

W.L. Bauerle · T.M. Hinckley · J. Cermak · J. Kucera
K. Bible

The canopy water relations of old-growth Douglas-fir trees

Received: 10 January 1998 / Accepted: 12 October 1998

Abstract We investigated whole tree water relations in 56–65 m tall, old-growth *Pseudotsuga menziesii* trees within the Wind River Canopy Crane site, Carson, Washington, USA. We measured at predawn and solar noon the vertical gradients in xylem pressure potential using a pressure chamber. On an *Abies amabilis* sapling located in the understory at the base of one of the study trees, predawn and solar noon xylem pressure potentials were also measured. Xylem pressure potential data were measured from late June through early September 1996 on foliage sampled from 1 to 64.5 m. Over this height gradient, predawn water potentials ranged from -0.23 to -1.10 MPa. Solar noon values showed an even greater range (from -0.44 to -2.51 MPa). At predawn, the water potential gradient approached the theoretical hydrostatic gradient (-0.0105 vs -0.010 MPa m^{-1}). The gradient at solar noon was steeper (-0.0331 MPa m^{-1}). Instantaneous stomatal conductances were not greatly different between young, sapling-sized and old-growth trees [0.094 ± 0.033 (SD) vs 0.086 ± 0.045 cm s^{-1} , respectively]. Stomata of both size classes of trees appeared very sensitive to increasing vapor pressure deficits. A comparison of stable carbon isotope values from the old-growth and sapling-sized trees indicated lower stomatal conductances in the old-growth. This study provides sound documentation regarding the utility of the cohesion theory in the interpretation of water potential gradients. This study also emphasizes inherent differences between sapling-sized and tall, old-growth trees.

T.M. Hinckley (✉) · K. Bible
College of Forest Resources, Box 352100,
University of Washington, Seattle, WA 98195, USA

W.L. Bauerle
Department of Floriculture and Ornamental Horticulture,
Cornell University, Ithaca, NY 14853, USA

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

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

Introduction

Under static conditions of no water flow and assuming cohesive forces in water conducting columns, a theoretical gradient in water potential due to gravity of about -0.01 MPa m^{-1} should be observed between the soil and some measurement point in the plant above the soil (Scholander et al. 1965; Zimmermann 1983). One of Scholander et al.'s (1965) gradients was derived using branches shot from a Douglas-fir tree (*Pseudotsuga menziesii*) between 0730 and 1700 hours. In a review of these data, Zimmermann acknowledged the closeness of the observed to the theoretical hydrostatic gradient, but remarked about how little the gradient observed by Scholander et al. varied during the day (Zimmermann and Brown 1977). An examination of the older literature illustrates considerable deviation in observed gradients (ranging from much steeper to even inverted gradients) from the theoretical gravitational gradient (Hellkvist et al. 1974; Hinckley and Ritchie 1970; Hinckley et al. 1978; Richter 1973; Tobiessen et al. 1971; Zimmermann 1978). More recent literature has questioned the entire cohesion theory (e.g., Zimmermann 1993; Zimmermann et al. 1995; Canny 1997, 1998a, b, c).

Three relatively recent developments suggest that this is an appropriate time to re-examine the nature of water potential gradients in tall trees. First, Zimmermann et al. (1995) and Canny (1998a–c) have called into question the cohesion theory, the use of the pressure chamber and whether highly negative water potentials really do exist in tall trees. Although papers by Holbrook et al. (1995), Pockman et al. (1995), Tyree (1997), and Sperry (1998) provide excellent data refuting these challenges, still the perception exists that the cohesion theory is inadequate. Our paper, using the canopy crane to provide rapid and repeated sampling of foliage from several heights in several large Douglas-fir trees, clearly illustrates the nature of the gradients and provides a parsimonious conceptual framework, based on the cohesion theory, to interpret them. Second, Ryan and Yoder (1997), building on the concepts of hydraulic architecture and the constraints it

places on water flow (e.g., Zimmermann 1983, Sperry 1995), hypothesize that there are limits to the maximum heights trees can achieve and these limits are most often set by stem hydraulic conductivity. Our data illustrate both the water potential values found in the tops of tall trees and how these values compared with values from younger, shorter trees. Finally, there is clear evidence that seedlings, saplings and large trees react very differently to both natural and anthropogenic stresses (Chapelka and Samuelson 1998; Fredericksen et al. 1996a,b; Grulke and Miller 1994; Kelly et al. 1995; Kolb et al. 1997; Samuelson and Edwards 1993). Our data on stomatal conductances and stable isotopes of carbon provide further information about these differences.

Materials and methods

Site location and description

The Wind River Canopy Crane Research Facility (WRCCRF) is located in the T.T. Munger Research Natural Area of the Gifford Pinchot National Forest, near Carson in Skamania County, Washington. The site is an old-growth Douglas-fir/western hemlock (*Pseudotsuga menziesii*/*Tsuga heterophylla*) forest positioned on gentle topography near the base of Trout Creek Hill, an extinct volcano. Elevation is 340 m; the latitude is 45°49'13.76"N and the longitude is 121°57'06.88"W.

The WRCCRF is the second site in the world with a high-rise, free-standing construction crane (Liebherr 550 HC, top of mast 87 m) and the first in a temperate forest (Holden 1995, Stork et al. 1997). Researchers ride in a gondola attached to a 85 m long crane jib (the highest point the gondola can reach is 69 m). The gondola accesses an area of 2.3 ha.

Climate and soils

The maritime Pacific climate of the region is characterized by a wet winter and dry summer. The mean annual precipitation is approximately 2528 mm. Most of the precipitation falls between October and May, and the decreased precipitation between June and September (~119 mm) creates potential summer drought conditions. The mean annual snowfall is 233 cm and the mean annual temperature is 8.7°C. The site experiences the following extremes in temperature: January 0°C (mean) and -3.7°C (mean minimum), July 17.5 °C (mean) and 26.9 °C (mean max.) (U.S. Weather Bureau 1965). The soils are classified as entic dystrandepts, medial, mesic belonging to the Staebler series and these entisols are coarse-textured (homogenous loamy sands and sandy loams) developing in 2–3 m of volcanic tephra over lahar and olivine basal bedrock (Wise 1970). There is no evidence to suggest there have been wildfires within the natural area during the last 200–300 years.

Experimental stand

The dominant tree species, estimated to be 460 years old, are Douglas-fir and western hemlock. The projected leaf area index is estimated to be around 10.3 (Thomas and Winner, personal communication). A complete description of the site can be found in Franklin et al. (1972), Franklin and DeBell (1988), Kemp and Shuller (1982) and on the WRCCRF web site (<http://weber.u.washington.edu/~wrccrf>).

On the crane plot all trees with diameter at breast height (DBH) equal to or greater than 5 cm were measured, marked, numbered and mapped (Freeman, Ford, Shaw and Bible, unpublished data). Altogether there are 446 living trees and 97 dead

trees per ha. Stand basal area is 114.3 m² ha⁻¹ of which 72.6% is alive.

The upper canopy is uneven, with groups and individuals of the large, dominant Douglas-fir trees separated by gaps. Such a configuration allows the crowns of large trees to be quite long (20–35 m) and to grow in relatively open conditions similar to a solitary tree. Leaf area distribution in this canopy has been estimated from light extinction (Parker 1997).

Study trees

Three old-growth, dominant Douglas-fir trees were selected for intensive study. These trees were numbered as follows: 40 (56 m tall), 91 (65 m), and 1373 (57 m). These trees were selected based on the following criteria: healthy crown, low, live branches on the south side and accessible from gondola, healthy new growth, and abundant lateral branches. A 1.1 m Pacific silver fir (*Abies amabilis*) near the base of tree 1373 was incorporated into the study to provide a ground level measure of water potential. In addition, several 2–4 m tall, exposed, 5- to 10-year-old Douglas-fir trees (hereafter referred to as "sapling-sized trees"), located about 800 m south of the canopy crane circle at the border between the old-growth forest and the Wind River nursery, were included for comparative purposes.

Measurement techniques

A Scholander-Hammel pressure chamber was used to measure branchlet water potential (Soil Moisture, Santa Barbara, Calif.). A LI-1600 steady-state porometer (Li-Cor Inc., Lincoln, Neb.), equipped with an enclosed conifer cuvette (Li 1600-07), was used to measure stomatal conductance, photosynthetic photon flux density, relative humidity, and transpiration. Additional meteorological data were collected at 70 m on the canopy crane using a Campbell Scientific Weather Station maintained by the WRCCRF.

Measurement protocols

On 6 days (June 20, July 9, 30, August 14, 29, and September 18) during the summer of 1996, predawn and solar noon water potential were measured at three canopy positions (top, middle, and bottom) in old-growth Douglas-fir trees and from a single canopy position in the 1 m tall, understory Pacific silver fir. For July 26, 27, 29 and August 2, water potential and stomatal conductance were measured on the exposed, sapling-sized Douglas-fir trees.

For water potential readings, branchlets were removed with a sharp razor blade from the three canopy positions using the gondola, and from ground level foliage on foot. The use of the gondola meant that times between excision and initial pressurization rarely exceeded 20 s.

For porometer readings, foliage samples were prepared 24 h prior to first reading. A foliated lateral branchlet was selected from near the area where water potential branchlets were to be sampled, enough foliage was removed so that the chamber could be sealed over the branch. At least two branchlets were prepared at each sample location. Because foliage was still expanding on June 20, porometer readings were not taken until almost 3 weeks later on July 9.

Measurement methods for tall trees

For each sample date and tree, two sets of three foliated twigs were selected for water potential measurements from the upper, middle, and lower parts of the crown on the south side of each tree. One individual of each of the twig sets was covered with aluminum foil before sunset ("covered"). Before dawn, two twigs of the first pair ("uncovered") were removed and their water potential was measured. Immediately thereafter, the third twig of the set was removed and, while still covered with foil, its water potential

measured. At solar noon, the second sample set was measured in a similar fashion. A comparison of water potential in two nearby twigs, one covered and the other uncovered, is a possible way to examine the role of xylem hydraulic capacity on friction potential (after Richter 1973) and its effect on water potential gradients. The measurement of water potential in the covered twig provides an estimate of the local water potential of the xylem stream to which the second, exposed twig is attached.

Stomatal conductance was measured in the top and middle canopy positions at predawn and solar noon in all study trees on July 9 and 30, August 14 and 29, and September 18. Additional readings between 0700 and 0830 hours were taken on 2 days in order to measure stomatal conductances when light and vapor pressure deficit were not likely limiting.

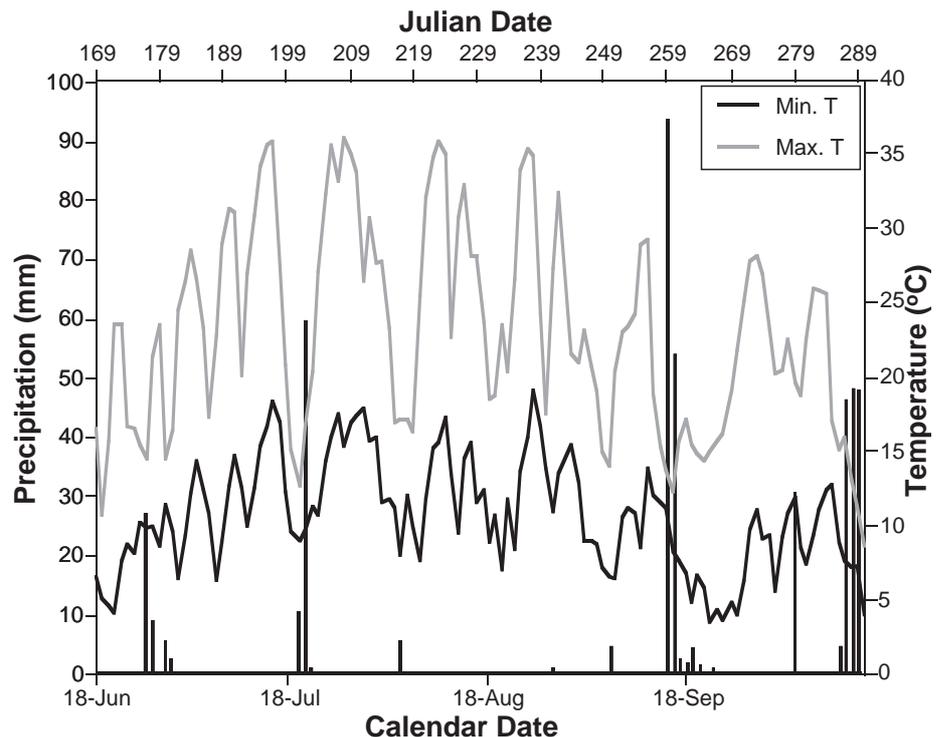
Measurement methods for sapling-sized trees

For July 26, 27, 29, and August 2, water potential and stomatal conductance were measured at predawn and solar noon on 5- to 10-year-old Douglas-fir saplings located outside of the old-growth forest at the edge of the nursery. On July 26 and 29, additional readings were taken every 3 h from predawn to 2100 hours. At predawn and solar noon, water potential in two uncovered and one foil-covered twig was measured. At all other times, water potential and stomatal conductance were measured from two twigs. Sample twigs were located between 1 and 2.5 m above the ground on the south side of these saplings.

Twig samples

Branchlets used for porometer measurements were harvested in October 1996, sealed in plastic bags, and brought to the University of Washington for further analysis. Projected leaf area of the samples was measured with a PC-based video image analysis system (OPTIMAS, Optimas Digital Area Analyzer). The needle samples were then dried at 70°C, and after 24 h, dry weights were recorded. The needles were then crushed and ground with a mortar and pestle, and a 1 mg sub-sample was sent to the Duke University Phytotron for $\delta^{13}\text{C}$ and %N analysis.

Fig. 1 Precipitation and air temperature at 70 m throughout the study period (both calendar and Julian Date shown). Two lines are shown; the *solid light line* illustrates maximum daily air temperature whereas the *solid black line* illustrates minimum daily air temperature. Precipitation is illustrated with *solid vertical lines*



Results and discussion

Seasonal patterns

Figure 1 illustrates the pattern of temperature and rainfall from 18 June to 15 October 1996. Two nested patterns of maximum and minimum temperature variation were observed over this time period. First, maximum temperature increased from nearly 20°C in the middle of June to just over 35°C by mid-July, remained near this maximum until late August, and then declined to less than 10°C by the middle of October. Second, within this broad pattern, another pattern was observed. This pattern was associated with the movement of marine air masses inland and resultant decreases in temperature and increases in humidity and cloudiness. Often precipitation occurred during these periods of cloudiness; however, precipitation was highly variable, ranging from less than 1 to 56 mm.

Table 1 shows values for predawn and solar noon water potential (Ψ) for the three old-growth trees and for the understory Pacific silver fir. For foliage samples taken from the top of the old-growth Douglas-fir trees, predawn Ψ ranged from highs of -0.78 MPa to lows of -1.10 MPa. Seasonal differences were minimal, and values less than -1.1 MPa for foliage from the tops of these overstory study trees were never observed. Tree 91 always had more negative predawn Ψ values than trees 40 and 1373; however, these more negative values could mostly be attributed to the 9 m greater measurement height in tree 91 (mean difference = 0.12 MPa; hydrostatic difference = 0.09 MPa). For understory Pacific silver fir, predawn Ψ ranged from -0.23 to -0.38 MPa. These relatively high values suggested that soil water stresses did not occur in this tree during the summer of 1996.

Table 1 Data on predawn and solar noon water potentials in the three old-growth (OG) Douglas-fir trees (40, 91, 1373) and the understory Pacific silver fir sapling. For predawn values, average value for the overstory trees is given for foliage covered in aluminum foil ($n=3$) whereas for the understory sapling $n=2$. For solar noon

values, data are for foliage not covered in foil ($n=6$ for overstory trees and $n=2$ for understory sapling). For the old-growth trees, only data for the tops of the crown are given. Missing data are left blank

Date	Predawn water potentials				Solar noon water potentials			
	OG average	OG max	OG min	Understory	OG average	OG max	OG min	Understory
June 20	-1.02	-0.97	-1.09 ^a		-1.81	-1.77	-1.84 ^a	
July 9	-1.04	-1.01	-1.10 ^a		-1.71	-1.66	-1.78 ^a	
July 30	-0.87	-0.82	-0.93 ^a	-0.33	-2.17	-2.09	-2.24 ^b	-0.62
August 14				-0.35	-2.28	-2.22	-2.38 ^c	-0.55
August 29	-0.95	-0.88	-1.05 ^a	-0.38	-2.30	-2.09	-2.51 ^b	-0.75
September 18	-0.84	-0.78	-0.90 ^a	-0.23	-2.16	-2.00	-2.33 ^a	-0.44

^a Minimum value measured in tree 91

^b Minimum value measured in tree 40

^c Minimum value measured in tree 1373

Even the exposed Douglas-fir saplings located at the edge of the old-growth forest and the nursery did not have predawn values less than -0.6 MPa (data not shown, Bauerle 1997). For all three groups of trees, predawn water potentials were surprisingly high considering the summer drought (e.g., Zobel et al. 1976).

Table 1 also lists the water potential values at solar noon for the study trees. Solar noon Ψ values ranged from -1.66 to -2.51 MPa in the top of the old-growth Douglas-fir trees and from -0.44 to -0.75 MPa in the understory Pacific silver fir. Average differences among the three overstory trees were slightly greater at solar noon (0.21 MPa) than at predawn (0.12 MPa). These differences at solar noon could not be explained by differences in measurement height.

Because of the maritime-Mediterranean climate of western Washington, soil water content is high at the beginning of the growing season and then generally declines as the season progresses. Flows of maritime air inland during the summer (and associated precipitation events) may temporarily reduce or even alleviate the rate of soil drying; however, soil moisture does not begin to recover until late in the growing season. In spite of these climatic patterns and other indices of summer drought such as the mid-June cessation of water flow in the intermittent stream, predawn water potentials varied very little and remained relatively high in overstory, understory and exposed, sapling-sized trees. Stand level adjustments in canopy conductance and leaf area leading to low rates of whole-tree transpiration (Cermak et al. unpublished data), and deep moisture moving along the top of the buried lava flow may have resulted in an adequate supply of moisture for the entire summer of 1996.

Except for the first two measurement periods, when soil moisture was still relatively high, solar noon water potential values were less than -2.0 MPa in the tops of the study overstory trees. These water potential values are lower than those previously reported in 15–30 m Douglas-fir trees (Lassoie 1973). The most negative solar noon water potential measured in the exposed, sapling-sized Douglas-fir at Wind River was -1.75 MPa (data not shown, Bauerle 1996). There is considerable evi-

dence of crown stress and dieback for large, old-growth canopy trees at the site. Gravity's effect on the water column (described in the next section) may impede growth at the top of the crown in tall trees and may lead to branch and top dieback as the result of sheer height and hydraulic limitations (Ryan and Yoder 1997).

Water potential gradient

Figure 2 illustrates the relationship between predawn water potential and height for the three overstory Douglas-fir trees and the single understory Pacific silver fir. The values shown were averaged for July 30, August 29 and September 18. It is noteworthy that the estimated predawn water potential at 1 m in the tall Douglas-fir trees matched the measured value in the understory Pacific silver fir. There was a statistically significant relationship between predawn water potential and height ($P=0.001$ and $R^2=0.96$). Based upon the 95% confidence limits, the slopes of the lines derived from covered (-0.0105 MPa m^{-1}) or uncovered foliage (-0.0108 MPa m^{-1}) and the theoretical hydrostatic gradient imposed by gravity on a standing water column (-0.010 MPa m^{-1}) were statistically identical.

In contrast to the predawn situation, the relationship between solar noon water potential and height showed a steeper slope (-0.019 MPa m^{-1}), a more negative intercept (-1.19), and a lower R^2 (0.83) (Fig. 3). The change in slope from predawn to solar noon indicates that water potential declines more steeply with height at solar noon because of combination of the frictional and hydrostatic components of water transport (Richter 1973). Differences at any point in the crown between the predawn and the solar noon lines illustrate the effect of friction on the water potential value (at 30 m, the contribution is about 1.1 MPa and at 65 m, it is almost 1.4 MPa). The intercept for the solar noon regression line is not only more negative than the predawn intercept, it is also considerably more negative than the water potential measured in the understory Pacific silver fir (-0.69 MPa). The difference in water potential between predawn and solar noon

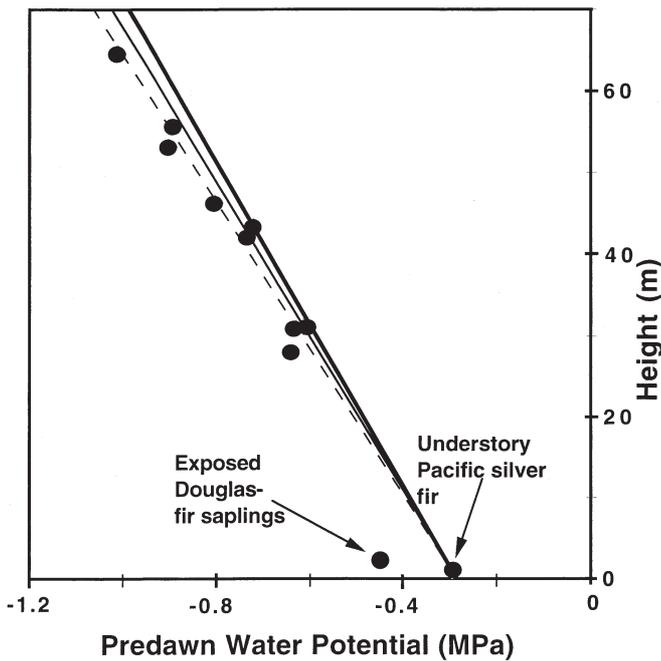


Fig. 2 Relationship between height and predawn water potential in the three old-growth Douglas-fir trees, the exposed Douglas-fir saplings, and the single, understory Pacific silver fir sapling. Three lines are shown; the *thick, solid line* illustrates the theoretical hydrostatic gradient (-0.01 MPa m^{-1}) whereas the *thin, solid line* is the least squares regression line for foliage samples covered with aluminum foil (slope= $-0.0105 \text{ MPa m}^{-1}$) and the *dashed line* is for samples not covered (slope= $-0.0108 \text{ MPa m}^{-1}$). The actual mean data points are shown for the later case. Each data point is for the top, middle and bottom crown positions in the overstory trees and is the average of 6 (not covered) readings. The readings were from July 20, August 29 and September 18. The readings for the understory Pacific silver fir come from the same dates and $n=6$. Data for the exposed, Douglas-fir saplings come from July 26, 27, 29 and August 2 ($n=12$). The Type II regression model was also explored (Sokal and Rohlf 1981) and gave the following results: $Y=-0.225-0.011 X$ for covered foliage and $Y=-0.243-0.012 X$ for uncovered foliage. Lines were not statistically different from each other or from the theoretical line

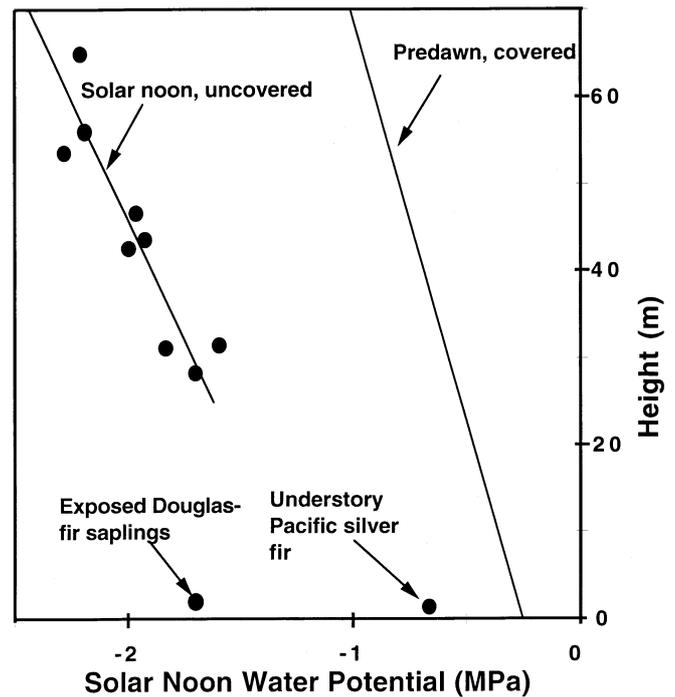


Fig. 3 Relationship between height and solar noon water potential in the three old-growth Douglas-fir trees, the exposed Douglas-fir saplings and the single, understory Pacific silver fir sapling. Two lines are shown: the first line is the least squares regression line observed for predawn water potential of Al-foil covered foliage. The second is the least squares regression line for solar noon values of water potential in foliage from only the old-growth trees and not covered with Al foil ($Y=-1.19-0.019X$, $R^2=0.83$). Each data point is the average of 8 (non-Al foil covered) readings (2 per time, 4 days). The readings were from July 20, August 14 and 29 and September 18. Data for the understory Pacific silver fir come from the same dates and $n=8$. Data for the exposed, Douglas-fir saplings come from July 26, 27, 29 and August 2 ($n=12$) saplings. The Type II regression model was also explored (Sokal and Rohlf 1981) and gave the following results: $Y=-1.189-0.017 X$ for uncovered foliage. The slope was not statistically different from the predawn slopes (Fig. 2), but was from the theoretical line. The intercept was statistical different from the predawn intercept

ranged from 0.2 to 0.4 MPa in the understory Pacific silver fir, to around 1.1 MPa at the base of the crown of the Douglas-fir trees to 1.3 MPa at the very top. The brighter, hotter and drier microenvironment of the canopies of the overstory trees versus the dimmer, cooler, more humid microenvironment near the forest floor was largely responsible for this difference (Parker 1997). When solar noon values of water potential from the understory Pacific silver fir (-0.59 MPa) are compared with those from the exposed Douglas-fir saplings (-1.68 MPa), again differences in microenvironment may have led to the difference.

Stomatal conductance

Only a limited number of stomatal conductance values were taken in both the old-growth and sapling-sized trees

($n=116$). From these values, the following results were noted. First, mean stomatal conductance at predawn was 0.004 ± 0.007 (SD) cm s^{-1} whereas solar noon values averaged 0.075 ± 0.026 cm s^{-1} in the old-growth, a statistically significant difference ($P=0.001$, paired t -test). Second, there were tree-to-tree differences in the old-growth trees, but these were small (0.065 , 0.057 and 0.078 cm s^{-1} for trees 40, 91 and 1373, respectively), statistically insignificant ($P=0.147$, ANOVA) and appeared to be related to differences in height and crown exposure. Third, the mean difference in stomatal conductance between old-growth and sapling-sized trees was small [mean of all stomatal conductance values when $\text{PAR}=300 \mu\text{mol m}^{-2} \text{ s}^{-1}$ was 0.086 ± 0.045 (SD) cm s^{-1} for the old-growth trees and 0.094 ± 0.033 cm s^{-1} for the sapling-sized trees; $P=0.145$, paired t -test]. Finally, stomatal conductances of both old-growth and sapling-sized trees were sensitive to vapor pressure deficit, decreasing rapidly at vapor pres-

sure deficits greater than 1 kPa (data not shown, Bauerle 1997).

The plant tissue value of the stable carbon isotope ratio ($\delta^{13}\text{C}$) provides a measure of the degree of biochemical and biophysical discrimination between the two stable isotopes of carbon, ^{12}C and ^{13}C (Farquhar et al. 1989). For C_3 plants with relatively open stomata, one expects values of $\delta^{13}\text{C}$ to be between -28 and -32‰ . In contrast, with stomatal closure, values should be between -23 and -25‰ . In contrast to mean stomatal conductances, mean values for $\delta^{13}\text{C}$ were statistically different [mean for the upper exposed current foliage of old-growth trees and exposed sapling sized trees was -25.184 ± 0.237 (SD) ‰ versus $-29.62 \pm 0.388\text{‰}$; $P=0.001$, paired t -test]. Since $\delta^{13}\text{C}$ is an integrated indicator of the ratio between photosynthesis and stomatal conductance (Ehleringer et al. 1993), differences in $\delta^{13}\text{C}$ can result from differences in stomatal conductance, differences in rates of photosynthesis or both. Our porometer measurements do not indicate large differences in stomatal conductance between foliage of sapling-sized and old-growth trees. While we did not measure photosynthetic rates, differences in N concentration (which should be linearly correlated with photosynthetic capacity, Evans 1989) between sapling and old-growth foliage were small (1.34 and 1.23%, respectively) and not statistically different ($P=0.089$, paired t -test), implying only small differences in photosynthesis. In contrast, the large differences in $\delta^{13}\text{C}$ suggest large differences in one or both of these processes. The work of Ryan and Yoder (1997) indicates that in tall trees, differences in stomatal conductance are more likely. Therefore, it is likely that our very limited temporal sampling of stomatal conductances failed to characterize fully existing differences between these two very differently sized and aged tree types. Clearly more work needs to be done to understand the difference between the instantaneous measurements of stomatal conductance and the longer-term $\delta^{13}\text{C}$ values better. However, the direction of the difference was consistent whether instantaneous or integrated values of stomatal conductances were used.

Frictional potential

As presented earlier, it is possible to compare the two lines in Fig. 3 and thereby visualize the influence of friction on measured water potential. Based on this comparison, friction accounted for 0.4 MPa in the understory tree and between 1.1 and almost 1.4 MPa in the overstory trees. Unfortunately, it is not possible to isolate what part of the soil-plant-atmospheric continuum is responsible, and in what proportion, for this frictional influence. Possibilities range from xylem hydraulic capacity to localized drying in the soil.

At predawn, Ψ in covered branchlets from all canopy positions in the old-growth trees averaged -0.76 MPa, whereas in uncovered branchlets, it averaged -0.81 MPa, a statistically insignificant difference ($P=0.487$, paired t -test). However, the difference at solar noon exceeded

0.30 MPa ($P < 0.001$, paired t -test). An even larger difference was noted in the sapling-sized trees at solar noon, 0.46 MPa. These differences suggest that, even at a very local, relatively small scale, considerable friction exists in the water conduction pathway of a branch. Combining these results with those from the consideration of the hydrostatic gradients suggest that water potentials in the tops of tall trees are often quite negative. As hypothesized by Ryan and Yoder (1997), the water potential of the foliage at the tops of tall trees exists near critical values for cavitation, a condition largely set by the distance from the water table and the hydraulic capacity of the xylem. As a result, stomata are more often closed and carbon gain is reduced.

In conclusion, differences in stomatal conductances (i.e., small in instantaneous and large in integrated estimates) between tall and short trees were observed and support an emerging hypothesis developed by Ryan and Yoder (1997). As originally noted by Scholander et al. (1965), water potential measured at pre-dawn followed the predicted hydrostatic gradient. Although no foliage was located below 28 m in the old-growth trees, inclusion of data from an understory, 1 m tall sapling did not affect the slope of the line. It is important to note that the cohesion theory effectively explained the behavior of water potential in both types of trees. At solar noon, gradients in water potential were steeper than the hydrostatic; however, these gradients were understandable in light of transpirational water movement and decreases in water potential due to friction. These steeper gradients contrasted with those observed by Scholander et al. (1965), but nicely fit the conceptual considerations of Richter (1973) and Zimmermann (1978, 1983).

Acknowledgements The authors thank E. Van Volkenburgh and F. Meinzer for technical assistance, T.A. Martin, P. Gayaldo, J. Reynolds, K.J. Brown, D.W. Peterson, J. Rombold, C. Wright, and D. Gilbert for helpful discussions, and the Wind River Canopy Crane staff (D. Shaw, M. Creighton, B. Baker, and P. Foster) for assistance with the research study. Excellent critical reviews were provided by Drs. M. Abrams and T.E. Kolb. Funding support was provided by DOE's Westgec sub-program of NIGEC.

References

- Bauerle WL (1997) Diurnal water potential gradients in relation to water loss from old growth Douglas-fir *Pseudotsuga menziesii* tree. Unpublished M.S. thesis, University of Washington, Seattle, Wash.
- Canny MJ (1997) Vessel contents during transpiration-embolisms and refilling. *Am J Bot* 85:1223–1230
- Canny MJ (1998a) Transporting water in plants. *Am Sci* 86: 152–159
- Canny MJ (1998b) Dr. Canny replies (letter to the editors). *Am Sci* 86: 214–215
- Canny MJ (1998c) Applications of the compensating pressure theory of water transport. *Am J Bot.* 85:897–909
- Chappelka AH, Samuelson LJ (1998) Ambient ozone effects on forest trees of the eastern United States: a review. *New Phytol* 139:91–108
- DeBell DS, Franklin FF (1987) Old-growth Douglas-fir and western hemlock: a 36-year record of growth and mortality. *West J Appl For* 2:111–114

- Ehleringer JR, Hall AE, Farquhar GD (1993) Stable isotopes and plant carbon-water relations. Academic Press, San Diego, Calif
- Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia* 78:9–19
- Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. *Annu Rev Plant Physiol Plant Mol Biol* 40:503–537
- Franklin JF, DeBell DS (1988) Thirty-six years of tree population change in an old-growth *Pseudotsuga-Tsuga* forest. *Can J For Res* 18:633–639
- Franklin JF, Hall FC, Dyrness CT, Maser CH (1972) Federal research natural areas in Oregon and Washington: a guidebook for scientists and educators. USDA For. Serv. Pac. Northwest For. and Range Exp. Stn., Portland, Ore.
- Fredericksen TS, Skelly JM, Steiner KC, Kolb TE, Kouterick KB (1996a) Size-mediated foliar response to ozone in black cherry trees. *Environ Pollut* 91:53–63
- Fredericksen TS, Steiner KC, Skelly JM, Joyce BJ, Kolb TE, Kouterick KB, Ferdinand JA (1996b) Diel and seasonal patterns of leaf gas exchange and xylem water potentials of different-sized *Prunus serotina* Ehrh trees. *Forest Sci* 42:359–365
- Grulke NE, Miller PR (1994) Gas exchange characteristics from seedlings to mature trees in giant sequoia: implications for response to current and future concentrations of atmospheric ozone. *Tree Physiol* 14:659–668
- Hellkvist J, Richards GP, Jarvis PG (1974) Vertical gradients of water potential and tissue water relations in Sitka spruce trees measured with the pressure chamber. *J Appl Ecol* 11:637–668
- Hinckley TM, Ritchie GA (1970) Within-crown patterns of transpiration, water stress, and stomatal activity in *Abies amabilis*. *Forest Sci* 16:490–493
- Hinckley TM, Lassoie JP, Running SW (1978) Temporal and spatial variations in the water status of forest trees. *For Sci Monogr* 20:1–78
- Holbrook NM, Burns MJ, Field CB (1995) Negative xylem pressures in plants: a test of the balancing pressure technique. *Science* 270:1193–1194
- Holden C (1995) Canopy open for business. *Science* 268:645–647
- Kelly JM, Samuelson L, Edwards G, Hanson P, Kelting D, Mays A, Wullschlegel S (1995) Are seedlings reasonable surrogates for trees? An analysis of ozone impacts on *Quercus rubra*. *Water, Air Soil Pollut* 85:1317–1324
- Kemp L, Shuller R (1982) Checklist of the vascular plants of Thorton T. Munger Research Natural Area. USDA Forest Service PNW-4, February 1982
- Kolb TE, Fredericksen TS, Steiner KC, Skelly JM (1997) Issues in scaling tree size and age responses to ozone: a review. *Environ Pollut* 98:195–208
- Lassoie JP (1973) Diurnal dimensional fluctuations in a Douglas-fir stem in response to tree water status. *Forest Sci* 19:251–255
- Parker GG (1997) Canopy structure and light environment of an old-growth Douglas-fir/western hemlock forest. *Northwest Sci* 71:261–270
- Pockman WT, Sperry JS, O'Leary JW (1995) Sustained and significant negative water pressure in xylem. *Nature* 378:715–716
- Richter H (1973) Frictional potential losses and total water potential in plants: a re-evaluation. *J Exp Bot* 24:983–994
- Ryan RG, Yoder BJ (1997) Hydraulic limits to tree height and tree growth. *Bioscience* 47:235–242
- Samuelson LJ, Edwards GS (1993) A comparison of sensitivity to ozone in seedlings and trees of *Quercus rubra* L. *New Phytol* 125:373–379
- Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA (1965) Sap pressure in vascular plants. *Science* 148:339–346
- Sokal RR, Rohlf FJ (1981) *Biometry*. W.H. Freeman&Co., New York, p 859
- Sperry JS (1995) Limitations on stem water transport and their consequences. In: Gartner BL (ed) *plant stems*. Academic Press, San Diego, pp 105–124
- Sperry JS (1998) A water fight (letter to the editors). *Am Sci* 86:214
- Stork NE, Wright SJ, Mulkey SS (1997) Craning for a better view: the canopy crane network. *TREE* 12:418–420
- Tobiessen P, Rundel PW, Stecker REW (1971) Water potential gradient in a tall *Sequoiadendron*. *Plant Physiol* 48:303–304
- Tyree MT (1997) The cohesion-tension theory of sap ascent: current controversies. *J Exp Bot* 48:1753–1765
- U.S. Weather Bureau (1965) Climatic summary of the United States supplement for 1951 through 1960, Washington, Climatology of the United States 86–39
- Wise WS (1970) Cenozoic volcanism in the Cascade Mountains of southern Washington. Washington Department Conserv, Div Mines and Geol Bull 60, p 45
- Zimmermann MH (1978) Hydraulic architecture of some diffuse-porous trees. *Can J Bot* 56:2286–2295
- Zimmermann MH (1983) Xylem structure and the ascent of sap. Springer, Berlin Heidelberg New York, pp 1–143
- Zimmermann MH, Brown CL (1977) *Trees structure and function*. Springer, Berlin Heidelberg New York, p 336
- Zimmermann U, Meinzer FC, Benkert F, Zhu JJ, Schneider H, Goldstein G, Kuchenbrod E, Haase A (1994) Xylem water transport: is the available evidence consistent with the cohesion theory? *Plant Cell Environ* 17:1169–1181
- Zobel DB, McKee A, Hawk GM, Dyrness CT (1976) Relationships of environment to composition, structure, and diversity of the forest communities of the central western Cascades of Oregon. *Ecol Monogr* 46:135–156