

Crown conductance and tree and stand transpiration in a second-growth *Abies amabilis* forest

T.A. Martin, K.J. Brown, J. Cermák, R. Ceulemans, J. Kucera, F.C. Meinzer, J.S. Rombold, D.G. Sprugel, and T.M. Hinckley

Abstract: We measured whole-tree sap flow in a 43-year-old *Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes – *Tsuga heterophylla* (Raf.) Sarg. forest in western Washington, U.S.A. We calculated whole-tree crown conductance to water vapor (g_{crown}) by substituting the sap flow data and meteorological measurements into the inverted Penman–Monteith equation. Individual tree sap flow and crown conductance varied widely with tree size, with the smallest tree sampled having average g_{crown} (on a ground-area basis) of $0.57 \text{ mm}\cdot\text{s}^{-1}$ and transpiring up to $4.9 \text{ kg}\cdot\text{day}^{-1}$, while the largest tree measured had an average g_{crown} of $7.20 \text{ mm}\cdot\text{s}^{-1}$ and lost as much as $98 \text{ kg}\cdot\text{day}^{-1}$. Crown conductance responded linearly and positively to radiation, and had a negative exponential response to vapor pressure deficit. These response patterns were utilized to construct an empirical model of g_{crown} that explained from 52 to 73% (average 66%) of the variation in g_{crown} . The dominant and codominant trees in the stand transpired for longer periods during the day than trees in the smaller size classes, and contributed disproportionately to total stand transpiration. Daily total sap flow for individual trees was strongly correlated with tree basal area; we used the relationship between these variables to estimate daily stand transpiration. Stand transpiration calculated for 28 days between August 6 and October 12, 1993, ranged from 0.01 to $3.52 \text{ mm}\cdot\text{day}^{-1}$. Stand transpiration increased curvilinearly with increasing average daily vapor pressure deficit, reflecting the negative response of g_{crown} to vapor pressure deficit.

Résumé : Nous avons mesuré l'écoulement de la sève d'arbres entiers dans une forêt de *Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes et de *Tsuga heterophylla* (Raf.) Sarg. âgée de 43 ans et située dans l'ouest de l'État de Washington aux États-Unis. Nous avons calculé la conductance à la vapeur d'eau (g_{cime}) d'arbres entiers en solutionnant l'équation de Penman–Monteith pour ce terme après y avoir introduit les données d'écoulement de la sève et les mesures météorologiques. La conductance de la cime et l'écoulement de la sève d'arbres individuels variaient beaucoup en fonction de la taille des arbres, le plus petit arbre ayant une valeur moyenne de g_{cime} (par unité de surface au sol) de $0,57 \text{ mm}\cdot\text{s}^{-1}$ et un taux de transpiration de $4,9 \text{ kg}\cdot\text{jour}^{-1}$, alors que le plus gros arbre avait une valeur moyenne de g_{cime} qui pouvait atteindre $7,20 \text{ mm}\cdot\text{s}^{-1}$ et perdait jusqu'à $98 \text{ kg}\cdot\text{jour}^{-1}$ d'eau. La conductance de la cime répondait de façon linéaire et positive au rayonnement et de façon exponentielle et négative au déficit de pression de vapeur. Ces comportements ont servi à construire un modèle empirique pour prédire la valeur de g_{cime} . Ce modèle explique de 52 à 73% (66% en moyenne) de la variation dans la valeur de g_{cime} . Les arbres dominants et codominants transpiraient plus longtemps pendant la journée que les arbres des plus petites classes de diamètre et ils contribuaient de façon disproportionnée à la transpiration totale du peuplement. L'écoulement total journalier de sève chez un arbre était fortement corrélé à la surface terrière de cet arbre. Nous avons utilisé la relation entre ces variables pour estimer la transpiration journalière du peuplement. Calculée sur 28 jours entre le 6 août et le 12 octobre 1993, la transpiration variait de 0,01 à $3,52 \text{ mm}\cdot\text{jour}^{-1}$. L'augmentation de la transpiration du peuplement avec une augmentation du déficit journalier de pression de vapeur suivait une courbe curviligne, ce qui reflète la réponse négative de la valeur de g_{cime} au déficit de pression de vapeur.

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T.A. Martin,¹ K.J. Brown, J.S. Rombold, D.G. Sprugel, and T.M. Hinckley. College of Forest Resources, P.O. Box 352100, University of Washington, Seattle, WA 98195-2100, U.S.A.

J. Cermák. Institute of Forest Ecology, Mendel's Agricultural and Forest University, Zemedelska 3, CS-61300 Brno, Czech Republic.

R. Ceulemans. Department of Biology, University of Antwerp, B-2610 Wilrijk, Belgium.

J. Kucera. Laboratory of Ecological Measuring Systems, Turisticka 5, CS-62100 Brno, Czech Republic.

F.C. Meinzer. Hawaii Agriculture Research Center, Aiea, HI 96701-3911, U.S.A.

¹ Author to whom all correspondence should be addressed. Present address: School of Forest Resources and Conservation, P.O. Box 110410, University of Florida, Gainesville, FL 32611-0410, U.S.A.

Introduction

As Kelliher et al. (1993) emphasized in a recent review, stand-level measurements of evapotranspiration from naturally occurring coniferous forest are relatively rare. Most stand-level measurements have been conducted on low-elevation pine, spruce, or Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantations located on flat terrain (see Jarvis et al. 1976 and Kelliher et al. 1993 for reviews). However, in western North America, at least, the majority of forest land is naturally regenerated, mountainous, and at higher elevations. Because such forests are so widespread, it is important to understand physiological processes and components of the water balance in stands of this type. While insight has been gained by using transpiration models coupled with stand structural and meteorological data to predict stand transpiration in naturally regenerated montane forest in western North America (Running 1984; Kaufmann 1985; Running et al. 1987, 1989), technological limitations have restricted the number of direct measurements of water loss of individual trees or entire stands under these conditions. This paper describes direct measurement of tree sap flow and calculation of crown conductance to water vapor and stand transpiration in a naturally regenerated forest of Pacific silver fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) located in mountainous terrain in western Washington, U.S.A.

The main reason most previous studies have focused on flat plantations is because of the fetch and aerodynamic requirements that must be met for stand-level measurements of evapotranspiration (such as eddy correlation and Bowen ratio). One alternative to stand-level measurements of evapotranspiration, with their associated assumptions, is to measure the transpiration of representative individual trees in a stand and then integrate those measurements upward to obtain stand-level estimates of transpiration. Of course, there are numerous assumptions involved with this method as well, but there are also several advantages. First, no assumptions about the topography of the site need be made to determine the source of water vapor, since tree sap flux is measured directly. Second, the measurements can continue under any weather conditions and are not limited to the "fine" summer day often favored by physiologists and meteorologists. Finally, the measurements of sap flow in individual trees make it possible to examine the components of stand-level transpiration, revealing the functional contributions of different classes of trees within the stand (cf. Granier 1987; Köstner et al. 1992; Cermák et al. 1995; Vertessy et al. 1995; Arneeth et al. 1996). As large-scale, long-term measurements of gas flux become increasingly common (Wofsy et al. 1993; Hollinger et al. 1994a; Grace et al. 1995; Jensen and Hummelshoj 1995), this type of analysis will be helpful in determining how individual plant processes interact to produce emergent ecosystem-level responses.

Materials and methods

Site description

This study was conducted in an *A. amabilis* – *T. heterophylla* stand located on a bench within a south-facing slope at 1300 m elevation in the Cedar River watershed, 70 km southeast of Seattle, Wash., on the west slope of the Cascade mountain

Fig. 1. Distributions of diameter at 1.3 m (A) and basal area at 1.3 m (B) for an *Abies amabilis* (open bars) – *Tsuga heterophylla* (hatched bars) stand at 1300 m elevation in the Cedar River watershed in western Washington. Solid circles indicate classes of sap flow sample trees. The inventory sample plot was 650 m² and contained 145 trees.

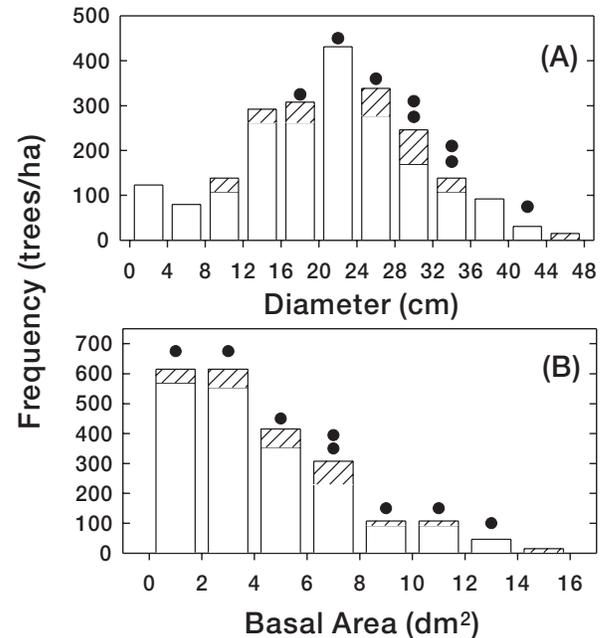


Table 1. Forest inventory data for an *Abies amabilis* – *Tsuga heterophylla* stand on the west slope of the Cascade range in Washington state.

	<i>A. amabilis</i>	<i>T. heterophylla</i>
Density (trees/ha)	1941	300
Basal area (m ² ·ha ⁻¹)	78.7	16.1
Diameter at breast height (cm)	20.7±1.8	24.7±5.7
Height (m)	14.6±0.45	16.3±0.75
Height (m), 10th percentile	7.3	5.3
Height (m), 90th percentile	20.1	19.8
Leaf area index (m ² ·m ⁻²)	7.8	1.6

Note: Values for diameter at breast height and height are mean ± SE.

range. The stand was regenerated from seed and advanced regeneration following a wind storm and subsequent salvage logging in approximately 1950. The stand was very dense (>2000 trees/ha; Table 1), with complete crown closure and no herbaceous forest floor vegetation. *Abies amabilis* represented 83% of the stand's basal area. The only other tree species present in the measurement plot was *T. heterophylla*. Average tree height was 14.9 m but varied widely. Ten percent of the trees in the stand were less than 8 m tall, and 25% were taller than 18.5 m. The tallest tree within the inventory plot was 23.2 m tall. Tree diameters at breast height (DBH) ranged from 1.5 to 40.3 cm for *A. amabilis* and from 11.3 to 45.0 cm for *T. heterophylla* (Fig. 1A). The only understory vegetation present were small (1–2 m tall), shade-adapted *A. amabilis*. Leaf area index of the stand was 9.4 m²·m⁻².

Throughout this paper, we will use diameter as a convenient surrogate for tree social position or crown class within the

Table 2. Biometric and physiological parameters of sap flow measurement trees.

Diameter at breast height (cm)	Height		Projected crown area (m ²)	Crown volume ^a (m ³)	Projected leaf area (m ²)	Avg. g_{crown} (mm·s ⁻¹)	Max. g_{crown} (mm·s ⁻¹)	$\frac{\text{Max.}(g_{\text{crown}})^d}{\text{Max.}(g_s)}$	Avg. g'_{crown} ^e (mm·s ⁻¹)	Radiation slope parameter ^f ($\times 10^{-2}$)	Vapor pressure deficit
	Total height (m)	crown base (m)									exponential parameter ^g
40.1	18.0	8.5	18.4	58.3	150.9 ^b	7.20	19.64	3.3	0.88	5.84	-0.485
36.0	19.2	8.8	12.6	43.7	121.4 ^b	7.47	22.13	3.7	0.78	6.92	-0.563
34.6	19.5	9.1	15.4	53.4	111.6 ^b	4.43	13.99	2.3	0.62	3.40	-0.384
31.0	18.6	8.8	16.0	52.3	89.6 ^b	3.41	7.06	1.2	0.61	2.13	-0.338
28.5	19.7	11.3	8.1	22.7	57.3 ^c	4.52	14.07	2.3	0.64	4.10	-0.512
24.4	19.2	10.7	6.0	17.0	44.5 ^c	3.38	10.53	1.8	0.46	2.45	-0.375
21.2	18.5	11.0	3.5	8.8	33.4 ^c	2.43	6.68	1.1	0.26	1.19	-0.105
16.9	14.9	8.5	7.4	15.8	29.7 ^c	0.57	1.85	0.3	0.14	0.26	-0.069 ^a

^aCrown volume calculated as a cone.

^bFrom leaf area – diameter relationship described in text.

^cLeaf area measured as described in text.

^dRatio of maximum crown conductance to maximum shoot stomatal conductance (mm·s⁻¹/mm·s⁻¹).

^e $g'_{\text{crown}} = g_{\text{crown}}/\text{tree LAI}$.

^fCrown conductance unlimited by D (g_{max} (mm·s⁻¹) = $R_n \times \text{slope parameter}$).

^gVapor pressure deficit limiting function ($f(D)$, fraction) = $\exp(\text{parameter} \times D \text{ (kPa)})$.

stand. This simplification is justified because of the strong correlation between tree diameter and crown-size parameters (Table 2). Although there was little variation in total height within our sap flow measurement sample, there was a broad range of DBHs and crown widths and lengths, reflecting the variation from dominant to suppressed crown classes. For the purposes of this study, suppressed trees will refer to the smallest trees within the overstory canopy stratum, as distinguished from the very small (1–2 m tall), suppressed advanced regeneration *Abies* within the forest understory.

Leaf area

A relationship between total tree leaf area (projected) and DBH was used to estimate tree and stand leaf area. This relationship was developed by subsampling within the crowns of nine trees from a range of diameter classes. Four of these trees were also sampled for sap flow. The foliage area sampling was performed after cessation of sap flow measurement in the fall. We measured the length, diameter, and azimuthal orientation of each branch on each of the nine trees. Within each of the nine trees, we randomly chose and removed a branch from every whorl within the top 10 whorls, and from every other whorl from the rest of the crown. To determine the leaf area of each sampled branch we cut the branch into annual shoot segments and divided the segments into piles representing 2-year age-classes (except for current foliage, which was treated as a separate age-class). The total length of segments in each age-class was measured, and a random subsample was taken to determine dry weight of needles per unit shoot length and mean needle thickness. Area per unit shoot length was calculated from needle thickness and dry weight using a relationship developed from a smaller subsample of shoots. (For current foliage, area (cm²) = $24.6 \times \text{dry weight (g)} / \text{thickness (mm)}$, $R^2 = 0.711$, $n = 60$. For older foliage, area = $23.3 \times \text{dry weight/thickness}$; $R^2 = 0.809$, $n = 184$.) Area per unit length was then converted to total projected leaf area by multiplying by the total length of segments in that age-class. These data were then used to predict the leaf area of the remaining

branches on the sample trees, and the branch leaf areas were summed to obtain total one-sided leaf area for each sample tree. A relationship between tree leaf area and DBH developed from the nine leaf area sample trees was used to predict leaf area for the other trees in the stand.

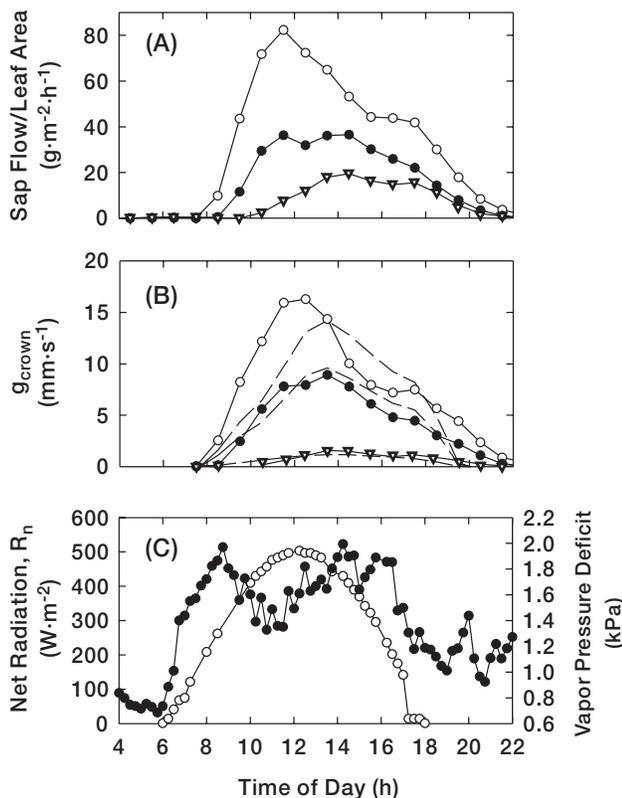
Tree sap flow

Tree sap flow was measured using the tissue heat balance technique described in detail by Cermák et al. (1973, 1982), Kucera et al. (1977), and Cermák and Kucera (1981). This involves heating a portion of the conducting tissue of the sample tree with an electrical current passed between electrodes inserted into the trunk. With constant power input, sap flow is calculated from the temperature difference between thermocouples inserted into the heated and unheated portions of the xylem. Heat losses due to conduction through the wood are accounted for by subtracting the “fictitious flow” obtained from the system under low- or no-transpiration conditions. Measurements of sap flow were taken every minute and stored as 15-min averages with a P-6 sap flow meter and datalogger (Ecological Measuring Systems, Ltd., Brno, Czech Republic).

The measurement sensors and 0.5 m of trunk above and below the measurement point were shielded from ambient temperature fluctuations by a 2.5 cm thick open cell foam layer, which was in turn covered by 1 mm thick reflective aluminum sheeting. Plastic sheeting sealed to the trunk above the measurement point with wax was used to protect the apparatus from moisture.

Sap flow gauges were installed on eight trees chosen to represent a broad range of diameters (Table 2, Fig. 1). Sample trees were chosen using the “quantiles of total” technique (Cermák and Kucera 1990; Cermák and Michálek 1991). This technique produces a sample skewed toward the larger diameters, concentrating measurement resources in tree size-classes that tend to dominate stand transpiration (Köstner et al. 1992). The smallest sap flow tree sampled had a DBH of 16.9 cm, which placed it in the bottom 33rd percentile of the diameter distribution. The largest sap flow tree was in the 98th DBH percentile

Fig. 2. Diurnal water loss and crown conductance (g_{crown}) for three *Abies amabilis* trees on September 9, 1993. (A) Whole-tree sap flow per unit leaf area for trees with diameter at breast height of 40.1 cm (open circles), 28.5 cm (solid circles), and 16.9 cm (open triangles). (B) Measured (symbols as defined in A) and modeled (broken line) g_{crown} . Data from September 9 were not used in the construction of the g_{crown} model. (C) Net radiation (open circles) and vapor pressure deficit (solid circles) on September 9.



at 40.1 cm. Sap flow measurements began in early August and continued until mid-October.

Branch sap flow

Branch sap flow was measured using branch sap flow gauges (Dynagage, Dynamax Inc., Houston, Tex.). This method and instrumentation are described in detail by Sakuratani (1981), Baker and van Bavel (1987), and Steinberg et al. (1989). These devices utilize the same heat-balance principles described for whole-tree sap flow measurements, except that heat application and temperature sensing are both performed external to the branch, with a flexible solid-state heater and thermocouples pressed against the outside of the branch. We followed the insulation and installation precautions described by Gutierrez et al. (1994).

Sap flow gauges were installed on three branches on each of two trees. Branches were chosen to represent a range of branch diameters and exposures. Sap flow was monitored every minute and stored as 15-min averages by a datalogger (CR-10, Campbell Scientific, Inc., Logan, Utah).

Meteorological measurements

Meteorological variables were measured from a weather station positioned at the top of a 20-m tower, at the approximate

height of the dominant trees in the stand. Global shortwave radiation was measured with a pyranometer (LI200S, LI-COR, Lincoln, Nebr.). Because of limited tower height, the pyranometer was shaded by adjacent trees at several times throughout the day. The radiation data were corrected for shading by linearly interpolating data points during shaded periods. On partly cloudy days, artificially shaded periods were distinguished from cloudy periods by their timing (artificial shading events occurred at the same time each day) and by their shape (artificial shading events started and ended abruptly and usually reduced irradiance to a greater degree than did cloud cover). A shielded combination capacitive relative humidity sensor – thermistor probe (HMP35C, Campbell Scientific, Inc., Logan, Utah) 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, Mich.). Variables were read every minute and averages recorded every 15 min by a datalogger. Precipitation data obtained from a weather station 9 km to the north and 740 m lower in elevation served as a qualitative indicator of precipitation at the study site.

Stand transpiration

Tree-level sap flow data were integrated to the stand level as described by Cermák and Kucera (1990) and Cienciala et al. (1994). This was accomplished by quantifying the relationship between size of the sampled sap flow trees (in this case, basal area) and daily sap flow. This relationship was then applied to the diameter distribution of the stand to calculate transpiration for a day. Because transpiration was not measured in *T. heterophylla* trees, their transpiration rates were assumed to be identical to those of equally sized *A. amabilis* for the purposes of the integration.

Crown conductance

The well-known Penman–Monteith combination equation (Monteith 1965) provides a useful framework for analysis of the interaction between plant and environmental control of transpiration. This equation describes the relationship between tree transpiration (E_{crown} ; $\text{kg}\cdot(\text{m}^2 \text{ ground area})^{-1}\cdot\text{s}^{-1}$), boundary-layer and crown conductance (g_a and g_{crown} , respectively, expressed in $\text{m}\cdot\text{s}^{-1}$ on a ground-area basis), radiation absorbed by the tree crown (R_{crown} ; $\text{W}\cdot\text{m}^{-2}$) and vapor pressure deficit (D ; kPa) as

$$[1] \quad E_{\text{crown}} = \frac{sR_{\text{crown}} + \rho_a C_p D g_a}{\lambda \left[s + \gamma \left(1 + \frac{g_a}{g_{\text{crown}}} \right) \right]}$$

where s is the slope of the saturation vapor pressure deficit versus temperature curve at air temperature ($\text{kPa}\cdot\text{K}^{-1}$), ρ_a is the density of dry air ($\text{kg}\cdot\text{m}^{-3}$), C_p represents the specific heat capacity of air ($\text{J}\cdot\text{kg}^{-1}\cdot\text{K}^{-1}$), λ is the latent heat of evaporation of water ($\text{J}\cdot\text{kg}^{-1}$), and γ is the psychrometer constant ($\text{kPa}\cdot\text{K}^{-1}$).

When the transpiration rate of an individual tree (E_{crown}) is known, as in this study, crown conductance (g_{crown} ; $\text{m}\cdot\text{s}^{-1}$) can be calculated by substituting E_{crown} , g_a , and weather station data into the inverted Penman–Monteith equation. We used a formulation given in Granier and Loustau (1994):

$$[2] \quad \frac{1}{g_{\text{crown}}} = \left[\frac{s}{\gamma} \left(\frac{R_{\text{crown}} - \lambda E_{\text{crown}}}{\lambda E_{\text{crown}}} \right) - 1 \right] \frac{1}{g_a} + \frac{\rho_a}{E_{\text{crown}}} \frac{C_p}{\lambda \gamma} D$$

Because of the time difference between transpiration from the crown and sap flow at the measurement point, it was necessary to lag the weather station data to utilize eq. 2. Lagging the meteorological data by 2 h resulted in the highest correlation of sap flow with the weather data, and comparison of time traces of radiation (R_n), D , and sap flow confirmed that this was a satisfactory match. Other researchers have found it necessary to lag meteorological data to apply similar analyses to sap flow data (Granier and Loustau 1994).

The radiation absorbed by each tree (R_{crown}) was calculated in three steps. First, above-stand net radiation was calculated from global shortwave radiation using a linear relationship between net radiation and shortwave radiation developed over a different *A. amabilis* stand in 1994. Second, the net radiation at the top of the tree (R_{top}) was calculated using the tree height and the average light extinction profile of the stand. Finally, the radiation absorbed by the tree was calculated as in Granier and Loustau (1994):

$$[3] \quad R_{\text{crown}} = [1 - \exp(-k \text{LAI})] R_{\text{top}}$$

where k is the Beer's law extinction coefficient (0.47) calculated from the stand average vertical light and leaf area profiles (D.G. Sprugel, unpublished data) and LAI is the individual tree leaf area index ($\text{m}^2 \cdot \text{m}^{-2}$) calculated by dividing the projected tree 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; Parker 1995).

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} ; $\text{m} \cdot \text{s}^{-1}$) was estimated from a relationship between wind speed (ws ; $\text{m} \cdot \text{s}^{-1}$) and g_{aS} developed for shoot models in a wind tunnel:

$$[4] \quad g_{aS} = 0.0425, \quad ws \leq 0.1 \text{ m} \cdot \text{s}^{-1}$$

$$g_{aS} = \frac{1}{7.27 ws^{-0.5101}}, \quad ws > 0.1 \text{ m} \cdot \text{s}^{-1}$$

and was converted to a ground-area basis for each tree by multiplying by the tree's leaf area index. Crown aerodynamic conductance (g_{aM} ; $\text{m} \cdot \text{s}^{-1}$) was calculated from the wind profile equation (Monteith 1965):

$$[5] \quad g_{aM} = \frac{k^2 ws}{\{\ln[(z-d)/z_0]\}^2}$$

where values of displacement height (z_0) and roughness length (d) were estimated using the graphs in Shaw and Pereira (1982), z is anemometer height (m), and k is Von Karman's constant.

Results and discussion

Within-tree time lags

Stem sap flow lagged branch sap flow by approximately 2–4 h in the two trees on which both branch and stem sap flow gauges were installed. This lag was greatest during the rising leg of flow and was reduced at peak flows and during the falling leg. Morning time lags between sap flow and transpiration have been observed in other field studies on both large (Penka et al. 1979; Cermák et al. 1982; Schulze et al. 1985; Diawara et al. 1991; Lu et al. 1995) and small (Day et al. 1990) coniferous trees, although lags or discontinuities have also been observed starting at midday (Veselkov and Tikhov 1984). In contrast, most studies on broad-leaved trees have revealed relatively small time lags (Cermák et al. 1984; Dye and Olbrich 1993; Green 1993; Hinckley et al. 1994; Hollinger et al. 1994b; Cienciala and Lindroth 1995).

The lags we observed are presumably the result of the uptake and transpiration of water stored in tree tissues, although the change in the magnitude of the time lag throughout the day could be attributed to diurnal variations in radiation at the crown positions where branch sap flow was measured. Estimation of the water storage capacity of the *A. amabilis* stems (cf. Cermák et al. 1982) indicated that this forest contained an average of 12.6 kg/tree of stored water or 27.2 mm. This equates to approximately 8 days of mean summer transpiration. Waring and Running (1978) estimated that large *P. menziesii* trees contained up to 27 mm of stored water in their sapwood, 75% of which was contained in stem sapwood (although Tyree and Yang (1990) have taken issue with the methods used by Waring and Running). In contrast, simultaneous observations of sap flow at breast height and crown base by Schulze et al. (1985) in *Larix decidua* Mill. \times *Larix leptolepis* (Sieb. & Zucc.) Gord. and Köstner et al. (1992) in *Notofagus fusca* (Hook.f.) Oerst. suggested that most of the stored water used during the day came from tissues above the base of the live crown, rather than from the stem. Because we measured sap flow only at breast height and in branches, we were not able to determine the source of the stored water.

Sap flow and crown conductance

We observed large variations in sap flow and crown conductance with tree size. The highest daily total sap flow for the smallest tree measured (16.9 cm DBH) was less than 5 $\text{kg} \cdot \text{day}^{-1}$, while the largest tree measured (40.1 cm DBH) transpired up to 98 $\text{kg} \cdot \text{day}^{-1}$. This was partially a result of greater leaf area on larger trees (Table 2), although sap flow per unit leaf area was also dependent on tree size, with larger, dominant trees having greater rates of leaf area normalized transpiration (Fig. 2A). Variation in crown conductance was also large, ranging from an average of 0.57 $\text{mm} \cdot \text{s}^{-1}$ (maximum 1.85 $\text{mm} \cdot \text{s}^{-1}$) for the 16.9 cm diameter tree to 7.47 $\text{mm} \cdot \text{s}^{-1}$ (maximum 22.13 $\text{mm} \cdot \text{s}^{-1}$) for the second largest tree measured (Table 2).

Previous reports of sap flow in forests differ in the degree of variation with tree size. For example, Granier (1987), Köstner et al. (1992), Vertessy et al. (1995), Arneth et al. (1996), and Teskey and Sheriff (1996) all found that absolute sap flow varied by an order of magnitude between the smallest and largest trees sampled. In contrast, both Diawara et al. (1991) and Lu et al. (1995) found very little variation in sap flow

Table 3. Duration of sap flow per day for sample trees.

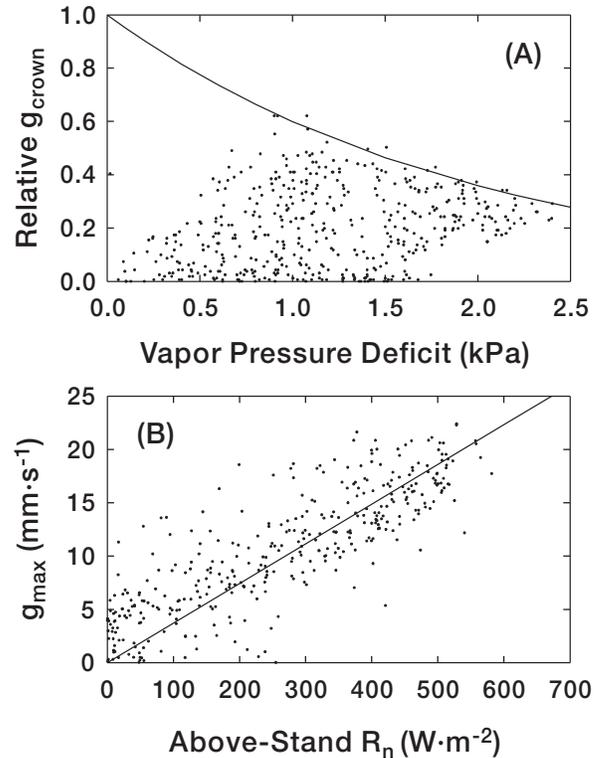
Sample tree diameter (cm)	Avg. daily sap flow duration (h)	SD	Min. sap flow duration (h)	Max. sap flow duration (h)	<i>N</i> (days)
40.1	18.31	3.34	9.0	23.0	36
36.0	17.38	4.21	6.0	24.0	37
34.6	18.69	2.61	13.0	24.0	32
31.0	16.46	5.73	1.0	24.0	35
28.5	15.56	4.40	1.0	24.0	48
24.4	13.58	3.84	4.0	20.0	36
21.2	11.45	4.90	1.0	20.0	40
16.9	10.35	3.92	2.0	17.0	43

between trees, although variation did increase as the soil dried in the Lu et al. (1995) study. In contrast, variation of sap flow with tree size was less pronounced under dry conditions in *Eucalyptus* trees in South Australia (Thorburn et al. 1993). Increased among-tree variation of sap flow under dry conditions could be attributable to increases in soil moisture heterogeneity as the soil dries. Cermák et al. (1995) attributed increased within-tree variation in sap flow rates during a drought to differential availability of water to various portions of the root system. Some variation in sap flow with tree size may be attributed simply to variation in leaf area. When Teskey and Sheriff (1996) normalized sap flow in *Pinus radiata* D. Don by tree leaf area, small and large trees transpired at approximately the same rate. Similarly, Vertessy et al. (1995) reported that variation in tree sap flow of *Eucalyptus regnans* F.J. Muell. was linearly correlated with tree leaf area (in contrast to the present study). In general, the amount of variation in transpiration follows the degree of stratification of the stand. As Swanson (1994) points out, it is probably reasonable to assume that "...variation in transpiration between trees of the same species is at least equal to the variation in their diameter. If one also adds variation in crown structure or dominance, then one should be able to account for the range of possibilities present in most stands."

In addition to having low crown conductance and rates of transpiration, the duration of transpiration was also shorter for suppressed trees compared with the larger size-classes (Table 3). The largest tree we measured (40.1 cm DBH) transpired an average of 18 h·day⁻¹, while the smallest tree measured (16.9 cm DBH) transpired only 10 h·day⁻¹ on average (Table 3). Sap flow occasionally continued throughout a 24-h period, with very low levels of nighttime flow present (Table 3). Figure 2A shows the differential sap flow duration for different-sized trees for a diurnal period. The large tree in Fig. 2A begins transpiration earlier in the day and continues to transpire later in the day than the smaller tree. This can be attributed to the shorter "effective day" experienced by suppressed trees. During the hours near sunrise and sunset, when solar angles are low, trees with smaller crowns lower in the canopy are shaded by larger adjacent trees. This effect is probably exaggerated in this stand because of the high leaf area index and the relatively closed, homogeneous nature of the canopy. Differences between small and large trees in less dense canopies would not be expected to be as great.

The magnitude of g_{crown} in this study can be compared with porometric measurements of stomatal conductance in this spe-

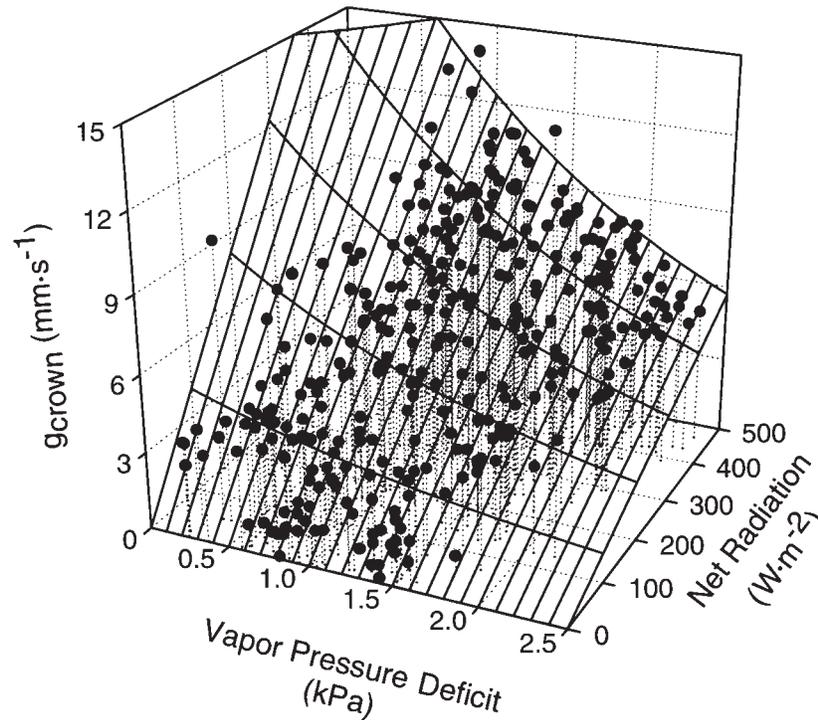
Fig. 3. (A) Response of normalized crown conductance (g_{crown}) to vapor pressure deficit (D) for a 28.5 cm DBH *Abies amabilis* tree. The regression line represents the upper boundary response to D (eq. 7, $a = -0.512$). (B) Response of maximum conductance (g_{max}) to above-stand net radiation (R_n) for a 28.5 cm DBH *A. amabilis* tree. Regression line through the origin has a slope of 0.041.



cies by evaluating g_{crown} on a leaf-area basis (g'_{crown} ; Table 2, calculated by dividing g_{crown} by tree LAI). Stomatal conductance measured with a porometer on sunlit and partially shaded foliage on two codominant trees in this stand throughout the growing season ranged from a mean of 2.2 mm·s⁻¹ (maximum 6 mm·s⁻¹) for current foliage to a mean of 1.5 mm·s⁻¹ (maximum 3.8 mm·s⁻¹) for 5-year-old foliage. In comparison, g'_{crown} was less than half of these values. This is not surprising, considering that most of the porometer measurements were taken on well-lit samples, while much of the foliage in the crown was in more heavily shaded environments. The values of g_{crown} obtained in this study are also comparable with canopy-scale conductance measurements in other conifer species. Since larger trees dominate transpiration in this system, the value of canopy conductance for the stand should be similar to the g_{crown} of the larger trees. The maximum g_{crown} for the three largest trees in this study ranged from 13.99 to 22.13 mm·s⁻¹ (Table 2). In comparison, maximum canopy conductance for *P. menziesii*, *Picea sitchensis* (Bong.) Carrière, and *Picea abies* (L.) Karst. stands in the literature range from 16 to 20 mm·s⁻¹ (Jarvis et al. 1976; Milne 1979; Price and Black 1990; Cienciala et al. 1992).

Work by Meinzer and Grantz (1989, 1991) suggests that homeostasis between bulk stomatal conductance and boundary layer conductance results in relatively steady rates of maximum water loss and total conductance across a range of LAI within a vegetation type and perhaps even between different

Fig. 4. The response to vapor pressure deficit and radiation of measured (symbols) and modeled (solid lines) crown conductance for a 28.5 cm DBH *Abies amabilis* tree. The model explained 73% of the variability in g_{crown} . Coefficients of determination for the model for the other trees ranged from 0.52 to 0.73 (average 0.66).



vegetation types (see Kelliher et al. 1993; Hinckley et al. 1994). Meinzer and Grantz (1989, 1991) observed in sugarcane canopies that, as LAI and stand boundary layer conductance changed, canopy bulk stomatal conductance also changed such that relatively steady rates of water loss and total conductance (boundary layer plus stomatal components) were maintained over a range of LAI. Kelliher et al. (1995) also presented observations of correspondence between shoot-scale and stand-scale parameters across a range of LAI and vegetation types. They observed that across a range of LAI and vegetation types, the ratio between maximum canopy-scale or bulk conductance and maximum shoot-scale stomatal conductance tends to maintain a value of approximately three. Kelliher et al. (1995) hypothesize that two factors combine to hold this ratio relatively steady within a species or vegetation type across a wide range of LAI. First, the maximum value of stomatal conductance appears to be quite conservative within vegetation types (Körner 1994). Second, in stands with lower LAI, canopy conductance due to vegetation will also be lower, therefore decreasing bulk conductance. However, decreases in LAI will also tend to increase soil evaporation because of increased radiation flux to the soil surface, which compensates for decreased plant conductance, resulting in relatively steady maximum bulk conductances across a range of LAI.

Our data appear to agree with the ratio of three presented by Kelliher et al. (1995). The ratio of maximum g_{crown} (for each tree) to maximum shoot stomatal conductance (from samples taken as described previously) for the three largest trees in this study (presumed to reflect canopy-scale conductance) ranged from 2.3 to 3.7, averaging 3.1 (Table 2). Our estimate

of g_{crown} does not include a soil evaporation component, but because of the high stand LAI, soil evaporation probably contributes little to ecosystem water loss. It is not possible with our single stand data set to discern whether the mechanisms proposed by Meinzer and Grantz (1989, 1991) or Kelliher et al. (1995) are at play, although our data are not inconsistent with either.

Empirical modeling

To summarize the response of g_{crown} and tree and stand transpiration to environmental variables, and to allow us to quantitatively explore these relationships, we developed an empirical model of g_{crown} for each sap flow measurement tree. Many recent field studies of stomatal conductance and crown and canopy conductance have observed that conductance responds primarily to radiation and vapor pressure deficit (Kaufmann 1982; Massman and Kaufmann 1991; Köstner et al. 1992; Dye and Olbrich 1993; Whitehead et al. 1994; Cienciala and Lindroth 1995). Our results concurred with this in that the addition of air temperature terms did not improve the fit of any of the models we tested. In our final model, g_{crown} has a negative exponential response to D and a positive linear response to R_n , and takes the form

$$[6] \quad \hat{g}_{\text{crown}} = f(R_n) f(D)$$

where \hat{g}_{crown} is predicted crown conductance and $f(R_n)$ is a net radiation function which produces g_{max} , defined as the hypothetical value of g_{crown} under a given level of radiation if there was no reduction in g_{crown} due to vapor pressure deficit. The

Fig. 5. Response of daily tree transpiration per unit leaf area to average daily vapor pressure deficit for 40.1 cm (open circles), 28.5 cm (solid circles), and 16.9 cm (open triangles) DBH *Abies amabilis* trees.

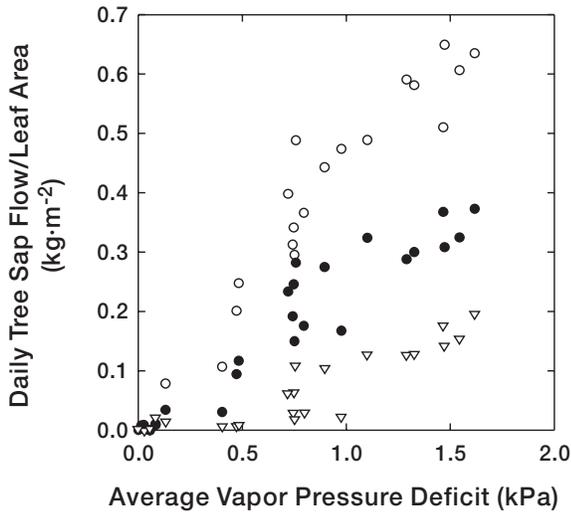
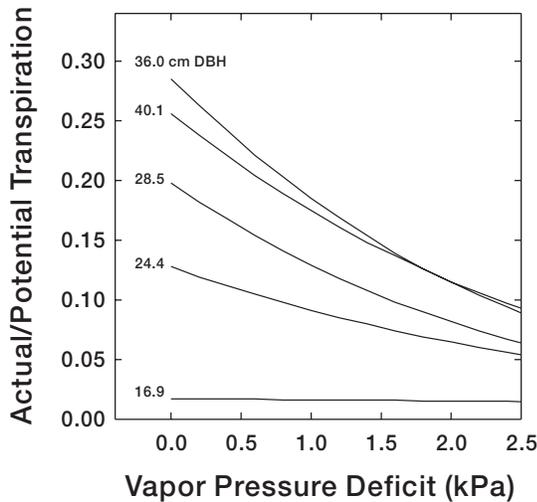


Fig. 6. Modeled response of actual/potential transpiration to increasing vapor pressure deficit for *Abies amabilis* trees of different diameters. To generate this graph, the empirical model described in the text was used to simulate g_{crown} at varying vapor pressure deficits with net radiation = $300 \text{ W}\cdot\text{m}^{-2}$, air temperature = 20°C , wind speed = $1.0 \text{ m}\cdot\text{s}^{-1}$. Equation 1 was then used to calculate actual and potential ($g_{\text{crown}} \rightarrow \infty$) transpiration.



maximum conductance is then reduced by $f(D)$, a function of vapor pressure deficit.

The vapor pressure deficit function was constructed first and was then used to derive the net radiation function. The function describing the reduction in g_{max} due to vapor pressure deficit was constructed using boundary line analysis (Webb 1972; Jarvis 1976; Livingston and Black 1987). This was accomplished by fitting a boundary line to the upper limit of scatterplots of normalized values of g_{crown} versus D (Fig. 3A). There are apparent missing values in the “corners” of these scatterplots, especially at low D , where normalized g_{crown} appears to decrease. This is because the simultaneous occurrence

Table 4. Contribution (percent) of trees of different social classes to stand transpiration and leaf area.

Percentage of:	Social class		
	Suppressed	Intermediate	Codominant
Stand density	33.3	33.3	33.3
Stand transpiration	9.8	16.5	73.7
Stand leaf area	8.6	28.0	63.4

Note: Trees were divided into social classes by diameter at breast height.

of high R_n and low D in the field is rare. Working under the premise that g_{crown} responds negatively to D and positively to R_n (Köstner et al. 1992; Dye and Olbrich 1993; Granier and Loustau 1994), we assume that the “true” maximum conductance of the stand would occur at high R_n and 0 kPa D . This led to a vapor pressure deficit function of the form

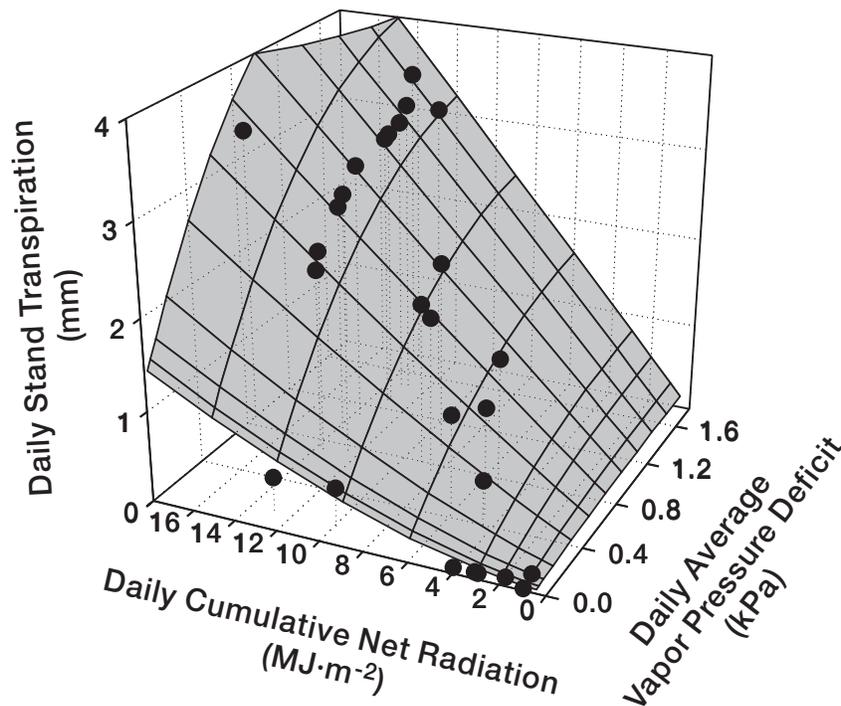
$$[7] \quad f(D) = \exp(-aD)$$

where $1 - f(D)$ represents the fractional reduction in maximum conductance due to nonzero vapor pressure deficit. The function was fitted using least squares linear regression on log-transformed upper boundary data so that, when $D = 0$, the function returns a value of 1. The vapor pressure deficit function was used to adjust measured values of g_{crown} upward to arrive at an estimate of g_{max} , the conductance unlimited by vapor pressure deficit. Maximum conductance was then modeled as a linear function of net radiation (Fig. 3B). Crown conductance could then be predicted for any combination of R_n and D by first predicting g_{max} from the net radiation function, then reducing g_{max} using the vapor pressure deficit function.

This model explained from 52 to 73% (average 66%) of the variation in g_{crown} for the sample trees. The behavior of the model was realistic (Fig. 2B), and by running the model under hypothetical climate conditions and substituting the simulated g_{crown} into eq. 1, transpiration of individual trees could be simulated, which in turn could be integrated upward in scale to predict stand transpiration under the hypothetical conditions.

As shown by the model summary and data in Fig. 4, g_{crown} increases linearly with above-canopy radiation and decreases in a nonlinear fashion with increases in D . While our model appears to agree with much of the literature in terms of its D response, it differs somewhat in the radiation response. Several studies in coniferous forests have shown conductance at constant D to increase in a rectangular hyperbolic fashion with radiation, with an initial steep increase, followed by a leveling off of conductance at a “saturated” light level (Gash et al. 1989; Breda et al. 1993; Granier and Loustau 1994; Whitehead et al. 1994). Our data, on the other hand, show conductance at any particular level of D to continue increasing as R_n increases. This may be characteristic of the deep, dense forest canopy at this site. Because light penetration is greatly attenuated within the upper canopy, lower portions of the canopy remain in relatively low light (at 10 m above the ground, radiation was less than 5% of that above the stand). As radiation increases, more light penetrates into the shaded portions of the canopy, raising stomatal conductance of leaves in those regions (which, in turn, raises g_{crown}), even as leaves in the upper canopy are light saturated. The LAI of the canopies described by Gash et al. (1989), Breda et al. (1993), Whitehead et al. (1994), and Granier and Loustau (1994) were 2.3, 6.0, <6.0, and $1.7 \text{ m}^2\cdot\text{m}^{-2}$, respectively.

Fig. 7. The response of measured (symbols) and modeled (shading) daily stand transpiration to daily cumulative net radiation and daily average vapor pressure deficit.



In these forests, most of the leaves within the canopy probably reach light saturation at lower above-canopy radiation levels than in a denser, higher LAI forest such as the one described in this paper.

Larger trees had higher rates of transpiration per unit leaf area than did smaller trees at equal above-stand vapor pressure deficits (Fig. 5). This could be due to decreased water vapor pressure deficit with depth into the canopy, although this seems unlikely, as the air in tall coniferous stands is well mixed, with only small humidity gradients within the canopy (Jarvis et al. 1976). Another possible explanation is that small trees absorbed less radiation than large trees, resulting in reduced transpiration in smaller trees (eq. 1). While there were small differences in calculated quantities of radiation absorbed by the different sample trees, there was not much systematic variation in this parameter with tree size (data not shown). In addition, because of the relative magnitudes of g_{crown} and g_a in this system (total crown boundary layer conductance calculated from eqs. 4 and 5 was usually at least two orders of magnitude larger than g_{crown}), radiation is not as important in determining transpiration as the prevailing level of D . This phenomenon was described in detail by Jarvis and McNaughton (1986), who explored the relative importance of radiation and vapor pressure deficit as controllers of transpiration by separating eq. 1 into imposed (D driven) and equilibrium (R_n driven) components. Jarvis and McNaughton (1986) pointed out that, when boundary layer conductance is considerably larger than canopy conductance, transpiration from vegetation is determined primarily by canopy conductance and the prevailing magnitude of D . Vegetation in this state is considered to be well coupled to the evaporative environment. In vegetation in which large leaf size results in decreased shoot-

level boundary layer conductance (e.g., *Populus*; Hinckley et al. 1994) or stand structure results in low canopy aerodynamic conductance (e.g., agronomic crops; Baldocchi 1994), boundary layer conductances (and, as a result, net radiation) become more important in determining the transpiration rate. The highly coupled nature of the *Abies* stand, therefore, also implies that our estimates of g_{crown} are not very sensitive to errors in calculation of R_{crown} .

A third explanation for the differences in rates shown in Fig. 5 is that g_{crown} of trees in the smaller size-classes was lower than in larger trees, resulting in lower transpiration than larger trees at equal vapor pressure deficits. This explanation is supported by our data, which show that g_{crown} decreases with tree size and crown class (Table 2). The degree to which stomata are limiting transpiration can be quantified by comparing transpiration with stomatal control (eq. 1) to potential transpiration, calculated from evaluating eq. 1 assuming no stomatal limitation to water loss ($g_{\text{crown}} \rightarrow \infty$, equivalent to a tree crown constructed out of wet filter paper). As shown in the model simulation in Fig. 6, stomata become increasingly important in limiting water loss as D increases and g_{crown} decreases. The magnitude of this effect varied with tree size. Stomatal control in the smaller trees sampled remained relatively constant across a range of vapor pressure deficits. Larger trees had more variation in stomatal control, transpiring up to 30% of potential transpiration at low D , but decreasing to near the level of stomatal control of the smaller trees (<10% of potential transpiration) at high D .

Stand transpiration

Because of intermittent equipment and battery failure, every sample tree was not monitored every day. Stand transpiration

was calculated for 28 days with complete data between August 6 and October 12, 1993. Transpiration during this period ranged from 0.01 to 3.52 mm·day⁻¹ and averaged 1.70 mm·day⁻¹. The maximum rate of transpiration was comparable with values reported for other coniferous forests (see reviews by Kelliher et al. 1993; Pallardy et al. 1995). Hatton et al. (1995) assessed the potential errors associated with scaling sap flow measurements at the tree scale upward to the stand level. They estimated (from their measurements of six trees within a *Eucalyptus populnea* F.J. Muell. woodland) that, when measurement trees are stratified according to size (as they were in our study), the coefficient of variation associated with the stand-level estimate of transpiration is approximately 5%.

The contribution of the different size-classes of trees to total stand transpiration is summarized in Table 4. The smallest third of the stand (by diameter; 744 trees/ha) contributed less than 10% of the total transpiration of the stand. In contrast, the largest 744 trees/ha (consisting of trees greater than 25.0 cm DBH) contributed more than 70% of the total stand transpiration. As discussed previously, the low absolute transpiration rate in suppressed trees is attributable to lower leaf area per tree and to reduced g_{crown} compared with larger trees.

Daily stand transpiration was strongly dependent on average vapor pressure deficit and daily radiation sum (Fig. 7). The response of stand transpiration to average daily D was curvilinear, reflecting the increasing control of transpiration by stomata as D increased (Fig. 6). To summarize stand responses and to determine the response of the stand to environmental conditions not captured during the measurement period, we ran the empirical model of g_{crown} under varying radiation and vapor pressure deficit regimes. Hourly predicted values of g_{crown} were substituted into eq. 1 to estimate tree transpiration, which was summed for the day and integrated to the stand scale to produce the response surface in Fig. 7. This surface represents the hypothetical response of stand transpiration to environmental conditions not occurring during the measurement period. While caution must be exercised when interpreting model predictions made for conditions different than the conditions under which the model was developed, the behavior of the surface in Fig. 7 is reasonable and is probably a realistic prediction of the transpiration response of this stand during the growing season.

Our model takes into account only radiation and vapor pressure deficit, atmospheric factors that directly affect the above-ground portion of the forest. In contrast, some researchers have found it necessary to include functions which describe soil moisture depletion (Running 1984; Granier and Loustau 1994). During the measurement period, significant rainfall events were separated by at most 18 days, so it is unlikely that stand water relations were strongly affected by soil water deficits. The fact that the pattern of residuals for the stand transpiration model did not vary with precipitation events further supports this supposition. These results are also in accordance with Teskey et al. (1984), who concluded from gas exchange measurements in *A. amabilis* that summer drought is not commonly a limiting factor in this conifer's subalpine environment.

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