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Forest Ecology and Management 152 (2001) 211–224

Forest Ecology
and
Management

www.elsevier.com/locate/foreco

Control of transpiration in a 220-year-old *Abies amabilis* forest

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Received 15 February 2000; accepted 2 September 2000

Abstract

We measured sap flow at the branch and tree levels, and calculated tree transpiration at the stand level, in a 220-year-old *Abies amabilis* (Dougl.) Forbes forest. Temporal and spatial patterns of branch sap flow rate per unit leaf area reflected differences in canopy position and diurnal variation in radiation exposure. Average leaf area normalized branch conductance of upper canopy branches ranged from 0.50 to 1.01 mm s⁻¹. Maximum leaf area normalized tree sap flow rates were similar to those previously measured in a younger *A. amabilis* forest (about 80 g m⁻² leaf area h⁻¹), but dominant trees in the old growth stand transpired approximately three times more per day (up to 281 kg H₂O per day) than dominant trees in the younger forest. This difference was attributed primarily to leaf area: dominant trees in the old growth stand had approximately three times more leaf area than those in the younger *Abies* stand. Crown conductance on a ground area basis varied by an order of magnitude between the smallest and largest trees measured (maximum 4.84 mm s⁻¹ and mean 1.44 mm s⁻¹ versus maximum 37.54 mm s⁻¹ and average 12.16 mm s⁻¹, respectively). There was considerable spatial and temporal variation in stomatal versus boundary layer control of transpiration as expressed by the Ω decoupling coefficient. Ω for the largest measured tree ranged from less than 0.1 to greater than 0.6, and remained above 0.3 for more than 9% of the daylight hours monitored. The degree of decoupling decreased with tree size, with Ω of the smallest tree sampled never exceeding 0.3. Daily stand transpiration ranged from less than 0.4 mm to greater than 3.3 mm depending on radiation and vapor pressure deficit. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Transpiration; *Abies amabilis*; Forest; Sap flow; Decoupling coefficient; Leaf area

1. Introduction

In the Pacific Northwest region of the US, about 45% of the total land area, or 2×10^7 ha, is forested

(Powell et al., 1994). About 20% of these forests retain the distinctive characteristics of primary or old growth forest that were widespread prior to European settlement, such as large, old trees, multi-layer canopy structure, and presence of standing and downed dead woody material (Bolsinger and Waddell, 1993). Because of logging and development pressures, most remaining old growth forests in the Pacific Northwest are found in remote, inaccessible, and/or high-elevation locations. For this reason, old growth forests are a component of many municipal and wildland watersheds in

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the region. Limited studies in other ecosystems have shown that tree age may affect stand or watershed water balance (Dunn and Connor, 1993; Jayasuriya et al., 1993; Cienciala et al., 1997). An understanding of the dynamics and controls of water flux in Pacific Northwest old growth forests could be useful for predicting the effects of management actions and forest succession on watershed-level function. Despite the obvious biological and applied interest, little information exists about the water relations of old growth trees and forests in the Pacific Northwest.

The objective of this study was to investigate the dynamics and control of branch-, tree- and stand-level water flux in a Pacific Northwest old growth forest. Our research approach was motivated by our previous work in younger *Abies amabilis* (Dougl.) Forbes forests (Martin et al., 1997, 1999). Specifically, we were interested in three main issues: (1) our previous work has shown that water loss at the shoot and branch scales in *A. amabilis* is well-coupled. This means that transpiration at these scales is regulated almost entirely by stomatal conductance and the prevailing vapor pressure deficit, and that boundary layer conductance and net radiation do not significantly impact water flux (Martin et al., 1999). In the present study, we investigate the role of stomatal and boundary layer conductances in regulating transpiration at the individual tree crown level, with emphasis on both temporal and spatial (tree-to-tree) variation in decoupling. (2) Our work (Martin et al., 1997) and the research of others (Granier, 1987; Köstner et al., 1992; Arneth et al., 1996) has revealed great variation in transpiration rates with tree size and has shown that stand water loss is dominated by the largest few trees in the stand. We wanted to quantify these relationships for an old growth *A. amabilis* stand. (3) Finally, we were interested in quantifying the magnitude and patterns of transpiration of an old growth forest at the stand level.

2. Materials and methods

2.1. Study site description

The study site is in the Findley Lake Research Area (47°19'N, 121°35'W), located at 1130 m elevation in the Cedar River Watershed, 65 km southeast of Seattle, WA. There is an extensive history of research

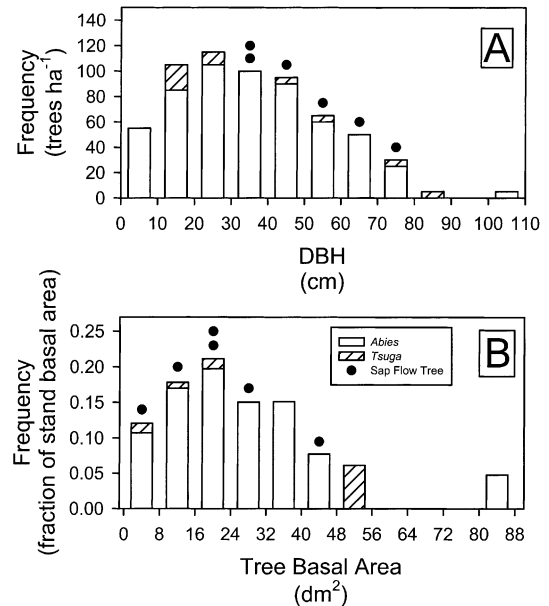


Fig. 1. Distributions of diameter at breast height, 1.3 m (A) and basal area at breast height (B) for a 220-year-old *Abies amabilis* forest. Inventory data were taken from a 0.2 ha circular plot surrounding the access tower system. The diameter and basal area classes of sap flow measurement trees are indicated by ●.

in soils and nutrient cycling, community ecology and production ecology at the site (Turner and Singer, 1976; Singer et al., 1978; Grier et al., 1981; Vogt et al., 1983; Meier et al., 1985). The stand is composed primarily of *A. amabilis* (Pacific silver fir), with approximately 15% of the basal area occupied by *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) and *Tsuga mertensiana* (Bong.) Carr. (mountain hemlock) (Fig. 1B). Increment cores from the dominant trees showed approximately 220 growth rings. At the time of the study, the dominant trees ranged in height from 35 to 42 m. The stand density was 625 trees ha⁻¹, with a basal area of 83.4 m⁻² ha⁻¹. The canopy was accessed by a 38 m tall system of towers and catwalks.

The climate of the site is characterized by mild, dry summers (mean July air temperature 12°C) and cool, wet winters (mean January air temperature -3.2°C). Annual precipitation averages 2700 mm, the majority of which falls as snow. Maximum snow accumulations range from 2 to 4 m, and the ground remains snow covered from mid or late November until late May or early June (Lassoie et al., 1985). During the present

study, maximum, minimum and mean air temperatures were 28.8, 1.3 and 13.0°C, respectively; 107 mm of precipitation reached the forest floor as throughfall during the same period (Rombold, unpublished data).

2.2. Tree sap flow

Tree sap flow was measured with the stem heat balance technique described in detail by Cermák et al. (1973, 1982), Kucera et al. (1977), and Cermák and Kucera (1981). Sap flow gauges (P-6, Ecological Measuring Systems, Ltd., Brno, Czech Republic) were installed on six trees chosen to represent a broad range of diameters as described in Cermák and Kucera (1990) and Cermák and Michálek (1991). The stainless steel electrodes and thermocouples for each gauge were inserted to the approximate depth of the functional xylem, and measured sap flow over a circumferential distance of approximately 80 mm. These sensors measure mass flux of water per unit circumference, so assumptions regarding radial flow profiles were not necessary. Because it is not practical to measure sap flow around the entire tree circumference, measurements of sap flow per unit circumference were made on opposite sides of the tree, then averaged and scaled to the tree level by multiplying the averaged sap flow measurement by under-bark tree circumference (Cermák et al., 1982). To avoid large variations in sap flow around the circumference of the tree (Cermák and Kucera, 1990), the measurement sensors were placed as far above the ground as was practical (1.5–2.0 m). Sample tree diameter at breast height (DBH) ranged from 31.5 to 78.0 cm (Fig. 1). Sap flow was measured from 12 July to 10 October 1994.

2.3. Branch sap flow

Branch sap flow was measured with heat balance sap flow gauges (Dynagage, Dynamax Inc., Houston, TX). This method and instrumentation are described in detail by Sakuratani (1981), Baker and van Bavel (1987) and Steinberg et al. (1989). Gauges were installed using the precautions outlined in Gutierrez et al. (1994) on four branches on each of the two largest sap flow measurement trees. On each tree, two sap flow gauges were located on branches in the top third of the crown (approximate height 33 m) and near the bottom third of the crown (approximate height

25 m). The branches ranged from 1.38 to 2.64 cm in diameter at the point of measurement. Sap flow was monitored every min and stored as 30 min averages by a datalogger (CR-10, Campbell Scientific, Inc., Logan, UT).

2.4. Tree and stand leaf area

Foliage area sampling was performed after the cessation of sap flow measurement in the fall of 1994 and in the summer and fall of 1995. We measured the diameter, height from the ground and azimuthal orientation of every living branch on each of seven leaf area sample trees, and also on the six trees on which sap flow was measured. From each of the seven leaf area sample trees, we randomly chose and removed approximately 20 branches. The leaf area of each sampled branch was determined as in Martin et al. (1997), then the branch leaf area data were integrated to the tree level using the branch diameter and height measurements. Total tree height (in m) was the best predictor of tree projected leaf area (leaf area in $\text{m}^2 = 23.9 + 2.9 \times 10^{-6} \times \text{height}^{5.04}$, $R^2 = 0.956$) and was used to predict leaf area for the rest of the trees in the stand.

2.5. Meteorological measurements

Meteorological variables were measured from a weather station at the top of a 39 m tall tower. Global shortwave and net radiation were measured with a pyranometer (Li200S, Li-Cor, Lincoln, NE) and Fritschen miniature net radiometer (Micromet Instruments, Bothell, WA), respectively. A shielded combination capacitive relative humidity sensor/thermistor probe (HMP35C, Campbell Scientific, Inc., Logan, UT) monitored relative humidity and air temperature. Wind speed and wind direction were measured with a cup anemometer and wind vane, respectively (Model 03001-5, R.M. Young, Traverse City, MI). Variables were read every minute and averages recorded every 30 min by a datalogger.

2.6. Crown and branch conductance

Crown conductance (g_c , m s^{-1}) was calculated by substituting tree transpiration rate (T_c , $\text{kg H}_2\text{O m}^{-2}$ ground area s^{-1}), boundary layer conductance

(g_a , ms^{-1} on a ground area basis), vapor pressure deficit (D , kPa) and net radiation absorbed by the tree crown (R_c , W m^{-2}) into the Penman–Monteith equation (Monteith, 1965)

$$T_c = \frac{sR_c + \rho_a C_p g_a D}{\lambda[s + \gamma(1 + (g_a/g_c))]} \quad (1)$$

where s is the slope of the saturation vapor pressure versus temperature curve at air temperature (kPa K^{-1}), ρ_a is the density of dry air (kg m^{-3}), C_p represents the specific heat capacity of air ($\text{J kg}^{-1} \text{K}^{-1}$), λ is the latent heat of evaporation of water (J kg^{-1}) and γ is the psychrometer constant (kPa K^{-1}). Eq. (1) was then solved for g_c as in Granier and Loustau (1994). It should be emphasized that g_c is the vapor phase conductance for an individual tree, expressed per unit ground area occupied by the tree crown. This can be considered equivalent to a tree-level canopy conductance. Crown conductance on a ground area basis (g_c) was converted to crown conductance on a leaf area basis (g'_c) by dividing g_c by the individual tree's leaf area index.

The net radiation absorbed by each tree (R_c) was calculated in two steps. First, the net radiation at the top of the tree was calculated from the tree height assuming that the light extinction coefficient for the stand was equivalent to that in a second growth *Abies* stand (0.47, Martin et al., 1997). Second, the radiation absorbed by the tree was calculated as in Granier and Loustau (1994) using the Beer's law extinction coefficient and individual tree LAI ($\text{m}^2 \text{m}^{-2}$) calculated by dividing the tree projected leaf area by the crown plan area.

Vapor pressure deficit was assumed to be constant throughout the canopy. This is a reasonable assumption in tall conifer stands, where the air within the canopy is well mixed with the air above the stand (Jarvis et al., 1976; Granier and Loustau, 1994; Ewers and Oren, 2000).

Crown boundary layer conductance (g_a) was calculated as the series sum (sum of inverse conductances, since resistances are additive in series) of a shoot boundary layer conductance (g_{aS}) and a crown aerodynamic conductance (g_{aM}) as in Köstner et al. (1992) and Arneth et al. (1996). Shoot boundary layer conductance on a projected leaf area basis (g_{aS} , m s^{-1}) was estimated from a relationship between wind speed

(w , m s^{-1}) and g_{aS} developed from measurements on *A. amabilis* branch models in a wind tunnel (Martin et al., 1999) and was converted to a ground area basis for each tree by multiplying by the tree's leaf area index. Because this approach does not account for reductions in wind speed with canopy depth, it overestimates tree-level g_{aS} . Crown aerodynamic conductance (g_{aM} , m s^{-1}) was calculated from the wind profile equation (Monteith, 1965) with values of displacement height and roughness length estimated from graphs in Shaw and Pereira (1982). From these calculations, $g_{aM} = 0.335 \times w$; at wind speeds below 0.1 m s^{-1} , $g_{aM} = 0.034 \text{ m s}^{-1}$. This results in higher g_{aM} than if we had used the approximation of $g_{aM} = 0.1 \times w$ that is frequently used for forests (Jarvis et al., 1976; Kelliher et al., 1992).

Branch conductance on a leaf area basis (g'_{branch} , mm s^{-1}) was calculated from Eq. (1), with all the terms evaluated at the branch level instead of the tree level. Radiation absorption by the branch on a leaf area basis was evaluated by multiplying R_n measured at the weather station by the average silhouette to projected area ratio of the branch determined from shoot samples (Martin et al., 1999). Because R_n was not measured low in the crown, g'_{branch} was calculated only for branches in the upper canopy.

2.7. Decoupling coefficient and related parameters

The relative importance of stomatal and boundary layer limitations to transpiration was quantified by a dimensionless decoupling coefficient, Ω (Jarvis and McNaughton, 1986)

$$\Omega = \frac{(s/\gamma) + 2}{(s/\gamma) + 2 + (g_a/g_c)} \quad (2)$$

We partitioned tree transpiration into components attributable to radiation (T_{R_c}) and to vapor pressure deficit (T_D) as

$$T_{R_c} = \Omega T_{\text{equ}} = \Omega \frac{R_c}{\lambda(1 + (\gamma/s))} \quad (3)$$

$$T_D = (1 - \Omega) T_{\text{imp}} = (1 - \Omega) g_c D \frac{\rho_a C_p}{\lambda \gamma} \quad (4)$$

where T_{equ} and T_{imp} are the equilibrium and imposed rates of transpiration, respectively, as defined in Jarvis and McNaughton (1986). The equilibrium rate of

transpiration is the rate of transpiration that would occur with very low boundary layer conductance (Eq. (1) evaluated with $g_a = 0$), while T_{imp} is the rate of transpiration that would occur with infinite boundary layer conductance (Eq. (1) evaluated with $g_a = \infty$).

3. Results and discussion

3.1. Tree and stand leaf area

Projected leaf area of sap flow measurement trees ranged from 70.9 to 460.8 m² (Table 1). Leaf area index of individual sap flow measurement trees, calculated by dividing tree leaf area by projected crown area ranged from 4.8 to 14.5. Stand leaf area index was 6.4, at the lower end of the range reported for other Pacific Northwest old growth coniferous forests (Marshall and Waring, 1986; Runyon et al., 1994) and about 30% lower than the LAI reported for second-growth *A. amabilis* (Martin et al., 1997).

3.2. Time lags between stem sap flow and transpiration

In order to utilize Eq. (1) to calculate g_c , it is necessary to synchronize sap flow data with meteorological data (Ewers and Oren, 2000). In this study, sap flow at the base of the stem lagged behind branch sap flow and meteorological variables (Fig. 2),

presumably due to the effects of water storage between the stem sap flow gauge and transpiring leaves (Martin et al., 1997; Phillips et al., 1997). The correlation between sap flow at the stem base and D or branch sap flow rate was highest when D or branch sap flow was lagged by 30 min. The correlation peaks at the 30 min time lag were broad; correlation coefficients for real time data or data lagged by 60 min were only about 1% lower than those for data lagged by 30 min. Crown conductance calculations were relatively insensitive to the choice of time lag; average values of g_c calculated with real time, 30 min, or 60 min lagged meteorological data generally differed by less than 4%. Based on this information, we lagged meteorological data by 30 min when applying Eq. (1) to calculate whole-tree conductances. Although more sophisticated and biologically realistic methods exist for dealing with capacitance (Phillips et al., 1997), we made the pragmatic assumption of a constant time lag, as other researchers have (Granier and Loustau, 1994; Hogg and Hurdle, 1997), since we were not focusing on capacitance issues.

3.3. Branch sap flow and conductance

Branch sap flow rates varied with meteorological conditions and crown position (Fig. 2B). On cloudless days, branches could be distinguished from each other by their unique diurnal sap flow “signature” resulting from the changing radiation environment as the branch

Table 1
Biometric and physiological parameters of sap flow measurement trees in a 220-year-old *Abies amabilis* stand^a

Diameter at 1.3 m (cm)	Total height (m)	Height crown base ^b (m)	Projected crown area ^c (m ²)	Projected leaf area (m ²)	Maximum daily sap flow (kg H ₂ O per day)	Average g_c^d (mm s ⁻¹)	Maximum g_c (mm s ⁻¹)	Average g_c^e (mm s ⁻¹)	Maximum g_c^e (mm s ⁻¹)	Duration of $\Omega > 0.3$ (%) ^f
78.0	41.6	14.7	39.9	460.8	281.3	12.16	37.54	1.05	3.25	9.4
61.8	35.0	11.0	18.0	260.7	74.7	9.12	44.60	0.630	3.08	4.3
54.1	37.4	13.6	23.1	241.0	101.4	9.00	35.53	0.863	3.41	4.3
45.7	31.8	14.4	16.2	141.6	72.9	7.93	28.33	0.907	3.24	2.2
38.6	32.8	17.4	14.0	67.0	34.6	3.24	13.72	0.676	2.87	0.5
31.5	25.9	12.1	14.8	70.9	9.2	1.44	4.84	0.300	1.01	0.0

^a Sap flow parameters are averages of all measured daylight, 0.5 h time periods.

^b Measured to the lowest branch with green foliage.

^c Calculated from radii measured from the ground in four cardinal directions.

^d Crown conductance on a ground area basis calculated using Eq. (1).

^e Crown conductance on a leaf area basis calculated by dividing g_c by the individual tree leaf area index.

^f Percent of 0.5 h daylight periods during which the Ω decoupling coefficient exceeded 0.3.

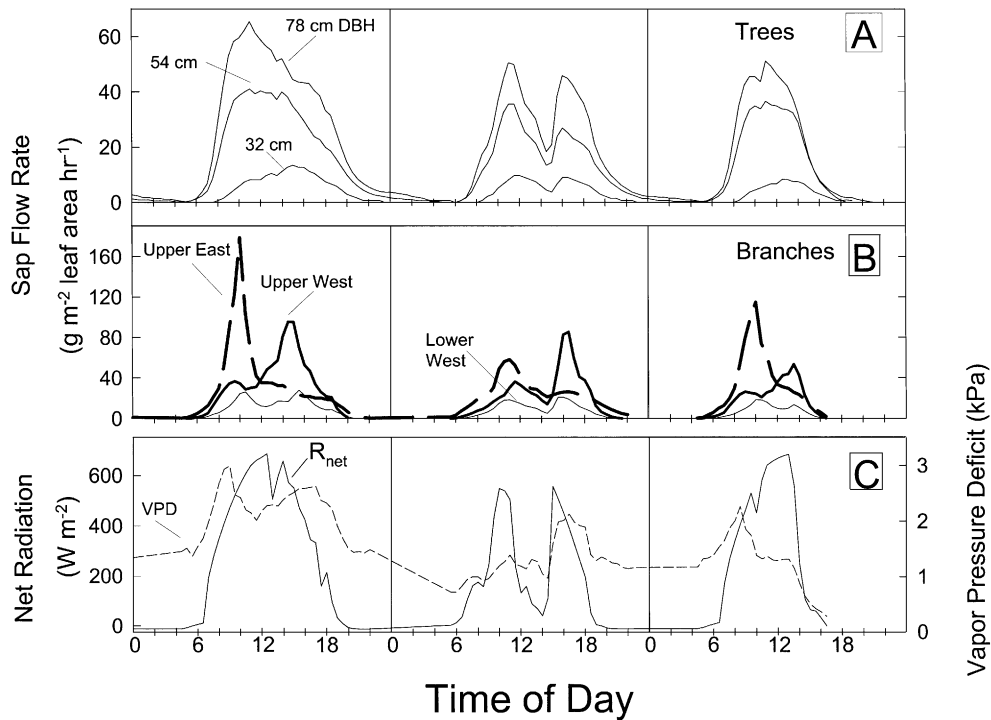


Fig. 2. Sap flow and meteorological data on 22–24 July 1994 for a 220-year-old *Abies amabilis* forest. (A) Sap flow for dominant (78 cm diameter), co-dominant (54 cm diameter) and suppressed (32 cm diameter) trees. (B) Sap flow rates of branches located in the upper canopy (east and west exposures) and lower canopy. (C) Net radiation and vapor pressure deficit. Meteorological data are not lagged in time.

moved in and out of the shade of other branches and adjacent trees. For example, the upper crown east facing branch shown in Fig. 2B had a characteristic peak in sap flow rate at the beginning of each cloudless day, followed by a decline as the branch moved into the shade caused by the tree to which it was attached. In contrast, sap flow in a branch on the upper west side of the crown was relatively low early in the day as the branch remained in partial shade, but then increased as the sun moved into the western sky. Branches lower in the canopy had considerably smaller amplitude of variation throughout the day.

Sap flow rates per unit leaf area of upper branches tended to be higher than those of branches in the lower crown. Peak water loss rates per unit leaf area of the upper branches exceeded peak rates of water loss per unit leaf area of the co-dominant trees to which they were attached, while branches lower in the canopy had sap flow rates that were considerably lower than rates at the crown level (compare Fig. 2A and B). These patterns of branch versus tree canopy-level variation

are similar to patterns observed in *Pinus taeda* (Phillips et al., 1997; Oren et al., 1998).

Average g'_{branch} for the four branches measured in the upper canopy ranged from 0.50 to 1.01 mm s⁻¹; maximum g'_{branch} for the same branches ranged from 2.07 to 4.71 mm s⁻¹ (Table 2). This variation did not appear to be correlated with variation in branch size, position or exposure. While there are several reports of

Table 2
Conductance statistics for branches in the upper canopy of a 220-year-old *Abies amabilis* stand

Branch position (exposure, height)	Branch leaf area (m ²)	g'_{branch} ^a (mm s ⁻¹)		
		Average	S.D.	Maximum
NW, 33 m	0.50	0.52	0.43	3.70
W, 33 m	1.17	0.76	0.67	4.35
NE, 33 m	0.78	1.01	0.72	4.71
SE, 32 m	1.05	0.50	0.35	2.07

^a Branch conductance on a leaf area basis calculated as described in text.

g'_{branch} for broad-leaved trees (Meinzer et al., 1993; Hinckley et al., 1994), there are none for coniferous trees to which to compare our measurements (Rayment et al., 2000). The mean values of g'_{branch} in this study are consistent with shoot-scale stomatal conductance measured in *A. amabilis* in previous studies (Teskey et al., 1984; Brooks et al., 1994). Because the calculations of g'_{branch} utilized radiation measurements from the weather station, it was assumed that the branches were unshaded, which is clearly not the case as discussed previously. However, because *A. amabilis* foliage at the branch level has been shown to be well coupled (Martin et al., 1999), the contribution of radiation to transpiration will be small (see Eq. (3)), and the errors in g'_{branch} due to errors in radiation inputs to Eq. (1) will be small.

3.4. Circumferential variation in tree sap flow

In most of the trees measured, variation in sap flow rate between the two opposite measured sides was relatively small (average ratio of the two measurements ranging from 1.00 to 1.44). However, in the second largest and largest trees measured, the average ratio between the rates measured on the two sides was 2.66 and 2.91, respectively. In both of these trees, very large (>35 cm diameter) roots entered the tree stem below the measurement point producing the larger values of sap flow. In comparison, most of the other visible coarse roots entering the base of these stems were 20 cm diameter or less. Despite our precautions in locating the sap flow sensors 1.5–2.0 m above the ground, it appeared that these large roots may have caused the flow rate in the area measured by the sensor to be substantially greater than that in the remainder of the tree. This led to problems with the calculation of tree sap flow for the two largest trees we measured. Using the unweighted average of the two sides to calculate whole tree sap flow rates produced large rates of sap flow in the two trees (up to 450 kg per day in the largest tree measured). Using an average of the two measurement sensors weighted so that the high sensor represented only the proportion of the tree circumference occupied by the large root produced sap flow rates 60–75% of the rates calculated from unweighted averages.

To determine whether tree sap flow rates calculated from the weighted or unweighted sensor averages

were more realistic, we compared values of crown conductance on a leaf area basis (g'_c , calculated from both the weighted and unweighted averages of sap flow using the methods described previously) to shoot level measurements of stomatal conductance (g_s) measured with a porometer, and to g'_{branch} of upper crown branches (Table 2). The value of g'_c obtained in this fashion is equivalent to the average g_s of all leaves on the tree (Arneeth et al., 1996). Because g_s decreased with depth in the canopy (data not shown), g'_c should be lower than the g_s of upper canopy shoots. Our work in a second growth *A. amabilis* stand has confirmed this (Martin et al., 1997). When we compared g'_c obtained from the unweighted sap flow data for the two largest trees to upper-canopy g_s or g'_{branch} , g'_c tended to be two to three times larger than the upper crown conductances; when we did the same comparison with g'_c calculated using a weighted sap flow measurement, values of g'_c were usually similar in magnitude or lower than the independent upper-canopy conductance measurements (Tables 1 and 2). Considering this information, we decided to use values of tree sap flow calculated from weighted averages for the two largest trees sampled.

3.5. Tree sap flow

Rates of sap flow per unit leaf area for the dominant trees in the old growth stand approached $80 \text{ g m}^{-2} \text{ h}^{-1}$ on warm, dry days (Figs. 2 and 3), intermediate to rates observed at the branch level in the upper and lower canopy (Fig. 1). These maximum leaf area normalized rates were comparable to maximum rates observed in dominant trees in a second-growth *A. amabilis* stand measured 1 year earlier (Martin et al., 1997). In contrast, Hubbard et al. (1999) found that leaf area normalized sap flow rates were 53% lower in old (250 years) than in young (40 years) *Pinus ponderosa* Dougl. ex Laws. trees.

Despite similarities in leaf area normalized transpiration rates, there were large differences in the absolute magnitudes of whole tree transpiration between old growth and young *A. amabilis* stands. Daily transpiration from the largest tree measured in the present study was more than 100 kg per day on 70% of the days we measured, and occasionally exceeded 200 kg per day (9% of the days measured). In contrast, the largest tree in the second growth

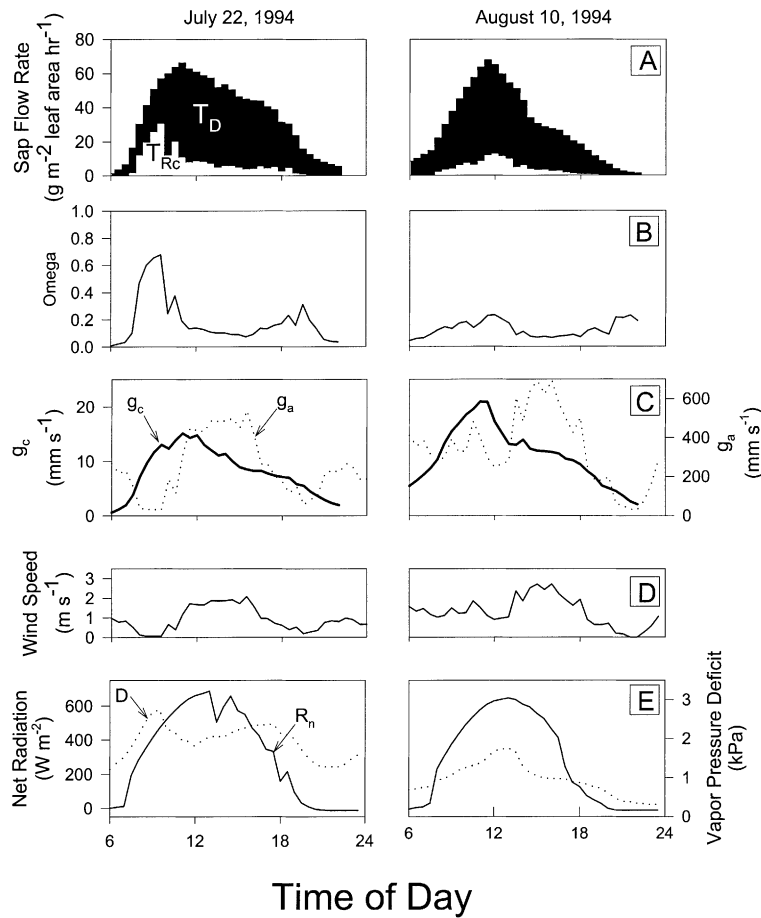


Fig. 3. Sap flow, conductance and meteorological data from a 220-year-old *Abies amabilis* stand during two days in 1994 with similar vapor pressure deficit and net radiation regimes. (A) Sap flow rate per unit leaf area for the largest tree measured. The dark region represents the portion of sap flow attributable to vapor pressure deficit, while the light region represents sap flow attributable to radiation (see Eqs. (3) and (4)). (B) Variation in the decoupling coefficient Ω . (C) Variation in crown conductance and boundary layer conductance for the largest tree measured. Note the differences in scale for g_a and g_c . (D) Wind speed measured at a weather station above the canopy. (E) Net radiation and vapor pressure deficit measured at a weather station above the canopy. The meteorological variables are lagged by 30 min to account for the time difference between transpiration at the leaf surface and sap flow at the base of the stem (see text for further explanation).

A. amabilis stand never transpired more than 98 kg per day (Martin et al., 1997); for 75% of the days measured, that tree transpired less than 80 kg per day. These large differences in total daily transpiration can be explained primarily by the greater leaf area on the largest trees in the old growth stand. The largest measured tree in the second growth stand had 151 m² of leaf area (Martin et al., 1997), one-third of the leaf area of the largest tree measured in the old growth stand (461 m², Table 1). As a result, on days with similar D and R_n , the largest tree in the old growth

stand lost 244 kg of water, while the largest measured second growth stand tree transpired only 89 kg.

Daily cumulative transpiration of the magnitude observed in the large trees in this study are rare in the literature, primarily because most studies have been carried out on smaller material in the higher latitudes, where evaporative demand tends to be lower. In conifers, individual tree transpiration of dominant and co-dominant trees on the order of 50–100 kg per day is typical (Schiller and Cohen, 1995; Arneth et al., 1996; Loustau et al., 1996; Wullschlegel et al., 1998),

although single-tree transpiration rates of fast-growing species under high evaporative demand, such as *Pinus radiata* D. Don in Australia, do sometimes exceed 300 kg per day (Teskey and Sheriff, 1996). As researchers begin to measure sap flux in larger trees (e.g. Cermák et al., 1982; Barker and Becker, 1995), reports of daily individual tree water loss rates of the magnitude we observed here will likely become more common.

Rates of tree sap flow varied with tree size. For example, the smallest tree we measured transpired 7.5 kg on 22 July; on the same day, the largest tree we measured transpired almost 40 times more water, 281.3 kg (Fig. 4). We investigated the implications of this variation at the stand level by ranking all of the trees in the measurement plot by diameter, then dividing the trees into three groups with equal numbers of trees in each group. We then calculated the contribution of each group to leaf area and transpiration at the stand level. The largest third of the trees dominated stand leaf area and transpiration, accounting for 77.7% of the stand's leaf area, and over 83% of stand transpiration. In contrast, the smaller two-thirds of the stand accounted for less than 30% of the leaf area of the stand and only 17% of the transpired water. We found similar domination of water loss by the larger size classes of trees in a second growth *A. amabilis*

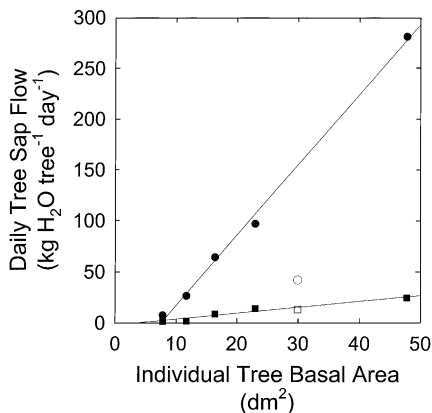


Fig. 4. Whole tree sap flow totals for days with relatively high sap flow (●, 22 July 1994) and low sap flow (■, 16 August 1994). The lines indicate scaling relationships for the high sap flow day (sap flow (kg) = $6.91 \times \text{tree BA (dm}^2) - 52.12$, $R^2 = 0.997$) and low sap flow day (sap flow = $1.08 \times \text{tree BA} - 11.18$, $R^2 = 0.998$). The 30 dm² BA tree (hollow symbols) was excluded from the regressions (see text for explanation).

stand, where the largest third of the trees accounted for 74% of the stand's water loss (Martin et al., 1997). Similarly, Köstner et al. (1992) found that the largest 20% of the trees in their *Nothofagus* measurement plot transpired more than 50% of the water lost from the plot.

3.6. Crown conductance

Crown conductance on a ground area basis (g_c) also varied widely with tree size (Table 1). Crown conductance of the largest tree sampled averaged 12.16 mm s^{-1} , and reached as high as 37.54 mm s^{-1} . The smallest tree sampled, in contrast, had average (1.44 mm s^{-1}) and maximum (4.84 mm s^{-1}) values of g_c that were an order of magnitude smaller than g_c of the largest trees. Diurnally, g_c tended to rise early in the morning, peak before noon, and then decline through the rest of the day (Fig. 3C).

Few estimates of g_c or g'_c for individual conifer trees exist in the literature. The maximum g_c of the dominant trees in this *Abies* forest were 8–15 times larger than the maximum g_c of emergent *Larix gmelinii* (Rupr.) Rupr. trees measured by Arneth et al. (1996) in Siberia. This is not surprising, considering the very high vapor pressure deficits (reaching peaks of 4 kPa), low soil moisture and very low leaf area indices ($1.5 \text{ m}^2 \text{ m}^{-2}$) in the larch forest. In contrast, the maximum g'_c of 8-year-old *Pinus taeda* trees were two to three times larger than maximum g'_c of the largest *Abies* trees in this study (Pataki et al., 1998). The average g_c of the various size classes of trees in this study were slightly larger than average g_c of a second growth *Abies* forest (Martin et al., 1997). For example, the largest and second-largest trees measured in this study had average g_c of 12.16 and 9.12 mm s^{-1} , respectively (Table 1), compared to the corresponding averages of 7.20 and 7.47 mm s^{-1} for the two largest trees measured in a younger *A. amabilis* stand (Martin et al., 1997).

In comparison to the paucity of single-tree estimates of g_c for conifers, estimates of conductance for entire canopies are more numerous (see reviews by Jarvis et al. (1976), and Kelliher et al. (1993)). While we did not calculate forest canopy conductance in this study, the maximum values of g_c for the emergent trees (which would be expected to dominate any calculation of canopy conductance) are somewhat

larger than maximum conifer canopy conductance reported in the literature, which typically range from 16 to 20 mm s⁻¹.

3.7. Decoupling — stomatal versus boundary layer control of transpiration

The value of Ω varies between 0.0 and 1.0. Vegetation with values of Ω near 1.0 is considered to be decoupled. Transpiration from decoupled vegetation is controlled primarily by radiation absorption — g_c is not an important controller of T_c (see Eq. (3)). Vegetation with typically high g_c and smooth, short, dense canopies (resulting in low g_a) such as agronomic crops tend to have higher values of Ω (Meinzer, 1993; Baldocchi, 1994). On the other hand, when Ω approaches 0.0, transpiration is controlled primarily by g_c and D (see Eq. (4)). Vegetation with both low values of g_c and tall, open canopies and small leaf size (resulting in high g_a), such as coniferous forest, tend to have values of Ω between 0.0 and 0.2 (i.e. they are well coupled). Broadleaved forests usually fall somewhere between the two extreme cases, with values of Ω ranging from 0.4 to 0.6 (Meinzer, 1993; Hinckley et al., 1994).

Measurements of boundary layer conductance and stomatal conductance at the branch scale in a previous study (Martin et al., 1999) showed that transpiration in *A. amabilis* branches is well coupled; values of Ω at the branch scale seldom exceeded 0.25, and almost always remained below 0.1. In other words, g_s and D were the primary determinants of transpiration rate. Some of the measurements taken in the present study suggest that this conclusion may be scale dependent. When the relative magnitude of the boundary layer and stomatal conductances are compared at the tree level, under certain conditions the boundary layer conductance component becomes an important regulator of transpiration. For example, on the morning of 22 July, when g_c of the largest tree we measured was at its diurnal maximum, and wind speed was low (resulting in low g_a), Ω exceeded 0.25 for quite some time, and exceeded 0.6 for over 1 h (Fig. 3). Over the entire season, the Ω decoupling coefficient of the largest tree measured exceeded 0.3 for over 9% of the daylight hours (Table 1).

In addition to their implications for stomatal versus boundary layer control of transpiration, these

decoupling data also imply shifts in the relative contributions of R_c and D to tree transpiration. Under well-coupled conditions when Ω is low, D is the primary meteorological factor controlling transpiration (Eqs. (3) and (4), Fig. 3). However, the role of radiation as a factor driving transpiration increases in proportion to Ω (Eq. (3)), resulting in relatively equal influences of R_c and D under less well coupled conditions (Fig. 3A). (It should be noted that under conditions with very low boundary layer conductance, the assumption of uniform within-canopy D may be violated. We tested the effects of a “worst case scenario” violation of this assumption by re-calculating the 22 July data in Fig. 3 with D decreased by 25%. The resulting g_c values were up to 50% higher than those calculated with the constant D assumption; Ω was less sensitive, increasing by at most 15%.)

The reason for the difference in coupling between the branch (Martin et al., 1999) and tree levels is that at the tree level, an additional component of the boundary layer conductance must be considered. This aerodynamic conductance (g_{aM}) accounts for the conductance to water vapor transfer between the outside of the leaf boundary layer and some reference point above the stand (which in this study was the weather station) (Smith et al., 1997; Rayment et al., 2000). This decrease in coupling with an increase in the spatial scale of reference is expected. The coupling literature explicitly predicts that as spatial scale increases, decoupling will increase (Jarvis and McNaughton, 1986).

It is important to note that the degree of coupling is highly dependent on wind speed. For example, although 22 July and 10 August had similar radiation and humidity regimes (Fig. 3E), half-hourly average wind speed on 10 August never fell below 1 m s⁻¹, while the morning of 22 July was calm. This difference in wind speed resulted in large differences in tree coupling between the 2 days and, as a result, differences in the relative importance of R_n and D in determining transpiration (Fig. 3A). Similarly, Rayment et al. (2000) attributed the high mean Ω (0.52) of an interior *Picea mariana* [Mill.] B.S.P. stand to frequent days with high radiation and low wind speeds. Because Ω is determined by the relative magnitude of g_c and g_a , the timing of wind speed changes is also quite important. A lull in wind speed (and the resultant decrease in g_a) will have little effect

on coupling when g_c is low, such as late in the day on 10 August, while decreased g_a will have a large effect when g_c is high, such as early in the day on 22 July (Fig. 3).

The degree of decoupling was also dependent on tree size. Because smaller trees tended to have smaller g_c , coupling increased with decreasing tree size (Table 1). This phenomenon introduces the interesting concept of spatial variation in coupling. In other words, in addition to the temporal variation in Ω resulting from changing wind speed and g_c (Fig. 3), there is also, at any particular time, variation in the degree of coupling from tree to tree.

3.8. Estimated stand transpiration

To estimate stand transpiration for any given day, we quantified the relationship between summed tree sap flow and tree size, then used this relationship to estimate the sap flow of all the trees on the 0.2 ha measurement plot as in Martin (2000). In all cases, the best fit for this relationship was obtained by using individual tree basal area as the size metric. The second-largest tree measured transpired considerably less than would be expected based on its size (0.30 m² BA tree, Fig. 4), and had abnormally low g'_c values (61.8 cm DBH tree, Table 1). We noted later in the summer that the bark at the base of this tree was sloughing off, suggesting that it may have been infected with a pathogen that could have affected its ability to take up water. For this reason, this tree was excluded from the calculations of stand transpiration.

The relationship between daily tree sap flow and tree basal area was linear (Fig. 4). Individual tree basal area explained from 91.1 to 99.9% of the variation in daily tree sap flow; in most cases, the R^2 for this relationship exceeded 0.99. These regressions were not forced through the origin, and most of them had X-axis intercepts significantly different than zero. This meant that trees with basal areas smaller than the X-axis intercept had negative estimated sap flow; when this occurred, those trees' sap flow sums were considered to be zero. The basal area "cutoff point" where calculated sap flow fell to zero ranged from 0.002 to 0.0977 m², and varied with daily sap flow (Fig. 4). By comparison, the smallest sap flow sample tree had a basal area of 0.0779 m² (Table 1). While we

sampled the full range of tree sizes present in the stand, our estimates of stand transpiration should be interpreted with caution because of the relatively small number of trees used to scale from the tree to the stand level. We quantified this uncertainty by calculating stand transpiration from both the upper and lower bounds of 90% tolerance intervals (Miller, 1981) for each scaling regression. The bounds of these stand transpiration "prediction intervals" varied by an average of 23% from the regression prediction.

We calculated stand transpiration for a total of 30 days. Although we monitored tree sap flow from 12 July to 10 October, there were numerous days with incomplete data collection because of battery failure — the remoteness of the site made it difficult to maintain electric power to the equipment. Daily stand transpiration ranged from 0.37 to 3.37 mm. As would be expected, stand transpiration varied in concert with changes in daily D and R_n (Fig. 5). In contrast to the scarcity of individual-tree estimates of g_c for conifers, there are numerous stand-level estimates of transpiration for coniferous forests obtained with micrometeorological methods (Kelliher et al., 1993), sap flow measurements (Wullschlegel et al., 1998) or both

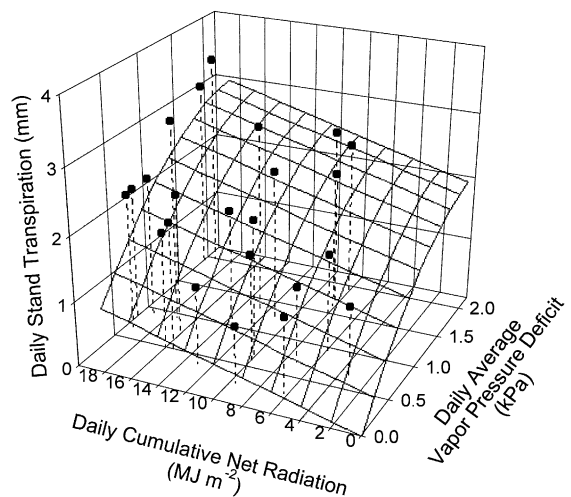


Fig. 5. The response of daily transpiration of a 220-year-old *Abies amabilis* stand to average daily vapor pressure deficit and daily cumulative net radiation. The surface represents a multiple regression of daily stand transpiration (T_{stand} , mm) with average daily vapor pressure deficit (D , kPa) and daily cumulative net radiation (R_c , MJ m⁻²), where $T_{\text{stand}} = 0.056 \times R_c + 1.97 \times D - 0.465 \times D^2$, $R^2 = 0.81$ (R^2 version 6 after Kvalseth (1985)).

(Granier et al., 1990; Diawara et al., 1991; Loustau et al., 1996; Oren et al., 1998). Although estimates of stand transpiration vary considerably with species, weather and soil conditions, rates of water loss seldom exceed 5.0 mm per day. An exception to this generality was a *Pinus radiata* stand in Australia that transpired a maximum of 6.8 mm per day (Teskey and Sheriff, 1996).

4. Conclusions

Old growth *Abies amabilis* tree transpiration per unit leaf area, tree crown conductance, and leaf area-normalized crown conductance were comparable to previously-reported measurements on younger, shorter coniferous forests. However, several aspects of water transport in this forest were unique. The values of daily single-tree transpiration of the dominant trees in this stand, attributable to the large leaf area of these trees, are higher than most in the literature. The dominant trees in this forest showed levels and duration of decoupling greater than usually reported for coniferous trees. Finally, decoupling, and by extension the relative importance of radiation and vapor pressure deficit and stomatal and boundary layer conductances for determining transpiration rate, was highly variable in time (hour to hour within trees) and space (between trees at the same time). These results emphasize the importance of considering structure (e.g. leaf area amount and distribution) and organizational level (shoot versus branch versus whole tree) in analyses of forest function.

Acknowledgements

Mark Redlin and John Rombold deserve special thanks for their leadership in the construction of the canopy access system. Michele Kruegel, Heather Norton and John Rombold helped with the field measurements. Martin Lechowicz provided helpful comments on an earlier version of the manuscript. The City of Seattle granted access to the study site. This study was funded in part by the United States Forest Service and the United States Environmental Protection Agency (cooperative agreement #CR 820462), and by an NSF Graduate Research

Fellowship to T.A.M. Florida Agricultural Experiment Station Journal Series Number R-077 68.

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