Environmental control of whole-plant transpiration, canopy conductance and estimates of the decoupling coefficient for large red maple trees

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Abstract

There is a strong need to extend whole-tree measurements of sap flow into broad-leaved forests where characteristics of stand structure, surface roughness, leaf dimension, and aerodynamic and canopy conductance may interact to partially decouple the canopy from the atmosphere. The implications partial decoupling to understanding the environmental control of canopy transpiration and to the modeling of forest water use are many. Therefore, thermal dissipation probes were used over a three-month period (June through August, 1997) to quantify day-to-day and tree-to-tree variation in whole-tree sap flow (Q) for 12 red maple (*Acer rubrum* L.) trees growing in an upland oak forest of eastern Tennessee. Whole-tree Q was calculated as the product of measured sap velocity, sapwood area and the fraction of sapwood functional in water transport. Daily canopy transpiration (E_c) was calculated from whole-tree Q and projected crown area, whereas average daily conductance (g_c) was derived by inverting the Penman–Monteith equation. Maximum Q averaged 73 kg per tree per day and varied between 45 and 160 kg per day for trees that ranged in stem diameter (DBH) from 17 to 35 cm, and from 19 to 26 m in height. Canopy transpiration peaked at 3.0 mm per day in early July and averaged 1.5 mm per day over the 3-month measurement period. Tree-to-tree variability for E_c was high. Maximum rates of E_c varied from 1.9 mm per day for the tree with the smallest projected crown area to 5.7 mm per day for one of the largest trees. Day-to-day variation in E_c was a function of daily differences in net radiation (R_n) and atmospheric humidity deficit (δ_e). Increases in daily R_n and δ_e led to linear increases in canopy transpiration and there was no indication that a plateau-style relationship existed between E_c and average daily δ_e. Mean daily g_c ranged from 1.4 to 6.7 mm s^{-1}, and averaged 3.4 mm s^{-1} across the 12 study trees. Some of the tree-to-tree variation observed for E_c and g_c was related to the fact that not all trees occupied the same vertical position within the stand. Variation in estimates of the daily decoupling coefficient ($0 \leq \Omega \leq 1$) was also considerable and for individual trees the seasonally-averaged Ω varied from 0.12 to 0.37, and averaged 0.23 for the 12 study trees. An Ω of this magnitude indicates that red maple canopies are partially decoupled from the atmosphere and suggests that significant vertical gradients of air temperature and δ_e from the canopy surface to the bulk air several meters above the canopy are possible. Model analysis of hourly data indicated that simulated surface temperatures in mid-July were 3.6–5.8°C higher than above-canopy reference temperatures, and δ_e at the canopy surface was 0.3 kPa higher than that of the bulk atmosphere. These calculations were partially supported by leaf-level measurements taken on one of the trees from a 20-m canopy-access tower. The implications

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of this partial decoupling to understanding and modeling the environmental control of canopy transpiration are discussed. © 2000 Elsevier Science B.V. All rights reserved.

1. Introduction

Canopy transpiration for trees and stands of the boreal, temperate and tropical forest have been well characterized both in terms of magnitude and environmental control of canopy and stomatal conductance (Kelliher et al., 1992; Köstner et al., 1992; Granier et al., 1996; Cienciala et al., 1997; Meinzer et al., 1997; Magnani et al., 1998; Granier et al., 2000). Coniferous forests have received the most attention in this regard and for species like pine and spruce, a simplified version of the Penman–Monteith equation is often used to estimate rates of canopy transpiration as the product of bulk surface conductance and atmospheric humidity deficit (Phillips and Oren, 1998). Canopies such as these are aerodynamically well-coupled to the atmosphere and have a decoupling coefficient ($0 \leq \Omega \leq 1$) near zero (Jarvis and McNaughton, 1986). One implication of $\Omega \rightarrow 0$ is that the stomatal control of transpiration is high and a fractional change in stomatal conductance leads to an equal fractional change in transpiration. Studies with broad-leaved species, however, indicate that characteristics of forest structure, surface roughness, leaf dimension, and aerodynamic and canopy conductance act to partially decouple the forest canopy from the atmosphere. Magnani et al. (1998) reported an average Ω of 0.28 for a 35-year-old beech stand in Italy, whereas Ω for a 100-year-old beech forest in Germany averaged 0.20 (Herbst, 1995). Stomata exert less control on canopy transpiration as $\Omega \rightarrow 1$ and, as a result, transpiration becomes increasingly dependent on net radiation received and less dependent on atmospheric humidity deficit (Jarvis and McNaughton, 1986).

Although estimates of Ω that range from 0.20 to 0.28 are not as large as those observed in tropical forests (Meinzer et al., 1997) and short-rotation plantations (Hinckley et al., 1994), they are nonetheless large enough to be of concern when assessing the response of canopy transpiration to a fractional change in stomatal conductance (Meinzer et al., 1997) and when addressing the extent to which transpiration rates for individual trees are controlled by net radiation and atmospheric humidity deficit (Jarvis and McNaughton, 1986). Our objectives in this study, therefore, were to examine whole-tree water use, canopy transpiration, bulk surface conductance, and estimates of Ω for mature red maple (*Acer rubrum* L.) trees. Our primary objective was to quantify day-to-day variation in these canopy processes and to examine the environmental control of transpiration in relation to prevailing climate. This was done for 12 co-dominant individuals of a mid-latitude deciduous forest in eastern Tennessee. A secondary objective was to investigate tree-to-tree variation in Ω and to assess the relationship between Ω and canopy and aerodynamic conductance. These results are discussed in terms of whether Ω varies among trees that occupy different positions within the forest canopy and how tree-specific information can be used to assess the collective contribution of individual trees to stand transpiration. The diurnal pattern of transpiration is also examined and the sensitivities of canopy and stomatal conductance to atmospheric humidity deficit are compared.

2. Materials and methods

2.1. Site description and environmental monitoring

Whole-tree studies of sap flow were conducted during the 1997 growing season within an upland oak forest on the Walker Branch Watershed, a part of the US Department of Energy's Oak Ridge Reservation in Anderson County, Tennessee ($35°58'$N and $84°17'$W). The study area is located on a southeast facing slope that extends 240 m along a ridge top and 80 m down a 20 m elevation gradient. Trees range in age from 40 to 75 years old. The basal area of the forest overstory is dominated by chestnut oak (27%, *Q. prinus* L.), white oak (20%, *Q. alba* L.), black gum (13%, *Nyssa sylvatica* Marsh.), red maple (12%, *Acer rubrum* L.), northern red oak (9%, *Q. rubra* L.), yellow-poplar (8%, *Liriodendron tulipifera* L.) and

sugar maple (3%, *A. saccharum* Marsh.). Overstory basal area was 22.4 m² ha⁻¹ and leaf area index was 6.2 m² m⁻² in 1996. The average height of all canopy trees was ≈24 m. Rainfall in 1997 was greater than normal with annual and growing season precipitation being 8 and 23% higher that the 50-year average of 1352 and 716 mm, respectively. Because of this ample and equally distributed rainfall throughout the growing season, there were no soil moisture deficits in 1997. Median temperature on Walker Branch Watershed is 14.4°C. Soils are mapped as Typic paleudults.

Instruments for measuring air temperature, relative humidity and PPFD were located on a tower near the study site. A capacitance-type sensor was used to measure relative humidity (Rotronics Instrument, Huntington, NY). Net radiation was measured 10 m above the canopy with a net radiometer (model 7, REBS, Seattle, WA), and soil heat flux was estimated from the average of three soil heat flux plates (model HFT-3, REBS). Mean and turbulent wind fields and sensible heat flux were measured at 10 Hz with a sonic anemometer (model SWS-211/3K, Applied Technology, Boulder, CO) placed on a meteorological tower 10 m above the canopy. Net radiation, soil heat flux and sensible heat flux were measured continuously and average data were recorded every half-hour. Rainfall was measured in the clearing with a tipping bucket rain gauge.

2.2. Tree selection and measurement of stem diameter, sapwood depth and crown area

Twelve trees were randomly selected from within a 1.9-ha study area for measurements of stem diameter, bark and sapwood thickness, height and crown area. These trees were largely canopy dominants, although one or two might be better classed as co-dominants based on height and crown area. Stem diameter at breast height (1.3 m) was measured with a diameter tape. Bark thickness was determined with a digital caliper at two to five locations around the stem circumference by drilling 1.3-cm holes through the bark and to the bark–sapwood interface. This transition between bark and sapwood was identified based on a visual assessment of color, texture and water content. Sapwood thickness was determined at the same locations as bark thickness by removing 5-mm diameter cores of wood with an increment bore. The transition between heartwood and sapwood was based on coloration. Tree heights were measured with a hand-held clinometer (Suunto USA, Carlsbad, CA), whereas crown areas were calculated from vertical projections of the crown perimeter. Total sapwood area was calculated from sapwood depth and stem diameter after accounting for bark thickness.

2.3. Whole-tree sap flow and estimates of sap velocity

Total sap flow (Q) for each of the 12 trees was calculated as the product of sap velocity, cross-sectional sapwood area and the fraction of sapwood functional in water transport. Sap velocity rates were determined with thermal dissipation probes (Dynamax, Houston, TX). These probes operated on the constant power principle (Granier, 1987) and consisted of two cylindrical probes, each 1.3 mm in diameter, that were inserted 3 cm into the sapwood of a tree. The two probes were inserted one above the other and separated along the stem by 4 cm. The upper probe was installed at a height of 1.3 m and contained a heating element that was heated at 200 mW with a 110 mA constant power source. The lower probe served as an unheated reference. Each probe contained a copper–constantan thermocouple and the temperature difference between the two probes was influenced by sap velocity in the vicinity of the heated probe. Thermal dissipation probes were installed on 22 May 1997 and left in place until 3 September. Köstner et al. (1998) indicated that probes can be installed and then left in place for up to an entire growing season without modifying the water transport properties of xylem. All probes were installed on the northern side of trees to avoid direct solar heating and shielded with aluminum foil to minimize temperature fluctuations in the sapwood.

The (compensation) heat pulse technique (SF-300, Greenspan Technology, Warwick, Queensland, Australia) was used to estimate the fraction of sapwood functional in water transport for two trees located off the study site. These trees varied in stem diameter from 24.6 to 29.3 cm. Heat pulse velocity was determined for probes implanted to each of four pre-determined depths in the sapwood (Hatton et al., 1990). Insertion depths were calculated so that thermistors of each probe were optimally located within concentric annuli of equal sapwood area (Wullschleger and King, 2000).

Probe positions were identified as P1, P2, P3 and P4 beginning with the outermost position (P1) and progressing to the probe closest to the heartwood (P4). Holes for the probes were drilled with a 1.98 mm bit. A drill guide was used to ensure that the holes were properly spaced and parallel. All probes were located at a height of 1.3 m and were positioned on the northern side of the tree. A data logger was programmed to provide a heat pulse for 1.8 s and measurements at each of four sapwood depths were recorded every 20 min. Sap velocity was estimated as outlined by Barrett et al. (1996) and all estimates were corrected for probe implantation effects based on a wound diameter of 2.2 mm (Swanson and Whitfield, 1981). An increment bore was used to extract a sample of sapwood near where the probes were implanted for determination of wood density and water content. The fraction of total sapwood area functional in water transport (a value between 0 and 1) was calculated for each tree as the sap velocity measured at P1 through P4, divided by the maximum sap velocity measured at one of the other four probe positions (usually at P1 or P2). Sap velocity nomenclature and units of expression are consistent with Edwards et al. (1996).

2.4. Calculation of canopy transpiration, surface conductance and Ω

Daily and hourly estimates of canopy transpiration (E_c) were calculated from whole-tree sap flow and measured crown area (Table 1). All calculations of canopy conductance were derived by inverting the Penman–Monteith equation (Stewart, 1988),

$$\lambda E_c = \frac{s(R_n - G) + \rho C_p \delta_e g_a}{s + \gamma[1 + (g_a/g_c)]} \quad (1)$$

where λ is the latent heat of vaporization of water ($J\,kg^{-1}$), R_n the net all-wave radiation above the stand ($J\,m^{-2}\,s^{-1}$), G the heat flux to soils ($J\,m^{-2}\,s^{-1}$), ρ the density of dry air ($kg\,m^{-3}$), C_p the specific heat of air at constant pressure ($J\,kg^{-1}\,K^{-1}$), δ_e the atmospheric humidity deficit (kPa), s the rate of change of saturation water vapor pressure with temperature ($kPa\,K^{-1}$), γ the psychrometric constant ($kPa\,K^{-1}$), g_a the aerodynamic conductance ($m\,s^{-1}$) and g_c the canopy conductance ($m\,s^{-1}$). Aerodynamic conductance for momentum was estimated from the mean wind and frictional velocity using Monin–Obukov similarity theory (Monteith and Unsworth, 1990). The aerodynamic conductance for water vapor and heat is slightly greater than that for momentum, so g_a was corrected for excess resistance (Verma, 1989). Eq. (1) was solved for g_c using daily averages of all quantities (Phillips and Oren, 1998). Thermodynamic variables were calculated based on air temperature averaged over daylight hours. Daily δ_e and R_n were obtained by averaging hourly values throughout the day (Fig. 1). Temperature dependencies for the parameters ρ, C_p, λ and γ were as shown in Table 2 of Phillips and Oren (1998). Hourly estimates of g_c were calculated using air temperature, δ_e and R_n specific to those hours.

Table 1
Characteristics of the 12 large red maple trees on which estimates of sap velocity were determined[a]

Tree #	Diameter (cm)	Height (m)	Sapwood thickness (cm)	Sapwood area (cm^2)	Crown area (m^2)
1018	28	19	7.0	426	14
1054	29	22	8.6	521	20
1076	28	23	6.8	414	19
1129	25	24	8.0	404	29
1147	32	26	7.8	571	23
1208	32	24	8.5	590	28
1211	32	23	9.2	610	28
1290	34	24	7.5	587	22
1298	35	23	8.5	671	34
1321	31	21	9.9	591	26
1389	26	21	7.3	404	28
2973	17	21	5.7	190	16

[a] Stem diameter, height, sapwood thickness, sapwood area and crown area were either measured directly or calculated for each tree.
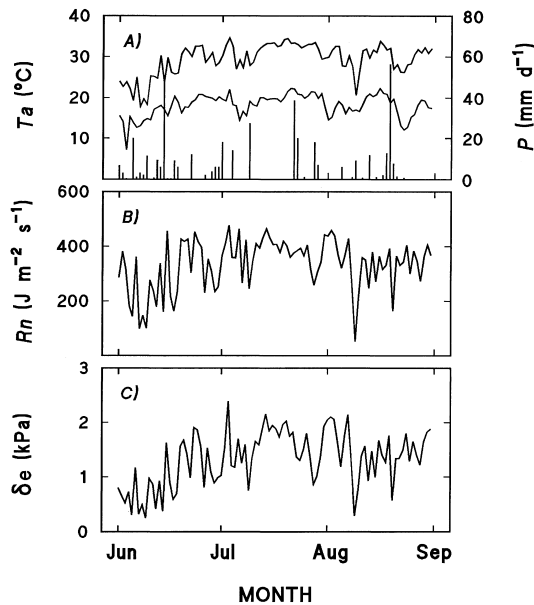
Fig. 1. Average daily estimates of (A) minimum and maximum air temperatures, and precipitation, (B) above-canopy net radiation and (C) atmospheric humidity deficit for the 3 months (June, July and August) during which whole-tree sap flow was measured on 12 red maple trees.

The decoupling coefficient (Ω) was calculated according to Jarvis and McNaughton (1986),

$$\Omega = \frac{(1 + \varepsilon)}{(1 + \varepsilon + g_a/g_c)} \qquad (2)$$

where ε is the change of latent heat relative to the

change in sensible heat of saturated air (2.91 at 25°C). The relative importance of radiative (E_{eq}) and advective (E_{imp}) energy for E_c was estimated using the equation,

$$E_c = \Omega E_{eq} + (1 - \Omega)E_{imp} \qquad (3)$$

where E_{eq} is the equilibrium transpiration rate that would be obtained over an extensive surface of uniform wetness and E_{imp} the transpiration rate imposed by the atmosphere on the natural canopy surface through the effects of δ_e (Schulze et al., 1995).

Diurnal measurements of stomatal conductance (g_s) were made on 26 August 1997 from the top of a 20-m canopy-access tower constructed on the study site. Only one of the 12 trees could be reached from this tower (#1290). An open-flow gas analysis system (LI-6400, Li-Cor, Lincoln, NE) was used to measure g_s for a total of eight leaves every half-hour from 0800 to 1600 h. All measurements were made at ambient conditions of temperature, atmospheric humidity deficit and PPFD. Air temperatures during the day varied between 21 and 36°C, whereas PPFD reached a maximum of 1475 μmol m^{-2} s^{-1} during mid-afternoon. Atmospheric humidity deficit ranged between 0.6 and 3.4 kPa.

3. Results

The 12 red maple trees selected for this study ranged in stem diameter from 17 to 35 cm, and varied between

Table 2
Seasonal estimates of mean daily transpiration, canopy conductance and the decoupling coefficient (omega) for 12 large red maple trees

Tree #	Canopy transpiration (mm d^{-1})	Canopy conductance (mm s^{-1})	Omega
1018	1.3 (3.2)[a]	2.7 (5.5)	0.20 (0.38)
1054	2.3 (5.1)	6.7 (13.9)	0.37 (0.68)
1076	1.2 (2.3)	2.5 (4.8)	0.19 (0.31)
1129	1.4 (3.2)	3.2 (8.0)	0.22 (0.47)
1147	1.6 (3.0)	3.7 (6.9)	0.26 (0.39)
1208	1.4 (2.7)	3.0 (6.0)	0.22 (0.44)
1211	2.5 (5.7)	6.3 (15.6)	0.35 (0.67)
1290	1.2 (3.0)	2.8 (7.4)	0.20 (0.45)
1298	1.3 (2.9)	2.7 (6.0)	0.20 (0.40)
1321	1.4 (2.8)	3.1 (6.0)	0.22 (0.37)
1389	1.2 (2.7)	2.5 (4.3)	0.19 (0.30)
2973	0.7 (1.9)	1.4 (4.1)	0.12 (0.29)
Average (±S.D.)	1.5±0.5	3.4±1.5	0.23±0.07

[a] The maximum value of daily transpiration, canopy conductance and the decoupling coefficient calculated for each tree during the season is shown in parentheses.

19 and 26 m in height (Table 1). Sapwood thickness ranged from 5.7 to 9.9 cm and, in general, was positively related to measured stem diameter (data not shown). Sapwood area per tree varied between 190 and 671 cm^2 (Table 1). The fraction of sapwood area functional in water transport was 0.74 as estimated from depth-dependent measurements of sap velocity in two trees. Sap velocity was greatest for probes located in outer sapwood (P1) and lowest for probes closer to the heartwood (P4). Relative sap velocities during the day averaged 0.99 at P1, 0.86 at P2, 0.80 at P3 and 0.44 at P4.

Whole-tree sap flow averaged across the 12 sample trees exhibited considerable day-to-day variation (Fig. 2a). Sap flow rates reached a maximum of 73 kg per tree per day early in July and averaged ≈38 kg per tree per day over the entire 89-day measurement period. The seasonal pattern of Q was similar among trees, although individual trees differed markedly in maximum and average sap flow. One of the largest trees (#1211) had a maximum daily Q of 160 kg per day and transpired almost 6350 kg of water during the 89-day study period. One of the smallest trees (#1076) had, by comparison, a maximum Q of 45 kg per day and transpired only 1990 kg of water from June through August. The seasonal (89 days) estimate of whole-tree Q averaged 3240 kg for the 12 trees.

Average rates of canopy transpiration followed a seasonal pattern identical to that of whole-plant Q
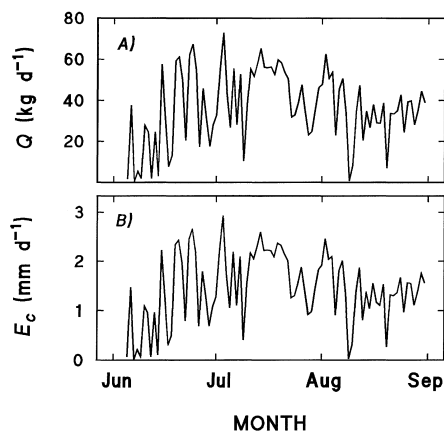

Fig. 2. Daily estimates of (A) whole-tree sap flow and (B) canopy transpiration averaged across the 12 study trees. Canopy transpiration (E_c) was calculated from daily whole-tree sap flow (Q) and projected crown area.
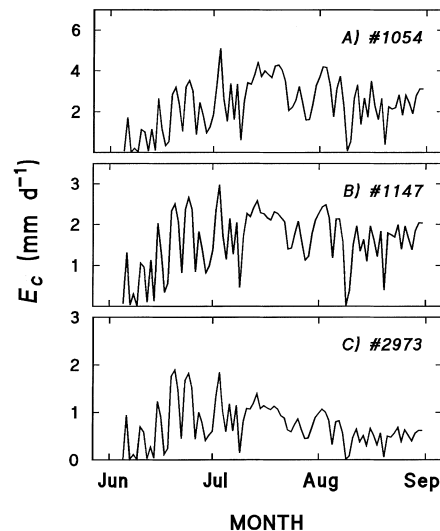

Fig. 3. Tree-to-tree variation in daily estimates of canopy transpiration (E_c) for three red maple trees representative of (A) high (#1054), (B) average (#1147) and (C) low (#2973) rates of canopy transpiration. Note difference in the y-axis scale for panel A compared to that of panels B and C.

(Fig. 2b). Estimates of E_c reached a maximum rate of 3.0 mm per day on 3 July and, for the 12 study trees, averaged 1.5 mm per day over the 89-day measurement period (Table 2). Tree-to-tree variability for E_c was high. Maximum rates of E_c varied 3-fold from 1.9 mm per day for one of smallest trees in the canopy (#2973) to 5.7 mm per day for tree #1211 (Table 2). Although variation among trees was substantial, the day-to-day patterns of E_c for three trees representative of high (#1054), average (#1147) and low (#2973) rates of E_c were qualitatively similar (Fig. 3). The seasonal pattern of E_c showed considerable daily fluctuations early in June, followed by a period of relatively stable E_c between 10 and 21 July due to favorable R_n and δ_e conditions, and then considerable fluctuations in E_c again throughout much of August.

The extent of day-to-day variation in E_c that was observed during June and August was largely a function of daily differences in R_n and δ_e (Fig. 4). Increases in the average daily receipt of R_n led to near linear increases in E_c for all the study trees. Daily R_n, however, had to exceed what appeared to be an apparent threshold of 150 J m^{-2} s^{-1} before non-zero rates of E_c were observed (Fig. 4a–c). Increases in average daily
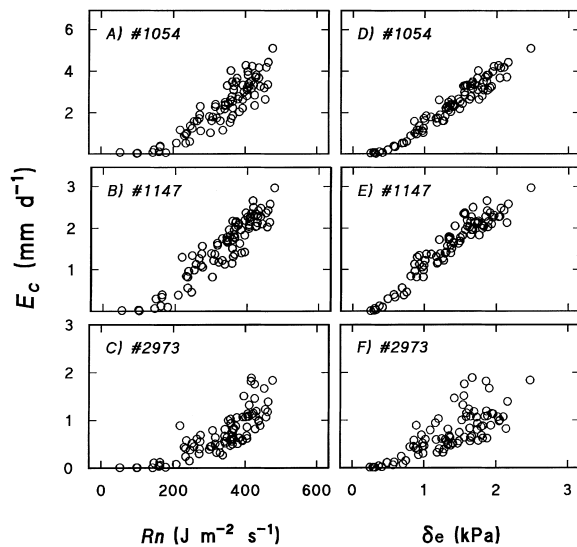
Fig. 4. Representative relationships between tree-specific daily canopy transpiration (E_c) and daily average net radiation (panels A–C) and daily canopy transpiration and daily average atmospheric humidity deficit (panels D–F). Note difference in the y-axis scale for panels A and D compared to other panels.

Fig. 5. Seasonal variation in (A) average daily canopy conductance and (B) average daily estimates of the decoupling coefficient (Ω) for three red maple trees. The upper dashed line is for a tree (#1054) with one of the greatest estimates of canopy conductance (g_c), the solid line is for the tree (#1147) that most represents the 12-tree population mean and the lower dashed line is for a tree (#2973) with one of the lowest estimates of canopy conductance.

δ_e also led to increases in E_c (Fig. 4d–f). A non-zero intercept was evident, but it was not as prominent as that observed for net radiation. Scatter among individual data points for trees #1054 and #1147 was noticeably lower for plots of E_c versus δ_e (Fig. 4d-e) than for plots of E_c versus R_n (Fig. 4a-b). The linear nature of the relationship between E_c and δ_e was less evident for the smallest tree in this study (#2973) and scatter was somewhat higher (Fig. 4f).

Considerable day-to-day variation in g_c was observed (Fig. 5a). Maximum daily estimates of g_c ranged from 15.6 mm s^{-1} for tree #1211 to 4.1 mm s^{-1} for tree #2973, and averaged 3.4 mm s^{-1} across the 12 study trees (Table 2). Similar variation was observed for estimates of daily Ω (Fig. 5b) and for individual trees the seasonally-averaged Ω varied from 0.12 to 0.37 (Table 2). Daily Ω averaged 0.23 across all trees. Much of the day-to-day variation in Ω was explained by changes in daily g_c (Fig. 6a). Daily variation in Ω was not, however, closely correlated with g_a (Fig. 6b).

Canopy transpiration, g_c and Ω exhibited not only day-to-day variation throughout the season, but also varied hourly throughout any given day. Hourly estimates of E_c for tree #1290 reached a maximum of
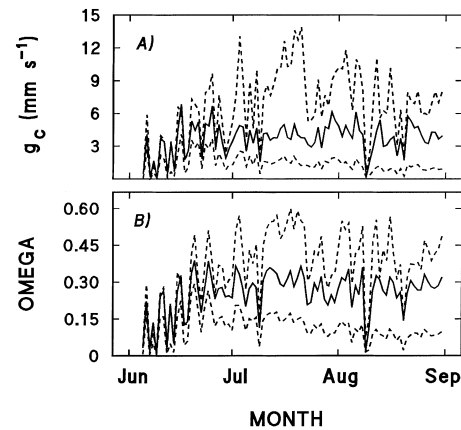
0.36 mm h^{-1} at 1200 h and then gradually declined throughout the afternoon (Fig. 7a). The hourly pattern of g_c was similar to that of E_c (Fig. 7b), although the afternoon decline was much more prominent. Hourly estimates of Ω were near zero early in the morning and increased to a fairly constant value of 0.32 during mid-day (Fig. 7c). Estimates of Ω dropped to near zero again at night. The mid-afternoon decline in g_c was closely correlated with increases in δ_e beyond an apparent threshold of 2.0 kPa (Fig. 8a). A mid-day decline of somewhat greater magnitude was evident for leaf-level estimates of g_s as δ_e increased beyond
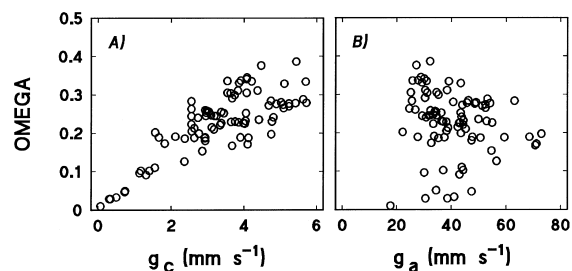

Fig. 6. Relationship between daily estimates of (A) the decoupling coefficient and canopy conductance (g_c), and (B) the decoupling coefficient and aerodynamic conductance (g_a). The data shown represent the mean of 12 trees.
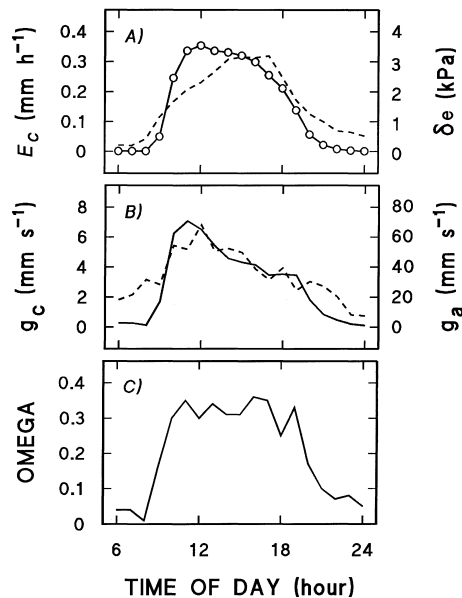
Fig. 7. Diurnal pattern of (A) canopy transpiration (solid line) and atmospheric humidity deficit (dashed line), (B) canopy (solid line) and aerodynamic conductance (dashed line), and (C) the decoupling coefficient for tree #1290 (3 July 1997).
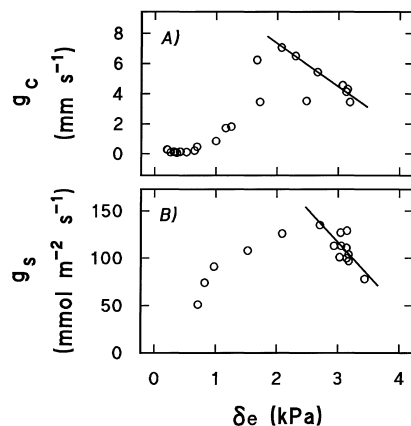

Fig. 8. Dependency of (A) canopy conductance and (B) stomatal conductance on atmospheric humidity deficit. Estimates of g_c were derived from sap-flow measurements on tree #1290, while estimates of g_s were collected using a Li-Cor 6400 gas-analysis system on individual leaves of tree #1290. Both data sets are from 3 July 1997. Leaf-level measurements were made from a 20-m canopy-access tower. Solid lines are 'best-fit' linear regressions for conductance data beyond an atmospheric humidity deficit of 2.0 and 2.5 kPa respectively.

2.5 kPa (Fig. 8b). The slopes of these two lines indicated that a 1 kPa increase in δ_e (e.g., 2.5→3.5 kPa) would result in a 35–40% reduction in both g_c and g_s (data not shown).

4. Discussion

There was considerable day-to-day variation in all the whole-tree and canopy-scale processes measured or estimated in this study. This variation was bounded on one extreme by rainy days and cloudy skies, and on the other by sunny days, clear skies and moderate atmospheric humidity deficits. Not surprisingly, estimates of whole-tree Q and E_c were lower on rainy days than those measured during dry-weather conditions. Canopy transpiration averaged <0.9 mm per day for the 41 days on which precipitation fell compared with more typical rates of 3.0 mm per day that were measured during cloudless weather. Jimenez et al. (1996) observed that the annual course of stand transpiration for a laurel forest on the Canary Islands was highly variable and noted that transpiration rates were lower during autumn and winter when there were more frequent rainy and foggy days. A similar conclusion was reached by Wullschleger et al. (2000) who reported that stand-level estimates of E_c for a multi-species upland oak forest in east Tennessee averaged <1.5 mm per day during the growing season largely as a result of rain and the meteorological conditions that accompany precipitation events (clouds and low R_n, and high relative humidity and low δ_e).

Most studies do not emphasize rates of whole-tree Q and E_c during cloudy or overcast days, but instead focus on the interpretation of data collected during periods when maximum rates of sap flow occur (Köstner et al., 1992; Arneth et al., 1996; Granier et al., 1996). An analysis of our data similarly restricted to 'dry canopies' indicated that daily estimates of whole-tree Q ranged from 24 to 73 kg per day and E_c ranged from 1.1 to 3.0 mm per day when averaged across the 12 study trees. Whole-tree Q was greatest for large trees, due primarily to larger trees having more sapwood and consequently more total sap flow. Sap flow was also greater for larger trees because these trees often occupied positions within the forest canopy that had a better radiation regime that tended to promote higher rates of sap flow. For example, whole-tree sap flow for one of

the largest trees in our study was 160 kg per day (6350 kg total), whereas it was only 45 kg per day (1990 kg total) for one of the smaller trees. Such differences in whole-plant Q suggest that trees of differing stature may have different rates of canopy transpiration. Although evidence to support this notion was observed (2.5 vs. 1.2 mm per day for trees #1211 and #1076, respectively), there was no generalized relationship between E_c and stem diameter or height among the trees measured in this study. Nonetheless, estimates of Q and E_c were well within the range of values previously reported for whole-tree Q (Köstner et al., 1992; Arneth et al., 1996; Martin et al., 1997) and compared favorably to a recent compilation of water-use studies where the majority of 52 investigations reported rates of whole-tree sap flow that ranged between 10 and 200 kg per day (Wullschleger et al., 1998). There are, unfortunately, fewer estimates of E_c for individual broad-leaved trees. Measured rates of whole-tree Q are instead more typically used to extrapolate estimates of stand transpiration based on one or more scalars (Hatton et al., 1995), as was recently done for a 35-year-old beech forest in Italy (Magnani et al., 1998). These authors reported rates of stand transpiration that ranged between 0.62 and 2.97 mm per day, and we note that these values closely match estimates in our study albeit for canopy (and not stand) transpiration.

Canopy transpiration in red maple was clearly related to R_n and δ_e, and it is therefore not surprising that daily differences in R_n and δ_e were reflected in daily variation for canopy transpiration. However, because estimates of R_n and δ_e co-vary throughout the season, it is often difficult to separate the relative contribution of these two climatic variables to canopy transpiration. Baldocchi and Vogel (1996) inferred from eddy covariance methods that available energy was the key environmental variable modulating LE over a temperate broad-leaved forest located <2-km from our study site. This conclusion was based on the observation that a greater proportion of the variation in LE was explained by variation in available energy than was explained by variation in vapor pressure deficit. Baldocchi and Vogel (1996) showed only the relationship between LE and available radiation, but it is obvious that the variation observed in their stand-level study was far greater than that reflected in our tree-specific relationships between canopy transpiration, R_n and δ_e

(Fig. 4). We note that an average Ω of 0.23 indicates that E_c is controlled by R_n and δ_e in a ratio of 1 to 3.3 (Schulze et al., 1995). This ratio can be inferred from published estimates of Ω for a range of broad-leaved trees to vary between a ratio of 1 to 2.6 (Magnani et al., 1998) and 1 to 4.0 (Granier et al., 1996). Ratios of such magnitude indicate that rates of E_c are determined more by daily δ_e than they are by daily R_n (Schulze et al., 1995). Moreover, a multiple regression analysis performed on the data set indicated that the majority of the day-to-day variation in E_c was explained by δ_e (data not shown).

Additional information on the environmental control of E_c is reached by substituting an Ω of 0.23 into Eq. (3) and then solving for the relative contribution of E_{eq} and E_{imp} to total canopy transpiration. Jarvis and McNaughton (1986) used this approach to illustrate that transpiration in conifer plantations ($\Omega=0.1$) was largely dominated by 'imposed' transpiration (E_{imp}), while transpiration from a grassland ($\Omega=0.8$) was largely dominated by 'equilibrium' rates of transpiration (E_{eq}). Our data indicate that for a typical day in mid-July, estimates of E_{eq} were 0.75 mm h^{-1} whereas estimates of E_{imp} were 0.25 mm h^{-1} (data not shown). According to Eq. (3) the relative contribution of (ΩE_{eq}) and $(1-\Omega)E_{imp}$ to total E_c were approximately equivalent (0.17 versus 0.19 mm h^{-1}). The mid-day estimate of E_c (0.36 mm h^{-1}) agrees closely with that shown in Fig. 7a.

An average Ω of 0.23 indicates that red maple canopies are partially decoupled from the atmosphere. Magnani et al. (1998) recently argued that a partial decoupling of beech canopies ($\Omega=0.28$) could result in significant vertical gradients of air temperature and δ_e from the canopy surface to the atmosphere several meters above the canopy. Mid-day estimates of surface temperature (T_s) in their analysis were 1–2°C higher than above-canopy reference temperature (T_r) and δ_e at the canopy surface was up to 0.4 kPa higher than those above the canopy. This occurred even though transpiration served as a continuous source of water vapor that presumably led to a higher absolute humidity within the canopy. Application of equations 8 and 10 from Magnani et al. (1998) to a limited data set for red maple indicated that hourly estimates of T_s during July were 3.6–5.8°C higher than T_r, and that mid-day differences in δ_e between the canopy surface and the atmosphere averaged 0.3 kPa and could on occasion

exceed 1.0 kPa. These calculations of $T_s - T_r$ are qualitatively supported by leaf-level measurements made on 26 August with the LI-6400; leaf temperatures measured during the afternoon (1400–1600 h) were up to 2.5°C warmer than air temperatures. Meinzer et al. (1997) argued that selecting the proper reference surface for calculations of $T_s - T_r$ and δ_e, either above the canopy or at leaf surface, could influence how we interpret the environmental control of canopy transpiration and conductance. This was clearly evident for the highly decoupled canopies of tropical trees ($\Omega > 0.82$) where stomatal conductance was not related to bulk-air humidity deficits, but instead was closely tied to that of the leaf surface (Meinzer et al., 1997). Magnani et al. (1998) similarly found that the relationship between δ_e and g_c in beech was more evident when the canopy, not the bulk atmosphere, was considered the reference surface. We too observed that a scattered relationship between hourly g_c and δ_e (restricted to $R_n \geq 500$ J m^{-2} s^{-1}) was improved in red maple by replacing bulk-air δ_e with one calculated for the canopy surface. It remains to be seen whether including this refinement in our analysis will ultimately improve either our understanding of canopy-scale processes or our ability to model the environmental control of canopy transpiration. Magnani et al. (1998) noted that while model estimates of E_c in their study were improved by relating g_c to δ_e calculated at the canopy surface, such improvements were not significantly different from those derived using δ_e measured in the bulk atmosphere. A comparative study that measured whole-tree Q and then estimated g_c in terms of δ_e defined both at the canopy surface and at some reference level above the canopy for species with inherently different estimates of Ω (e.g., species differing in leaf size) would help identify when partial decoupling was of a sufficient magnitude to impact model estimates of canopy transpiration.

The response of canopy transpiration to δ_e has been the subject of some debate, mostly regarding whether rates of E_c increase monotonically with increasing δ_e or whether they instead reach a plateau where stomatal closure beyond a threshold value of δ_e restricts further increases in canopy transpiration. The threshold-type response is often observed for hourly estimates of E_c (Granier et al., 1996; Infante et al., 1997) and there is evidence that in many species this also holds for daily estimates of E_c (Hogg et al., 1997; Martin et al.,

1997). Myers et al. (1998) reported a strong, positive correlation between daily transpiration and daytime mean δ_e for a young *Eucalyptus grandis* stand, but noted that as mean daytime δ_e increased above ca. 1.5 kPa there were no further increases in transpiration. Our results contrast with those of Myers et al. (1998) in that there was a steady increase in E_c for red maple canopies across all estimates of average daily δ_e. This conclusion is not, however, entirely consistent with the observation that marked mid-afternoon declines in hourly estimates of both g_s and g_c were correlated with increases in δ_e beyond a threshold of 2.0–2.5 kPa. Although such an inconsistency between hourly and daily data is difficult to resolve, it should be emphasized that values of mean daily δ_e beyond 2.0 kPa occurred at our study site on only six days during 1997. Furthermore, hourly estimates of δ_e greater than 2.5 kPa were observed on fewer than 17 days during our 89-day study and on only 2 days did hourly δ_e exceed 3.0 kPa. Apparently stomatal closure that occurred during these periods was not sufficient to impact daily rates of canopy transpiration. Additional analyses are needed in order to fully understand the tradeoffs between deriving daily versus hourly estimates of g_c and whether physiological information is lost (or gained) in going from one temporal scale to the other.

One of the more interesting aspects to emerge from our study and those of others relates to how forest structure or canopy stratification influences whole-tree Q, canopy transpiration, g_c and Ω (Köstner et al., 1992; Martin et al., 1997). Köstner et al. (1992) observed that emergent *Nothofagus* trees transpired at a higher rate (58–84 kg per tree per day) than did co-dominant (10–30 kg per tree per day) and suppressed trees (2–30 kg per tree per day), and it was noted that emergent individuals contributed disproportionately to total stand water use. Although we did not select trees from within the canopy to address a priori whether tree height and/or canopy position had a strong impact on whole-tree Q and associated processes, we suggest that this would be an interesting area of study. Martin et al. (1997) emphasized the importance of canopy position in his analysis of E_c and g_c for *Abies amabalis* trees that differed in height and location within the forest canopy. Rather than apply a uniform radiation regime to all trees in calculations of g_c via a traditional inverted Penman–Monteith

approach, Martin et al. (1997) derived tree-specific estimates of absorbed radiation based on the vertical distribution of leaf area index with the intent of simulating how tree position and associated radiation regime might impact estimates of g_c and the decoupling coefficient. It was unfortunate that these authors focussed on radiation since it was concluded that tree-specific estimates of g_c were relatively insensitive to changes in radiation (as in hindsight might be expected for a coniferous species). The conceptual framework developed by Martin et al. (1997) should not, however, be dismissed. We estimate that g_c and Ω for red maple canopies are indeed both relatively insensitive to height-dependent differences in absorbed radiation and to a lesser extent δ_e, but that calculations of Ω exhibit considerable sensitivity to height-dependent differences (if there are any) in wind speed or more specifically aerodynamic conductance. A sub-canopy tree, for example, characterized by a lower g_a environment than its' neighbors would have, all else being the same, a much greater Ω compared to trees of greater stature (e.g., a change in g_a from 60 to 30 mm s^{-1} is sufficient to increase Ω from 0.22 to 0.34). This apparent sensitivity of Ω to the balance between g_a and g_c (see Eq. (2)) is due to the fact that trees at our study site were routinely subjected to consistently low wind speeds throughout the day and on most afternoons g_a was only 4–10 times greater than canopy conductance. Such an aerial environment is much different than those reported for coniferous forests where g_a may be several orders of magnitude greater than g_c (Martin et al., 1997; Phillips and Oren, 1998).

Finally, our studies with red maple demonstrate that considerable variation exists for all measured and estimated canopy processes. Day-to-day variation suggests that trees are highly dynamic in their response to changes in R_n and δ_e, while tree-to-tree variation illustrates the potential significance of canopy demographics and forest structure in determining rates of canopy transpiration, bulk surface conductance and Ω for individual trees. Our calculations suggest that height-dependent differences in δ_e and wind speed are sufficient to influence the decoupling coefficient (Ω) of red maple canopies and, as a result, should have implications for stand transpiration. Application of the Penman–Monteith equation to the study of g_c and Ω for trees of different heights in a forest canopy may,

however, violate assumptions of the 'big leaf' model (Jarvis and McNaughton, 1986). If such is the case then other model formulations might be better suited for such an analysis and these possibilities should be explored. Studies that measure whole-tree sap flow for trees that occupy different canopy strata and then use these data in spatially-explicit, process-based modeling of stand transpiration may be one approach to pursue in attempting to better understand how water use is influenced by the arrangement of trees within a forest (Falge et al., 1997). In this regard, studies that provide estimates of whole-tree Q for individuals that occupy different positions within the forest would help quantify the role that tree height and canopy stratification play in determining rates of stand transpiration (Köstner et al., 1992; Martin et al., 1997). This information would be useful for evaluating the differential contribution of species to forest water use and in better defining the environmental control of canopy transpiration.

Acknowledgements

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