

Boundary layer conductance, leaf temperature and transpiration of *Abies amabilis* branches

TIMOTHY A. MARTIN,^{1,3} THOMAS M. HINCKLEY,¹ FREDERICK C. MEINZER² and DOUGLAS G. SPRUGEL¹

¹ College of Forest Resources, University of Washington, Seattle, Washington, USA

² Hawaii Agriculture Research Center, Aiea, Hawaii, USA

³ Present address: School of Forest Resources and Conservation, University of Florida, Box 110410, Gainesville, FL 32611-0410, USA

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Summary We used three methods to measure boundary layer conductance to heat transfer (g_{bH}) and water vapor transfer (g_{bV}) in foliated branches of *Abies amabilis* Dougl. ex J. Forbes, a subalpine forest tree that produces clumped shoot morphology on sun-formed branches. Boundary layer conductances estimated in the field from energy balance measurements increased linearly from approximately 10 mm s^{-1} at low wind speeds ($< 0.1 \text{ m s}^{-1}$) to over 150 mm s^{-1} at wind speeds of 2.0 m s^{-1} . Boundary layer conductances measured on shoot models in a wind tunnel were consistently higher than field measurements. The difference between wind tunnel values and field measurements was attributable to variation in path length between the two experimental environments. Boundary layer conductance estimated by subtracting stomatal resistance (r_{sV}) measured with a porometer from the total branch vapor phase resistance were unusually small. Sensitivity analysis demonstrated that this method is not suitable for coniferous foliage or when stomatal conductance (g_{sV}) is small compared with g_{bV} . Analysis of the relative magnitudes of g_{sV} and g_{bV} revealed that, under most conditions, *A. amabilis* branches are well coupled (i.e., g_{sV} is the dominant controller of transpiration). The boundary layer conductance to heat transfer is small enough that leaf temperature can become substantially higher than air temperature when radiation is high and wind speed is low. Over a two-month period, the maximum difference between leaf and air temperatures exceeded 6°C . Leaf temperature exceeded air temperature by more than 2°C on 10% of the daylight hours during this period. Consideration of both the photosynthetic temperature response of *A. amabilis* foliage as well as the summer air temperature conditions in its habitat suggests that these elevated leaf temperatures do not have a significant impact on carbon gain during the growing season.

Keywords: Pacific silver fir, stomatal conductance, stomatal resistance, water vapor transfer.

Introduction

Water loss from plant leaves is controlled by boundary layer conductance and stomatal conductance operating in series.

Stomatal conductance (g_{sV}) is a function of the density, size and degree of opening of stomata. Boundary layer conductance to water vapor (g_{bV}) depends on the thickness of the layer of air at the surface of the leaf through which water vapor must diffuse after leaving the stomata. Boundary layer conductance is controlled by leaf size and morphology and wind speed (Monteith and Unsworth 1990, Nobel 1991, Schuepp 1993). Because of the relationship between leaf size and boundary layer conductance, conifers are assumed to have very large g_{bV} .

High boundary layer conductances have important implications for leaf temperature. In addition to providing resistance to water vapor diffusion, the boundary layer around a leaf also provides resistance to the transfer of heat between a leaf and its surroundings. As a consequence, large boundary layer conductances to heat transfer (g_{bH}) result in small differences between air temperature and leaf temperature, because heat is easily convected from the leaf to the surrounding air. Because g_{bH} in conifers is assumed to be very large, it is commonly assumed that conifer needle temperatures seldom, if ever, differ from air temperature by more than one degree (e.g., Jarvis et al. 1976, Tan et al. 1978, Kaufmann 1984, Angell and Miller 1994). Some measurements of leaf temperature in conifers (e.g., Vanderwaal and Holbo 1984) support this assumption.

A high boundary layer conductance also has important implications in the control of transpiration. Because boundary layer conductance and stomatal conductance operate in series, their relative magnitude determines which conductance is the dominant regulator of transpiration. The Omega factor (Ω), a dimensionless coefficient ranging from 0.0 to 1.0, was introduced by McNaughton and Jarvis (1983) and Jarvis and McNaughton (1986) as an index of the degree of stomatal control of transpiration. When g_{sV} is much smaller than g_{bV} , stomata are the dominant controller of water loss and a decrease in g_{sV} will result in a nearly proportional decrease in transpiration. Vegetation in this state has an Ω value near 0, and is said to be well coupled. In contrast, when g_{bV} is much smaller than g_{sV} , changes in g_{sV} will have little effect on transpiration rate, and input of radiation to the canopy is the primary driver of transpiration. Vegetation in this state has

values of Ω near 1.0, and is considered to be poorly coupled. Coniferous foliage, with its presumably high g_{bV} and low g_{sV} , is considered to be well coupled, with Ω values between 0 and 0.1 (Jarvis and McNaughton 1986). Agronomic crops, with lower g_{bV} and higher g_{sV} , are considered to be poorly coupled, with Ω values exceeding 0.8 (Jarvis and McNaughton 1986, Meinzer 1993). Broad-leaved tree species tend to be intermediately coupled, with Ω values between 0.3 and 0.6 (Lindroth 1993, Meinzer 1993, Meinzer et al. 1993, Hinckley et al. 1994).

Some measurements of conifer needle temperature indicate that g_{bV} and g_{bH} in conifers may not be as large as has been previously thought. Measurements of leaf temperature in *Pinus sylvestris* L. (Christersson and Sandstedt 1978), *Abies lasiocarpa* (Hook.) Nutt. (Hadley and Smith 1987, Smith and Carter 1988), *Picea engelmannii* Parry ex Engelm. (Hadley and Smith 1987) and *Abies amabilis* Dougl. ex J. Forbes (this paper) all show elevations in conifer needle temperature of at least 5 °C above air temperature, suggesting that boundary layer resistance to heat transfer is significant, at least with some needle arrangements and under certain meteorological conditions. Measurements of boundary layer conductance of shoot models of *Abies lasiocarpa* and two other subalpine conifers by Smith (1980) demonstrated that g_{bV} significantly impeded transpiration in all three species.

Given the inconsistencies among published observations and the common assumption that conifer boundary layer conductance is an insignificant impediment to water and heat transfer, we were interested in clarifying the significance of boundary layer conductance for the physiology of Pacific silver fir (*Abies amabilis*), a needle-leaved tree species. Our work had three main objectives: (1) to quantify the magnitude and response to wind speed of g_{bV} in *A. amabilis* shoots using both field and laboratory approaches; (2) to evaluate the role of g_{bV} in limiting transpiration from *A. amabilis* branches; and (3) to examine the degree of leaf temperature elevation resulting from g_{bH} and its significance for carbon gain in *A. amabilis*.

Materials and methods

Study species and stand description

Abies amabilis is common in montane forests of the Pacific northwest. Needles on *A. amabilis* shoots formed in the sun tend to cluster around the top half of the shoot in a "bottle brush" configuration (Tucker et al. 1987, Sprugel et al. 1996). Many other species have similar sun shoot morphology (Sprugel 1989), including *Picea sitchensis* (Bong.) Carrière (Leverenz and Jarvis 1980), *Picea mariana* (Mill.) BSP (Harlow et al. 1979) and *Abies lasiocarpa* (Smith and Carter 1988). Because silver fir foliage persists on the tree for up to 25 years (T.A. Martin, unpublished observation), foliage with sun shoot morphology can exist throughout the canopy, not just in well lit portions (Brooks et al. 1994).

Field measurements were performed in the summer of 1995 in a Pacific silver fir stand at 1100 m elevation in the Cascade mountains (47°40' N, 121°36' W), 65 km southeast of Seattle, Washington. The stand had regenerated naturally after clear-

cutting in 1955, and at the time of measurements had a mean dominant-tree height of 6.4 m, a density of 13,000 stems ha⁻¹, a basal area of 35.9 m² ha⁻¹, and a projected leaf area index of about 5.5 (D.G. Sprugel, unpublished data).

Wind speed measurements

Wind speed was measured above the canopy with a cup anemometer (Wind Sentry 03101-5, R.M. Young, Traverse City, MI). Cup anemometers (Model 6101, R.M. Young) were installed at heights of 6.8 and 5.0 m, and low stall speed propeller anemometers (Model 05305 Wind Monitor AQ, R.M. Young) were installed at heights of 3.3 and 1.5 m. Wind speed and all other automated instruments were measured once each second and averaged over 5-min intervals.

Field boundary layer conductance measurements—energy balance method

We used two methods to estimate g_{bV} of *A. amabilis* branches in the field. The first method utilized measurements of leaf temperature, branch transpiration, and solar radiation to quantify the components of the energy balance of a branch. The boundary layer conductance to heat transfer was then found by solving an equation that described the energy balance and sensible heat transfer budget of the branch:

$$g_{bH} = \frac{R_n - \lambda E}{(T_{\text{leaf}} - T_{\text{air}})\rho_a c_p}, \quad (1)$$

where T_{leaf} and T_{air} represent leaf and air temperature, respectively, g_{bH} is boundary layer conductance to heat transfer (m s⁻¹), R_n is radiation absorbed by the branch (W m⁻² leaf area), λ is latent heat of evaporation of water (J kg⁻¹), E is evaporation rate from the branch (kg m⁻² s⁻¹), ρ_a is density of dry air (kg m⁻³), and c_p is heat capacity of air (J kg⁻¹ °C⁻¹).

Radiation absorbed by the branch (R_n , W m⁻² leaf area) was calculated as:

$$R_n = (\alpha_{\text{sw}}R_{s,\downarrow} + R_{l,\downarrow} + \alpha_{\text{sw}}R_{s,\uparrow} + R_{l,\uparrow} - 2R_1)A_m, \quad (2)$$

where α_{sw} is the shortwave absorption coefficient for conifer foliage (0.88, Gates 1980), $R_{s,\downarrow}$ and $R_{l,\downarrow}$ are shortwave solar radiation and longwave sky radiation, respectively, $R_{s,\uparrow}$ is shortwave radiation reflected from below, $R_{l,\uparrow}$ is longwave radiation from the surface below the branch, R_1 is longwave re-radiation from the branch, and A_m is the mean silhouette to projected area ratio of the branch. Shortwave solar radiation was measured with a pyranometer (Li-200S, Li-Cor, Inc., Lincoln, NE). For branches lower in the canopy, $R_{s,\downarrow}$ and the other incoming radiation components were adjusted downward with an attenuation coefficient developed from measurements of light at the branch level taken during extensive sampling with the light sensor on a porometer. Shortwave radiation reflected from below ($R_{s,\uparrow}$) was calculated from the pyranometer data, assuming that the canopy (or forest floor) reflected a fraction of $R_{s,\downarrow}$ equal to $(1 - \alpha_{\text{sw}})$. Longwave radiation ($R_{l,\downarrow}$) was calculated from a relationship between air temperature and longwave radiation from clear skies (Swin-

bank 1963). The application of this equation was warranted, because all measurements were conducted on cloudless days. Conifer foliage was assumed to have a longwave emissivity of 0.96 (Gates 1980, Jones 1983). The other longwave radiation components ($R_{l\uparrow}$, R_l) were calculated with the Stefan Boltzman law and the appropriate surface temperature.

To convert absorbed radiation from a ground area basis to a leaf area basis, the summed radiation terms were multiplied by the mean silhouette to projected area ratio (A_m) of the branch. The A_m is calculated as the ratio of silhouette area of the branch (the projected area of the intact branch) to projected leaf area of the branch, averaged over many different hemispherical angles (Stenberg et al. 1995). This calculation accounts for the influence of shoot architecture and sun angle on radiation interception. With this approach, the simplifying assumption is made that the longwave radiation field is directionally similar to the short-wave radiation field. The silhouette to projected area ratio as viewed from directly above the branch (A_{max}) was measured on shoot samples in the laboratory with a video camera and a computerized image analysis system. The A_m was then calculated from a relationship between A_{max} and A_m developed from sampling in the same stand ($A_m = 0.4 (0.136 + A_{max})$, $r = 0.905$, H. Smolander, Finnish Forest Research Institute, Suonenjoki Research Station, Suonenjoki, Finland, and P. Stenberg, Department of Forest Ecology, University of Helsinki, Helsinki, Finland, pers. comm. 1997).

Leaf temperature (T_{leaf} , °C) was measured with 0.07-mm diameter copper/constantan thermocouples placed against the underside of the needle. Four thermocouples were wired in parallel to needles on each of four reference branches that remained attached to the trees. Two reference branches were located at the upper sampling height, and two at the lower height. Mean leaf temperatures measured with an infrared thermometer (Model 110/F, Everest Interscience, Tustin, CA) over two days were not significantly different from the thermocouple measurements. Air temperature was measured with a thermistor (HMP35C, Campbell Scientific, Logan, UT) on a 10-m tall tower in the stand.

Branch transpiration (E) was measured by recording the amount of water lost from potometers at 3- to 5-min intervals. Branches were cut from trees in the morning, immediately recut under water, and fitted with potometers. During each sampling day, one potometer-fitted branch was affixed to the tower at the top of the stand at 7 m height, and another at 1.5 m above the forest floor, near the base of the live crown. Three branches at the upper height and three branches at the lower height were measured over three sampling days in August 1995. Rates of water loss measured with potometers were comparable to water loss rates measured with branch sap flow gauges on intact *A. amabilis* branches (Martin 1997). In addition, previous sampling has shown that detached, hydrated *A. amabilis* branches retain normal physiological function for up to five days (Martin 1997). All sample branches at the upper height and one of the sample branches at the lower height were taken from sunny microsites and had sun morphology (mean $A_{max} = 0.42$). Diameters of the sampled branches were less than 10 mm and branch projected leaf area ranged from 0.04 to 0.25 m². To evaluate the effect of shoot morphology on g_{bV} at

low wind speeds, two branches at the lower measurement position were taken from shady microsites, and had foliage more typical of foliage formed in the shade (mean $A_{max} = 0.66$).

Boundary layer conductance to heat transfer (g_{bH}) was estimated by substituting measured leaf and air temperature, transpiration rate, and absorbed radiation into Equation 1. Boundary layer conductance to heat transfer was converted to g_{bV} by dividing by 0.93 (Monteith and Unsworth 1990).

Field boundary layer conductance measurements: resistance subtraction (RS) method

A method described by Meinzer et al. (1993) was used to make an independent field measurement of g_{bV} on the same branches used for the energy balance calculations. This method takes advantage of the fact that the total vapor phase conductance of a branch is the series sum of stomatal and boundary layer conductances. Because resistances (inverse conductances) are additive in series, g_{bV} can be estimated as:

$$g_{bV} = \frac{1}{1/g_{tV} - 1/g_{sV}}, \quad (3)$$

where g_{sV} is stomatal conductance of the branch estimated by measuring stomatal conductance of each age class of needles on the branch with a steady-state porometer and scaling to the branch level using the distribution of leaf area by age class. Total branch vapor phase conductance (g_{tV} , m s⁻¹) was calculated as:

$$g_{tV} = \frac{\lambda E \gamma}{\rho_a C_p (e_l - e_a)}, \quad (4)$$

where e_a is air vapor pressure (Pa) measured with the opened porometer's humidity sensor and e_l is leaf intercellular space vapor pressure (Pa), calculated as saturated vapor pressure at leaf temperature. Branch transpiration (E) was measured with potometers as described previously. Cuticular conductance was assumed to be negligible (Körner 1994).

Wind tunnel boundary layer conductance measurements: branch models

We also estimated g_{bV} by measuring water loss from plaster-coated branches (Landsberg and Ludlow 1970). This approach is analogous to using filter paper replicas of leaves to estimate boundary layer conductance of broad-leaved plants (Jarvis 1971, Roberts et al. 1990). Because water evaporates from the surface of the shoot model, eliminating the g_{sV} term, the g_{bV} of the shoot model can be estimated by:

$$g_{bV} = \frac{\lambda E \gamma}{\rho_a C_p (e_s - e_a)}, \quad (5)$$

where e_s and e_a are the vapor pressures at the model surface and bulk air in Pa, respectively, and E is evaporation rate from the

model ($\text{kg m}^{-2} \text{s}^{-1}$). Evaporation rate was measured with a balance (Model 1500D, Ohaus, Florham Park, NJ) on which the shoot model was mounted in the wind tunnel. Vapor pressure at the model surface was calculated by assuming the air at the surface of the shoot model was at saturated vapor pressure at the model temperature. The temperature of the model was measured with four thermocouples that were wired into the branch before covering the branch with plaster. After the plaster was applied, the coated thermocouples were the same size, shape and orientation as adjacent needles. Wind tunnel e_a was measured with the humidity sensor used in the field study.

The shoot model experiments were conducted in an open-circuit low speed wind tunnel (Model 2035, Meteorology Research, Inc., Altadena, CA). Wind speed within the tunnel was measured with a heated thermocouple anemometer (B-22, Hastings-Raydist, Hampton, VA) placed 15 cm upwind from the model, at the same height and distance from the sides of the tunnel as the model. Because the anemometer probe was only 6 mm wide, it was assumed to have negligible effects on the wind regime experienced by the shoot model. For each single wind speed run, the shoot model was dipped in water and shaken to remove excess, then mounted on the balance. The weight of the model was recorded every 30 s. Calculation of g_{bV} was made based on data for the period when rate of water loss from the branch model was constant. This period ranged from more than 10 min at the lowest wind speed (0.05 m s^{-1}) to about 2 min at the highest wind speed (5.0 m s^{-1}). Four branch models were measured over a range of wind speeds from 0.05 to 5.0 m s^{-1} . All branches used to make the shoot models were taken from sunny microsites. The branch model one-sided leaf areas ranged from 0.03 to 0.08 m^2 , and branch A_{max} ranged from 0.59 to 0.68 .

Coupling calculations

The decoupling coefficient (McNaughton and Jarvis 1983) was calculated as:

$$\Omega = \frac{s/\gamma + 2}{s/\gamma + 2 + g_{bV}/g_{sV}}, \quad (6)$$

where s is the slope of the saturated vapor pressure *versus* temperature curve ($\text{Pa } ^\circ\text{C}^{-1}$) and γ is the psychrometer constant ($\text{Pa } ^\circ\text{C}^{-1}$).

Results and discussion

Boundary layer conductances measured by the energy balance method were less than 20 mm s^{-1} at wind speeds less than 0.5 m s^{-1} , and increased linearly with increasing wind speed (Figure 1, $g_{bV} = 5.0 + 74.4v$, $R^2 = 0.56$). No differences in boundary layer conductance measured at 1.5 m were detected between branches with sun morphology and those with shade morphology.

Boundary layer conductance of shoot models measured in

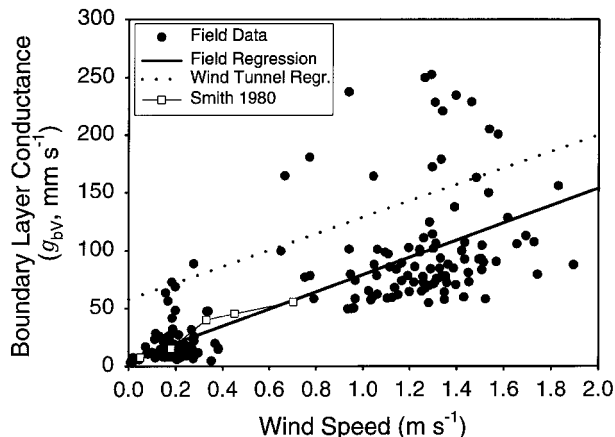


Figure 1. Relationship between boundary layer conductance to water vapor (g_{bV} , mm s^{-1}) and wind speed (v , m s^{-1}) for *Abies amabilis* branches in the field (solid circles and solid regression line, $g_{bV} = 5.0 + 74.4v$, $R^2 = 0.56$) and plaster-coated branch models in a wind tunnel (dotted regression line, $g_{bV} = 57.6 + 70.8v$, $R^2 = 0.66$). The slopes of the regression lines are statistically similar, whereas the intercepts are statistically different. Boundary layer conductance to heat transfer (g_{bH}) from the field data was determined by substituting measurements of leaf and air temperature, absorbed radiation and latent heat loss in Equation 2, and converted to g_{bV} as described in the text. Open squares denote field measurements from *Abies lasiocarpa* branch models reported by Smith (1980).

the wind tunnel were approximately 50 mm s^{-1} at a wind speed of 0.05 m s^{-1} and increased with increasing wind speed to approximately 300 mm s^{-1} at wind speeds approaching 5.0 m s^{-1} (Figure 1, $g_{bV} = 57.6 + 70.8v$, $R^2 = 0.66$). The orientation of the branch (perpendicular or parallel to the wind tunnel flow) did not affect the results.

The energy balance and wind tunnel estimates of g_{bV} were similar to those for other conifer species with clumped sun shoot morphology such as *Picea sitchensis* (Landsberg and Ludlow 1970, Landsberg and Thom 1971), *Abies lasiocarpa* (Smith 1980, see Figure 1), *Abies concolor* (Gord.) Lindl. and *Picea pungens* Engelm. (Tibbals et al. 1964). All of these studies utilized either plaster-coated or metal shoot models and, with the exception of the study conducted by Smith (1980), all were carried out in wind tunnel environments. Although several studies have measured g_{bV} on intact branches of broad-leaved trees (Meinzer et al. 1993, Hinckley et al. 1994, Meinzer et al. 1995), and on broad-leaved shoot models in field and laboratory conditions (Grace et al. 1980, Domingo et al. 1996, Smith et al. 1997), the present study is one of the first to estimate *in situ* g_{bV} of conifer branches, although the RS method was recently applied to *Picea mariana* (Mill.) BSP branches (D. Kubien and L. Flanagan, Carleton University, Ottawa, Ontario, pers. comm.) and Teklehaimanot et al. (1991) used elegant manipulations of precipitation and interception data to estimate mean g_{bV} for entire stands of *Picea sitchensis*.

Boundary layer conductances to water vapor estimated from the field energy balance data were consistently lower than the wind tunnel branch model estimates (Figure 1). The discrepancies between the data sets are probably attributable to the

difference in path length in the two experimental environments. The g_{bV} as calculated in our study describes water vapor or heat transfer between the leaf surface and the point at which air vapor pressure (or temperature) is measured; this distance is referred to as the path length. In the wind tunnel, the path length was short (< 30 cm) because ambient vapor pressure was measured adjacent to the branch. In contrast, the field measurements incorporated a longer path length between the leaf surface and the temperature sensor above the stand. This increased path length is reflected in the lower g_{bV} for the field data than for the wind tunnel data (see Smith et al. (1997) for a detailed discussion of path lengths).

In contrast to the energy balance and wind tunnel measurements, the resistance subtraction (RS) estimates of g_{bV} were not consistent with conifer boundary layer literature. Mean g_{bV} estimated by the RS method (1.6 mm s^{-1}) was an order of magnitude smaller than the lowest boundary layer conductance estimated with the energy balance and wind tunnel methods. The causes of these anomalous results became apparent when we examined the sensitivity of the various g_{bV} estimation methods to measurement errors.

Sensitivity analysis

The methods used to estimate boundary layer conductance varied in their sensitivity to measurement errors. The energy balance method (Equation 1) was somewhat sensitive to errors in leaf or air temperature measurements; variations of $0.1 \text{ }^\circ\text{C}$ in temperature measurement produced 5% errors in g_{bV} . Errors in estimation of net radiation produced approximately proportional deviations in g_{bV} , whereas the method was relatively insensitive to errors in transpiration measurement (Table 1). Similarly, with the shoot model method (Equation 5), errors in measurement of e_s , e_a , or E produced approximately proportional deviations in g_{bV} . In contrast, the resistance subtraction method (Equations 3 and 4) was very sensitive to errors in measurement of any of its parameters. Variations of only 5% in any one of the input parameters to Equation 3 or 4 resulted in departures from the "true" value of g_{bV} of up to 183%

(Table 1). Thus, the large discrepancies in our RS data probably were the result of small, simultaneous measurement errors in several input parameters, causing large errors in the estimation of g_{bV} .

Although the RS approach is theoretically sound, and has been successfully applied several times with broad-leaved tree species (Meinzer et al. 1993, Hinckley et al. 1994, Meinzer et al. 1995), it appears that with coniferous foliage it is problematic. When g_{bV} is large compared with g_{sV} (as it is in conifers), estimates of g_{bV} based on the RS approach are very sensitive to errors in estimating g_{tV} and g_{sV} (Table 1, Figure 2). When g_{sV} is considerably smaller than g_{bV} , accurate estimates of g_{bV} are exceedingly difficult to achieve with the RS approach. In contrast, when g_{bV} and g_{sV} are of similar magnitude, as they are in many broad-leaved trees, the RS approach is much less sensitive to small measurement errors (Figure 2). Because of the uncertainty associated with our RS estimates of g_{bV} , estimates of g_{bV} presented below are based on regression through the field dataset shown in Figure 1.

Boundary layer conductance and water loss

To assess the degree to which g_{bV} limited water loss, we calculated Ω (Equation 6) for August 22, 1995 based on the field relationship between g_{bV} and wind speed shown in Figure 1 and porometer measurements of g_{sV} . The upper-canopy branch remained well coupled (Ω 0.10) throughout the day (Figure 3). The branch in the lower canopy, where wind speeds were much lower, was less well coupled. For both branches, Ω declined through the day as g_{sV} decreased (Figure 3). This pattern of increasing coupling throughout the day was also observed at the whole-tree scale in *Nothofagus fusca* (Hook. f.) Ørst. (Köstner et al. 1992), whereas the average coupling of Amazonian rain forest tended to decrease in the morning to an Ω of approximately 0.2, and then remain stable throughout the day (Granier et al. 1996). Obviously, variations in these patterns will occur depending on how g_{sV} and wind speed (which determines g_{bV}) vary.

Wind speed decreased dramatically with depth in the canopy

Table 1. Sensitivity analysis showing the effects of parameter measurement errors when g_{bV} is estimated by the energy balance (Equation 1), resistance subtraction (Equations 3 and 4), and shoot model (Equation 5) methods. Deviations were calculated as $(\text{Error } g_{bV} - \text{"true" } g_{bV})/(\text{"true" } g_{bV})$.

| Method | Parameter | Typical parameter value | g_{bV} (mm s^{-1}) with no parameter measurement error | Parameter measurement error | Fractional deviation in g_{bV} for positive error | Fractional deviation in g_{bV} for negative error |
|--|--|-------------------------|---|------------------------------|---|---|
| Energy balance (Equation 1) | T_{leaf} ($^\circ\text{C}$) | 20 | 111 | $0.1 \text{ }^\circ\text{C}$ | 0.05 | -0.05 |
| | T_{air} ($^\circ\text{C}$) | 18 | 111 | $0.1 \text{ }^\circ\text{C}$ | -0.05 | 0.05 |
| | R_n (W m^{-2}) | 300 | 111 | 10% | -0.10 | 0.13 |
| | E ($\text{mg m}^{-2} \text{s}^{-1}$) | 12.2 | 111 | 10% | 0.01 | -0.01 |
| Resistance subtraction (Equations 3 and 4) | e_t (Pa) | 3000 | 75.6 | 5% | -0.87 | -1.17 |
| | e_a (Pa) | 2000 | 75.6 | 5% | -1.28 | -0.82 |
| | E ($\text{mg m}^{-2} \text{s}^{-1}$) | 12.2 | 75.6 | 5% | -1.83 | -0.71 |
| | g_{sV} (mm s^{-1}) | 1.7 | 75.6 | 5% | -0.68 | -1.72 |
| Shoot model (Equation 5) | e_s (Pa) | 1300 | 108.7 | 5% | -0.12 | 0.15 |
| | e_a (Pa) | 800 | 108.7 | 5% | 0.09 | -0.07 |
| | E ($\text{mg m}^{-2} \text{s}^{-1}$) | 407 | 108.7 | 5% | 0.05 | -0.05 |

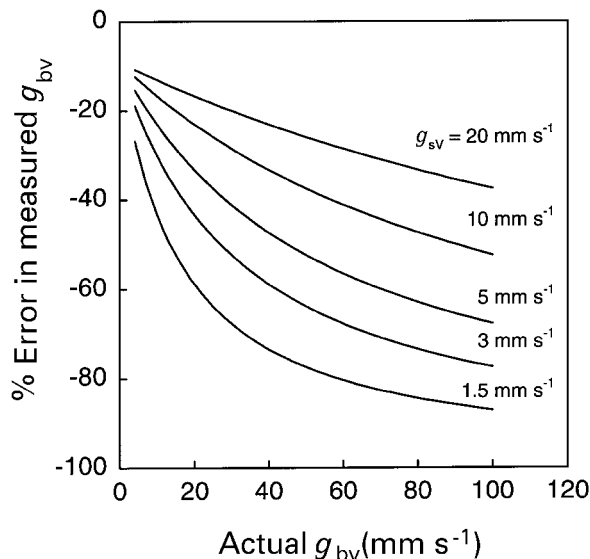


Figure 2. Analysis of the error resulting from using the resistance subtraction approach to estimate boundary layer conductance to water vapor (g_{bv}) and assuming the total resistance to water vapor ($1/g_{tV}$) is overestimated by 10%.

(Figure 3), and this might be expected to cause large decreases in coupling, as Roberts et al. (1990) found in a tropical broad-leaved forest. However, this was not the case with *A. amabilis*. Branches in the lower canopy did experience longer periods of low g_{bv} because of decreased wind speeds, but they also tended to have lower g_{sv} , which increased their degree of coupling (decreased the value of Ω). In the lower canopy (1.5 m), 5-min mean wind speeds remained below 0.5 m s^{-1} for 97% of the 504 daylight hours monitored, implying that g_{bv} in the lower canopy would almost always be below 42 mm s^{-1} (based on the equation shown in Figure 1). However, g_{sv} of intact branches at that crown position never rose above 3 mm s^{-1} , and were usually below 2 mm s^{-1} . Because conditions will rarely prevail when g_{bv} is small at the same time that g_{sv} is large (high radiation, low VPD, low wind speed), we postulate that *Abies amabilis* branches are well coupled ($\Omega < 0.3$) most of the time. In contrast, Smith (1980) concluded that g_{bv} of *Abies lasiocarpa* and two other subalpine conifers was small enough to limit water loss significantly for most of the growing season. The g_{bv} values measured by Smith (1980) in the young, well-lit *Abies lasiocarpa* trees are similar to our measurements in *A. amabilis* (Figure 1), but g_{sv} in *A. lasiocarpa* was relatively high, resulting in a larger ratio between g_{sv} and g_{bv} (and higher Ω) than in our study, where g_{sv} was lower.

Boundary layer conductance and needle temperature

Although branch g_{bv} was seldom small enough (compared with g_{sv}) to limit water loss from the foliage substantially, g_{bH} was small enough to allow significant elevation of leaf temperature above air temperature. Figure 4 demonstrates the potential range of leaf temperature elevations over air tempera-

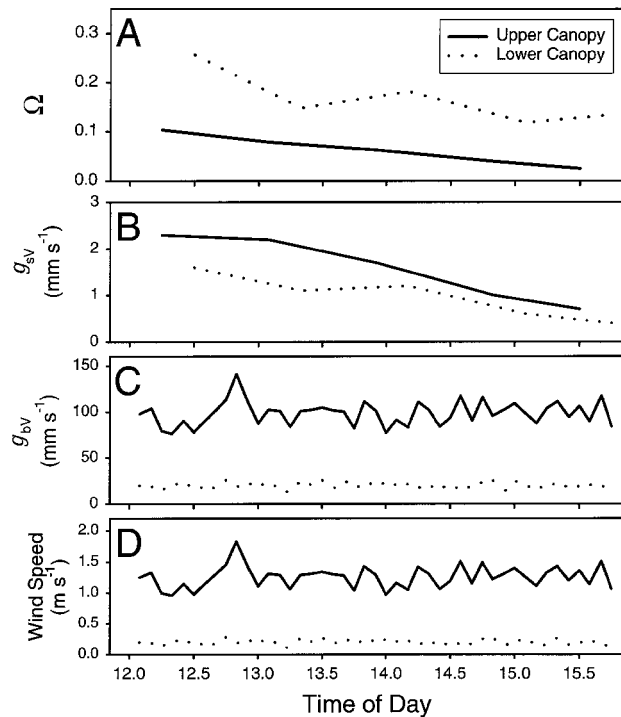


Figure 3. Diurnal variation of (A) the Ω decoupling coefficient, (B) g_{sv} , stomatal conductance to water vapor measured with a porometer, (C) g_{bv} , boundary layer conductance to water vapor calculated from the field regression equation in Figure 1, and (D) wind speed on August 22, 1995, for branches in the upper canopy (solid line) and lower canopy (dotted line) of an *Abies amabilis* stand.

ture under a set of typical conditions. These simulations show that leaf temperature elevations increase as wind speed decreases (causing g_{bH} to decrease) and radiation increases. Although leaf temperatures remained near air temperature at low values of absorbed radiation and at wind speeds higher than 1.5 m s^{-1} , leaf temperature exceeded air temperature by $2 \text{ }^\circ\text{C}$ or more under a large range of conditions. When radiation was high and wind speed was low, leaf temperature elevations could potentially approach $10 \text{ }^\circ\text{C}$; however, leaf temperature elevations of this magnitude were rare in the field. Between August 18 and October 4, 1995, the daytime difference between leaf and air temperature of the upper-canopy branches ranged from -4.2 to $4.7 \text{ }^\circ\text{C}$ (Figure 5A). Leaf temperature of the upper branches was within $1 \text{ }^\circ\text{C}$ of air temperature for 62% of the daylight hours measured, exceeded air temperature by more than $1 \text{ }^\circ\text{C}$ for 30% of the daylight hours measured, and exceeded air temperature by more than $2 \text{ }^\circ\text{C}$ during 10% of the daylight measurements (Figure 5A). The largest difference between leaf and air temperature ($6.6 \text{ }^\circ\text{C}$) occurred on the lower branches.

Smith and coworkers (Hadley and Smith 1987, Smith and Carter 1988, Smith and Brewer 1993) have hypothesized that the clumped shoot structures of high-elevation species such as *Abies lasiocarpa* and *Picea engelmannii* are an adaptation to low air temperatures. According to this hypothesis, the

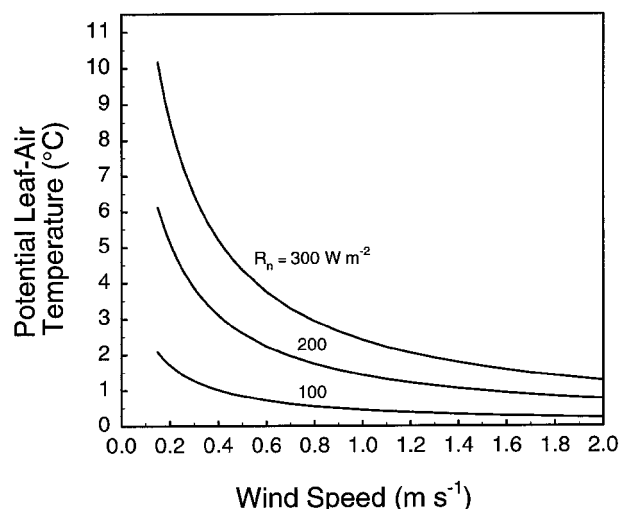


Figure 4. Potential leaf–air temperature difference over a range of wind speeds and absorbed radiation values, given a vapor pressure deficit of 1.5 kPa, an air temperature of 20 °C and stomatal conductance ($g_{s,v}$) of 2 mm s⁻¹. Boundary layer conductance to water vapor transfer was calculated by the field regression described in Figure 1 and converted to r_{bH} as described in the text. Latent heat loss, simulated with the Penman-Monteith equation (Monteith 1965), was allowed to vary with changes in wind speed and radiation.

clumped foliage causes decreased boundary layer conductance to heat loss, and the associated leaf heating brings the leaves closer to the optimum temperature for photosynthesis than if the leaves were at air temperature. This does not appear to be the case for *A. amabilis*. The photosynthesis versus temperature relationship for *A. amabilis* has a broad optimum, with little change in light-saturated net photosynthesis or light response between 10 and 20 °C (Teskey 1982). Although there was a difference between leaf and air temperature distributions in the field (Figure 5B), generally, leaf (and air) temperature remained between 10 and 20 °C, within the flat portion of the photosynthesis temperature response function. Empirical modeling of the response of net photosynthesis to elevated leaf temperature (leaf temperature \geq air temperature) and non-elevated leaf temperature (leaf temperature = air temperature) support these conclusions (Martin 1997). In contrast, air temperatures at the higher elevations where *Abies lasiocarpa* is usually found are frequently far below the photosynthetic temperature optimum for that species (Smith and Carter 1988), making leaf temperature elevations more important for carbon gain in *Abies lasiocarpa* than in *A. amabilis*.

It is unlikely that leaf temperature elevation resulting from sun shoot geometry is important for carbon gain in *Abies amabilis* during most of the growing season. On the other hand, sun shoot geometry may influence carbon gain through its effects on radiation transfer within shoots (Carter and Smith 1985) and within the canopy (Sprugel 1989, Leverenz and Hinckley 1990). Sprugel (1989) pointed out that the arrangement of needles on coniferous sun shoots decreases the interception of light by any individual needle in the upper canopy.

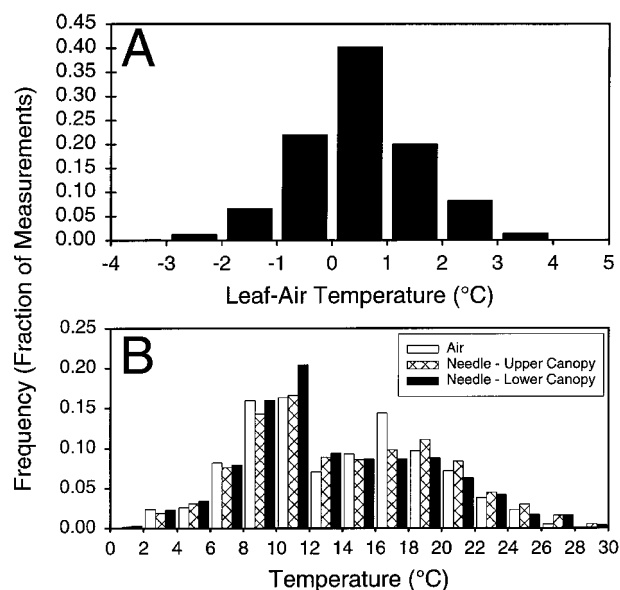


Figure 5. Distributions of five-minute mean daytime leaf and air temperatures in an *Abies amabilis* canopy between August 18 and October 4, 1995 ($n = 6052$). (A) Frequency distribution of five-minute mean leaf-air temperature difference for two branches in the upper canopy. (B) Frequency distribution of five-minute mean temperatures of the air (open bars) and of foliage in the upper canopy (hatched bars) and lower canopy (solid bars).

This serves to “spread” the available radiation throughout the canopy, rather than allowing large fractions of the radiation to be absorbed by the upper leaves, where the amount of light absorbed would exceed the photosynthetic capacity of the foliage. Simulations by Stenberg (1996) support this hypothesis, showing that if productive canopy leaf area is to be maximized, it is necessary for the well-lit foliage in the upper canopy to be less efficient at light interception than foliage lower in the canopy. In other words, the foliage in the upper canopy must be inclined at an angle to illumination from the sun, as is the case with sun shoots in *Abies amabilis* and the other coniferous species mentioned.

Finally, we note that our measurements and those of other researchers demonstrate that, given certain combinations of shoot morphology, wind speed and radiation, leaf temperature of some conifers can depart significantly from air temperature. Although this finding does not eliminate the utility of assuming leaf and air temperature equality, it emphasizes the importance of considering both shoot morphology and environmental conditions when invoking this assumption.

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References

- Angell, R.F. and R.F. Miller. 1994. Simulation of leaf conductance and transpiration in *Juniperus occidentalis*. *For. Sci.* 40:5–17.
- Brooks, J.R., T.M. Hinckley and D.G. Sprugel. 1994. Acclimation responses of mature *Abies amabilis* sun foliage to shading. *Oecologia* 100:316–324.
- Carter, G.A. and W.K. Smith. 1985. Influence of shoot structure on light interception and photosynthesis in conifers. *Plant Physiol.* 79:1038–1043.
- Christersson, L. and R. Sandstedt. 1978. Short-term temperature variation in needles of *Pinus sylvestris* L. *Can. J. For. Res.* 8:480–482.
- Domingo, F., P.R. van Gardingen and A.J. Brenner. 1996. Leaf boundary layer conductance of two native species in southeast Spain. *Agric. For. Meteorol.* 81:179–199.
- Gates, D.M. 1980. *Biophysical ecology*. Springer-Verlag, New York, 611 p.
- Grace, J., F.E. Fasehun and M. Dixon. 1980. Boundary layer conductance of the leaves of some tropical timber trees. *Plant Cell Environ.* 3:443–450.
- Granier, A., R. Huc and S.T. Barigah. 1996. Transpiration of natural rain forest and its dependence on climatic factors. *Agric. For. Meteorol.* 78:19–29.
- Hadley, J.L. and W.K. Smith. 1987. Influence of krummholz mat microclimate on needle physiology and survival. *Oecologia* 73:82–90.
- Harlow, W.M., E.S. Harrar and F.M. White. 1979. *Textbook of dendrology*. McGraw-Hill Book Company, New York, 510 p.
- Hinckley, T.M., J.R. Brooks, J. Ěermák, R. Ceulemans, J. Kušera, F.C. Meinzer and D.A. Roberts. 1994. Water flux in a hybrid poplar stand. *Tree Physiol.* 14:1005–1018.
- Jarvis, P.G. 1971. The estimation of resistances to carbon dioxide transfer. *In* *Plant Photosynthetic Production, Manual of Methods*. Eds. Z. Šesták, J. Ěatsky and P.G. Jarvis. Junk Publishers, The Hague, pp 556–631.
- Jarvis, P.G. and K.G. McNaughton. 1986. Stomatal control of transpiration: scaling up from leaf to region. *Adv. Ecol. Res.* 15:1–49.
- Jarvis, P.G., G.B. James and J.J. Landsberg. 1976. Coniferous forest. *In* *Vegetation and the Atmosphere, Vol. II, Case Studies*. Ed. J.L. Monteith. Academic Press, London, pp 171–240.
- Jones, H.G. 1983. *Plants and microclimate*. Cambridge University Press, Cambridge, 323 p.
- Kaufmann, M.R. 1984. A canopy model (RM-CWU) for determining transpiration of subalpine forests. I. Model development. *Can. J. For. Res.* 14:218–226.
- Körner, C. 1994. Leaf diffusive conductances in the major vegetation types of the globe. *In* *Ecophysiology of Photosynthesis*. Eds. E.-D. Schulze and M.M. Caldwell. Springer-Verlag, Berlin, pp 463–490.
- Köstner, B.M.M., E.-D. Schulze, F.M. Kelliher, D.Y. Hollinger, J.N. Byers, J.E. Hunt, T.M. McSeveny, R. Meserth and P.L. Weir. 1992. Transpiration and canopy conductance in a pristine broad-leaved forest of *Nothofagus*: an analysis of xylem sap flow and eddy correlation measurements. *Oecologia* 91:350–359.
- Landsberg, J.J. and M.M. Ludlow. 1970. A technique for determining resistance to mass transfer through the boundary layers of plants with complex structure. *J. Appl. Ecol.* 7:187–192.
- Landsberg, J.J. and A.S. Thom. 1971. Aerodynamic properties of a plant of complex structure. *Q. J. R. Meteorol. Soc.* 97:565–570.
- Leverenz, J.W. and T.M. Hinckley. 1990. Shoot structure, leaf area index and productivity of evergreen conifer stands. *Tree Physiol.* 6:135–149.
- Leverenz, J.W. and P.G. Jarvis. 1980. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). IX. The relative contribution made by needles at various positions on the shoot. *J. Appl. Ecol.* 17:59–68.
- Lindroth, A. 1993. Aerodynamic and canopy resistance of short-rotation forest in relation to leaf area index and climate. *Boundary-Layer Meteorol.* 66:265–279.
- Martin, T.A. 1997. Transpiration and boundary layer resistance from the shoot to the canopy scale in *Abies amabilis* forests. Ph.D. Dissertation, Univ. of Washington, Seattle, WA, 172 p.
- McNaughton, K.G. and P.G. Jarvis. 1983. Predicting effects of vegetation changes on transpiration and evaporation. *In* *Water Deficits and Plant Growth, Vol. VII*, Ed. T.T. Kozlowski. Academic Press, Inc., San Diego, pp 1–47.
- Meinzer, F.C. 1993. Stomatal control of transpiration. *Trends Ecol. Evol.* 8:289–294.
- Meinzer, F.C., G. Goldstein, N.M. Holbrook, P. Jackson and J. Cavelier. 1993. Stomatal and environmental control of transpiration in a lowland tropical forest tree. *Plant Cell Environ.* 16:429–436.
- Meinzer, F.C., G. Goldstein, P. Jackson, N.M. Holbrook, M.V. Gutierrez and J. Cavelier. 1995. Environmental and physiological regulation of transpiration in tropical forest gap species: the influence of boundary layer and hydraulic properties. *Oecologia* 101:514–522.
- Monteith, J.L. 1965. Evaporation and environment. *Symp. Soc. Exp. Biol.* 19:205–234.
- Monteith, J.L. and M.H. Unsworth. 1990. *Principles of environmental physics*. Edward Arnold, New York, 291 p.
- Nobel, P.S. 1991. *Physiochemical and environmental plant physiology*. Academic Press, San Diego, 635 p.
- Roberts, J., O.M.R. Cabral and L.F. DeAguiar. 1990. Stomatal and boundary-layer conductances in an Amazonian *terra firme* rain forest. *J. Appl. Ecol.* 27:336–353.
- Schuepp, P.H. 1993. Leaf boundary layers: Tansley Review No. 59. *New Phytol.* 125:477–507.
- Smith, D.M., P.G. Jarvis and J.C.W. Odongo. 1997. Aerodynamic conductances of trees in windbreaks. *Agric. For. Meteorol.* 86:17–31.
- Smith, W.K. 1980. Importance of aerodynamic resistance to water use efficiency in three conifers under field conditions. *Plant Physiol.* 65:132–135.
- Smith, W.K. and C.A. Brewer. 1993. The adaptive importance of shoot and crown architecture in conifer trees. *Am. Nat.* 143:528–532.
- Smith, W.K. and G.A. Carter. 1988. Shoot structural effects on needle temperatures and photosynthesis in conifers. *Am. J. Bot.* 75:496–500.
- Sprugel, D.G. 1989. The relationship of evergreenness, crown architecture and leaf size. *Am. Nat.* 133:465–479.
- Sprugel, D.G., J.R. Brooks and T.M. Hinckley. 1996. Effects of light on shoot geometry and needle morphology in *Abies amabilis*. *Tree Physiol.* 16:91–98.
- Stenberg, P. 1996. Simulations of the effects of shoot structure and orientation on vertical gradients in intercepted light by conifer canopies. *Tree Physiol.* 16:99–108.
- Stenberg, P., S. Linder and H. Smolander. 1995. Variation in the ratio of shoot silhouette area to needle area in fertilized and unfertilized Norway spruce trees. *Tree Physiol.* 15:705–712.
- Swinbank, W.C. 1963. Longwave radiation from clear skies. *Q. J. R. Meteorol. Soc.* 89:339–348.

- Tan, C.S., T.A. Black and J.U. Nnyamah. 1978. A simple diffusion model of transpiration applied to a thinned Douglas-fir stand. *Ecology* 59:1221-1229.
- Teklehaimanot, Z., P.G. Jarvis and D.C. Ledger. 1991. Rainfall interception and boundary layer conductance in relation to tree spacing. *J. Hydrol.* 123:261-278.
- Teskey, R.O. 1982. Acclimation of *Abies amabilis* to water and temperature stress in a natural environment. Ph.D. Dissertation, Univ. of Washington, Seattle, WA, 135 p.
- Tibbals, E.C., E.K. Carr, D.M. Gates and F. Dreith. 1964. Radiation and convection in conifers. *Am. J. Bot.* 51:529-538.
- Tucker, G.F., T.M. Hinckley, J. Leverenz and S.-M. Jiang. 1987. Adjustments of foliar morphology in the acclimation of understory Pacific silver fir following clearcutting. *For. Ecol. Manag.* 21:249-268.
- Vanderwaal, J.A. and H.R. Holbo. 1984. Needle-air temperature differences of Douglas-fir seedlings and relation to microclimate. *For. Sci.* 30:635-644.

