

Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees

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Summary We tested the hypotheses that hydraulic conductance is lower in old (about 250 years old and 30 m tall) compared to young (about 40 years old and 10 m tall) *Pinus ponderosa* Dougl. ex Laws. trees and that lower hydraulic conductance of old trees limits their photosynthesis. Hydraulic conductance at the end of summer 1995, calculated from leaf water potential and leaf gas exchange measurements on one-year-old needles, was 44% lower in old trees compared to young trees growing in a mixed age-class stand on the east slope of the Oregon Cascades. Whole-tree sapflow per unit leaf area averaged 53% lower in old trees compared to young trees and mean hydraulic conductance calculated from sapflow and water potential data was 63% lower in old trees than in young trees. For the entire summer, stomatal conductance (g_s) and assimilation (A) declined more steeply with air saturation deficit (D) in old trees than in young trees. For both old and young trees, mean g_s and A were approximately 32 and 21% lower, respectively, at typical midday D values (2.5–3.0 kPa). We hypothesized that if hydraulic conductance limits g_s and A , then increasing or decreasing the leaf specific conductance of a branch will result in proportional changes in the responses of g_s and A with D . Removal of 50% of the foliage from a set of experimental branches on old trees caused g_s and A to decline less steeply with D in early summer, but values were not significantly different from control values in late summer. Cutting transverse notches in branches on young trees had no effect on the responses of g_s and A with D . Leaf nitrogen content and photosynthetic capacity were similar suggesting that differences in g_s and A between old and young trees were not caused by differences in photosynthetic capacity.

Keywords: air saturation deficit, assimilation, ponderosa pine, stomatal conductance.

Introduction

Water transport in trees is regulated by the hydraulic conductance of the soil–root–shoot–leaf pathway, and whole-tree hydraulic conductance is a function of the path lengths and permeability of these tissues. Because stomatal conductance (g_s) and photosynthesis (A) depend on the transport of water

from soil to leaf to atmosphere, changes in whole-tree hydraulic conductance may affect leaf gas exchange.

Leaf specific hydraulic conductance of the flow path from soil to leaf (K_L), can be described by Darcy's law:

$$K_L = F_L / (\Psi_{\text{soil}} - \Psi_{\text{leaf}}), \quad (1)$$

where F_L is flux of liquid water per unit leaf area in the xylem tissue, and Ψ_{soil} and Ψ_{leaf} are soil and leaf water potentials, respectively. For conifer leaves that are well coupled to the atmosphere and when leaf temperature is equal to air temperature, the transpirational flux from leaf to atmosphere can be described as:

$$E_L = g_s D, \quad (2)$$

where E_L is transpiration flux per unit leaf area, g_s is stomatal conductance to water vapor per unit leaf area and D is air saturation deficit. Under steady-state conditions, F_L is approximately equal to E_L such that K_L can be described by combining Equations 1 and 2:

$$K_L = g_s D / (\Psi_{\text{soil}} - \Psi_{\text{leaf}}). \quad (3)$$

Trees undergo significant changes in size, growth form and physiology as they proceed from seedlings to maturity to old age (Ryan et al. 1996, Ryan and Yoder 1997). If these changes significantly reduce K_L , then rearranging Equation 3 to solve for g_s :

$$g_s = K_L (\Psi_{\text{soil}} - \Psi_{\text{leaf}}) / D, \quad (4)$$

predicts that g_s will be reduced in old trees compared to young trees (if the water potential gradient and vapor pressure deficits are equal). Therefore, effects of hydraulic conductance on g_s may be important when comparing net carbon assimilation (A) in old and young trees because stomata control the flux of CO_2 from the atmosphere into the leaf.

Tree age and height may both affect K_L (hereinafter we refer only to "old trees" and "young trees," recognizing that size increases along with age). Old trees often have lower assimila-

tion rates per unit leaf area than young trees (Kull and Koppel 1987, Grulke and Miller 1994, Schoettle 1994, Yoder et al. 1994) and there is evidence that whole-tree hydraulic conductance declines as trees age (Mattson-Djos 1981, Köstner et al. 1996). The lower hydraulic conductance in old trees may be caused by the increased length of the pathway that water must travel from soil to leaf (Waring and Silvester 1994). Other possible causes include reduced xylem conductivity in roots, stems and branches, and changes in root surface area and permeability. Ryan and Yoder (1997) hypothesized that, with diurnal increases in D , lower hydraulic conductance causes stomatal closure earlier in the day in old trees compared to young trees, leading to lower assimilation rates in old trees (the hydraulic limitation hypothesis). They suggested that hydraulic limitation may explain both why all trees eventually reach a maximum height as well as the decline in forest stand net primary production commonly observed after canopy closure.

Several studies have shown that changes in K_L can affect stomatal behavior. Reducing whole-plant hydraulic conductance by notching (Sperry and Pockman 1993), injecting air into xylem conduits (Sperry et al. 1993), or root pruning (Teskey et al. 1983) results in almost immediate stomatal closure. Other studies have shown that experimental alterations in leaf turgor induced by root pressurization, independent from soil or atmospheric water status, result in reversible changes in g_s (Saliendra et al. 1995, Fuchs and Livingston 1996). Furthermore, improving K_L of foliage either by foliage removal (Meinzer and Grantz 1990) or by shading (Whitehead et al. 1996) results in increased g_s and assimilation (A).

To understand how K_L can limit g_s and A in old trees we have considered how hydraulic conductance changes with path length. Pothier et al. (1989) described hydraulic conductance (K) as:

$$K = (k_s A) / (L \eta), \quad (5)$$

where k_s is sapwood permeability, A is sapwood cross-sectional area per unit leaf area, L is length of the flow path and η is viscosity of xylem water. Consider two hypothetical trees, Tree A is 10 m tall and Tree B is 40 m tall. Each tree is identical with respect to the parameters in Equation 5 except for L ; such that hydraulic conductance for Tree B is four times lower than for Tree A. If Ψ_{soil} is 1 MPa, Tree B would have to maintain a Ψ_{leaf} that is approximately four times lower than that of Tree A to maintain the same flux of water from soil to leaf (Equation 1). However, there is a limit to the negative pressure that can be maintained in the xylem. Significant negative pressures do occur in xylem tissue (Holbrook et al. 1995, Pockman et al. 1995) but it has been suggested that stomata close when leaf water potential reaches a critical value beyond which the water column will cavitate (Tyree and Sperry 1988, Jones and Sutherland 1991). If this is true, Tree B cannot maintain a Ψ_{leaf} four times lower than that of Tree A and must reduce its stomatal opening to prevent cavitation, which in turn limits the diffusion of CO_2 into the leaf.

Understanding the link between hydraulic conductance and photosynthetic performance of old and young trees may be

particularly important for modeling forest growth and response to climate change. Physiological forest process models for trees or stands typically simulate A and g_s using mechanistic or empirical sub-models and scale up to the canopy level using leaf area (e.g., BIOMASS (McMurtrie et al. 1990, 1992), FOREST-BGC (Running and Coughlan 1988, Running and Gower 1991), HYBRID (Friend et al. 1993), FORGRO (Mohren et al. 1984, Mohren 1987) and MAESTRO (Wang 1988)). An assumption common to all of these models (but see Williams et al. 1996) is that foliage from old and young trees of the same species, growing on the same site, are identical with respect to their photosynthetic response to air saturation deficit (given similar illumination, leaf nitrogen concentration and energy balance). However, if K_L is lower in old trees than in young trees, then assimilation per unit leaf area may differ between old trees and young trees, which may significantly affect annual carbon gain.

We estimated K_L of old and young *Pinus ponderosa* Dougl. ex Laws. trees using leaf gas exchange and leaf water potential measurements to determine if tree age and size affects K_L and, in turn, g_s and A . We also experimentally altered K_L of branches on old and young trees and determined the effects on g_s and A . Our specific hypotheses were: (1) leaf specific hydraulic conductance is lower in old trees than in young trees causing g_s and A to be significantly lower in old trees throughout the day; and (2) increasing the K_L of branches on old trees by removing foliage will shift the short-term responses of g_s and A of the remaining needles toward that of the young trees. Likewise, reducing the K_L of branches on young trees by notching will shift the short-term responses of g_s and A toward that of old trees.

Materials and methods

Site description

The study site, which has been described by Yoder et al. (1994), is a mixed-age ponderosa pine stand near Black Butte, OR (44°25' N, 121°40' W). The site is located at an elevation of 1032 m with deep volcanic ash derived soils. The site receives most of its annual 360 mm of precipitation during the winter months, and summers are hot and dry with long periods of sunny, cloudless days. Many years of partial harvesting and thinning at this site have resulted in an open stand and most trees receive full sunlight throughout the day. Tree height ranges from 3 to 35 m and tree age ranges from less than 30 to more than 250 years old.

Experimental design and treatment installation

We selected two old and three young trees that were located approximately 50 m apart. The old trees had a mean height of 33 m and were 230 years old, whereas the young trees had a mean height of 12 m and were 40 years old.

We used scaffolding to sample the upper third of the canopies, and installed three treatments (control, 50% defoliation of a branch, and four notches cut through 50% of the xylem tissue) on south-facing branches of old and young trees in late June 1995. Each treatment was replicated on four branches for

a total of twelve experimental branches in old and young trees. For the defoliation treatments, we removed every other fascicle in all needle age classes except current-year needles. We did not remove current-year needles because the buds were just beginning to expand at the time of treatment and removing any needles would have damaged those remaining. The amount of leaf area removed (50% of leaf area in June 1995) was verified by determining the dry weights of removed needles and of the remaining needles at the end of the experiment. We decreased K_L by means of a notching technique described by Sperry et al. (1993). The notching treatment involved four overlapping transverse notches through 50% of the branch diameter at the base of each branch. Wooden dowels prevented the wind from breaking the notched branches.

To test Hypothesis 1, we collected water potential and gas exchange data in September 1995 (Days 254–256). We measured both Ψ_{leaf} and predawn (Ψ_{predawn}) water potential with a pressure chamber (PMS, Corvallis, OR) for individual fascicles on the treatment branches concurrently with the leaf gas exchange measurements. We used Ψ_{predawn} from the young trees (adjusting for gravitational potential) to estimate Ψ_{soil} for both old and young trees. Based on the water potential, leaf gas exchange and D values measured at our site, we used Equation 3 to calculate K_L for the flow path from soil to leaf for old and young trees. We determined the effect of gravity on K_L by subtracting the gravitational component from Equation 3 as:

$$K_L = g_s D / (\Psi_{\text{soil}} - \Psi_{\text{leaf}} - h \rho g), \quad (6)$$

where $h \rho g$ is the gravitational pull on a column of water of height h and density ρ .

Additionally, we measured whole-tree sapflow at the base of each experimental tree by the heat balance method (Ěermák et al. 1973, Kuèera et al. 1977, Ěermák and Kuèera 1981, Ěermák et al. 1982). We measured sapflow every minute with a P6 sap flow meter and data logger (Ecological Measuring Systems, Ltd., Brno, Czech Republic) and stored 15-min means. We insulated the gauges 0.5 m above and below the measurement point with foam and reflective aluminum sheeting to protect the measurement point from ambient temperature fluctuations.

Sapflow and water potential data were used to calculate an independent estimate of hydraulic conductance in old and young trees. We calculated the leaf specific hydraulic conductance from soil to leaf (K_{L*}) as:

$$K_{L*} = F_{\text{tree}} / (\Psi_{\text{soil}} - \Psi_{\text{leaf}}), \quad (7)$$

where F_{tree} is mean hourly sapflow ($\text{kg h}^{-1} \text{m}^{-2}$ of projected leaf area (PLA)). We did not make adjustments for lag times between sapflow and transpiration (e.g., Ěermák et al. 1982, Schulze et al. 1985) because sapflow did not change significantly for the hours for which we had water potential data (0900–1500 h). We assumed that Ψ_{leaf} was similar throughout the canopy and determined the effect of gravity on K_{L*} as in Equation 6.

To estimate leaf area for old and young trees, we developed a branch diameter and leaf area relationship at a logging site

near our experimental area. We sampled four branches each from the upper, middle and lower portions of the canopy of freshly cut ponderosa pine trees that were similar in size to our experimental trees. We measured branch diameter and determined dry weights of all the needles on the branch. Leaf area for individual fascicles was determined for the sampled branches by a regression of weight and leaf area on a subsample of 10 needles per age class from each branch. Leaf area was determined for the experimental trees by measuring the branch diameter of every branch on old and young trees. The leaf area for each branch was determined by separate regression equations for old and young trees and summed for the entire tree.

If water supply to the foliage of old trees is reduced relative to that of young trees, photosynthesis will be limited more by stomatal conductance than by enzymatic capacity for photosynthesis. Therefore, older trees should show less discrimination to ^{13}C , and the $\delta^{13}\text{C}$ value of the cellulose in old tree foliage should be higher (less negative) than that of young trees (e.g., Evans et al. 1986, Farquhar et al. 1989). We extracted cellulose from foliage on control branches in old and young trees as described by Wise et al. (1945). These branches were in well-ventilated canopies and the branches received minimum shading throughout the day. The extracted cellulose was analyzed by mass spectrometry at the Stable Isotope Facility at the University of Waikato, New Zealand.

To determine the response of leaf gas exchange to D , we measured g_s and A diurnally on 1-year-old foliage of control and treatment branches. Measurements were taken between July and September on year Days 197–199, 210–212, 226, 244 and 254–256. We began each set of measurements at approximately 0700 h and measured gas exchange hourly until approximately 1600 h, unless clouds or high winds caused us to stop measuring early. We measured photosynthesis concurrently on old and young trees with two open-system infrared gas analyzers (Field et al. 1989, LCA3 or LCA4, Analytical Development Company, Hoddesdon, England). Before each set of diurnal measurements, the gas analyzers were calibrated with standard gas for CO_2 , and a dew point generator (LI-610, Li-Cor, Inc., Lincoln, NE) for H_2O vapor. Because photosynthesis in ponderosa pine saturates at photosynthetically active radiation (PAR) above $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Hadley 1969), we measured photosynthesis at PAR greater than $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ on foliage that was in full sunlight for at least 20 minutes before measurement. We determined leaf temperature in the cuvette by the energy balance calculation and determined the responses of g_s and A with D based on the natural variation of D in a day. We measured three control and three treatment branches for each set of hourly diurnal measurements.

Statistical analyses

For our estimates of K_L and K_{L*} , we used the mean hourly values for all three days of gas exchange, water potential and sapflow data (Days 254–256, Equations 3 and 7). Significant differences ($\alpha = 0.05$) were determined by one-way analysis of variance (Neter et al. 1990).

To test Hypotheses 1 and 2, we examined the response surfaces of g_s and A with D for old and young control and

treatment branches. We examined several nonlinear models but found that a linear regression model best described our data. We tested for differences in slopes by analysis of covariance and determined the significance ($\alpha = 0.05$) of the interaction between the regression lines of interest (Neter et al. 1990). One of the assumptions of linear regression is that the y -values are statistically independent of one another. Residuals for regressions of g_s and A with D were randomly scattered around zero indicating no bias from lack of independence.

Results

At the end of the summer (Days 254–256), mean K_L , calculated from leaf gas exchange, Ψ_{leaf} and Ψ_{soil} measurements (Equation 3), was 51% lower in old trees compared to young trees (Figure 1A, $P < 0.001$). The effect of gravity accounted for approximately 20% of K_L in old trees compared with 10% in young trees.

Mean daily sapflow per unit leaf area during Days 254–256 was 53% lower in old trees than in young trees (Figure 2, $P <$

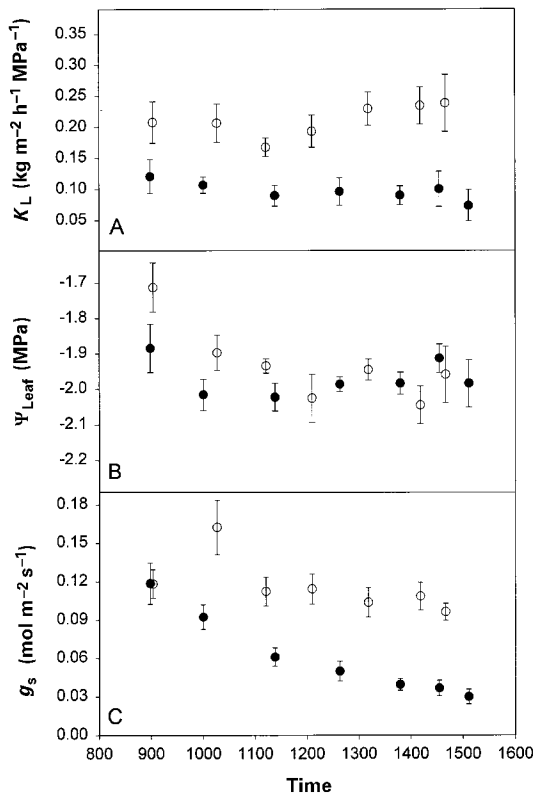


Figure 1. (A) Mean hourly leaf specific hydraulic conductance (K_L); (B) leaf water potential (Ψ); and (C) stomatal conductance (g_s) on Days 254–256 for old (●) and young (○) trees. Error bars are ± 1 standard error. Mean K_L was 44% lower in old compared to young trees ($P < 0.001$). The contribution of height to K_L in old and young trees was 20 and 10%, respectively. Leaf water potential was not significantly different between branches of old and young trees ($P = 0.21$) and mean stomatal conductance declined more steeply throughout the day in old trees compared to young trees ($P < 0.01$).

0.01) and K_{L*} calculated from sapflow measurements and water potential data (Equation 7) was 62% lower in old trees compared to young trees (Figure 3, $P < 0.001$). Mean projected leaf area was 150 m^2 for old trees and 24.9 m^2 for young trees. Leaf area to sapwood area ratios were significantly lower in old trees compared to young trees (0.09 and $0.14 \text{ m}^2 \text{ cm}^{-2}$ sapwood, respectively). The effect of gravity on K_{L*} was similar to its effect on estimates of K_L —approximately 20 and 10% of old-tree and young-tree K_{L*} , respectively. Both estimates of leaf specific conductance (K_L and K_{L*}) indicated lower conductance in old trees than in young trees; however, K_L averaged 50 and 37% higher than K_{L*} for old and young trees, respectively.

During the summer, g_s declined more steeply with D in old trees than in young trees (Hypothesis 1) (Figure 4A, $P < 0.01$).

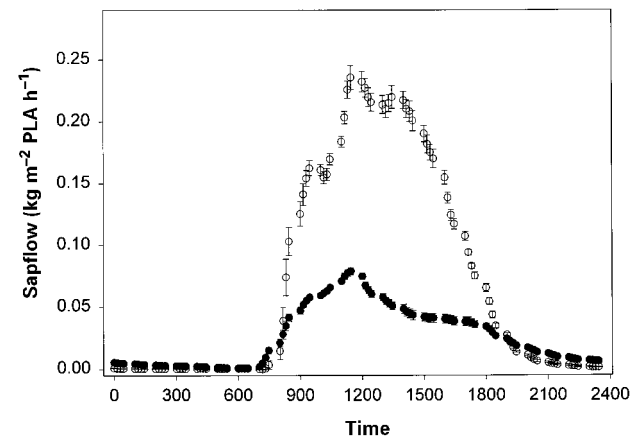


Figure 2. Mean hourly whole-tree sapflow per m^2 projected leaf area (PLA) during Days 254, 255 and 256 for old (●) and young (○) ponderosa pine trees. Error bars are ± 1 standard error. Mean sapflow was 53% lower in old trees than in young trees for the three-day time period.

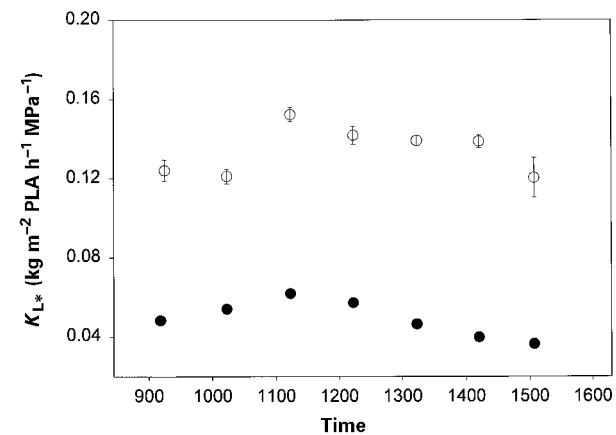


Figure 3. Mean hourly leaf specific conductance (K_{L*}), (calculated from Equation 7) for old (●) and young (○) ponderosa pine trees. Error bars represent ± 1 standard error. Mean K_{L*} was 63% lower in old trees than in young trees. The contribution of height to K_{L*} in old and young trees was 20 and 10%, respectively.

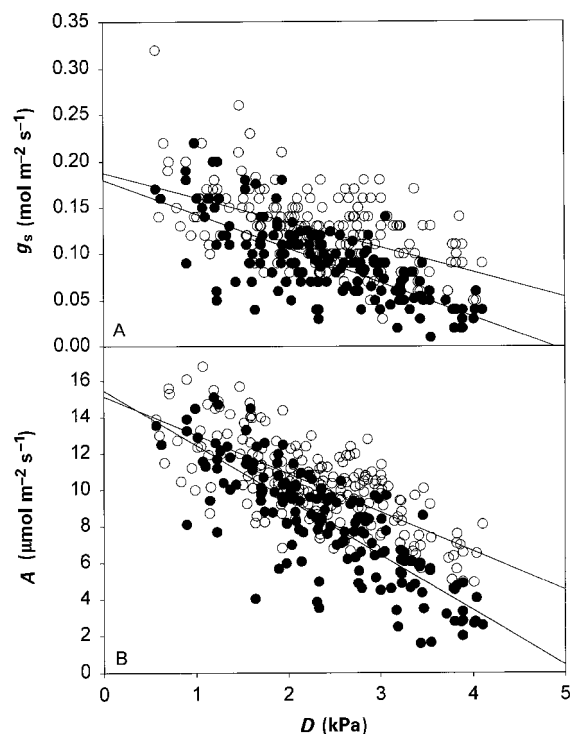


Figure 4. (A) Light-saturated stomatal conductance (g_s); and (B) CO_2 assimilation (A) versus air saturation deficit (D) for 1-year-old needles on control branches from old (●) and young (○) *Pinus ponderosa* trees. The slopes of the responses of g_s and A versus D of needles from branches on old trees were significantly more negative than those on young trees ($P < 0.01$). Values of R^2 for g_s versus D for old and young trees were 0.55 and 0.34, respectively. The response of A with D had R^2 values of 0.69 for old trees and 0.43 for young trees.

Because CO_2 diffusion into the leaf is limited by reduced g_s (Wong et al. 1985), we also observed a decline in carbon assimilation with increasing D in both old and young trees, with a significantly steeper decline in old trees (Figure 4B, $P < 0.01$). At typical midday D values (2.5 to 3.0 kPa), mean g_s and A were 32 and 21% lower, respectively, in control branches of old trees compared to young trees. At the end of the summer, mean $\delta^{13}\text{C}$ of cellulose taken from foliage on control branches was significantly higher in old trees compared to young trees (-23.4‰ versus -25.9‰ ; $P < 0.01$).

Defoliation treatments of branches on old trees resulted in short-term increases in the responses of g_s and A with D on the remaining needles on the branches (Figures 5A and 5B, $P < 0.01$). However, measurements of g_s and A later in the summer showed no difference between treatment and control branches ($P > 0.05$). Defoliation treatments of branches on young trees did not change the responses of g_s and A with D relative to those of the controls ($P > 0.05$; data not shown).

Our efforts to reduce K_L by notching branches in old and young trees did not yield expected results. In young trees, notching branches had no effect on the responses of g_s and A with D (data not shown; $P > 0.05$). In branches of old trees, the notching treatments caused two of the replicates to die and the remaining two showed no response to treatment.

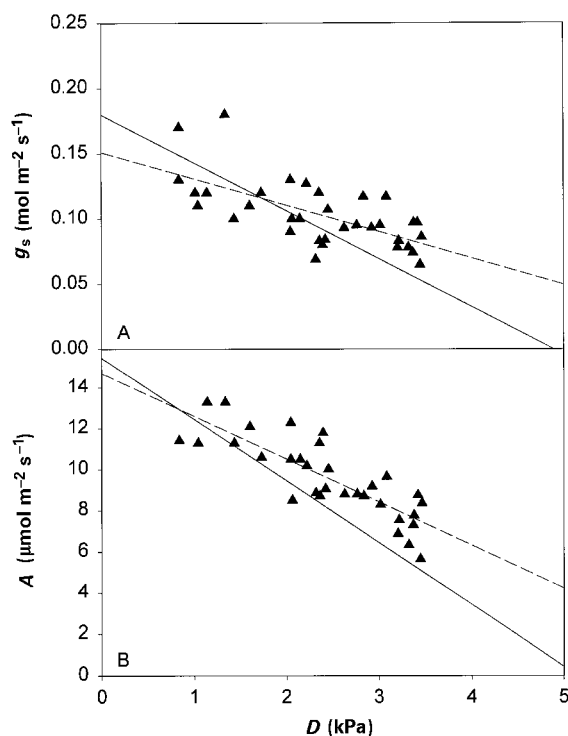


Figure 5. (A) Light-saturated responses of stomatal conductance (g_s); and (B) assimilation (A) for 1-year-old needles on defoliation treated branches on old trees in early summer. Regression line for control branches (—) is shown for comparison. The slope of the light-saturated responses of g_s and A with D for treated branches (—▲—) was significantly less negative than for control branches ($P < 0.01$). Values of R^2 for the response of g_s with D of foliage from treatment branches in early summer was 0.42. Values of R^2 for the response of A with D of foliage from treatment branches in early summer was 0.78.

Discussion

Our estimates for K_L and K_{L*} were much lower in old trees than in young trees (Figures 1A and 3), supporting Hypothesis 1. However, for both K_L and K_{L*} , the effects of gravity only accounted for 10–20% of the differences between old and young trees. We suggest that the remaining 80–90% is caused by the longer path length that water must flow from soil to leaf in the old trees. Old trees were approximately three times taller than young trees and supported longer branches throughout the crown. Because branch junctions have lower conductivity compared with the rest of the flow path (Zimmerman 1983), the large number of branch junctions in old trees may also contribute to lower K_L in old trees compared with young trees.

Estimates of K_L (estimated from gas exchange measurements) were 50 and 37% higher than estimates of K_{L*} (estimated from whole-tree sapflow) for old and young trees, respectively. The gas exchange measurements were made on 1-year-old needles, whereas whole-tree sapflow measurements estimated flow to the entire canopy, including older age class needles. We suggest the lower estimate for K_{L*} compared with K_L reflects higher resistance of the soil to leaf pathway for the > 1 -year-old needles.

Mean daily sapflow per unit leaf area (F_L) was significantly

lower in old trees than in young trees (Figure 2). Because water and carbon cycles are linked through canopy conductance, differences in F_L suggest lower canopy carbon gain in old trees than in young trees. Additionally, Equation 1 (using our estimates of Ψ_{soil} and Ψ_{leaf}) suggests that these differences are caused by lower mean K_L in the old trees than in the young trees.

During the summer, g_s and A declined more steeply in old trees than in young trees, supporting Hypothesis 1 (Figures 4A and 4B). Taken together with our estimate of K_L and the higher $\delta^{13}\text{C}$ values in foliage of old trees compared with young trees, these data suggest that hydraulic conductance limits photosynthesis in old ponderosa pine trees. However, the possibility exists that the differences may be partially attributable to differences in Ψ_{leaf} or photosynthetic capacity between old and young trees.

Because we did not measure Ψ_{leaf} with our early season measurements of leaf gas exchange, we can only speculate that the pattern of lower leaf specific hydraulic conductance in old trees than in young trees was present in early as well as late summer (Figure 1A). However, Yoder et al. (1994) found that diurnal leaf water potential did not vary significantly between old and young ponderosa pine trees at our experimental site in early August. Additionally, in a separate experiment, there was no significant difference in early season predawn and midday Ψ_{leaf} between old and young ponderosa pine trees at a nearby study site (Law et al., Oregon State University, unpublished data). Based on these findings and our data at the end of the summer that directly links a steep diurnal decline in leaf g_s of old trees with decreasing hydraulic conductance (Figures 1A, 1C and 3), we suggest that the pattern in Figure 4 is most probably caused by differences in hydraulic conductance, not differences in Ψ_{leaf} .

Differences in the responses of g_s and A with D for old and young trees do not appear to be the result of differences in photosynthetic capacity. Photosynthetic capacity is strongly linked to leaf nitrogen content because of the high nitrogen content of Rubisco, the primary carboxylating enzyme in C_3 photosynthesis (Field and Mooney 1986). We found no significant difference in leaf nitrogen concentration of 1-year-old needles from young and old trees (1.12 and 1.07%, respectively; $P > 0.6$). Similarly, in a separate study, we found no significant difference in leaf nitrogen concentration or specific leaf area between old and young trees at the same site (Bond et al., unpublished data). According to the Farquhar model of photosynthesis (Farquhar et al. 1980), the initial slope of assimilation (A) versus the internal CO_2 concentration of the leaf (C_i) is determined by the efficiency of carboxylation by Rubisco. Yoder et al. (1996) showed no significant difference in the initial slope of $A-C_i$ curves from foliage of our experimental trees, suggesting that there is no difference in Rubisco activity between the foliage of old and young trees at our site.

Lower g_s and A for values of D above 1.0 kPa indicate that there may be a significant difference in annual carbon gain between old and young ponderosa pine trees if a large portion of the growing season experiences saturating irradiance and high air saturation deficits. Values of PAR were greater than saturation ($800 \mu\text{mol m}^{-2} \text{s}^{-1}$) for approximately 72% of the

1996 growing season (April–September 30). During 32% of the time when irradiance was above $800 \mu\text{mol m}^{-2} \text{s}^{-1}$, D was greater than 2 kPa. Calculations from the relationships in Figure 4 indicate that g_s and A for a sunlit needle at the top of an old tree would be at least 22 and 11% lower, respectively, than a sunlit needle at the top of a young tree when $D = 2.0$ kPa. Therefore, lower g_s and A for a needle of an old tree compared with a young tree would be apparent for at least 25% of the growing season with actual differences being proportionally larger at higher air saturation deficits. These differences may translate into significantly lower annual carbon gain for old trees than for young trees, depending on the light environment of the canopy and how K_L changes with canopy position.

If lower g_s and A in old trees than in young trees is a result of lower hydraulic conductance, then experimentally increasing the K_L of individual branches on old trees should cause an increase in the responses of g_s and A with D (Equation 4, Hypothesis 2). For old trees in early summer, the slopes of g_s and A versus D for the defoliation treatments were significantly less than those for the controls (Figures 5A and 5B). There was no difference between defoliation treatments and controls for young trees (data not shown).

We did not measure Ψ_{leaf} concurrently with our leaf gas exchange measurements until the end of the experiment; however, during the early season measurements, Ψ_{leaf} of treatment branches must have been lower, higher, or similar to that of the control branches. If treatment Ψ_{leaf} was lower than that of the controls, g_s may have increased as a result of the increase in $\Psi_{\text{leaf}} - \Psi_{\text{soil}}$ (Equation 4) and we could observe the same pattern present in Figures 5A and 5B. If Ψ_{leaf} for treatment branches was higher or equal to that for control branches, then the K_L of the remaining foliage on branches in the defoliation treatment must have been increased by the treatment (Equation 4), causing the observed pattern of increased g_s and A . Because we did not measure Ψ_{leaf} , these data are only consistent with our hydraulic limitation hypothesis and not a direct test. However, recent experiments on ponderosa pine in the foot hills near Fort Collins, CO, indicate that removing needles on individual branches has no effect on Ψ_{predawn} or midday Ψ_{leaf} of the remaining foliage (Hubbard, unpublished data).

Late in the summer, there was no significant difference in the responses of g_s and A with D between defoliation treatments and controls. The seasonal response to the defoliation treatment may be associated with the presence of current-year needles, because these needles were not removed in the defoliation treatments. At the beginning of the summer, removing 50% of the leaf mass on branches in the defoliation treatment resulted in a 50% increase in branch K_L ; however, as current-year needles expanded throughout the summer, the differences in K_L between treatment and control branches may have become progressively less.

Our efforts to alter K_L by notching an individual branch in old and young trees were unsuccessful. Notching had no effect on the responses of g_s and A with D , and notching killed two of our replicate branches on old trees. We conclude that notching is a less effective technique than defoliation for modifying K_L . The notching treatment may not significantly reduce K_L of young tree branches because there is a redundancy in the

sapwood of ponderosa pine branches. Branch conductivity measurements of notched branches support this hypothesis because leaf specific conductivity of notched branches was not significantly different from controls ($P = 0.51$, data not shown).

Our experimental manipulations of K_L on branches in old and young trees were designed to examine the short-term responses of g_s and A to changes in K_L . However, results from these treatments do not indicate how hydraulic conductance will change with increased size and age or how long-term changes in hydraulic conductance affect leaf gas exchange. As trees grow larger, xylem permeability and sapwood per unit leaf area may increase, somewhat compensating for longer path lengths (Pothier et al. 1989, Carlquist 1975). These changes may partially mitigate lower hydraulic conductance and steeper responses of g_s and A with D , but the extent to which this occurs and over what time scales are not known.

In summary, we have shown that K_L and K_{L*} are lower and that g_s and A decline more steeply as a function of D in old, tall trees compared to young, short trees. The short-term responses of g_s and A of needles on partially defoliated branches of old trees declined less steeply with D compared to those of needles on control branches, suggesting that increasing K_L in old trees leads to increases in g_s and A . Although these data do not prove that g_s and A are limited by hydraulic conductance in ponderosa pine, they are consistent with the hydraulic limitation hypothesis.

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References

- Carlquist, S. 1975. Ecological strategies of xylem evolution. University of California Press, Berkeley, CA, 259 p.
- Ěermák, J. and J. Kuèera. 1981. The compensation of natural temperature gradient at the measuring point during the sap flow rate determination in trees. *Biol. Plant.* 67:191–220.
- Ěermák, J., M. Deml and M. Penka. 1973. A new method of sap flow rate determination in trees. *Biol. Plant.* 23:469–471.
- Ěermák, J., J. Ulehla, J. Kuèera and M. Penka. 1982. Sap flow rate and transpiration dynamics in the full-grown oak (*Quercus robur* L.) in floodplain forest exposed to seasonal floods as related to potential evapotranspiration and tree dimensions. *Biol. Plant.* 24:446–460.
- Evans, J.R., T.D. Sharkey, J.A. Berry and G.D. Farquhar. 1986. Carbon isotope discrimination measured concurrently with gas exchange to investigate CO_2 diffusion in leaves of higher plants. *Aust. J. Plant Physiol.* 13:281–292.
- Farquhar, G.D., S. von Caemmerer and J.A. Berry. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. *Planta* 149:78–90.
- Farquhar, G.D., J.R. Ehleringer and K.T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. *Annu. Rev. Plant Physiol.* 40:503–537.
- Field, C.B. and H.A. Mooney. 1986. The photosynthesis–nitrogen relationship in wild plants. *In* On the Economy of Plant Form and Function. Ed. T.J. Givnish. Cambridge University Press, Cambridge, UK, pp 25–55.
- Field, C.B., J.T. Ball and J.A. Berry. 1989. Photosynthesis: principles and field techniques. *In* Plant Physiological Ecology: Field Methods and Instrumentation. Eds. R.H. Pearcy, J. Ehleringer, H.A. Mooney and P.W. Rundel. Chapman and Hall, New York, pp 209–248.
- Friend, A.D., H.H. Shugart and S.W. Running. 1993. A physiology-based model of forest dynamics. *Ecology* 74:792–797.
- Fuchs, E.E. and N.J. Livingston. 1996. Hydraulic control of stomatal conductance in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and alder (*Alnus rubra* (Bong.)) seedlings. *Plant Cell Environ.* 19:1091–1101.
- Grulke, N.E. and P.R. Miller. 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.
- Hadley, E.B. 1969. Physiological ecology of *Pinus ponderosa* in Southwestern North Dakota. *Am. Midl. Nat.* 81:289–315.
- Holbrook, M.N., M.J. Burns and C.B. Field. 1995. Negative xylem pressures in plants: A test of the balancing pressure technique. *Science* 270:1193–1194.
- Jones, H.G. and R.A. Sutherland. 1991. Stomatal control of xylem embolism. *Plant Cell Environ.* 14:607–612.
- Köstner, B., P. Biron, R. Siegwolf and A. Granier. 1996. Estimates of water vapor flux and canopy conductance of Scots pine at the tree level utilizing different xylem sap flow methods. *Theor. Appl. Clim.* 53:105–113.
- Kuèera, J., J. Ěermák and M. Penka. 1977. Improved thermal method of continual recording the transpiration flow rate dynamics. *Biol. Plant.* 19:413–420.
- Kull, O. and A. Koppel. 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.
- Mattson-Djos, E. 1981. The use of pressure bomb and porometer for describing plant water stress in tree seedlings. *In* Proc. Nordic Symp. On vitality and Quality of Nursery Stock. Ed. P. Puttonen. Dept. of Silviculture, University of Helsinki, Finland, pp 45–57.
- McMurtrie, R.E., D.A. Rook and F.M. Kelliher. 1990. Modeling the yield of *Pinus radiata* on a site limited by water and nitrogen. *For. Ecol. Manag.* 39:381–413.
- McMurtrie, R.E., R. Leuning, W.A. Thompson and A.M. Wheeler. 1992. A model of canopy photosynthesis and water use incorporating a mechanistic formulation of leaf CO_2 exchange. *For. Ecol. Manag.* 52:261–278.
- Meinzer, F.C. and D.A. Grantz. 1990. Stomatal and hydraulic conductance in rowing sugarcane: stomatal adjustment to water transport capacity. *Plant Cell Environ.* 13:383–388.
- Mohren, G.M.J. 1987. Simulation of forest growth, applied to Douglas fir stands in the Netherlands. Ph.D. Diss., Landbouwniversiteit te Wageningen, Wageningen, The Netherlands, 183 p.
- Mohren, G.M.J., C.P. Van Gerwen and C.J.T. Spitters. 1984. Simulation of primary production in even-aged stands of Douglas-fir. *For. Ecol. Manag.* 9:27–49.
- Neter, J., W. Wasserman and M.H. Kutner. 1990. Applied linear statistical models: regression, analysis of variance and experimental design. Irwin, Boston, MA, 547 p.
- Pockman, W.T., J.S. Sperry and J.W. O’Leary. 1995. Sustained and significant negative water pressure in xylem. *Nature* 378:715–716.
- Pothier, D., H.A. Margolis and R.H. Waring. 1989. Patterns of change of saturated sapwood permeability and sapwood conductance with stand development. *Can. J. For. Res.* 19:432–439.

- Running, S.W. and J.C. Coughlan. 1988. A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. *Ecol. Model.* 42:125–154.
- Running, S.W. and S.T. Gower. 1991. Forest-BGC, a general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiol.* 9:147–160.
- Ryan, M.G. and B.J. Yoder. 1997. Hydraulic limits to tree height and tree growth. *BioScience* 47:235–242.
- Ryan, M.G., D. Binkley and J.H. Fownes. 1996. Age-related decline in forest productivity: pattern and process. *Adv. Ecol. Res.* 27:213–262.
- Saliendra, N.Z., J.S. Sperry and J.P. Comstock. 1995. Influence of leaf water status on stomatal response to humidity, hydraulic conductance, and soil drought in *Betula occidentalis*. *Planta* 196:357–366.
- Schoettle, A.W. 1994. Influence of tree size on shoot structure and physiology of *Pinus contorta* and *Pinus aristata*. *Tree Physiol.* 14:1055–1068.
- Schulze, E.-D., J. Ěermák, R. Matyssek, M. Penka, R. Zimmerman, F. Vasicek, W. Gries and J. Kuèera. 1985. Canopy transpiration and water fluxes in the xylem of the trunk of *Larix* and *Picea* trees—a comparison of xylem flow, porometer and cuvette measurements. *Oecologia* 66:475–483.
- Sperry, J.S. and W.T. Pockman. 1993. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. *Plant Cell Environ.* 16:279–287.
- Sperry, J.S., N.N. Alder and S.E. Eastlack. 1993. The effect of reduced hydraulic conductance on stomatal conductance and xylem cavitation. *J. Exp. Bot.* 44:1075–1082.
- Teskey, R.O., T.M. Hinckley and C.C. Grier. 1983. Effect of interruption of flow path on stomatal conductance of *Abies amabilis*. *J. Exp. Bot.* 34:1251–1259.
- Tyree, M.T. and J.S. Sperry. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? *Plant Physiol.* 88:574–580.
- Wang, Y.P. 1988. Crown structure, radiation absorption, photosynthesis and transpiration. Ph.D. Diss., University of Edinburgh, Edinburgh, Scotland, 188 p.
- Waring, R.H. and W.B. Silvester. 1994. Variation in foliar ¹³C values within the crowns of *Pinus radiata* trees. *Tree Physiol.* 14:1203–1213.
- Whitehead, D., N.J. Livingston, F.M. Kelliher, K.P. Hogan, S. Pepin, T.M. Mcseveny and J.N. Byers. 1996. Response of transpiration and photosynthesis to a transient change in illuminated foliage for a *Pinus radiata* D. Don tree. *Plant Cell Environ.* 19:949–957.
- Williams, M., E.B. Rastetter, D.N. Fernandes, M.L. Goulden, S.C. Wofsy, G.R. Shaver, J.M. Melillo, J.W. Munger, S.M. Fan and K.J. Nadelhoffer. 1996. Modeling 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.
- Wise, L.F., M. Murphy and A.A. D'Addieco. 1945. Chlorite holocellulose, its fractionation and bearing on summative wood analysis and on studies on the hemicelluloses. Section of the Technical Association of the Pulp and Paper Industry 122:11–19.
- Wong, S., I.R. Cowan and G.D. Farquhar. 1985. Leaf conductance in relation to rate of CO₂ assimilation. III. Influences of water stress and photoinhibition. *Plant Physiol.* 78:830–834.
- Yoder, B.J., M.G. Ryan, R.H. Waring, A.W. Schoettle and M.R. Kaufmann. 1994. Evidence of reduced photosynthetic rates in old trees. *For. Sci.* 40:513–527.
- Zimmerman, M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, New York, 143 p.