

Michael G. Ryan · Barbara J. Bond · Beverly E. Law
Robert M. Hubbard · David Woodruff
Emil Cienciala · Jiri Kucera

Transpiration and whole-tree conductance in ponderosa pine trees of different heights

Received: 19 April 1999 / Accepted: 23 March 2000

Abstract Changes in leaf physiology with tree age and size could alter forest growth, water yield, and carbon fluxes. We measured tree water flux (Q) for 14 ponderosa pine trees in two size classes (12 m tall and ~40 years old, and 36 m tall and ~290 years old) to determine if transpiration (E) and whole-tree conductance (g_t) differed between the two sizes of trees. For both size classes, E was approximately equal to Q measured 2 m above the ground: Q was most highly correlated with current, not lagged, water vapor pressure deficit, and night Q was <12% of total daily flux. E for days 165–195 and 240–260 averaged 0.97 mmol m^{-2} (leaf area, projected) s^{-1} for the 12-m trees and 0.57 mmol m^{-2} (leaf area) s^{-1} for the 36-m trees. When photosynthetically active radiation (I_p) exceeded the light saturation for photosynthesis in ponderosa pine ($900 \mu\text{mol m}^{-2}$ (ground) s^{-1}), differences in E were more pronounced: 2.4 mmol m^{-2} (leaf area) s^{-1} for the 12-m trees and 1.2 mmol m^{-2} s^{-1} for the 36-m trees, yielding g_t of 140 mmol m^{-2} (leaf area) s^{-1} for the 12-m trees and 72 mmol m^{-2} s^{-1} for the 36-m trees. Extrapolated to forests with leaf area index = 1, the 36-m trees would transpire 117 mm between 1 June and 31 August compared to 170 mm for the 12-m trees, a dif-

ference of 15% of average annual precipitation. Lower g_t in the taller trees also likely lowers photosynthesis during the growing season.

Key words Transpiration · Whole-tree conductance · Hydraulic conductance · Humidity response of stomatal conductance

Introduction

Our understanding of the ecophysiological response of forest trees to the environment largely comes from studies of young, plantation-grown specimens and seedlings, and few studies have examined how physiology changes with tree size or tree age. However, sequestration of nutrients in biomass, changes in hydraulic conductance of stems, and differences in gene expression with age can alter tree physiology (Ryan et al. 1997). These changes in physiology that occur with tree size or age are important for modeling the growth of forests through time (Ryan et al. 1997), determining whether tropical forests are net sources or sinks of carbon (Lugo and Brown 1992), understanding whether the conversion of old-growth forests to plantations will increase rates of carbon storage (Harmon et al. 1990), and predicting the interaction of hydraulic properties and canopy gas exchange (Williams et al. 1996).

Several studies suggest that physiology can differ with tree size or age. Photosynthesis (A) and stomatal conductance (g_s) declined more rapidly with increasing saturation vapor pressure deficit (D) in older taller conifers (Hubbard et al. 1999; Yoder et al. 1994) and broadleaves (Fredericksen et al. 1996). Hydraulic conductance declined with increasing tree age and height in Scots pine (Mencuccini and Grace 1996), potentially lowering canopy conductance, assimilation and wood growth. Foliage of the same age growing on older, taller trees can have lower photosynthetic capacity and g_s (Grulke and Miller 1994; Kull and Koppel 1987; Schoettle 1994), lower dark respiration (Grulke and Miller 1994) and

M.G. Ryan (✉) · R.M. Hubbard
USDA Forest Service, Rocky Mountain Research Station,
240 West Prospect RD, Fort Collins, CO 80526, USA
e-mail: mryan@lamar.colostate.edu
Tel.: +1-970-4981012, Fax +1-970-4981010

M.G. Ryan
Graduate Degree Program in Ecology, Colorado State University,
Fort Collins, CO 80523, USA

B.J. Bond · B.E. Law · D. Woodruff
Department of Forest Science, Oregon State University,
Corvallis, OR 97331, USA

E. Cienciala
Department of Soil Sciences (Environmental Physics),
Swedish University of Agricultural Sciences,
PO Box 7014, 75007, Uppsala, Sweden

J. Kucera
Environmental Measuring Systems,
Turisticka 5, 62100 Brno, Czech Republic

lower foliar N (Kull and Koppel 1987). Transpiration per unit leaf area was lower in older stands of Norway spruce (Alsheimer et al. 1998), *Eucalyptus* (Olbrich 1994), and Scots pine (Cienciala et al. 1997).

Differences in g_s at the leaf level and transpiration at the stand level suggest that transpiration and whole-tree conductance might be lower in older, taller trees (Ryan and Yoder 1997). Such differences might be caused by changes in the hydraulic conductance of the soil-to-leaf pathway because of differences in path length (Walcroft et al. 1996), in sapwood permeability (Mencuccini and Grace 1996), or in gravitational potential. Differences in canopy conductance could also be caused by differences in g_s at the leaf level related to differences in photosynthetic capacity (Grulke and Miller 1994; Kull and Koppel 1987; Schoettle 1994; Schulze et al. 1994).

An earlier study at our study site showed leaf gas exchange and leaf-specific hydraulic conductance of 1-year ponderosa pine needles at the top of the crown differed between 12-m and 36-m trees (Hubbard et al. 1999). The objective of this study was to determine if the differences between tree sizes seen at the leaf level in the upper crown applied to the entire crown, throughout the growth season, for a larger population of trees. To accomplish our objectives, we measured xylem water flux on seven 12-m and 36-m ponderosa pines and estimated transpiration and whole-tree conductance. The study was performed where trees of different sizes and ages grew in the same forest, under the same environment. Measured trees had the same photosynthetic capacity, and competition between tree crowns for light was minimal.

Materials and methods

Site description

We measured water use of individual ponderosa pine (*Pinus ponderosa* Laws.) trees from May to September 1995 and 1996 on a site near Black Butte, Oregon, USA (N44° 25' W121° 40') at elevation 1030 m. We selected this site because many years of partial

harvesting and thinning (with the objective of restoring pre-settlement stand conditions) have resulted in an open stand (leaf area index, LAI <1), where most trees receive full sunlight throughout the day, and both tall, old trees (~36 m, 290 year) and short, young trees (3–16 m, 10–80 year) exist on the same site. In general, trees left after harvest were of high quality and free from mistletoe infection. The understory is sparse, with bitterbrush (*Purshia tridentata* L.) and bunchgrasses.

Warm, dry summers and wet, cool winters characterize the climate. Annual precipitation at a weather station 15 km east of the site (Sisters, Ore., USA) averaged 360 mm between 1960 and 1990 (Oregon Climate Service, Oregon State University, Corvallis, Ore., USA, www.ocs.orst.edu). On average, only 17% of the annual precipitation falls between May and September. Precipitation for 1995 and 1996 at Sisters was 110% and 132% of the 1960–1990 mean. Precipitation for the preceding September–May (soil recharge period) was 303 mm for 1995 and 411 mm for 1996. Precipitation during June–August was 80 mm for 1995 and 28 mm for 1996. Average annual temperature is 7.7°C, with a mean of 13.9°C in July and –0.5°C in January. The soil is a sandy loam, derived from volcanic ash and classified as a light-colored andic inceptisol. Based on the root systems of a few wind-toppled trees, rooting depth is about 3–5 m.

Water flux measurements

We selected sample trees from two size classes: trees from 9 to 16 m height (average 12 m) and trees from 31 to 41 m height (average 36 m). In 1995, we measured water flux on two 12-m and two 36-m ponderosa pine trees. These trees were in groups to allow canopy access from towers for measurements of canopy gas exchange (Hubbard et al. 1999): trees of the same size were 3 m apart, and 50 m from the other size class. The long axis of the tree clumps was oriented to the south, so that shading by adjacent crowns was minimal. In 1996, we measured five 12-m and five 36-m trees located within a 200-m-diameter area. Each tree was 10–20 m from any neighboring trees. Tree characteristics are in Table 1.

Water flux (Q) through the xylem of each tree was measured using a heat-balance approach (EMS, Brno, Czech Republic; Cermák et al. 1973; Köstner et al. 1996; Kucera et al. 1977) and the methods specified by the instrument manufacturer. Measuring points were 2–3 m above the ground, and measurements were collected each minute and averaged and stored every 15 min. Heat loss from conduction was estimated by assuming zero flow during heavy rain or a humid night for each measuring point for each 30-day period. Stems were shielded with aluminum-faced insulation for 0.75 m above the measuring points to the base of the tree to

Table 1 Characteristics of sample trees

Size class	Year measured	Diameter 1.4 m (m)	Height (m)	Age when measured (year)	Leaf area (m ²)	Sapwood area (m ²)	Growth in year measured (kg year ⁻¹)	Growth per leaf area (kg m ⁻² year ⁻¹)
12	1996	0.31	12	30	63	0.044	12.3	0.20
12	1996	0.30	13	37	73	0.051	12.1	0.17
12	1996	0.29	11	25	63	0.044	12.1	0.19
12	1996	0.24	13	42	43	0.030	5.9	0.14
12	1996	0.36	16	81	98	0.068	13.9	0.14
12	1995	0.19	10	54	24	0.018	3.32	0.14
12	1995	0.19	9	34	26	0.018	2.07	0.08
36	1996	0.62	34	84	130	0.150	5.4	0.04
36	1996	0.66	34	266	120	0.130	6.9	0.06
36	1996	0.82	41	274	210	0.230	18.2	0.09
36	1996	0.79	35	302	220	0.240	5.4	0.02
36	1996	0.98	42	297	330	0.370	20.8	0.06
36	1995	0.70	34	286	120	0.160	8.1	0.07
36	1995	0.70	31	292	180	0.170	10.5	0.06

eliminate bias caused by radiation heating. Ponderosa pine has thick sapwood (average of 105 mm for the 12-m trees and 127 mm for the 36-m trees). We used the largest electrodes (80 mm) manufactured. Undersampling Q may be a potential problem because the electrode length < sapwood depth. However, Q in inner sapwood is typically low relative to outer sapwood (e.g. Cermák et al. 1992; Köstner et al. 1998; Phillips et al. 1996; Swanson 1994). Therefore, we assumed that the installation sampled 100% of the water flow.

Each EMS device provided estimates of water flow through a sapwood area of about 0.008 m²; we estimated water flow for the entire tree with 1, 2, or 4 devices per tree. Each tree had one device that remained in place for the season, and any other devices were placed either opposite the primary gauge (two short trees in 1995, three tall trees in 1996), or in quadrants (two tall trees in 1995) for 20–30 days. Water flux from different measuring points on the same tree differed by 5–20% for the short trees in 1995, and 11–25% for the tall trees in 1996. Relationships among the measuring points on a tree were quite stable (SD of the ratio between daily total flux for gauges was ~ 10%). Water flux for each measuring point (Q_i) for the entire sampling period was estimated as:

$$Q_i = Q_p \cdot \bar{Q}_i / \bar{Q}_p \quad (1)$$

where Q_p is the 15-min value for the primary gauge, \bar{Q}_i is the mean water flux for gauge i , and \bar{Q}_p is the mean water flux for the primary gauge during the period when both the primary gauge and gauge i were present. Tree water flux was the average of all Q_i for the tree.

We measured photosynthetically active radiation (I_p , LiCor 190SB), air temperature, and relative humidity (Campbell Scientific 207) from a 12-m tower located in a small clearing. In 1996, we periodically measured pre-dawn and mid-day leaf water potential from the mid-crown of three 12-m and three 36-m trees about 2 km away. Branches were felled with a shotgun and leaf fascicles immediately measured with a Scholander pressure chamber (PMS, Corvallis, Ore., USA).

Leaf area and tree growth

We estimated leaf area for the two small and two large trees in 1995 by measuring branch diameter for each branch on each tree and using a site-specific allometric relationship between branch diameter and leaf mass and between leaf mass and leaf area for each tree size class. To develop allometric equations, we selected 30 primary branches from short and tall trees harvested at a similar site 5 km distant. We measured branch diameter 4 cm from the trunk, dried the branch (70°C for 48 h), and separated and weighed the foliage. We measured leaf area on about 100 fascicles per tree size class (distributed over 5 foliage age classes) and estimated projected leaf area per fascicle from fascicle dry mass. The equations for estimating branch leaf mass (W_L , g) from branch diameter (D_b , mm) are:

$$W_L = 0.19D_b^2 - 0.00043D_b^3 \quad (2)$$

$$W_L = 0.22D_b^2 \quad (3)$$

Equation 2 was used for 36-m trees ($R^2=0.94$, $D_b=20$ –160 mm, SE=290), and Eq. 3 was used for 12-m trees ($R^2=0.84$, $D_b=11$ –40 mm, SE=79). The equations for estimating foliage area (A_L , projected, mm²) from fascicle mass (W_F , g) are:

$$A_L = 330 + 1630W_F \quad (4)$$

$$A_L = 250 + 2220W_F \quad (5)$$

Equation 4 was used for 36-m trees ($R^2=0.92$, SE=48) and Eq. 5 was used for 12-m trees ($R^2=0.93$, SE=47). We estimated projected leaf area for trees in 1996 from sapwood area at 1.4 m, and the ratio of projected leaf area to sapwood area at 1.4 m from the 1995 trees (1440 (SE=61) m² m⁻² for 12-m trees and 909 (SE=140) m² m⁻² for 36-m trees). Sapwood area was estimated from four increment cores per tree at 1.4 m height.

Annual aboveground wood growth for the measurement year was estimated from radial growth at 1.4 m using a general equa-

tion that estimates ponderosa pine biomass from diameter (Gholz et al. 1979).

Soil moisture

Soil moisture (0–120 cm) was measured every 7–14 days using time-domain reflectometry, with 19 rod-pairs (1.2 m length) systematically located throughout the forest. We assumed the standard calibration curve for the dielectric constant and soil water content (Dalton et al. 1984; Topp et al. 1980).

Data analysis

To derive E and g_t from Q , we assumed that capacitance was negligible. Support for this assumption was derived from two analyses—correlation of Q with D and with D lagged for 15 min to 3 h in 15-min increments (Phillips et al. 1997), and the proportion of total Q that occurred when $I_p < 5 \mu\text{mol m}^{-2} \text{s}^{-1}$ (recharge). For all except one large tree, the correlation of Q with D was always greater than that for any lagged D . When the analysis was restricted to the linear portion of the relationship between Q and D ($D < 1.5$ kPa), the correlation of Q with D was always greater than that for any lagged D . Additionally, Q for the largest and smallest tree measured in 1996 was strongly correlated ($R=0.90$), and the correlation was greater for current Q than any Q offset from –3 to +3 h in 15-min increments. The proportion of daily Q that occurred at night was always 2–3% for 12-m trees; for the 36-m trees, it was 5% in June and July, rising to 12% in August.

We estimated g_t (mmol m⁻² leaf area s⁻¹) as:

$$g_t = Q_l / D \quad (6)$$

where Q_l is xylem water flux per unit leaf area (mmol m⁻² s⁻¹) and D is vapor pressure deficit in partial pressure units (kPa/kPa) (Whitehead et al. 1996). g_t represents the total water vapor conductance or the conductance of the average leaf in the tree canopy, and consists of both aerodynamic (g_a) and canopy (g_c) components (Köstner et al. 1992; Thom 1972). However, because g_a is generally an order of magnitude higher than g_c in coniferous forests (Granier et al. 1996; Lindroth 1985), $g_t \cong g_c$, especially in these well-ventilated, open-canopy ponderosa pine forests. We estimated hydraulic conductance (K_H , mmol m⁻² s⁻¹ MPa⁻¹) of the pathway from soil to leaf as:

$$K_H = Q_l / (\Psi_{\text{soil}} - \Psi_{\text{mid}}) \quad (7)$$

where Ψ_{mid} is mid-day leaf water potential and Ψ_{soil} is soil water potential (estimated from pre-dawn leaf water potential, corrected for the gravitational effect of the measurement height), and Q_l was measured between 1100 and 1300 hours.

Our sampling unit was the individual tree. We compared the differences in Q_l , Q_s (water flux per unit sapwood area), and g_t between 12-m and 36-m tall trees by combining data from 1995 and 1996. We selected the same two periods for each year (days 165–195 and days 240–260) because we had complete data for all trees during these periods for both years. We partitioned the summer into periods because average tree water flux was substantially lower later in the year in response to lower soil moisture. The climate was very similar for both periods for 1995 and 1996 (<18% difference in mean air temperature, D , and I_p , and very little precipitation for either period for either year). Soil moisture was lower in 1996 for days 240–260 (Fig. 1A), but pre-dawn leaf water potential did not differ between the two periods in 1996 for nearby trees (Fig. 1B). Differences in diurnal patterns in tree Q_l were assessed by averaging the flux for each tree for each hour of the day for each of the two periods, and estimating a t -value comparing size classes for each hourly period (functional analysis of variance, see Ramsay and Silverman 1997). Differences in Q_l , Q_s , and g_t between the tree size classes were assessed with repeated measures ANOVA on the mean Q and mean g_t for each tree for each period. In this analysis, size class is the main factor, and time period (days 165–195 or 240–260) was the repeated measure. Differences

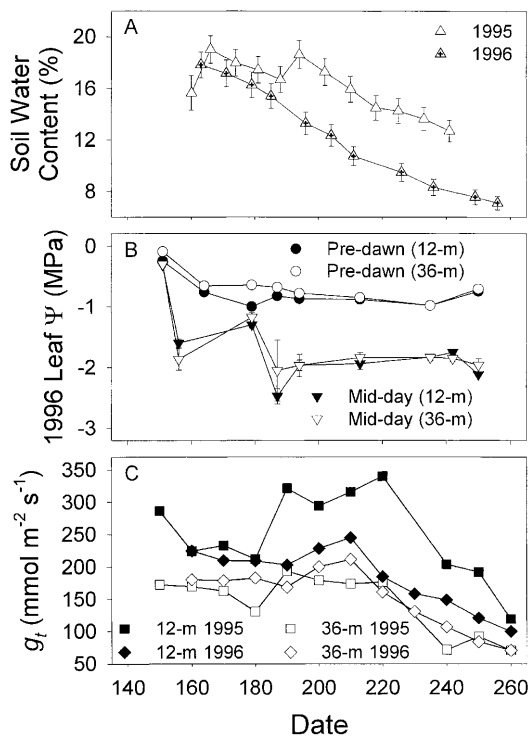


Fig. 1 **A** Mean soil water content (%) over 1.2 m depth for the summers of 1995 and 1996 ($n=19$). Error bars are standard error among sampling points. **B** Mean leaf water potential in 1996 (MPa) for nearby trees of a size similar to those measured for sap-flow ($n=3$). Error bars are standard error among trees. Pre-dawn values are corrected to a reference height of 0 m. **C** Mean reference canopy conductance ($I_p > 900 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $D=1.5 \text{ kPa}$) for 12-m and 36-m trees in 1995 ($n=2$ in each size class) and in 1996 ($n=5$ in each size class)

in the relationships of Q_1 and g_t to D were assessed by averaging the Q_1 for each tree for each sample period by 0.25 kPa classes and estimating a t -value comparing tree size classes for each 0.25 kPa class (Ramsay and Silverman 1997).

Results

Water flux was substantially lower for the average 36-m tree ($P < 0.02$). Under high light ($I_p > 900 \mu\text{mol m}^{-2} \text{s}^{-1}$), average Q_1 of the 12-m trees was 2.4 (SE=0.4) mmol m^{-2} (leaf area) s^{-1} , compared with 1.2 (SE=0.1) $\text{mmol m}^{-2} \text{s}^{-1}$ for the 36-m trees. For a 24-h day, Q_1 averaged 0.97 (SE=0.14) mmol m^{-2} (leaf area) s^{-1} for the 12-m trees compared with 0.57 (SE=0.06) $\text{mmol m}^{-2} \text{s}^{-1}$ for the 36-m trees. The interaction of Q_1 and sample period was not significant for either the high light or the 24-h measurements ($P > 0.55$), indicating that the decline of Q_1 in response to lower soil moisture in days 240–260 was similar for both 12- and 36-m trees.

Whole-tree conductance under high light was also substantially lower for the 36-m trees ($P < 0.01$), and averaged 140 (SE=22) mmol m^{-2} (leaf area) s^{-1} for the 12-m trees and 72 (SE=9.3) $\text{mmol m}^{-2} \text{s}^{-1}$ for the 36-m trees. The interaction of g_t and sample period was not significant ($P=0.53$).

Differences in Q_s between the two sizes of trees were more pronounced than those for Q_1 ($P < 0.01$). For $I_p > 900 \mu\text{mol m}^{-2} \text{s}^{-1}$, Q_s was 3.4 (SE=0.50) mol m^{-2} (sapwood) s^{-1} for 12-m trees and 1.1 (SE=0.13) $\text{mol m}^{-2} \text{s}^{-1}$ for 36-m trees; over 24 h, Q_s was 1.4 (SE=0.19) $\text{mol m}^{-2} \text{s}^{-1}$ for 12-m trees and 0.52 (SE=0.05) $\text{mol m}^{-2} \text{s}^{-1}$ for 36-m trees. If we assume that average $Q_1 \approx E$ and extrapolate the average difference in transpiration to a forest with a LAI of 1, the 36-m trees would transpire 0.6 mm day^{-1} less water than the 12-m trees— or 53 mm (15% of annual precipitation) less between 1 June and 31 August.

Sapwood thickness averaged 105 mm for 12-m trees and 127 mm for 36-m trees, and measurements were taken with 80 mm electrodes for heating sapwood. Our water flux values assume that all of the flux occurred in the outer 80 mm of sapwood. While it is unlikely that the deep sapwood contributes much to total flux (Cermák et al. 1992; Phillips et al. 1996; Swanson 1994), we did estimate the effect of a potential undersampling on the estimates of Q and the potential differences between tree size classes. If we assume that Q for sapwood deeper than 80 mm equals that in the outer 80 mm, then Q_1 would be 1.1 times that reported for the 12-m trees, and 1.4 times that reported for 36-m trees. Using these factors would decrease the ratio of E for 12-m trees:36-m trees from 1.7 to 1.4 over 24 h, and from 2.0 to 1.6 for $I_p > 900 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Soil moisture for days 240–260 was substantially lower than that for days 165–195 (15.0% versus 7.0% in 1996, Fig. 1A). Pre-dawn leaf water potential of nearby trees in 1996, however, did not differ among periods (-0.8 MPa, Fig 1B). Reference g_t ($D=1.5 \text{ kPa}$ and $I_p > 900 \mu\text{mol m}^{-2} \text{s}^{-1}$) began declining about day 210 for both size classes in both 1995 and 1996 (Fig. 1C). Q_1 averaged over 24-h and Q_1 for $I_p > 900 \mu\text{mol m}^{-2} \text{s}^{-1}$ were lower for days 240–260 than for days 165–195 (53% and 64%, respectively, $P < 0.01$). For comparison, whole ecosystem latent energy (LE) flux measured in a mixed-aged ponderosa pine forest 10 km north of our site showed a decrease from 2.0 mm day^{-1} for days 165–195 to 1.42 for days 240–260 (Anthoni et al. 1999).

Trees differed in their response to lower soil moisture: two 12-m and one 36-m tree nearly stopped transpiring by days 240–260, with Q_1 less than 10% of that in days 165–195. For the remaining trees, Q_1 for days 240–260 was at least 35% of Q_1 in days 165–195. The response of Q_1 to drought for the 36-m trees was less variable than for the 12-m trees (Levene's test for homogeneity of variances, $P=0.10$).

A functional analysis of variance of the mean diurnal pattern of water flux (Fig. 2) shows that differences between 12-m trees and 36-m trees occurred between 0800 and 1700 hours solar time (significant only for days 165–195), and between 2000 and 2400 hours solar time. Midday Q_1 of the 12-m trees was nearly twice that of the 36-m trees. Differences between tree sizes for 2000–2400 hours solar time reflects differences in recharge, as I_p was $< 5 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Q_1 for the two size classes responded differently to D (Fig. 3), resulting in lower g_t for the 36-m trees and lower

Fig. 2 Diurnal patterns in tree water flux (Q_l) for days 165–195 and 240–260. Q_l was averaged for each tree for each hour. *Error bars* are standard errors of the variation among trees within a size class ($n=7$ each). *T-value* is computed from *t*-test between size classes for each hour, and the dotted line gives *t* where $P=0.05$ for a single test

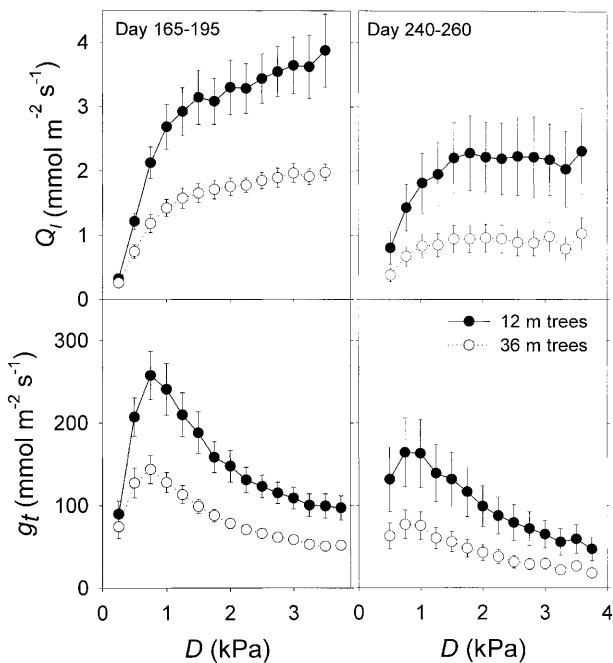
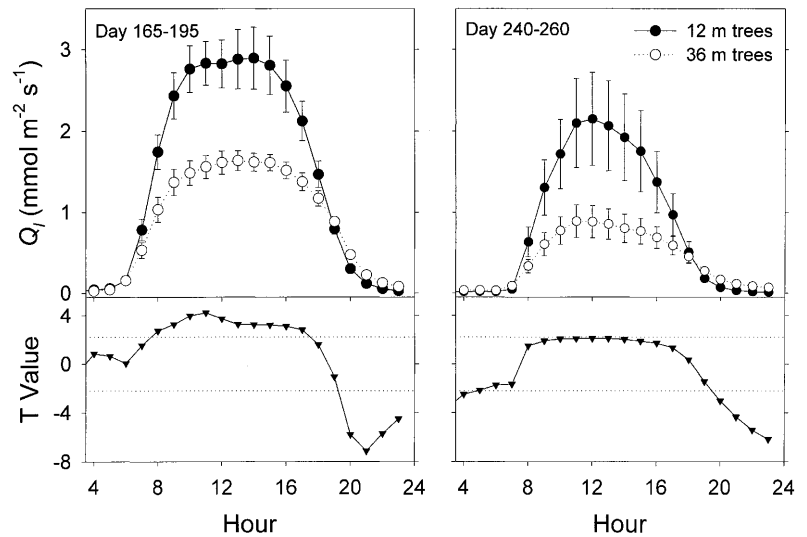


Fig. 3 Mean water flux (Q_l) and whole tree conductance (g_t) for 12-m and 36-m trees when $I_p > 900 \mu\text{mol m}^{-2} \text{s}^{-1}$, by 0.25 kPa class of leaf to air vapor saturation deficit (D). Fifteen-minute values were averaged by 0.25 kPa class for each tree. *Error bars* are standard errors of the variation among trees

maximum mid-day Q_l (Fig. 2). Q_l is statistically identical for the different tree sizes when $D < 1$ kPa ($t < 2.2$), but differs when $D > 1$ kPa. g_t differed between the two size classes when $D > 1.25$ kPa, and also when $D > 0.25$ kPa for days 165–195. Mid-day leaf-specific hydraulic conductance averaged $2.4 \text{ mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ for 12-m trees and $1.7 \text{ mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ for 36-m trees, based on leaf water potential of nearby trees and Q_l for days 179, 187, 194, 235, and 250.

Canopy g_t estimated from Q_l differed from g_s measured on a subset of the trees in our study in 1995. At the

Table 2 Stomatal conductance (g_s , $\text{mmol m}^{-2} \text{ s}^{-1}$) for 1-year foliage at the canopy top (Hubbard et al. 1999; R.M. Hubbard, unpublished data), and canopy conductance (g_t , $\text{mmol m}^{-2} \text{ s}^{-1}$) estimated from Q_l (xylem water flux per unit leaf area, $\text{mmol m}^{-2} \text{ s}^{-1}$). For all measurements, photosynthetically active radiation $> 900 \mu\text{mol m}^{-2} \text{ s}^{-1}$. For g_t , ‘early’ is days 165–195 and ‘late’ is days 240–260, both for 1995–96. For g_s , measurements were made for days 197–256 in 1995, and day of year did not affect the relationship between g_s and vapor pressure deficit (D , kPa)

D	Portion of growth season	12-m Size class		36-m Size class	
		g_s	g_t	g_s	g_t
Mean	All	129	140	87	72
1.0	Early		241		128
1.0	Late	192	163	166	76
2.5	Early		123		66
2.5	Late	153	79	109	32

leaf level, maximum g_s was about $200 \text{ mmol m}^{-2} \text{ s}^{-1}$ and similar for 12-m and 36-m trees (Hubbard et al. 1999). At the canopy level, maximum g_t was much greater for the 12-m trees (Table 2). Leaf g_s was greater than canopy g_t for days 240–260, and for $D > 1.5$ for days 165–195 (Table 2). For the entire measuring period, mean g_s of three 12-m and two 36-m trees in 1995 was similar to mean g_t in 1995–96 (Table 2). Leaf g_s for the 36-m trees decreased more rapidly as D increased (Hubbard et al. 1999), but the relative decrease of g_t as D increased was similar for both size classes.

Aboveground wood production per unit tree leaf area for the 36-m trees was 38% of that for the 12-m trees (Table 1, $P < 0.01$). Wood production per unit leaf area was correlated with height ($R^2 = 0.61$, $P < 0.01$), but the correlation of g_t with height was not significant ($R^2 = 0.23$, $P = 0.08$).

Discussion

The differences in E and g_t found between 12-m and 36-m trees in this study are similar to those found in other stud-

ies that compared different size trees growing in different even-aged closed-canopy stands. For example, E per unit of leaf area for 16-year, 56-m tall *Eucalyptus grandis* was 40% of that for 3-year, 18-m trees (Olbrich 1994), and E per unit of leaf area for 140-year, 25-m *Picea abies* was ~70% of that for 40-year, 16-m trees (Alsheimer et al. 1998). A reduction in E and g_t with tree height has also been observed among *Fagus sylvatica* growing in a closed-canopy stand (Schäfer et al. 2000). Because the differences in E and g_t found between size classes in this study were independent of environment, and because these differences were similar to those in closed-canopy stands, we suspect that some property of the tree that changes with size or age causes the differences.

Four factors could alter canopy conductance and transpiration between trees of different heights. First, a lower leaf water potential in 12-m trees would create greater potential gradient for transporting water and increase flux. However, mid-day leaf water potential was the same for nearby short and tall trees (Fig. 1B), and for short and tall trees at the same site in two earlier studies (Hubbard et al. 1999; Yoder et al. 1994). Second, lower photosynthetic capacity has been associated with lower stomatal conductance (Schulze et al. 1994), and photosynthetic capacity can be lower in older, taller trees (Ryan et al. 1997). However, photosynthetic capacity and leaf N concentration were the same for 1-year-old foliage for the two size classes in 1995 (Hubbard et al. 1999). Third, higher capacitance in larger trees could increase flux for taller trees. However, the influence of capacitance on flux was undetectable for the trees in this study. Finally, hydraulic conductance to liquid water flow from soil to leaf may be lower in taller trees, and could alter stomatal conductance (Hubbard et al. 1999; Ryan and Yoder 1997; Yoder et al. 1994).

Yoder et al. (1994) speculated that differences in photosynthetic performance between young and old trees results from increased hydraulic resistance in taller trees with longer branches. Stomatal conductance and the hydraulic resistance of a tree's vascular system have been linked (Sperry et al. 1993), and hydraulic resistance can change with tree height (Yoder et al. 1994) and branch length (Walcroft et al. 1996; Waring and Silvester 1994), or with stem or root permeability. Stomata close apparently to maintain leaf water potential above a level that would cause cavitation in xylem (Sperry 1995; Sperry et al. 1993; Sperry and Pockman 1993), and experimental increases in hydraulic resistance have induced stomatal closure without affecting leaf water potential (Sperry and Pockman 1993). These studies suggest that stomata may close to restrict transpiration, not simply in response to dry air (see Monteith 1995).

Measurements of water flux and canopy conductance showed that stomata for both short and tall ponderosa pine close to restrict transpiration when D exceeds 1 kPa. Similarly, whole ecosystem LE measurements in a nearby ponderosa pine forest showed that LE remained fairly constant for $D > 1$ kPa (Anthoni et al. 1999). Together, these measurements suggest that water transport may

have been limited by the hydraulic capacity of the whole plant system.

Average hydraulic conductance in our 36-m trees was 71% of the 12-m trees for the 5 days in 1996 when data on both sapflow and mid-day leaf water potential were available, and 44% of the 12-m trees on days 254–256 in 1995 (Hubbard et al. 1999). These results suggest that the lower hydraulic conductivity and lower g_t in the 36-m trees were related. The 36-m trees had more sapwood area per unit leaf area than the 12-m trees (1.6 times), and a much lower water flux per unit sapwood. These anatomical and functional changes would aid water supply for the 36-m trees by augmenting sapwood water storage and providing redundancy in the conducting system to mitigate the effects of xylem cavitation. Schäfer et al. (2000) show that a simple hydraulic model can account for the difference in g_t with height: the ratio of g_t for trees of two different heights is proportional to the product of the ratios of (1) sapwood area:leaf area, (2) the gradient in leaf water potential, corrected for gravitational differences, (3) sapwood conductivity, and (4) the inverse of tree height. We found no difference in the gradient in leaf water potential, corrected for gravitational differences. Applying the analysis of Schäfer et al. (2000) to data from this study gives (g_t 36 m/ g_t 12 m) \propto 1440/909 (sapwood area:leaf area) \times 12/36 (height) = 0.53, assuming sapwood conductivity is the same for both size classes. The ratio found for this study for $I_p > 900 \mu\text{mol m}^{-2} \text{s}^{-1}$ was 0.51.

Canopy g_t estimated from tree water flux was lower than leaf g_s measured during the same time of year, but relative differences in g_t with tree size were similar to those for leaf g_s . Because canopy g_t is an average over leaves of all ages and includes foliage growing in lower light, we expect g_t to be lower than leaf g_s measured on the most physiologically active foliage in the upper canopy. Canopy measurements show that differences in g_s with tree size were maintained for most of the average day and for the growth season. A difference in maximum canopy g_t with tree size, coupled with a lack of a corresponding difference in maximum leaf g_s at the canopy top, suggests that the foliage not measured at the leaf level (expanding foliage and foliage >1-year at the canopy top, and all foliage in the lower 2/3 of the canopy) has a higher average g_s in a 12-m tree than in a 36-m tree. The difference between the response of g_s and g_t to D suggests that capacitance may have a different effect on conductance for the entire canopy than on leaves at the canopy top.

Because of the open character of the study site, and the open character of ponderosa pine crowns, aerodynamic conductance is likely very large relative to stomatal conductance. Therefore, g_t , or whole-tree conductance, is approximately equal to canopy average stomatal conductance (Granier et al. 1996; Lindroth 1985). Because stomatal conductance and photosynthesis are closely related, lower g_t for the 36-m trees suggests that similar differences occur in photosynthesis per unit leaf area. At the same site, mid-day photosynthesis was 21% lower for

1-year-old foliage at the top of the crown for the tall trees measured in 1995 (Hubbard et al. 1999). Additionally, the difference in wood growth per unit leaf area ($0.15 \text{ kg m}^{-2} \text{ year}^{-1}$ for 12-m trees versus 0.06 for 36-m trees) was similar to the difference in g_t throughout the growing season ($140 \text{ mmol m}^{-2} \text{ s}^{-1}$ for 12-m trees versus $72 \text{ mmol m}^{-2} \text{ s}^{-1}$ for 36-m trees, $I_p > 900 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$). However, changes in allocation and respiration with tree size could also reduce wood growth per unit leaf area, so the difference in wood growth per unit leaf area does not necessarily indicate reduced canopy photosynthesis.

Differences in E and g_t with tree size could change many ecosystem processes as an even-aged forest or patch develops. Lower E in older, taller trees will increase soil moisture, and increased soil moisture can alter the pattern of seasonal water use or increase flows to groundwater or streamflow. Such an effect has been measured on a landscape scale in Australia. Streamflow declined $\sim 50\%$ from *Eucalyptus regnans* catchments when old, 100-m trees were replaced with a new forest after a large fire (Kuczera 1987) and the higher streamflow from catchments with older trees could not be entirely explained by differences in leaf area (Watson et al. 1999). Higher soil moisture may also increase decomposition and nutrient availability. In a lodgepole pine chronosequence, both soil moisture (Yoder et al. 1994) and nitrogen availability (Ryan and Waring 1992) were highest in the oldest forest. However, in an ecosystem with low leaf area, less E by the overstory may provide more water for understory E or for evaporation, and these processes may act to lessen any influence of tree size (Roberts 1983).

Existing old-growth forests of ponderosa pine often have multiple age-classes and heights, and would likely have transpiration rates between those of pure young or pure old stands. In a nearby old-growth ponderosa pine forest, there are dense patches of young (~ 45 year) trees, open patches of old trees (250 year) and about 50% of the area is mixed-age trees. In this forest (LAI ~ 1.6), whole ecosystem LE flux ranged from 2.0 to 1.4 mm day^{-1} during the growing season, and transpiration was about 80% of LE (Anthoni et al. 1999). In our study, average transpiration of all trees (both short and tall) on clear days varied from 2.3 mm to 0.95 mm .

Differences in canopy conductance and water use with tree size suggest that models of ecosystem-level water and carbon fluxes should consider the importance of tree size or age when estimating fluxes. These results also suggest that changes in the age distribution of forests, through harvesting, land-use change, or changes in disturbance regimes could alter fluxes of water and carbon at landscape scales.

Acknowledgements Research was supported by the US Department of Agriculture (NRICGP#9401021 and 97-35101-4376). We thank the US Forest Service, Sisters Ranger District for help in site selection and for access to study sites, Barbara Köstner, Ram Oren, and Dan Binkley for helpful comments, and Rudy King for assistance with statistical analysis.

References

- Alsheimer M, Köstner B, Falge E, Tenhunen JD (1998) Temporal and spatial variation in transpiration of Norway Spruce stands within a forested catchment of the Fichtelgebirge, Germany. *Ann Sci For* 55:103–123
- Anthoni PM, Law BE, Unsworth MH (1999) Carbon and water vapor exchange of an open-canopied ponderosa pine ecosystem. *Agric For Meteorol* 95:151–168
- Cermák J, Deml M, Penka M (1973) A new method of sap flow determination in trees. *Biol Plant* 15:171–178
- Cermák J, Cienciala E, Kucera J, Hällgren J-E (1992) Radial velocity profiles of water flow in trunks of Norway spruce and oak and the response of oak to severing. *Tree Physiol* 10:367–380
- Cienciala E, Kucera J, Lindroth A, Cermák J, Grelle A, Halldin S (1997) Canopy transpiration from a boreal forest in Sweden during a dry year. *Agric For Meteorol* 86:157–167
- Dalton FN, Herkelrath WN, Rawlins DS, Rhoades JD (1984) Time-domain reflectometry: simultaneous measurement of soil water content and electrical conductivity with a single probe. *Science* 224:989–990
- Fredericksen TS, Steiner KC, Skelly JM, Joyce BJ, Kolb TE, Kouterick KB, Ferdinand JA (1996) Diel and seasonal patterns of leaf gas exchange and xylem water potentials of different-sized *Prunus serotina* Ehrh. trees. *For Sci* 42:359–365
- Gholz HL, Grier CC, Campbell AG, Brown AT (1979) Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Research Paper 41. School of Forestry, Oregon State University, Corvallis, Ore., USA
- Granier A, Biron P, Köstner B, Gay LW, Najjar G (1996) Comparisons of xylem sap flow and water vapor flux at the stand level and derivation of canopy conductance for Scots pine. *Theor Appl Climat* 53:115–122
- Grulke NE, Miller PR (1994) Changes in gas exchange characteristics during the life span of giant sequoia: implications for response to current and future concentrations of atmospheric ozone. *Tree Physiol* 14:659–668
- Harmon ME, Ferrell WK, Franklin JF (1990) Effects on carbon storage of conversion of old-growth forests to young forests. *Science* 247:699–702
- Hubbard RM, Bond BJ, Ryan MG (1999) Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiol* 19:165–172
- Köstner BM, Schulze E-D, Kelliher FM, Hollinger DY, Byers JN, Hunt JE, McSevney TM, Meserth R, Weir PL (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
- Köstner B, Biron P, Siegwolf R, Granier A (1996) Estimates of water vapor flux and canopy conductance of Scots pine at the tree level utilizing different xylem sap flow methods. *Theor Appl Climat* 53:105–113
- Köstner B, Granier A, Cermák J (1998) Sapflow methods in forest stands: methods and uncertainties. *Ann Sci For* 55:13–27
- Kuczera GA (1987) Prediction of water yield reductions following a bushfire in ash-mixed species eucalypt forest. *J Hydrol* 94:215–236
- Kucera J, Cermák J, Penka M (1977) Improved thermal method of continual recording the transpiration flow rate dynamics. *Biol Plant* 19:413–420
- Kull O, Koppel A (1987) Net photosynthetic response to light intensity of shoots from different crown positions and age in *Picea abies* (L.) Karst. *Scand J For Res* 2:157–166
- Lindroth A (1985) Canopy conductance of coniferous forests related to climate. *Water Resour Res* 21:297–304
- Lugo AE, Brown S (1992) Tropical forests as sinks of atmospheric carbon. *For Ecol Manage* 54:239–255
- Mencuccini M, Grace J (1996) Developmental patterns of above-ground hydraulic conductance in a Scots pine (*Pinus sylvestris* L.) age sequence. *Plant Cell Environ* 19:939–948
- Monteith JL (1995) A reinterpretation of stomatal responses to humidity. *Plant Cell Environ* 18:357–364

- Olbrich BW (1994) The application of the heat pulse velocity technique to the study of transpiration from *Eucalyptus grandis*. PhD Dissertation, University of Natal, Durban, South Africa
- Phillips N, Oren R, Zimmermann R (1996) Radial patterns of xylem sap flow in non-porous, diffuse-porous and ring-porous tree species. *Plant Cell Environ* 19:983–990
- Phillips N, Nagchaudhuri A, Oren R, Katul G (1997) Time constant for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sapflow. *Trees* 11:412–419
- Ramsay JO, Silverman BW (1997) Functional data analysis. Springer, Berlin Heidelberg New York
- Roberts J (1983) Forest transpiration: a conservative hydrological process? *J Hydrol* 66:133–141
- Ryan MG, Waring RH (1992) Maintenance respiration and stand development in a subalpine lodgepole pine forest. *Ecology* 73:2100–2108
- Ryan MG, Yoder BJ (1997) Hydraulic limits to tree height and tree growth. *BioScience* 235–242:235–242
- Ryan MG, Binkley D, Fownes JH (1997) Age-related decline in forest productivity: pattern and process. *Adv Ecol Res* 27:213–262
- Schäfer KVR, Oren R, Tenhunen JD (2000) The effect of tree height on crown level stomatal conductance. *Plant Cell Environ* 23:365–375
- Schoettle AW (1994) Influence of tree size on shoot structure and physiology of *Pinus contorta* and *Pinus aristata*. *Tree Physiol* 14:1055–1068
- Schulze ED, Kelliher FM, Körner C, Lloyd J, Leuning R (1994) Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and plant nitrogen nutrition: a global ecology scaling exercise. *Annu Rev Ecol Syst* 25:629–660
- Sperry JS (1995) Limitations on stem water transport and their consequences. In: Gartner BL (ed) *Plant stems: physiology and functional morphology*. Academic Press, San Diego, pp 105–124
- Sperry JS, Pockman WT (1993) Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. *Plant Cell Environ* 16:279–287
- Sperry JS, Alder NN, Eastlack SE (1993) The effect of reduced hydraulic conductance on stomatal conductance and xylem cavitation. *J Exp Bot* 44:1075–1082
- Swanson RH (1994) Significant historical developments in thermal methods for measuring sap flow in trees. *Agric For Meteorol* 72:113–132
- Thom AS (1972) Momentum, mass, and heat exchange of vegetation. *Q J R Meteorol Soc* 98:124–134
- Topp GC, Davis JL, Annan AP (1980) Electromagnetic determination of soil water content: measurements in coaxial transmission lines. *Water Resour Res* 16:574–582
- Walcroft AS, Silvester WB, Grace JC, Carson SD, Waring RH (1996) Effects of branch length on carbon isotope discrimination in *Pinus radiata*. *Tree Physiol* 16:281–286
- Waring RH, Silvester WB (1994) Variation in foliar $\delta^{13}\text{C}$ values within the crowns of *Pinus radiata* trees. *Tree Physiol* 14:1203–1213
- Watson FGR, Vertessy RA, Grayson RB (1999) Large scale modelling of forest hydrological processes and their long-term effect on water yield. *Hydrol Proc* 13:689–700
- Whitehead D, Livingston NJ, Kelliher FM, Hogan KP, Peppin S, McSeveny TM, Byers JN (1996) Response of transpiration and photosynthesis to transient change in illuminated foliage area for a *Pinus radiata* D. Don tree. *Plant Cell Environ* 19:949–957
- Williams M, Rastetter EB, Fernandes DN, Goulden ML, Wofsy SC, Shaver GR, Melillo JM, Munger JW, Fan S-M, Nadelhoffer KJ (1996) Modelling the soil-plant-atmosphere continuum in a *Quercus-Acer* stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant Cell Environ* 19:911–927
- Yoder BJ, Ryan MG, Waring RH, Schoettle AW, Kaufmann MR (1994) Evidence of reduced photosynthetic rates in old trees. *For Sci* 40:513–527