



Water flux in a hybrid poplar stand

T. M. HINCKLEY,¹ J. R. BROOKS,¹ J. ČERMÁK,² R. CEULEMANS,³
J. KUČERA,² F. C. MEINZER⁴ and D. A. ROBERTS⁵

¹ College of Forest Resources, AR-10, University of Washington, Seattle, WA 98195, USA

² Faculty of Forestry, Institute of Forest Ecology, University of Agriculture, Brno-Sobesice 64400, Czech Republic

³ Biology Department, University of Antwerp, B-2610 Wilrijk, Belgium

⁴ Hawaiian Sugar Planters Association, Aiea, Hawaii 96701-1057, USA

⁵ Department of Geography, University of California, Santa Barbara, CA 93108, USA

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Summary

We studied water flux in a four-year-old stand of hybrid *Populus* during midsummer 1992. Study trees ranged in height from 11.0 to 15.1 m and in diameter from 8.3 to 15.1 cm. The large-leafed *Populus* hybrid was relatively poorly coupled to the atmosphere. The average value of the stomatal decoupling coefficient, Ω , was 0.66, indicating that, on average, a 10% change in stomatal conductance would result in only a 3 to 4% change in transpiration. During the middle of the summer, the smallest study tree used between 20 and 26 kg of water per day, whereas the largest tree used between 39 and 51 kg day⁻¹. The maximum observed rate of stand water loss was 4.8 mm day⁻¹ in this *Populus* clone. Maximum rates of sap velocity within the xylem were as high as 12.5 m h⁻¹; measured rates for exposed sunlit branches approached 90% of this maximum. Within-canopy patterns of stomatal conductance generally reflected patterns of incident radiation. Stomatal conductance of foliage grown in shade, even when exposed to non-limiting light and water source conditions, did not increase appreciably. Patterns of stomatal conductance under limiting and non-limiting conditions suggested that both stomatal conductance and leaf specific hydraulic conductivity (LSHC) were linked with the ability to exploit the light resource.

Keywords: hydraulic conductivity, *Populus*, stomatal conductance, stomatal decoupling coefficient, xylem sap velocity.

Introduction

Among physiologists, it is widely believed that stomata are invariably dominant in controlling transpiration, whereas meteorologists maintain that estimates of evapotranspiration for well-watered vegetation do not need to include stomatal response functions. This apparent conflict is not one of scientific evidence, but of interpretation of data gathered at incompatible scales. On a small scale, and especially under ventilated cuvette conditions where most physiologists measure transpiration, stomatal movements do control water loss from the leaf. However, at a larger scale, many canopies (especially dense, uniform canopies) are so decoupled from the atmosphere that the main factors controlling water loss are net radiation and those factors that influence canopy boundary layer properties (e.g., wind speed and canopy roughness) rather than atmospheric saturation deficit.

Canopy-atmospheric decoupling has been appreciated by micro-meteorologists for some time, and certain broad patterns have emerged. For example, it is known that the smoother and denser the canopy is, the more poorly it is coupled to the atmosphere. Also, broadleaf canopies are generally more poorly coupled than needle-leaved canopies. There are both physiological and ecological implications of canopy differences in atmospheric coupling—only recently have the conceptual and technical tools become available to approach measurements of canopy coupling (Kim and Verma 1991, Dawson 1993, Kelliher et al. 1993, Wofsy et al. 1993, Hollinger et al. 1994).

The broad objective of our research was to evaluate the extent to which different types of canopies are self-regulating, or homeostatic, in the face of changes in atmospheric variables such as vapor pressure deficit—in other words, how decoupled they are from the atmosphere. Similar to Schulze et al. (1985), Granier and Claustres (1989), Granier et al. (1990) and Köstner et al. (1992), an essential element of our approach was to make concurrent measurements of vapor fluxes and associated driving forces at multiple scales of observation from single leaves to entire trees. In addition to permitting compatible conclusions to be drawn from data gathered at contrasting scales (i.e., closure *sensu* Landsberg et al. 1991), the resulting information can be used to derive the decoupling factor (Ω), from which the sensitivity of transpiration to a marginal change in stomatal conductance can be evaluated (Jarvis and McNaughton 1986). The knowledge of the extent to which vapor pressure at the leaf surface is decoupled from that in the bulk atmosphere will enable us to evaluate the role of stomatal response to humidity in regulating transpiration under given conditions and to predict the impact on transpiration of changes in the atmospheric saturation deficit. In this paper, we report on a study of water loss from leaves, branches and trees in a hybrid poplar plantation.

Materials and methods

Study material and study site

The study was conducted at Washington State University's Farm 5 located near Sumner, Washington. Specifically, *Populus trichocarpa* × *P. deltoides* F₁ hybrid clone 50-194 from Stand I, Replication 1 of the Phase II trial (FT4.4) was used. Three replicates of this clone in 18-tree blocks were planted in the spring of 1989 along with 15 other F₁ hybrid clones. These clones were selected in 1988 because of their apparent high productivities in both field and operational trials. This study was initiated in late July 1992 (i.e., the fourth growing season) and ended in mid-October of the same year. On August 5, study trees ranged in height from 11.0 to 15.1 m and in diameter from 8.3 to 15.1 cm. A system of towers and scaffolding was constructed to gain access to the crowns of several trees (Figure 1). We measured whole-tree sap flux, branch sap flux, stomatal conductance, whole-stem and branch hydraulic conductivity, leaf area, canopy architecture, tree and stand inventory, stand microclimate, and reflected and scattered radiation.

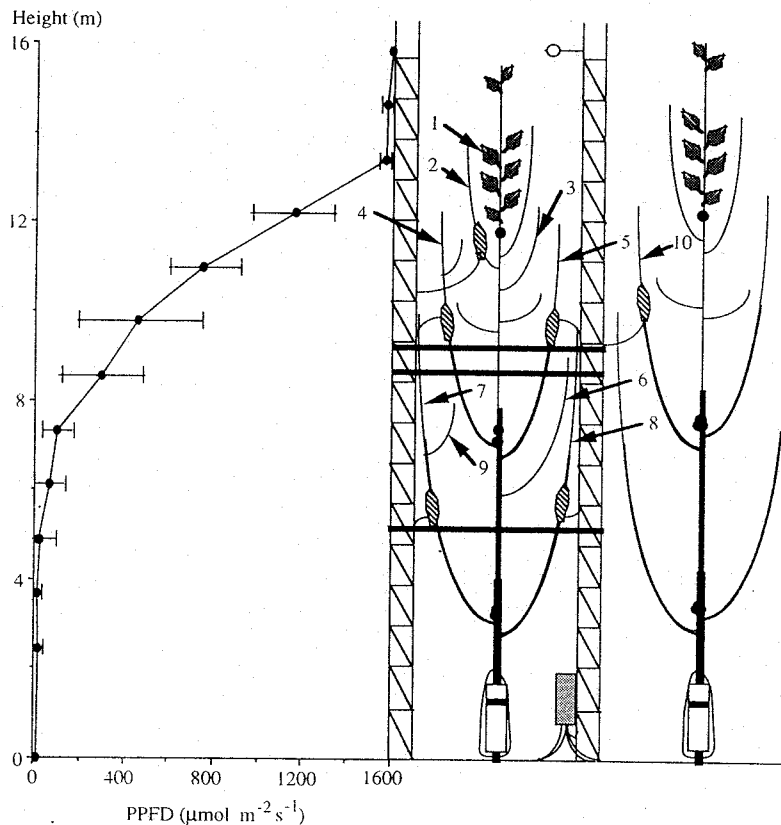


Figure 1. Scale diagram of the tower and scaffolding system surrounding a study tree (Tree No. 5, see Table 3) with single-sided access to five other study trees. The EMS sap flow system was located at the base of each tree, its associated data logger was on the tower. Six of the seven Dynamax stem gauges are shown (the insulated system is represented by a crossed-hatched area). Particular study branches are referenced by number with the terminal shoot being number 1. Branch 11 is not shown and was on a third tree. Solid circles on the stem represent the top of a given annual height increment. To the left is the photosynthetic photon flux density gradient through the canopy (included is the standard error of the mean).

Procedures

The study was divided into two phases. From July 29–August 6, whole-tree sap flow rates were measured simultaneously with microclimate, branch sap flow and stomatal conductance, while from August 15–September 20, 1992, only whole-tree sap flow rates and microclimate were monitored.

Microclimate Solar radiation, air temperature, dew (presence or absence) and relative humidity were measured above a turf grass clearing approximately 400 m from the plantation with a Campbell Scientific Weather Station (Campbell Scientific, Logan, UT) maintained by Washington State University. Additional measures of temperature and relative humidity were taken at mid-canopy in this stand (9.6 m) with a Vaisala sensor. Leaf temperatures were measured every 15 min with fine wire copper-constantan thermocouples on two to three representative leaves located on each study branch to calculate the leaf-to-air vapor pressure gradient and ultimately, total vapor phase conductance and crown conductance. In addition, a profile of photosynthetic photon flux density was constructed from 6 to 16 individual measure-

ments taken from the tallest tower at 1-m intervals through the canopy with a 1-m long LI Line Source Quantum Sensor (Li-Cor, Lincoln, NE). This profile was constructed from data collected on September 1 for the period 1100–1300 h solar time.

Stomatal conductance On the branches where Dynamax gauges were installed (see below), six to nine representative leaves were selected for measurements of stomatal conductance and transpiration with an LI-1600 steady state porometer (Li-Cor, Lincoln, NE). Recently mature to mature leaves were selected from both the terminal and secondary branch portions of each branch.

Xylem pressure potential The xylem pressure potential or water potential of leaves and twigs was measured on several days with a Scholander-Hammel pressure chamber (PMS Instruments, Corvallis, OR) according to the procedures of Ritchie and Hinckley (1975). Because these measurements are destructive, they were restricted to solar noon and to non-study branches (except on September 2). At solar noon, paired leaves were measured where one member of the pair was covered with aluminum foil 30 minutes before measurement, thus providing an estimate of stem water potential at the point of leaf insertion. These values were used to determine whether stress existed or not, and whether there were significant water potential gradients within the branch.

On September 2, solar noon xylem pressure potential values were taken on a covered and uncovered leaf from branches located at three positions within the canopy (positions 3, 6 and 9 shown in Figure 1). Immediately following these measures, the branch was cut under water, its base maintained in water and placed in an open environment with non-limiting light conditions. An additional pair of leaves (covered and uncovered) were measured after 30 min under these conditions.

Branch water loss Branch water loss was measured by means of an external heating and sensing system (Dynamax Inc., Houston, TX) following the modifications suggested by Gutierrez et al. (1994). Both the Dynamax and the EMS systems (used to measure trunk sap flow, see below) are based on a heat balance approach for measuring the volume flow of sap in the stem of a tree. Seven branches, placed into three groups, were studied. Each of the groups (e.g., branches 1 and 11 the upper group, branches 4, 5 and 10 the middle group, and branches 7 and 8 the lower group) occupied different vertical positions (and light environments) and represented the population of branches from that position (Figure 1). On August 7, the study branches were destructively harvested and the area of all leaves on each branch was measured with an LI-3200 leaf area meter (Li-Cor, Inc., Lincoln, NE).

Whole-stem and branch hydraulic conductivity Knowing the pattern and rate of dye movement in the stem of the study trees was important not only for calculating stem conductivity, but also for defining the sap velocity profile for proper insertion of heating elements and thermo-sensors of the EMS System. Before insertion of heating elements and thermo-sensors, two representative trees were supplied with a 0.5% acid fuchsin dye solution while their bases were immersed in water. Trees were

maintained in a vertical position for 30 minutes, then 10-cm sections were cut with a very sharp saw. The path of dye movement was determined based on the principles outlined in Čermák et al. (1992). Branch hydraulic conductivity was measured for branches from different positions on the main stem, with a range of diameters from 0.4 to 2.8 cm, by the methods of Sperry et al. (1988).

Whole-tree water loss For six trees larger than 12 cm in diameter, sap flow rate was measured by the trunk tissue heat balance (THB) method using internal (direct electric) heating and sensing (Čermák et al. 1976, 1984, 1992, Kučera et al. 1977). Sap flow rate was measured and recorded with an EMS sap flow meter P690-2 assembly (Brno, Czech Republic). Three electrodes and a battery of eight compensating thermocouples were used at each breast height measuring point (Čermák and Kučera 1981). Sap flow rate was measured from July 29 to September 20, 1992.

Tree and stand inventory measurements Diameters at breast height (DBH) were measured on all trees of Clone 50-194 as well as all other trees in Replicate 1 (Clones 11-11, 50-186, 49-177, 15-29, 50-184, 23-96, 44-148, 196-559, 184-411, 16-42, 55-258, 24-110, 44-133, 194-523 and 196-557). Results are summarized in Table 1. Similar data characterizing the specific study clone (50-194) are given in Table 2. In

Table 1. Forest inventory data for Replicate 1 of the Phase II trial (FT4.4) from Farm 5. Total area of Replicate 1 = 1336 m².

Diameter class (cm)	Tree density (stems ha ⁻¹)	Basal area (m ² ha ⁻¹)	Sum of basal area (m ²)
2	134	0.04	0.04
4	67	0.08	0.12
6	119	0.34	0.46
8	353	1.77	2.23
10	532	4.18	6.41
12	555	6.28	12.69
14	284	4.37	17.06
16	52	1.05	18.11

Table 2. Forest inventory data for the 18 trees of Clone 50-194 of Replicate 1 of the Phase II trial (FT4.4) from Farm 5. Total area of the study clone = 83 m².

Diameter class	Tree density (stems ha ⁻¹)	Basal area (m ² ha ⁻¹)	Sum of basal area (m ²)
2	0	0	0
4	0	0	0
6	241	0.68	0.68
8	241	1.21	1.89
10	602	4.73	6.62
12	603	6.82	13.44
14	361	5.56	19.00
16	121	2.43	21.43

addition, height increments and height during the study and at the end of the growing season were measured on all 18 trees of the study clone.

Scaling of sap flow rates from trees to stands Stand water loss was estimated from measures of stand basal area, stand conducting area and the rate of water flux through trees spanning a range of conducting areas (Čermák and Kučera 1990, Čermák et al. 1992). The biometric data for the six study trees are provided in Table 3. Diurnal courses of the sap flow rate between July 31 and August 6 were converted to a per unit cm of circumference and then regressed against the measured radiation at time t plus 1.5 h:

$$Q_{wt} = a(1 - \exp(-R/b)) ,$$

where Q_{wt} is the sap flow rate in $\text{kg tree}^{-1} \text{h}^{-1}$, R is radiation in W m^{-2} , and a and b are the tree specific coefficients.

Individual tree sap flow rates (daily sums of Q_{wt}) were scaled to the stand level (Q_{ws}) according to their relation to the xylem basal area of sample trees. First, Q_{wt} of a mean tree of each individual DBH class was calculated by the regression method outlined in Čermák et al. (1980). Then, Q_{wt} for each mean tree was multiplied by the corresponding numbers of trees in that DBH class. Finally, Q_{ws} was obtained by summing the values in the classes. Because all sample trees were of similar diameter which resulted in an insignificant regression line, the smallest still green tree of the stand was introduced into the set of sample trees where it was assumed that its transpiration approached zero, thus anchoring the regression line (Čermák et al. 1980).

Calculation of the Omega factor Total vapor phase conductance (crown conductance, g_c) was calculated as the sap flow per unit leaf area divided by the leaf-to-air vapor pressure gradient (Meinzer et al. 1993) determined to the mid-canopy humidity reference point (9.6 m). Stomatal conductance (g_s) and crown conductance (g_c) were used to calculate boundary layer conductance (g_b) as a residual:

Table 3. Biometric data of sap flow in trees of hybrid clone 50-194 (see Table 2 for all of the biometric data for this clone).

Tree no.	DBH (cm)	Height (m)	Stem circumference		Basal area	
			Plus bark (cm)	Without bark (cm)	Plus bark (cm^2)	Without bark (cm^2)
2	14.6	14.31	46	42.9	168.4	146.5
3	12.7	14.08	40.0	36.9	127.3	108.4
4	15.1	15.05	47.5	44.4	179.6	156.9
5	14.3	14.72	45.0	41.9	161.1	139.7
8	12.6	13.92	39.5	36.4	124.2	105.4
11	12.7	13.95	40.0	36.9	127.3	108.4

$$g_b = 1 / \left(\frac{1}{g_c} - \frac{1}{g_s} \right)$$

Stomatal and boundary layer conductance were then used to compute the stomatal decoupling coefficient, Ω , based on a recent formulation by McNaughton and Jarvis (1991) that takes radiative coupling between leaves and the atmosphere into account (Martin 1989). Data from branches 2, 4 and 5 (see Figure 1), upper and middle canopy branches, during the period July 31 to August 4, 1992 were used to calculate average values of Ω . The vapor pressure of the bulk air was determined at the mid-canopy reference point rather than at the nearby weather station, because it was discovered after the termination of the experiment that the humidity sensor at the weather station was malfunctioning. This resulted in a slight underestimation of the leaf-to-bulk air vapor pressure gradient because the vapor pressure at 9.6 m was partly influenced by the vapor flux from the canopy. This caused g_c and g_b to be slightly overestimated and Ω to be slightly underestimated.

Results and discussion

Whole-tree sap flux

Figure 2 illustrates the pattern of radiation and average sap flow through the six study trees (plus standard error) for the period August 2–4. It is important to note that sap flow is expressed per unit cm of circumference. Two significant observations were based on these results. First, only small differences in the quantity of sap flow were noted among the six trees, reflecting the small differences in crown position and the clonal nature of the material. Second, changes in sap flow were responsive to changes in solar radiation (regression data not shown, coefficients of determination ranged from 0.91 to 0.99 for the six study trees when solar radiation was lagged by 1.5 h). Others have noted no necessity to lag solar radiation (e.g., Köstner et al. 1992), or have found a more significant relationship with vapor pressure deficit (e.g., Granier and Claustres 1989). From the days shown on Figure 2, August 3 was chosen for further analysis because of the nature of the weather on the day and the completeness of the stomatal conductance data.

Diurnal branch and tree sap flow

August 3, 1992 was bright, warm and very dry (Figure 3). Minimum air temperature was 5.6 °C (0530 h solar time) and extensive dewfall occurred; as a consequence, dew did not evaporate from the canopy until after 0830 h. Peak solar radiation was observed between 1130 and 1230 h, whereas maximum air temperature was noted just before 1900 h, coincident with the maximum vapor pressure deficit. For August 3, stomatal conductances were highest for leaves on branches in the upper canopy and lowest for leaves in the lower canopy (Figure 4). Conductance values were slightly less in leaves from branches in the middle of the canopy than in the upper canopy, but they were considerably greater than in leaves located in the lower

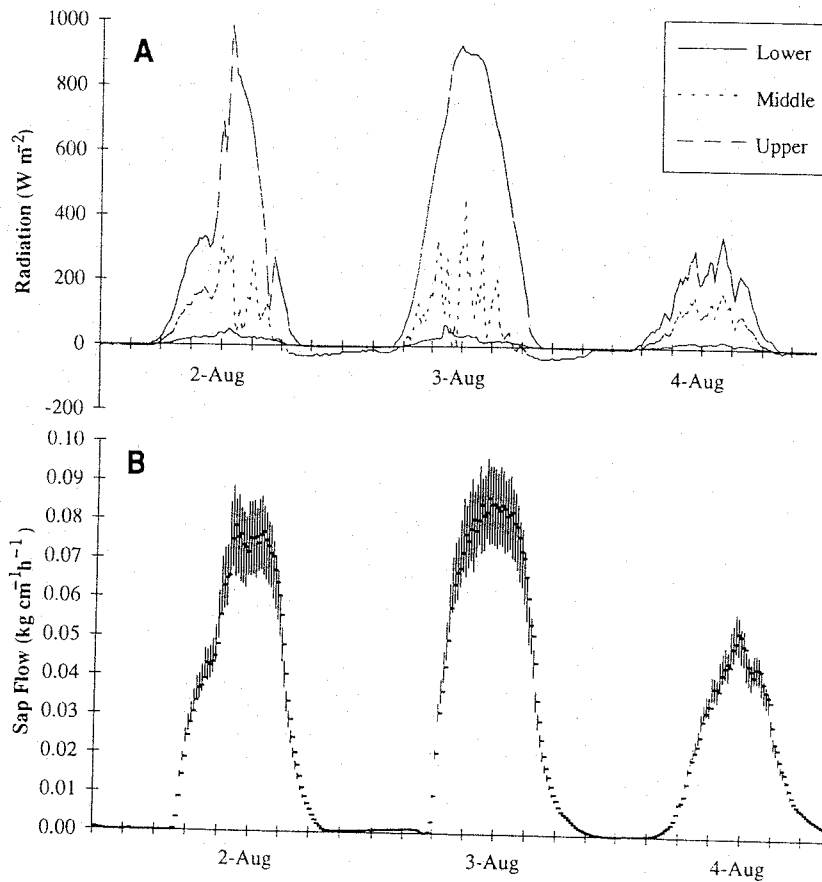


Figure 2. Radiation (A) and sap flow (B) for the period August 2–4, 1992. Three radiation values are given for each day (top is for a pyranometer while the middle and bottom are for net radiometers). Sap flow is the mean of the six study trees (Table 3) expressed as kg of water per unit of stem circumference per unit of time. Standard error is also shown.

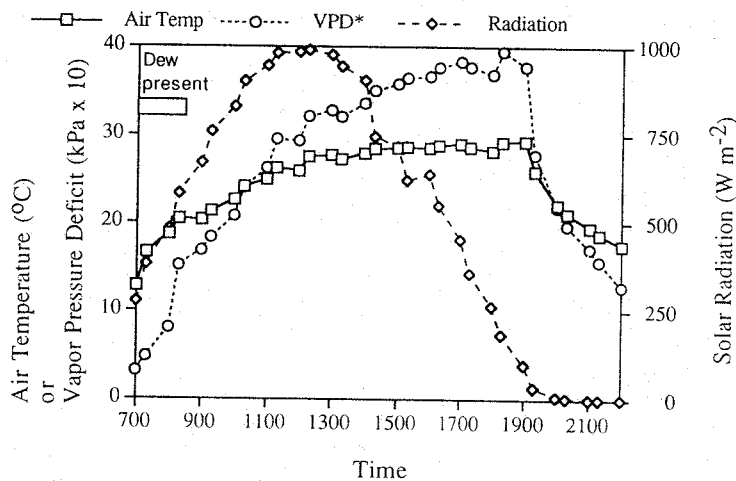


Figure 3. Weather data (solar radiation, air temperature and vapor pressure deficit) from the weather station for August 3, 1992 (water flux data illustrated in Figure 4).

canopy. Average midday PPFD was approximately $1350 \mu\text{mol m}^{-2} \text{s}^{-1}$ for upper-canopy branches, whereas for middle- and lower-canopy branches, it was 680 and $110 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. Above the top of the canopy, average maximum

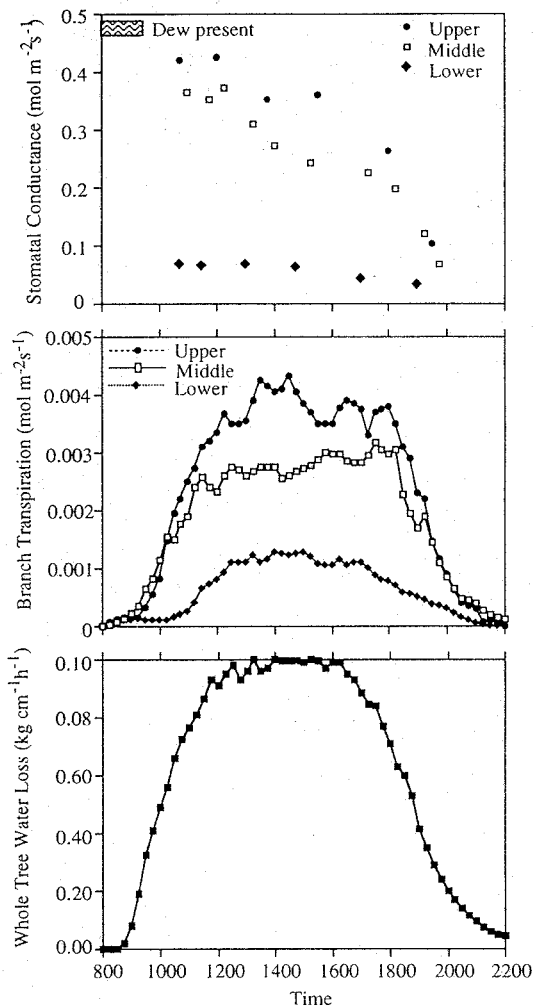


Figure 4. Whole-tree water loss (kg of water per unit of stem circumference per unit time), branch transpiration and leaf conductance for August 3, 1992. Data were collected from Tree No. 5 (see Table 3). The data for the upper, middle and lower branches correspond to locations number 2, 5 and 8, respectively, as shown in Figure 1. The period during which dew was present is also shown.

PPFDs were approximately $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 1). From 13 to 10 m, PPFD decreased to a little more than $400 \mu\text{mol m}^{-2} \text{s}^{-1}$, whereas between 10 and 7 m, it decreased to less than $50 \mu\text{mol m}^{-2} \text{s}^{-1}$. Maximum stomatal conductances occurred before solar noon and declined throughout most of the day. The most abrupt declines in stomatal conductances were noted between 1700 and 1900 h for leaves from upper- and middle-canopy branches and were associated with a sharp drop in solar radiation.

The highest rates of branch water loss were observed from upper-canopy branches and the lowest from lower-canopy branches. Water loss from middle- and upper-canopy branches was relatively constant from 1130 to almost 1930 h despite considerable declines in stomatal conductance (e.g., from more than 0.4 to less than $0.2 \text{ mol m}^{-2} \text{ s}^{-1}$). Transpiration remained high because vapor pressure deficit (Figure 3) continued to increase, compensating for reduced stomatal conductance. Transpirational differences between mid- and lower-canopy branches appeared to be related to

differences in stomatal conductances. In addition to differences between stomatal conductances between upper- and mid-canopy branches, there were also positional differences in leaf specific conductivities. Leaf specific conductivities of upper branches were almost twice those of middle and lower branches (6.14 versus 3.84 and 3.65 [$\times 10^{-4}$ kg s $^{-1}$ MPa $^{-1}$ m $^{-1}$], respectively).

Average leaf transpiration rates, estimated from porometer measurements (data not shown), were 50 to 100% higher than values obtained at the branch level (Dynamax gauges). Similar overestimations by the porometer were noted by Köstner et al. (1992) in *Nothofagus* and by Meinzer et al. (1993) in *Anacardium excelsum*. We noted a tendency for the highest porometer-based transpiration rates to be observed between 1500 and 1730 h. These differences reflect the inability of the porometer-based measurements to account properly for the boundary layer surrounding the leaf.

Patterns of whole-tree water loss demonstrated a plateau similar to the upper- and middle-crown branches; however, whole-tree rates decreased after 1700 h, whereas they did not for these branches. Because rates of upper-crown branch water loss were maintained beyond 1700 h, the decline in whole-tree water loss after 1700 h can be explained only by declines in water loss from middle and lower branches.

When we examined all of the stomatal conductance data collected during this study, maximum observed values decreased with canopy depth (Table 4). At branch (or leaf) position No. 1 (Figure 1), maximum stomatal conductance was 0.48 mol m $^{-2}$ s $^{-1}$, whereas at position No. 9, it was 0.074 mol m $^{-2}$ s $^{-1}$. This pattern of decreasing stomatal conductance with decreasing radiation has been observed in

Table 4. Spatial variation in maximum stomatal conductance for the period July 31–August 6, 1992, shown for six different positions within the canopy of a study tree (see Figure 1 for positions). In addition, stomatal conductance and xylem water potential measurements are given for midday on September 2 for leaves from branches before and after the branches were removed under water from the tree and placed in a fully illuminated, open location (the branch base was cut under water and was maintained under water during the entire experiment). For xylem water potential, the value in parentheses is the value obtained from a leaf covered with aluminum foil. One set of stomatal conductance and xylem water potential measurements was taken on the tree ("On") and the other set after 30 minutes under full sun, with unrestricted water supply ("Excised"). Branch sap velocity was estimated on excised branches from the movement of a 0.5% acid fuchsin dye solution.

Canopy position	Stomatal conductance (mol m $^{-2}$ s $^{-1}$)			Xylem water potential (MPa)		Sap velocity (m h $^{-1}$)
	Intensive	On	Excised	On	Excised	
1	0.480					
2	0.475					
3		0.350	0.380	-0.79(-0.55)	-0.41(-0.24)	12.6
4	0.436					
5	0.385					
6		0.255	0.280	-0.62(-0.52)	-0.45(-0.17)	11.1
7	0.085					
8	0.074					
9		0.068	0.075	-0.52(-0.34)	-0.38(-0.17)	7.0

other stand level studies. Granier and Claustres (1989) observed a decrease from 0.22 cm s^{-1} at the top of a *Picea abies* canopy to 0.06 cm s^{-1} at the bottom. Köstner et al. (1992) found a maximum stomatal conductance of $0.28 \text{ mol m}^{-2} \text{ s}^{-1}$ near the top of their *Nothofagus* canopy and a minimum of $0.15 \text{ mol m}^{-2} \text{ s}^{-1}$ near the bottom. A pattern similar to that found between July 31 and August 6 was noted on September 2, except that maximum conductances appeared to have decreased. Following individual branch removal from the tree and placement under relatively non-limiting conditions (light greater than saturation and water freely available), stomata opened slightly and stomatal conductances increased by 8.5–10.3%. In contrast, xylem water potentials increased considerably with the largest increase for the uppermost branch (from -0.79 to -0.41 MPa). *In situ* values of xylem water potential suggested that leaf water status played no role in controlling stomatal conductances. These results and the leaf specific hydraulic conductivity (LSHC) values of other branches obtained from similar positions in the canopy (Table 4) suggested that maximum values of both stomatal conductance and LSHC were determined by the light environment in which the leaves and branches had developed. Although stomatal conductance appeared to be coordinated with LSHC, the small stomatal response to branch excision and resulting increase in xylem water potential indicated that this coordination was not mediated by the dependence of xylem water potential on transpiration and LSHC.

For branches of this hybrid poplar, potential sap velocity within the xylem was as high as 12.6 m h^{-1} . The maximum observed rate in exposed sunlit branches approached 90% of the potential rate. The maximum observed sap velocity in *Nothofagus*, a ring-porous species, is 34.2 m h^{-1} (Köstner et al. 1992), three times faster than that observed in *Populus*, a diffuse-porous species. Sap flow is confined to the outer 0.2 cm of the xylem of *Nothofagus*, whereas in *Populus*, it was observed to depths of 4.0 cm. In contrast, sap velocity in *Picea abies* is less than 0.8 m h^{-1} (Granier and Claustres 1989). This rate is less than one tenth that observed in *Populus*; however, even more of the sapwood is functional in *Picea* than in *Populus*.

Tree-to-stand sap flow and water loss data

Maximum midday radiation ranged from 1006 to 372 W m^{-2} on July 31 and August 6, respectively. During this same period, daily maximum temperatures ranged from 33.1 to 20.2 °C (for July 31 and August 6, respectively). For average and maximum days during this short period, trees within the 12-cm diameter class were estimated to use about 20 and 26 kg of water per day, respectively, whereas those in the 14 cm class used between 29 and 38 kg day^{-1} , respectively, and those in the 16-cm diameter class used between 39 and 51 kg day^{-1} , respectively. Mean and maximum stand transpiration calculated for the July 31 through August 6 period were 3.64 and 4.81 mm day^{-1} , respectively.

Omega factor

For the period July 31 through August 4, the average g_s for branches 2, 4 and 5 was $0.311 \text{ mol m}^{-2} \text{ s}^{-1}$, whereas g_c was $0.190 \text{ mol m}^{-2} \text{ s}^{-1}$ (Table 5). This resulted in an

Table 5. Vapor phase conductances and the stomatal decoupling coefficient (Ω) for leaves on branches in the upper mid-crown of Tree No. 5 during the period July 31–August 4, 1992. Values for individual branches (\pm SE, $n = 8$) are averages of measurements taken between 1000 and 1500 h PST. Stomatal conductance (g_s) was measured in six to nine leaves on each branch to obtain the average value per branch. See Figure 1 for positions of branches. g_c is the crown conductance (calculated from branch transpiration rates, leaf and air temperatures, and the relative humidity). g_b , or boundary layer conductance, was calculated by difference.

Branch	g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	g_c ($\text{mol m}^{-2} \text{s}^{-1}$)	g_b ($\text{mol m}^{-2} \text{s}^{-1}$)	Ω
2	0.317 ± 0.027	0.207 ± 0.011	0.957 ± 0.241	0.61 ± 0.06
4	0.330 ± 0.027	0.184 ± 0.009	0.590 ± 0.188	0.71 ± 0.06
5	0.287 ± 0.026	0.181 ± 0.012	0.653 ± 0.124	0.65 ± 0.04
Mean	0.311 ± 0.016	0.190 ± 0.006	0.723 ± 0.111	0.66 ± 0.03

average g_b of $0.723 \text{ mol m}^{-2} \text{ s}^{-1}$. The average value of Ω was 0.66, but varied considerably between days and with time of day. For example, on July 31, Ω was approximately 0.82 before 1300 h but decreased to about 0.64 during the late afternoon when wind speed was higher. This indicates that, on July 31, the change in transpiration from the upper mid-canopy associated with a 10% change in g_s ranged from 1.8 to 3.4%. The upper mid-canopy was thus relatively poorly coupled to the bulk atmosphere with respect to stomatal control of transpiration. In general, rather smooth, uniform, broadleaf canopies (e.g., tropical rain forest) have rather high Ω values, whereas rough, small-leaf canopies (e.g., macchia, orchard trees, conifer forest) have rather low values (Jarvis 1985, Jarvis and McNaughton 1986, Verma et al. 1986, Valentini et al. 1991). Our data appear to fit the hypothesized relationship for a rather smooth, broadleaf canopy. Recently published values also indicate that Ω is not a constant for a given canopy, but varies as the environment interacting with a canopy changes. Similar to the pattern we observed, Köstner et al. (1992) found an Ω of 0.35 early in the day that declined to 0.05 by the evening in *Nothofagus*. Meinzer et al. (1993) noted an Ω of 0.5 during the dry season and 0.75 during the wet season in *Anacardium excelsum*, a large-leaf, emergent canopy species growing in central Panama.

We suspect that measurement of external vapor pressure at a greater height than 9.6 m would have yielded even higher values of Ω for *Populus*. Within the canopy, Ω would be expected to increase with decreasing height as a result of the expected decrease in g_b . This tendency may be partially compensated for by the observed decrease in g_s with decreasing height. Spatial variation in Ω within a canopy has been noted by others. For example, Roberts et al. (1990) observed an Ω of 0.3 near the top (36 m) of an Amazonian rain forest, whereas in the understory (1.5 m), Ω was 0.8. Unfortunately, only a limited number of measured Ω values appear in the literature; this clearly is changing.

The hybrid poplar was poorly coupled to the atmosphere with an average Ω value of 0.66 indicating that a 10% change in stomatal conductance would result in only a 3.4% change in canopy transpiration (at constant vapor density gradient, etc.). This

high value of ω contrasts with values near 0.1 reported for typical conifer stands (Jarvis and McNaughton 1986). As a very simple extrapolation, one would expect that water use in conifers with low Ω would be quite different from that in broadleaf trees with a high Ω . Yet, the maximum calculated rate of stand water loss was 4.81 mm day⁻¹ for *Populus* in our study, a value slightly less than the maximum of 5.0 mm day⁻¹ observed by Fritschen et al. (1973) for Douglas-fir (*Pseudotsuga menziesii*). Leaf area indices were approximately the same in the two species, whereas individual stomatal conductances were 3 to 5 times higher in *Populus* than in Douglas-fir. However, similar rates of stand transpiration in vegetation with very different ω values could arise from stomatal control of partitioning of total vapor phase conductance (crown or canopy conductance) between stomatal and boundary layer components. For example, in a conifer stand, g_b will be very high but g_s rather low. In our poplar stand, g_s was high and g_b was low. However, the total conductance may have been similar in the two stands. All other things being equal (LAI, soil water, net radiation), the two stands could then have similar rates of transpiration. Several authors have suggested that once canopies close, very similar rates of transpiration occur (Whitehead and Jarvis 1981, Kelliher et al. 1993). As demonstrated by Meinzer and Grantz (1991), a number of different structural, morphological and physiological properties and mechanisms may be responsible for these apparent similarities.

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