuals without a pattern).

As a third method of evaluating environmental effects, a non-linear model based on expected a priori behavior tested whether certain structural features existed in the data. The model was modified from one relating the response of stomatal conductance to environmental variables (Jarvis 1976) to describe the response of E_C , incorporating a soil moisture parameter:

$$E = \frac{Q_0}{Q_{\text{omax}}} \cdot (k_1 + k_2 \ln(D)) \cdot (1 - \exp(k_3 \text{RSM})) \cdot \frac{L}{L_{\text{max}}} \quad (3)$$

where Q_{omax} and L_{max} are the maximum Q_0 and L recorded during the study, k_1 , k_2 , and k_3 are empirically derived coefficients, and RSM is the relative soil moisture calculated based on Legates and Willmott (1995) as:

$$\text{RSM} = \frac{\text{SMD}_{\text{max}} - \text{SMD}}{\text{SMD}_{\text{max}}} \quad (4)$$

where SMD_{max} is the maximum SMD found during the study.

The model was originally developed to explain variation in stomatal conductance (Jarvis 1976), yet the modi-

fied model accounted for 81% of the variance in daily E_C throughout the growing season (residuals had no pattern).

Seasonal stand hydrologic budget

For the annual budget, missing daily E_C data were estimated based on the empirical relationship with Q_o (Fig. 3). Precipitation (P), P_T , and E_C for the 1993 growing season were 1,235 mm, 593 mm, and 278 mm, respectively. The sum of interception losses ($I=P-P_T=642$ mm) and E_C , accounting for most of the evapotranspiration, excluding litter and soil evaporation, and understory transpiration, was 920 mm, about 75% of P . However, relatively high stemflow in broadleaf forests may more than compensate for excluding litter and soil evaporation. At the end of the season, the E_C contribution of individuals >30 mm in diameter ($A_S=11.7$ m² ha⁻¹) represented 44% of seasonal P_T . During the stable L period, daily E_C averaged 1.30 (SE=0.05) mm day⁻¹.

We also estimated daily loss of water from bark surface (E_B) based on the relationship between D_Z and J_S of one *Q. alba* and three *A. rubrum* individuals for which sufficient values were available before budbreak ($P<0.01$; Fig. 4). By using D_Z values for the entire year and assuming that the relationship is valid for all conditions in which nighttime $T_a>0^\circ\text{C}$, regardless of whether foliage is present, we obtained an average E_B of 0.07 (SE=0.001) mm day⁻¹, reaching a maximum of 8% of the E_C obtained during the growing season on a day with a similar D_Z . For the 1993 period of nighttime $T_a>0^\circ\text{C}$, E_B averaged 0.05 (SE=0.002) mm day⁻¹, or about 16 mm during the growing season, accounting for 5% of E_C .

Effects of environmental factors on daily sap flux of individual species

Atmospheric variables

We calculated Q_o above the canopy position occupied by each species (Q_{oj}) to compare the responses of different species to incident radiation. Ring-porous species occupied the upper canopy. For these species, $Q_{oj}=Q_o$. For *A. rubrum* and *L. styraciflua*, Q_{oj} was calculated using the Beer equation:

$$Q_{oj} = Q_o e^{-kL} \quad (5)$$

where k is an extinction coefficient (Landsberg 1986). A mean k value of 0.4 for comparable hardwood forests was taken from Jarvis and Leverenz (1983). For *A. rubrum*, Q_{oj} was calculated after L was reduced by the L_j of this species (Table 1). For *L. styraciflua*, L was reduced by the sum of the L_j of both species in order to estimate total L above the lower and mid canopy positions, respectively.

During the period of stable L and SMD <10 mm, J_{Sj} of all species increased with Q_o in a manner best described

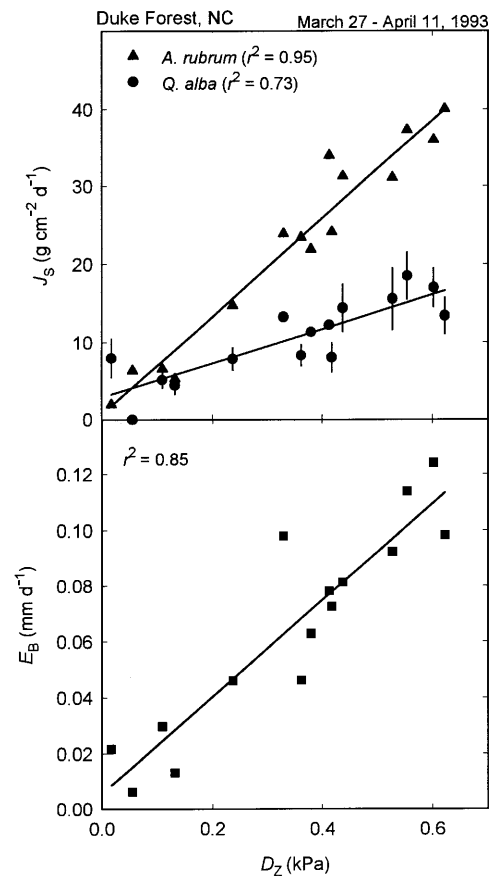
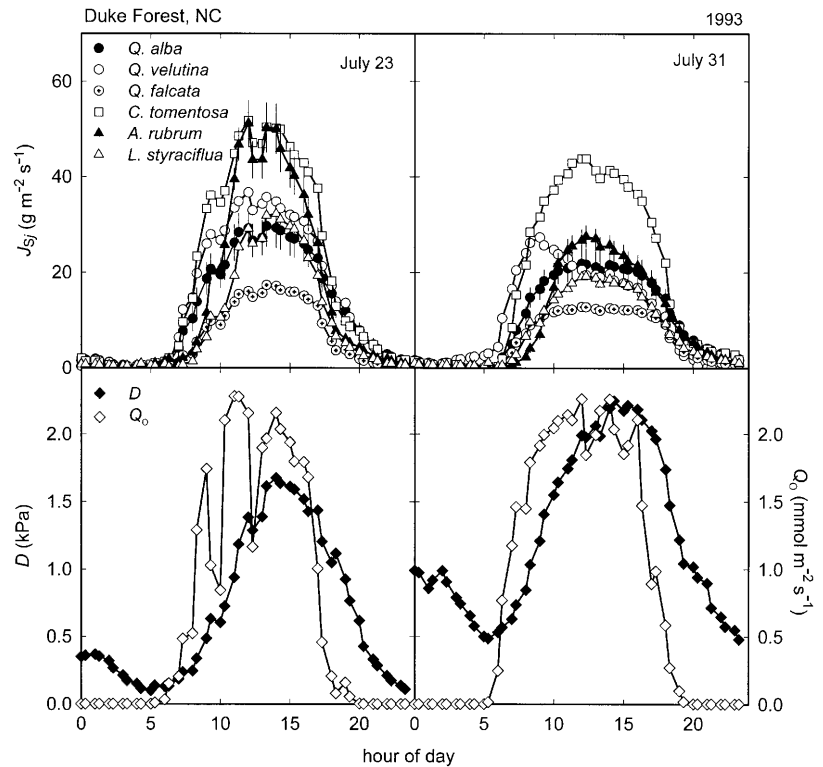


Fig. 4 Daily sap flux (J_S) values for one individual of *Acer rubrum* and averaged for three individuals of *Quercus alba*, and daily estimates of canopy water loss through bark (E_B) in relation to daylength-normalized mean daily vapor pressure deficit (D_Z) during the period before bud break

as a sigmoidal Gompertz function (*A. rubrum* and *L. styraciflua*, $r^2=0.84$ and 0.77 , respectively), or an exponential rise to a maximum (all *Quercus* species, and *C. tomentosa*, r^2 range: $0.55-0.82$). The increase in J_{Sj} with Q_{oj} was less for *Q. alba* than for *A. rubrum* ($P<0.01$, $n=6$; data not shown); when J_{Sj} was related to Q_o instead of Q_{oj} , the difference between the species was smaller, but clearly discernible ($P<0.05$; see daily J_{Sj} in Fig. 3). The relationships between J_{Sj} and D_Z were best described for all species as an exponential rise to a maximum (r^2 range: $0.49-0.85$). *Q. alba* responded less to D_Z than *A. rubrum* ($P<0.05$; Fig. 3).

Differences between *A. rubrum* and *Q. alba* in responses of daily J_{Si} to D_Z were tested by first obtaining the area between saturating curves describing the mean relationship for each species. Curves were generated with a generalized additive fit (gam function, S-Plus for Windows v. 3.3; Math Soft). The area was calculated at 0.05-kPa intervals of D_Z from values of 0.1–0.7 kPa. Then, using a random-number generator, individual trees were assigned to either *A. rubrum* or *Q. alba* categories designated 0 and 1, respectively. This procedure was repeated 2,000 times. At each repetition, the area between

Fig. 5 Diurnal sap flux density (J_{Sj}), overstory incident photosynthetically active radiation (Q_o), and vapor pressure deficit (D) for a clear day at the onset (23 July) and end (31 July) of a drought period



generalized additive fits of J_{Sj} versus D_Z for each category was calculated, generating a normal distribution of areas with a mean of 0. Then, the actual area between the two mean curves was compared to one tail of this distribution, and was found to be greater than 95% of the generated values, indicating that the response of the two species was different with $P < 0.05$.

The values of daily J_{Sij} for species with $n=1$ or 2 were tested against those with $n=6$ (comparing a value to a population). The responses of J_{Sj} to Q_o and D_Z were indistinguishable among the species in the genus *Quercus*, and between this genus and *L. styraciflua* ($P > 0.05$). Thus, three distinct groups are present in Fig. 3 ($r^2=0.79-0.88$ for relationships with Q_o , and $0.64-0.86$ with D_Z ; $P < 0.05$ for differences among groups for both Q_o and D_Z): *C. tomentosa*, the emergent, with the greatest sensitivity to increasing Q_o and D_Z , *A. rubrum*, the low- to mid-canopy species with intermediate responses, and all of the *Quercus* species together with *L. styraciflua* with the smallest response. Note that differences in responses are mostly apparent at high values of Q_o and D_Z reflecting differences in the maximum rates of J_{Sj} .

Soil moisture

Soil moisture conditions affected E_C as indicated by the poor correlation between E_C and Q_o or D_Z during periods of relatively high SMD. Species sensitivity to soil drying was evaluated during the longest period without precipitation in the 1993 record (13 days, from 21 July to 2 August). The diurnal J_{Sj} behavior of all species during two

relatively clear days, one near the beginning of the drying cycle (23 July), and the other near the end of the period (31 July) is shown in Fig. 5. Under non-limiting light and soil moisture conditions, J_{Sj} of *A. rubrum* and *C. tomentosa* was highest, while J_{Sj} of *Q. falcata* was lowest. With increasing SMD, J_{Sj} of *A. rubrum* showed the greatest relative decline, while *C. tomentosa* showed the smallest.

Mean canopy stomatal conductance responses to D

Half-hourly mean stomatal conductance of water vapor for individuals (G_{Sij} ; Martin et al. 1997; Oren et al. 1999) was estimated for the mid-season period of stable L_j . G_{Sij} was plotted against D , and the upper envelope, representing optimal conditions of light and soil moisture, was selected for further analysis (Martin et al. 1997; Schäfer et al. 2000). The selected data were analyzed based on a simplified Lohammar et al. (1980) model, reduced to the function:

$$G_{Sij} = b - c \times (\ln D) \quad (6)$$

in which b is G_{Sij} at a reference $D=1$ kPa, hereafter referred to as G_{Sijr} . All individuals of both species showed a log-linear relationship between G_{Sij} and D (Fig. 6). For *Q. alba*, individuals with higher G_{Sijr} showed a greater decrease in conductance with increasing D (Fig. 6). *A. rubrum* responses were more variable.

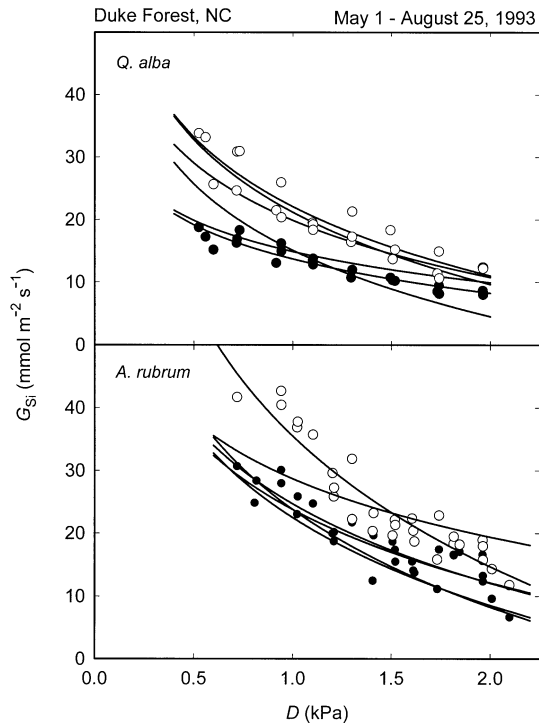


Fig. 6 Canopy stomatal conductance of individual trees (G_{Si}) of *Quercus alba* and *Acer rubrum* decreased with vapor pressure deficit (D). Data are half-hourly means representing the upper boundary of the data corresponding to best light and soil moisture conditions. Lines follow the least-square fit with $\ln D$ of all six individuals in each species, and the symbols are the actual data for two example trees

Discussion

Roberts (1983) found that where transpiration of canopy trees E_C is low, understory transpiration compensates, conserving total transpiration. In our stand, E_C reached a maximum of just over 2 mm-day^{-1} under moist soil conditions. The annual E_C (including E_B) of about 278 mm , most of which occurs during the 6-month growing season, was 73 mm less (Student t -test $P < 0.01$) than the average value of stand transpiration in a number of European forests (Roberts 1983). The difference cannot be accounted for by the sparse understory, and may reflect low ensemble mean stomatal conductance of all species caused by a fast depletion of moisture storage in the shallow soil.

In temperate deciduous forests, the dominant factor controlling seasonal canopy conductance and stand transpiration is the degree of foliation, with clear transitions between leafless, dormant periods, and periods of fully expanded foliage during the growing season (Körner 1994). Soil moisture can strongly affect water use by forests while canopy leaf area is high (Körner 1994). Both multiple-factor analyses showed that the variation in daily E_C over the entire period was accounted for by variations in Q_o , D_z , SMD, and L . However, Q_o accounted for more of the variability in E_C than did the other variables.

Over short rainless periods, SMD clearly affected water use (Fig. 5), thus, selecting data to represent $\text{SMD} < 10 \text{ mm}$ improved the relationships between both E_C and J_s , and the microclimatic variables (Fig. 3). Precipitation in 1993 was average, but SMD was $\geq 10 \text{ mm}$ for nearly half the growing season, causing soil moisture to limit transpiration, especially of *A. rubrum* (Fig. 5).

Water use during leafless and dynamic L periods

Although more synchronized than tropical trees, rates of leaf expansion and senescence differ among co-occurring temperate deciduous species (Borchert 1994; Sperry et al. 1994). Consequently, variation in stand-level water use should depend on species composition. A significant flux of water in the xylem of diffuse-porous species (*L. styraciflua* and *A. rubrum*) preceded that in ring-porous species (three *Quercus* species, and *C. tomentosa*; Fig. 2). Differences between ring- and diffuse-porous species in the timing of bud break include a complete embolism of the large-diameter earlywood vessels of ring-porous trees during winter freeze-thaw cycles (Ellmore and Ewers 1986; Cochard and Tyree 1990; Sperry et al. 1994). These vessels may conduct over 90% of xylem water in ring-porous species, necessitating production of new earlywood prior to bud break. In contrast, diffuse-porous species suffer less embolism in winter (Wang et al. 1992), and can also establish sufficient positive root xylem pressure in early spring to quickly refill embolized vessels, resulting in a recovery of hydraulic conductivity (Borchert 1994; Sperry et al. 1994).

In the 2 weeks prior to bud break, a low yet detectable flux of water was found in many individuals (Fig. 1). Although the flow may provide water used in bud swell before bud burst (Sperry et al. 1994), and for refilling the winter-embolized vessels, the linear response of the flux to D_z (Fig. 4), and the large quantity of water (ca 32 kg for an average-size tree over the 2 weeks) indicate that much of the water is lost to the atmosphere through the bark. We calculated the average loss rate for the stand as the average stand-level E_B (0.07 mm-day^{-1} during the 2 weeks before bud break) divided by stand bark surface area per ground area ($3.8 \text{ m}^2 \text{ m}^{-2}$, estimated based on a winter value of $1.2 \text{ m}^2 \text{ m}^{-2}$ of projected canopy area multiplied by π). The estimated loss rate through the bark of about 0.02 mm-day^{-1} is comparable to the average of leafless seedlings of several species (ca 0.03 mm-day^{-1}), which also varied with microclimate (after Weaver and Mogensen 1919; Kozlowski 1943). Lower rates through the bark of mature trees may indicate that only a portion of the surface, perhaps the thinner bark on younger branches and expanding buds, exchanges water with the atmosphere.

Water loss to the atmosphere through the bark was estimated at 4–5% of annual E_C , less than water uptake through the bark of a 30-year-old *Picea abies* stand following rain events (ca 13% of E_C ; after Werk et al. 1988; Katz et al. 1989a, 1989b; Oren and Zimmerman 1989).

Water loss along this pathway may be the consequence of maintaining a short pathway into stem portions where cavitation occurs, thus facilitating a reversal of embolism and a recovery of hydraulic conductivity (Grace 1993; Milburn 1993).

Leaf shedding in temperate deciduous species may occur prematurely if soil moisture is particularly scarce (Hatton and Wu 1995; D.E. Pataki and R. Oren, unpublished data), but is typically controlled by phenological interactions with environmental cues (Borchert 1992). In this study, leaf shedding began earlier in all of the ring-porous species, but proceeded at a slower rate than in diffuse-porous species (Fig. 2). It should be noted that certain *Quercus* species are marcescent and retain senesced leaves throughout the winter, thus Fig. 2 may under-represent the rate of senescence for some *Quercus* spp. The relative decline in J_{Sj} among species did not correlate with the relative decline in L_j in any species (compare Fig. 1 to Fig. 2). Inter-tree variation in senescence, marcescent behavior, and changes in the regulation of water loss by leaves during this time (Doley 1967) may combine to obscure the temporal relationship between J_S and leaf area in mature forests during fall (Bréda et al. 1993).

Water use during periods of peak canopy leaf area

During periods of a relatively constant L in deciduous forests, soil water availability controls the potential canopy conductance, while Q_o and D control the actual diurnal patterns of conductance (Körner 1994).

Responses of J_{Sj} and E_C to Q_o and D_Z

Diurnal values of J_S are often summed to daily values, thus avoiding the complication that stem capacitance introduces in the analysis of transpiration responses to variation in environmental conditions (Oren et al. 1998b; Phillips and Oren 1998; Ewers et al. 1999). Furthermore, by summing J_{Sj} to daily values, evaluating how the responses of different species are reflected in the daily-integrated stand-level E_C response is possible. Analysis of days in which SMD was small showed that daily E_C was linearly related to Q_o above the canopy, but tended to saturate with D_Z within the canopy (Fig. 3), as was found in tropical forests (Oren et al. 1996; Phillips et al. 1999). The response of E_C to D_Z was caused by J_{Sj} of all *Quercus* species reaching a maximum at low D_Z , in contrast to J_{Sj} of the other species that increased throughout the range of D_Z (Fig. 3). Both types of responses to D have been shown in co-occurring species (Oren et al. 1996; Sala et al. 1996; Phillips et al. 1999; Pataki et al. 2000).

Altogether, three separate relationships described the responses of J_{Sj} to both Q_o and D , with all the *Quercus* species forming a single group with *L. styraciflua*, and *C. tomentosa* and *A. rubrum* showing separate relationships above the multi-species group. The responsiveness

of J_{Sj} to both light and D_Z was unrelated to position in the canopy, as was also found in tropical forests (Phillips et al. 1999; Oren et al. 1996). Thus, the variations in species responsiveness to microclimate will cause forests of different composition to respond differently to variations in microclimate. Under high soil moisture, for example, compared with a forest composed of species behaving like *Q. alba*, the E_C of a forest with half the sapwood in species behaving like *A. rubrum* will be similar under low to moderate Q_o and D_Z , but roughly 25% higher under high Q_o and D_Z .

Responses to SMD

Indication of drought response of the six species can be qualitatively seen in the change in the diurnal pattern of J_{Sj} between days representing the beginning and end of a drying cycle (Fig. 5). The effect of soil drying on J_S is confounded by daily variation in Q_o and D_Z , which were shown to influence the flux (Fig. 3). *Q. alba* is considered a more drought-tolerant species than *A. rubrum* (Gebre et al. 1998; Tschaplinski et al. 1998). Daily J_S was evaluated during a 13-day drying cycle, focusing on days with relatively high Q_o ($>40 \text{ mol m}^{-2} \text{ day}^{-1}$) and D_Z ($>1.0 \text{ kPa}$) (data not shown). *Q. alba*, and even more so, *A. rubrum* increased transpiration following the rain, but returned to the pre-rain value after extracting only 6–8 mm from the soil, both reaching a minimum at $\text{SMD} \approx 10 \text{ mm}$. The increase in daily J_S following the rain may have reflected the recovery of hydraulic conductivity in the soil and soil-root interface and reversal of stem and root embolism (Nobel and Sanderson 1984; Tyree and Dixon 1986; Passioura 1988; Borghetti et al. 1993; Grace 1993; Milburn 1993). The relatively fast decrease in daily J_S following the initial rise is similar to findings in a nearby pine stand, which also has shallow roots (Oren et al. 1998a, 1998b; Phillips and Oren 1998), and is in contrast to a gradual decrease found in stands with deep root systems (Bréda et al. 1993; Oren and Sheriff 1995). At the end of the cycle, the daily J_S of *A. rubrum* decreased to a third of maximum, while that of *Q. alba* decreased to one-half, with the other species showing intermediate responses.

Thus, in forests on shallow soils, composed of species similar to *Q. alba*, transpiration will respond less to changes in soil moisture than in forests composed of species which behave as *A. rubrum*. As rainless periods increase in length, forests composed of species similar to *A. rubrum* will transpire less than forests of species behaving like *Q. alba*.

Species differences in sensitivity of stomatal conductance

Intra- and inter-specific variations in stomatal response to D result in a relationship between the sensitivity of stomatal conductance to D (i.e., $dG_s/d\ln D$) and the con-

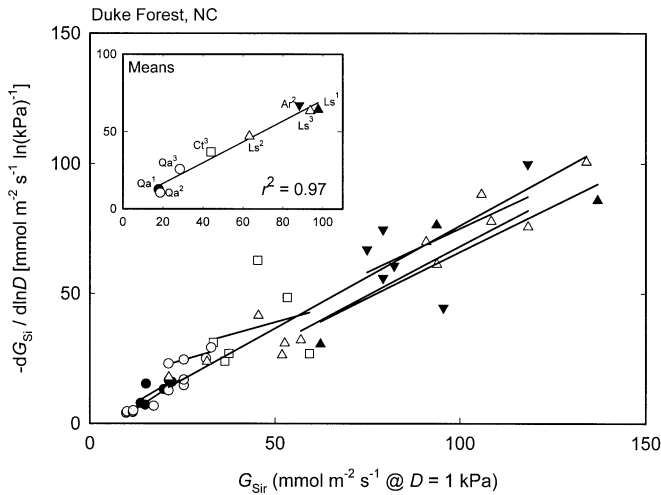


Fig. 7 The sensitivity of individual tree crown-level stomatal conductance to vapor pressure deficit ($-dG_{Sijr}/d\ln D$) increases proportionally to the conductance at a reference low $D=1$ kPa (G_{Sjr}). Lines are the least-square fit for each species-site combination. Symbols can be identified based on the codes shown in the inset, which shows the means of each species-site combination [*Qa* *Quercus alba*, *Ct* *Carya tomentosa*, *Ls* *Liquidambar styraciflua*, *Ar* *Acer rubrum*; superscripts: 1 data from a different study on the same upland site, after Phillips et al. (1996), 2 this study, 3 data from a study on a floodplain site (D.E. Pataki and R. Oren, unpublished data)]

ductance at a low, reference $D (=1$ kPa, i.e., G_{Sjr} ; Black and Squire 1979; Morison and Gifford 1983; Comstock and Ehleringer 1993). The average slope of the relationship is 0.6, increasing when the range in D is small, and when the ratio of boundary layer conductance to stomatal conductance decreases (Oren et al. 1999). Thus, D and G_{Sjr} can explain the variation in diurnal G_{Sij} . The variation in G_{Sijr} is partially explainable based on light, soil moisture, tree height, and species differences (Köstner et al. 1992; Oren et al. 1999; Schäfer et al. 2000).

We analyzed the relationship between G_{Sij} and D for *Q. alba* and *A. rubrum* (Fig. 6). It generally followed that individuals with higher G_{Sijr} showed greater sensitivity to D , and that *Q. alba* individuals had lower G_{Sijr} and sensitivity to D than individuals of *A. rubrum*. We summarized this information by displaying the relationship between stomatal sensitivity to D and G_{Sjr} (Fig. 7). We added to this summary data from another study at the same site (Phillips et al. 1996) and from a study at bottomland forest of the same species (D.E. Pataki and R. Oren, unpublished data). The results from all three investigations show that intra- and inter-specific variation in G_{Sijr} explains a large proportion of the variation in stomatal sensitivity to D (Fig. 7). The overall slope of the relationship (0.67; Fig. 7 inset) is steeper than the theoretical mean slope (ca 0.60) because the sensitivity of stomatal conductance was evaluated over a narrow D range (Oren et al. 1999).

At the species level in both the mesic and the more xeric sites, ring-porous species tended to have lower

G_{Sijr} , and with it lower stomatal sensitivity to D than the diffuse-porous species (Fig. 7, inset). Furthermore, contrary to our expectation, G_{Sjr} and the sensitivity to D of a given species were similar at both sites, indicating that trees at both sites developed conductive tissues (probably in fine roots) under similar hydraulic conditions (Alder et al. 1996; Ewers et al. 2000). Despite relatively frequent rains during the growing season, limited rooting volume due to shallow, rocky soils, coupled with high rainfall interception resulted in a small amount of readily available water between rain events (ca 10 mm based on the results discussed above).

The results of this study show that stands composed of a high proportion of ring-porous species similar to those studied here have lower mean canopy conductance and lower maximum E_C than stands composed of a high proportion of diffuse-porous species. As a result, the stomatal conductance of these ring-porous species should be less sensitive to variation in light, vapor pressure deficit, and soil moisture (Oren et al. 1999; Ewers et al. 2000).

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