

Responses of sap flux and stomatal conductance of *Pinus taeda* L. trees to stepwise reductions in leaf area

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Abstract

Herbivory or artificial foliage removal has been shown to affect gas exchange and canopy water relations. In this study, canopy architecture and water relations in response to progressive defoliation were examined in a stand of 8-year-old loblolly pine (*Pinus taeda* L.) trees, a shade-intolerant, pioneer species common in the south-eastern USA. Sap flux was measured with constant heat sap flow gauges in order to estimate canopy stomatal conductance (G_s) while foliage in the 6 m high stand was harvested in 1 m increments from the bottom up. Leaf-level stomatal conductance and water potential data were also collected. Profiles of silhouette area ratio and specific leaf area showed no trends with crown height, reflecting an open canopy (leaf area index = 1.55). Therefore, short-term changes in G_s with foliage removal were attributed to hydraulic effects rather than influences of changes in mean microclimate conditions on G_s of remaining foliage. A large increase in G_s was observed during the 6 h pruning period which fully compensated for the reductions in foliage area down to 45%. Canopy stomatal conductance and whole plant liquid phase conductance as calculated from sap flux were both influenced by the rate of growth as indicated by the annual basal area increment.

Key words: Canopy stomatal conductance, defoliation, hydraulic conductance, sap flux, stomatal conductance.

Introduction

Responses of plant water relations to reductions in leaf area may have implications for predicting whole plant responses to herbivory, as well as for evaluating relationships between stomatal conductance to water vapour (g_s)

and other hydraulic parameters. Increased gas exchange rates have been commonly observed in response to defoliation in a range of species (McNaughton, 1983; Gold and Caldwell, 1989; Welter, 1989; Reich *et al.*, 1993). While defoliation experiments have often focused on assimilation and growth (Alderfer and Eagles, 1976; Wallace *et al.*, 1984; Belsky, 1986), effects on g_s are less studied (Welter, 1989). Transpiration rate per unit leaf area and g_s have generally been found to increase with decreasing leaf area (Meinzer and Granz, 1991; Reich *et al.*, 1993; Kramer and Boyer, 1995). This effect has been attributed to changes in microclimate of remaining foliage (Parker, 1949), in addition to increases of leaf specific hydraulic conductance (Meinzer and Granz, 1990; Meinzer *et al.*, 1991), as g_s has been demonstrated to increase with hydraulic conductance (Teskey *et al.*, 1983; Reich and Hinckley, 1989). However, increases in stomatal conductance in tree species has not been consistently observed in response to partial defoliation by herbivores (Ellsworth *et al.*, 1994).

As large numbers of leaf-level g_s measurements within short intervals are required adequately to characterize the conductance of a canopy (Leverenz *et al.*, 1982; Jarvis, 1995), leaf-level measurements may not capture the effects of tree crown defoliation on whole plant water relations. In this study, successive canopy layers were removed from an 8-year-old *Pinus taeda* L. plantation while sap flux was measured continuously in 10 individuals in order to calculate whole plant liquid phase hydraulic conductance (L) and obtain continuous estimates of canopy stomatal conductance (G_s), or mean g_s weighted by leaf area. In field studies, hydraulic effects on g_s induced by reductions of leaf area are difficult to distinguish from effects of increased light penetration or wind exposure if the canopy was sufficiently closed prior to foliage removal. In addition, morphology and physiology of remaining foliage, which systematically affect g_s according to canopy posi-

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tion, may influence the results of vertically-progressing defoliation experiments. This effect has been well illustrated by multi-layer canopy models (Whitehead *et al.*, 1990; Stockle, 1992; Roberts *et al.*, 1993).

If light availability is limited in the lower crown, needles become more horizontal and less self-shading. In addition, shade leaves may contain fewer mesophyll layers, resulting in increased specific leaf area ($A_1 : M_1$; Shelton and Switzer, 1984; Oren *et al.*, 1986; Leverenz and Hinckley, 1990). High $A_1 : M_1$ is associated with low needle density in these layers and less clumping of foliage, or ratios between branch silhouette and leaf area ($A_p : A_1$) approaching the maximum efficiency value of 1. Silhouette area ratio has been shown to be more important than leaf angle in assessments of light capture efficiency in the lower crown (Leverenz and Hinckley, 1990). Thus, high leaf area index (LAI) and light attenuation result in pronounced canopy profiles of both parameters (Sampson and Smith, 1993).

In this study, LAI, $A_1 : M_1$, and $A_p : A_1$ profiles were generated for 5×1 m canopy layers in conjunction with the removal of foliage in order to assess short-term changes in g_s with explicit consideration of these confounding effects. Harvested branches and foliage were used to evaluate canopy architecture, which may influence water relations via effects on light penetration, temperature and humidity throughout the canopy profile (Kinerson *et al.*, 1974), either directly or in conjunction with changes in leaf physiology.

Materials and methods

Study site

The site was located in the Durham Division of Duke Forest, North Carolina (35°52'00" N, 79°59'45" W) in a transitional zone between the coastal plain and the Piedmont plateau. The surrounding terrain is rolling, with an average elevation of approximately 130 m above sea level. Mean annual temperature for this region is 15.5°C, while mean annual precipitation is 1140 mm. Rainfall is well distributed throughout the year as a whole (Ruffner and Bair, 1985).

Measurements were made in a *Pinus taeda* L. monoculture on Appling sandy loam subject to minimal erosion due to <2% slope. The trees were planted as 1-year-old seedlings during February, 1986 at 2.4×2.4 m spacing. At the time of the experiment the stand included subsequent *Pinus taeda* recruits in addition to a minor intrusion of understorey hardwood saplings, principally *Liquidambar styraciflua* L., *Juniperus virginiana* L., and *Quercus phellos* L. The plot chosen for study contained 65 trees covering 78.5 m² of ground area, or 0.83 trees m⁻². Mean height of *P. taeda* individuals within the plot was 3.7 ± 1.2 m, with the tallest individuals reaching *c.* 5 m. Diameter at breast height for all trees was approximately normally distributed and ranged from 2.7 to 10.3 cm, with a quadratic mean of 3.6 cm. The canopy area index, which includes the surface of all canopy elements (m² m⁻²) just before the experiment was 1.89, as measured with an LAI 2000 plant canopy analyser (Li-Cor, Lincoln, NE, USA).

Sap flux measurements

Twelve *P. taeda* individuals were chosen for sap flow measurements with heated and unheated thermocouple pairs after Granier (1987). Ten experimental trees represented suppressed, intermediate, and dominant classes having approximately the same population density as the rest of the stand. Two additional *P. taeda* individuals located just outside the plot were selected as references.

Granier-type stem flow sensors consisted of a copper-constantan thermojunction inserted 1 cm into a 2 cm long probe which is 2 mm in diameter. Two sensors were inserted radially into the trunk, with one spaced approximately 15 cm above the other. The upper sensor was equipped with a constantan heater supplied with constant 200 mW power. The two thermojunctions were joined as a thermocouple and the temperature difference between the two probes was recorded to obtain sap flux density J_s (g m⁻² s⁻¹), as derived empirically (Granier, 1987).

Canopy stomatal conductance (G_s) was calculated from sap flux density using a simplified form of the Penman–Monteith equation:

$$G_s = \frac{\dot{G}_c}{LAI} = \frac{\gamma \lambda J_s}{\rho c_p D A_1 : A_s} \quad (1)$$

where \dot{G}_c is canopy conductance, γ is the psychrometric constant (kPa K⁻¹), λ is the latent heat of vaporization (J kg⁻¹), ρ is the density of moist air (kg m⁻³), c_p is the heat capacity of moist air (J kg⁻¹ K⁻¹), D is the vapour pressure deficit (kPa), and $A_1 : A_s$ is the leaf to sapwood area ratio (m² m⁻²; Whitehead and Jarvis, 1981). This formulation assumes (1) that sap flux densities are uniform throughout the cross-sectional sapwood area, (2) that stem capacitance may be neglected, and (3) that canopy aerodynamic conductance is much larger than G_s (i.e. strong aerodynamic coupling), as has been commonly reported for young conifer stands (Whitehead and Jarvis, 1981).

In addition, whole plant liquid phase hydraulic conductance (L) was calculated after Loustau and Granier (1993):

$$L = \frac{J_s}{\psi_s - \psi_l} \quad (2)$$

where ψ_s and ψ_l are the soil and leaf water potentials, respectively.

Relative humidity and temperature were recorded in mid-canopy (RHA1 probe, Delta-T Devices, Ltd., Cambridge, England, UK) to calculate the vapour pressure deficit (D) of canopy air. In addition, a quantum sensor (190SB, Li-Cor, Inc) was elevated above the canopy and levelled to estimate incident overstorey photosynthetically active radiation (I_o). Three quantum sensors were distributed under the canopy to measure incident understorey photosynthetically active radiation (I). Sap flow and micrometeorological data were recorded continuously with a multi-channel data logger (Delta-T Devices, Ltd.) at a frequency of 1 min on the day of the experiment and for 3 d prior to the experiment.

Foliage removal experiment

Beginning 1 m above the ground, 5×1 m canopy layers of the 10 sap flow experimental trees, and all other individuals in the plot, were harvested from the bottom up at 1 h intervals between 11:40 and 18:00 EST on 30 March 1993. Due to the vertical distribution pattern in canopy leaf area, total stand biomass in the first and fifth canopy layers was negligible. The 10 sap flow experiment trees did not have branches from 0–1 m, so that defoliation effects were considered from 1–2, 2–3, 3–4,

and 4–5 m for the water relations analysis. Distances were marked on stems from 1–5 m above the ground, so that defoliation was conducted between marks by pruning of whole branches and needles. Needles at the tip of branches may actually overlap into the adjacent upper or lower layer. During the harvesting period microclimate measurements continued to be recorded as described.

One branch was left intact on each tree at 2.5 m so that stomatal conductance (g_s) and water potential (ψ_l) measurements could be taken just prior to the harvest, between successive harvests, and after the top layer was defoliated. These data were collected with a steady-state porometer (LI-1600, Li-Cor, Lincoln, NE, USA) and a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA, USA), respectively. Canopy area index measurements were also made following each pruning increment with an LAI 2000 plant canopy analyser (Li-Cor). The porometry branches were removed at the end of the experiment, at which time all remaining biomass, including stems and understorey vegetation, was also harvested.

Biomass and leaf area measurements

Fresh weight of whole harvested branches was recorded by layer for all branches in the field on the day of the experiment. In addition, three branches from each experimental tree at each layer were reserved for laboratory measurement of mass and area. These measurements included (1) projected one-sided silhouette area (A_p) using a digital scanning device (DIAS II, Decagon Devices, Inc., Pullman, WA, USA), (2) projected one-sided leaf area (A_l) on 10 fascicles randomly selected from each branch using the same method as A_p , (3) fresh weight of whole branches (including needles) before drying, and of needles (M_l) and branches separately after oven-drying for at least 48 h at 70 °C, and (4) mass of the 10 fascicles after oven-drying. Fascicles provided data for estimating specific leaf area ($A_l:M_l$, $\text{cm}^2 \text{g}^{-1}$). This, combined with M_l of the respective branch was used to estimate branch A_l . The silhouette area ratio ($A_p:A_l$, $\text{m}^2 \text{m}^{-2}$) was calculated from A_p and A_l . The ratio of M_l to total branch fresh weight was multiplied by the field-measured fresh weight of each canopy layer to estimate dry leaf mass; leaf area was then estimated by multiplying $A_l:M_l$ by the total leaf dry mass of that layer. This was done for each measurement tree using the mean values from the tree itself, and for the stand using the mean values from all trees. Summing leaf mass and area in each stand canopy layer provided an estimate of the vertical distribution of biomass and leaf area index (LAI , $\text{m}^2 \text{m}^{-2}$). Total leaf area for each measured tree was used to calculate the leaf to sapwood area ratio ($A_l:A_s$, $\text{m}^2 \text{cm}^{-2}$). Values of A_s measured on all trees in the plot provided an independent estimate of LAI . LAI obtained by harvest was compared to LAI 2000 values recorded after each canopy cut.

Stems were also harvested after branch removal, and cross-sections were taken from each stem to record sapwood area at sensor height, and calculate wood specific gravity from disc volume and dry mass obtained after drying the discs to constant weight. Total stem volume was then estimated from stem height for each individual by assuming a three-dimensional cone shape above 1.3 m and cylindrical volume from 1.3 m to the ground. Volumes were partitioned into 1 m canopy increments and stem mass was obtained with the wood specific gravity. Water mass in each canopy layer was obtained for needles plus branches from one minus dry-to-fresh weight ratio multiplied by the field-measured weight, and for the stem from water weight per unit of stem disc volume and the volume of stem in each layer.

Results

Canopy structure

Canopy biomass and leaf area distributions are summarized in Figs 1 and 2. Average $A_l:M_l$, $A_p:A_l$, and $A_l:A_s$ values were consistent with literature values for loblolly pine at $27.69 \pm 1.08 \text{ cm}^2 \text{g}^{-1}$, $0.82 \pm 0.14 \text{ m}^2 \text{m}^{-2}$, and $0.17 \pm 0.02 \text{ m}^2 \text{cm}^{-2}$, respectively (Leverenz and Hinckley, 1990; Samuelson *et al.*, 1992; Margolis *et al.*, 1995). Profiles of $A_l:M_l$ and $A_p:A_l$ indicated a high degree of canopy openness, as no vertical trend was apparent (Table 1). Canopy gap fraction as estimated by the LAI 2000 was found to be 0.19. After all branches were removed, stem area index was measured at $0.34 \text{ m}^2 \text{m}^{-2}$. A 95% confidence interval about the regression included the 1:1 relationship between actual and LAI 2000-derived

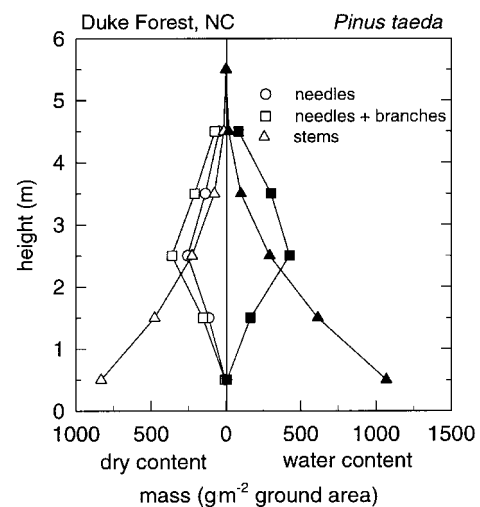


Fig. 1. Dry biomass and water content of needles, needles+branches, and stems at five one-meter canopy layers for 12 harvested trees located on a 78.5 m² plot.

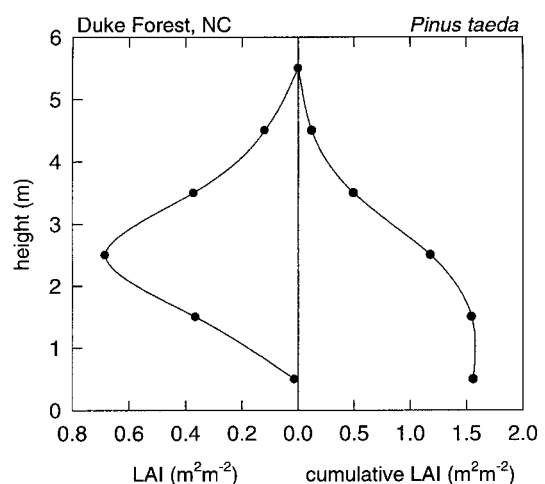


Fig. 2. Leaf area index (LAI) and cumulative LAI for 5 × 1 m canopy layers as determined by harvest of all trees in the experimental plot.

Table 1. Specific leaf area ($A_1:M_1$) and silhouette area ratio ($A_p:A_1$) for 10 *Pinus taeda* individuals by canopy layer

P-values are given for ANOVA. Leaf and silhouette area are reported as projected one-sided area.

Height (m)	$A_1:M_1$ ($\text{cm}^2 \text{g}^{-1}$)	$A_p:A_1$ ($\text{m}^2 \text{m}^{-2}$)
1-2	31.1 ± 2.0	0.84 ± 0.11
2-3	25.8 ± 1.9	1.00 ± 0.16
3-4	26.5 ± 8.7	0.71 ± 0.11
4-5	28.1 ± 3.7	0.72 ± 0.17
Mean	27.7 ± 1.1	0.82 ± 0.14
P	0.32	0.42

LAI when the stem-only LAI 2000 value was subtracted from total LAI 2000 measurements made after each layer was removed (Fig. 3). Other correction factors, such as values accounting for mutual shading of needles as has been previously suggested (Stenberg *et al.*, 1994), were not required.

Light extinction throughout the canopy was evaluated by relating LAI to $I \times I_0^{-1}$ measured before the defoliation began and after each layer was removed. A linear relationship between $\ln(I \times I_0^{-1})$ and LAI was found (Fig. 4), as predicted from Beer's equation for a homogeneous canopy with a low degree of clumped foliage (Jarvis and Leverenz, 1983). The absolute value of the slope, or the extinction coefficient, derived from this relationship was 0.17 ± 0.02 ($P < 0.05$).

Water relations

Sap flux for reference versus experimental trees is given in Fig. 5. A similar relationship is observed both on the day prior to the experiment and on the day of the experiment, with the exception of the last two measurement periods after 80% and 100% of leaf area had been

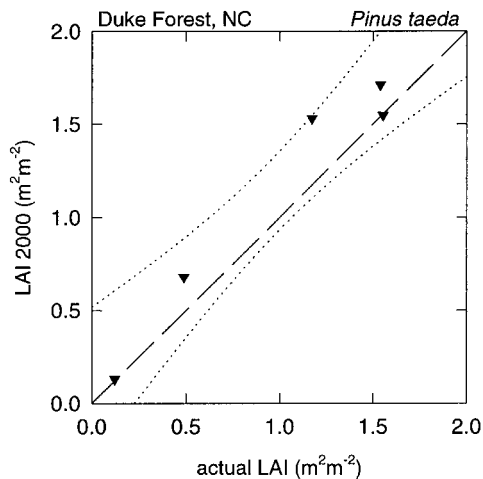


Fig. 3. Comparison of LAI 2000 leaf area index (LAI) values with actual LAI as determined by harvest. The 95% confidence interval of the regression line (dotted lines) are given with a 1:1 line (dashed line).

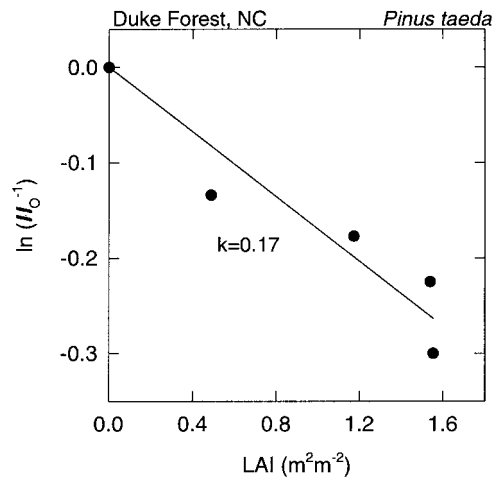


Fig. 4. Determination of the Beer extinction coefficient (k) as the slope of the relationship between the natural logarithm of incident fraction of photosynthetically active radiation ($I \times I_0^{-1}$) and leaf area index (LAI).

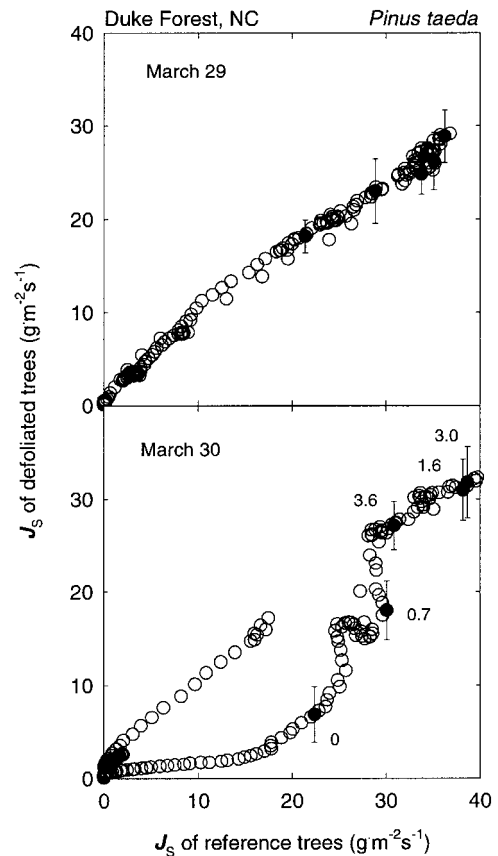


Fig. 5. One minute averages of sap flux (J_s) given every 5 min for reference versus experimental trees on the day prior to the experiment (March 29) and the experiment day (March 30; open circles). Data were missing for 1 h on the morning of experiment prior to defoliation. Afternoon values for both days are given for the first measurement point after sap flux stabilized following cutting on the experiment day (closed circles). Numerical values represent average leaf area per tree (m^2) before and after each cutting period.

removed, respectively. Standard errors are given for experimental trees only due to the small number of reference trees. Canopy stomatal conductance was calculated on a leaf area basis according to equation (1) and compared with measured g_s (Fig. 6). Mean g_s and G_S of the combined 10 experimental and two reference trees prior to the branch harvesting period were not different (paired t -test, $P > 0.05$) at 0.28 ± 0.03 and $0.27 \pm 0.03 \text{ mol m}^{-2} \text{ s}^{-1}$, respectively. The diurnal patterns of G_S for reference and experimental trees were similar on the day prior to the experiment. The relationship between the two groups (not shown, but indicated in Fig. 5, top, $P < 0.05$, $r^2 = 0.98$) was used to predict G_S for measurement trees on the experiment day in the absence of defoliation (closed circles). Actual G_S calculated with a stepwise reduction in leaf area is shown for experimental trees during this period (open circles). In contrast to reference trees, G_S of defoliated trees showed a rapid increase during the harvesting period. Values are given for 10 min periods between cuts during which sap flux appeared to reach steady state in all 10 trees. Stomatal conductance of the remaining measurement branch at 2.5 m as measured by porometry did not show the same pattern (closed squares).

In order to evaluate whether the observed increase in G_S during defoliation was compensatory on a whole-plant

basis, G_S was also calculated by maintaining constant, pre-harvest leaf area to estimate G_S during the defoliation period (open triangles). These values were equal to G_S predicted for the day of the experiment from reference trees in the absence of harvest, indicating full compensation of water uptake during foliage removal.

The effect of plant size on water relations parameters was evaluated with basal area increments obtained from diameter measurements of trees in the study plot during the experiment and 1 year prior to the experiment. These values were related to g_s and $A_1:A_s$.

The experiment was conducted during a period in which soil moisture was not limiting, as evidenced by the presence of the water table at the soil surface following a recent rain event (although the site was not permanently water-logged). Therefore ψ_s was assumed to be zero for calculations of L , neglecting soil solute potential.

Both g_s measured by porometry and L prior to defoliation increased with basal increment for the 10 experimental and two reference trees ($P < 0.05$, Fig. 7) while $A_1:A_s$ did not ($P > 0.05$).

Discussion

Canopy structure

The vertical distribution of leaf area and biomass measured in this study suggest an open canopy in this stand, indicating a similar g_s capacity in all canopy layers. An extinction coefficient of 0.17, low in comparison with previously reported k for conifer stands (Jarvis and Leverenz, 1983), was estimated. In addition, combining LAI ($= 1.55 \text{ m}^2 \text{ m}^{-2}$) and stem area index ($= 0.34 \text{ m}^2 \text{ m}^{-2}$) yielded a total canopy area index of $1.89 \text{ m}^2 \text{ m}^{-2}$ prior to harvest. Thus, the total light absorbing surface area in the stand was low.

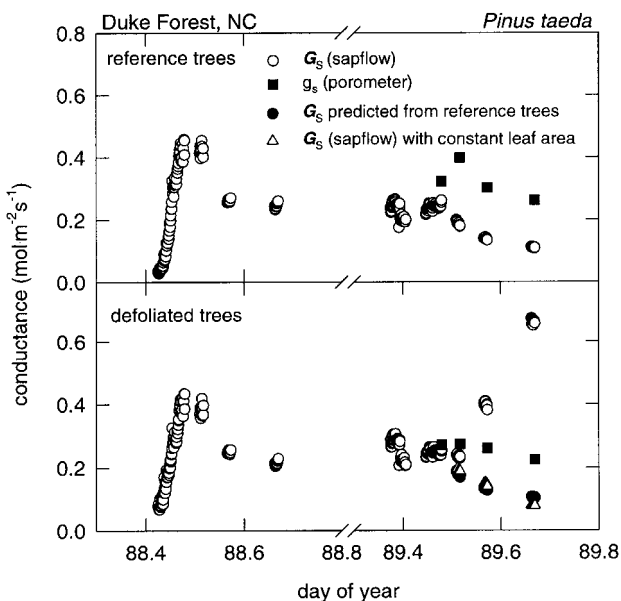


Fig. 6. Mean canopy stomatal conductance (G_S) of two reference and 10 experimental trees during defoliation (day of year 89) and 1 d prior to defoliation (day of year 88). Afternoon values for both days are given during 10 min intervals when sap flux stabilized following cutting on the day of the experiment. Open circles represent calculated values using actual leaf area. On the day of the experiment, closed circles show G_S as predicted from behaviour of reference trees. Open triangles show G_S calculated with constant rather than decreasing leaf area. Closed squares are mean stomatal conductance values measured by porometry ($n=2$ for reference trees, 10 for defoliated trees).

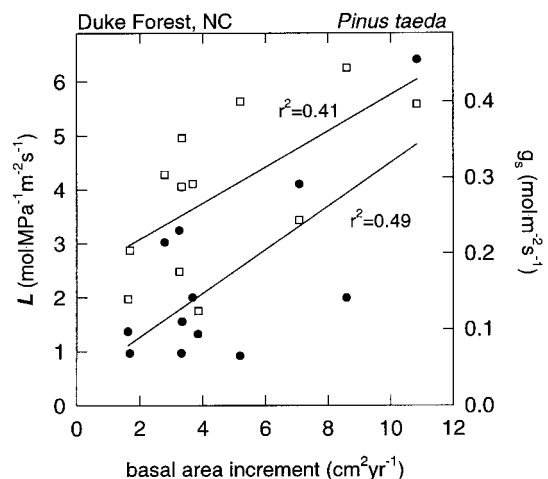


Fig. 7. Whole plant liquid-phase hydraulic conductance (L , circles) and stomatal conductance (g_s , squares) as a function of annual basal area increment ($P < 0.05$).

Given the low k and canopy area index, it is not surprising that $A_1:M_1$ and $A_p:A_1$ did not change with canopy height, reflecting relatively high light intensity in lower layers. This appears to be common in young loblolly pine stands. Shelton and Switzer (1984) reported similar fascicle density throughout the canopy of a 5-year-old stand. Similarly, for a 15-year-old loblolly stand, Sinclair and Knoerr (1982) found canopy light distribution similar to that expected from randomly arranged foliage, suggesting minimal vertical gradients in clumping of branches and foliage.

Negligible reductions in light were calculated as foliage in the lower canopy layers was highly illuminated prior to harvest. Averaging $I \times I_o^{-1}$ attenuated in each in canopy layer and weighting by the LAI of each layer, a mean ratio of 0.82 was obtained for the entire canopy. In comparison, $I \times I_o^{-1}$ at the lowest layer was calculated to be 0.74. In the absence of changes in leaf and shoot morphology with canopy depth due to high canopy openness, effects of microclimate and canopy position on g_s were probably small and can be neglected when evaluating responses to upwardly progressing leaf area reduction.

Water relations

Full compensation in J_s was observed until 55% of leaf area was removed. Following the removal of the third canopy layer, the experimental trees showed lower J_s than the reference, reflecting a reduction of leaf area to 20%. After the remaining foliage was removed, J_s decreased rapidly at first, and then slowly reached zero. These small flux rates were likely to reflect a combination of water loss through bark and stem recharge.

Canopy stomatal conductance calculated from sap flux was similar to leaf level g_s measured by porometry for the 10 experimental trees prior to defoliation. Maximum values of G_s were somewhat higher than previously reported in *Pinus* stands (Granier *et al.*, 1996; Köstner *et al.*, 1996), although g_s fell within the range of leaf-level conductance of seedlings adapted to well-watered conditions when adjusted for one-sided leaf area (Teskey *et al.*, 1987). In defoliated trees, leaf-level measurements did appear to show a departure from the diurnal evident in the reference trees (Fig. 6). However, canopy stomatal conductance estimated during the defoliation period indicated large increases in G_s with foliage removal, although the effect was not captured effectively with instantaneous leaf level measurements. Thus, although mean g_s was equivalent to G_s prior to defoliation for the experimental trees, the rapid increase in G_s was not reflected in g_s .

There may be two possible reasons for the incongruence of leaf- and canopy- level conductance estimates. First, G_s was calculated with sap flux values which had appeared to reach steady state at the end of each measurement

period, but g_s measurements were made throughout the period between canopy cuts. The number of measurements precluded conducting all g_s sampling at steady state, so that leaf-level measurements represent a transient period. Secondly, g_s was measured on a mid-canopy branch during the course of the experiment. As the canopy was defoliated from the ground up, the sun angle was simultaneously decreasing, resulting in mid-canopy shading from the uncut trees surrounding the experimental plot. The relatively constant g_s in this branch may partially reflect the compensatory effects of decreased leaf area above and decreasing sun angle relative to the remaining foliage, for which average light increased as lower layers were removed. These issues illustrate the advantages of estimating G_s with continuous measurements if associated assumptions, such as a well aerodynamically coupled canopy and low stem capacitance relative to sap flux, are reasonable. The first assumption is generally accepted for conifers, which have high aerodynamic conductance (Whitehead and Jarvis, 1981), especially in stands supporting low LAI (Granier and Loustau, 1994).

With regard to the second assumption, the total amount of water stored in stems above ground was equivalent to about 2 mm water depth, as estimated from Fig. 1. Waring and Running (1978) have shown a maximum of 8% daily withdrawal or recharge of plant stem capacitance in *Psuedotsuga menziesii*. It is likely that recharge had occurred prior to the experiment in this stand, and that stem water content was close to maximum, as the soil was saturated for several days prior to defoliation. However, if the estimate of Waring and Running is applied to the *P. taeda* individuals in this study, at most 0.16 mm of water were recharged during the midday-late afternoon experimental period. In comparison to 1.5 mm d^{-1} daily transpiration at this site on the day prior to the experiment, recharge can account for *c.* 11% of the compensation effect reported here, if evenly distributed over the experimental period. Given the high midday water potential measured prior to defoliation ($-0.73 \pm 0.07 \text{ MPa}$) it is unlikely that cavitation-induced withdrawal of stem water storage reached even these maximum values.

The similarity of G_s values predicted from reference trees on the experiment day and G_s simulated with constant rather than decreasing leaf area (Fig. 6) indicates almost fully compensatory increases in conductance in response to foliage removal. Thus the decrease in J_s after removal of the third layer (Fig. 5) resulted in only a slight relative decrease in G_s calculated with constant leaf area compared to that predicted from reference trees. In a defoliation study on sugarcane, Meinzer and Granz (1990) also found full compensation of water uptake in response to a 40% reduction in leaf area. In that study, increases in conductance were not accompanied by

changes in ψ_1 , but were attributed to other effects of increased hydraulic conductance. In a separate study, Meinzer *et al.* (1991) concluded that these effects are mediated by changes in xylem sap composition, as g_s of excised leaves from small sugarcane plants corresponded to g_s of larger plants when root xylem exudate of the larger plants was applied. Again, the authors attributed the chemical effects to differences in root hydraulic conductance in plants of varying sizes. A strong correlation between hydraulic conductance and g_s was also reported by Teskey *et al.* (1983), who observed declines in g_s when roots of 30-year-old *Abies amabilis* were removed, or cuts were made into branches to reduce L within the root and stem pathways, respectively. In a similar study, Sperry *et al.* (1993) proposed that adjustments of g_s in response to reduced hydraulic conductance were mediated by small, undetected changes in ψ_1 which maintained ψ_1 above the threshold value for xylem cavitation. Thus, both experimental increases and decreases in L have resulted in similar directional changes in g_s .

As changes in G_s observed in this study were associated with increases in hydraulic conductance, a similar trend may be present in unmanipulated trees of varying growth rate. Trees with large stem increments produce larger, more, or more porous tracheids, factors which may increase the wood specific conductivity, or stem $L \times$ stem length (Pothier *et al.*, 1989a; Tyree and Ewers, 1991). In fact, L increased with the rate of basal area increment (Fig. 7) for the individuals in the study plot. Increases in stem permeability with site quality have been observed in *Pinus* stands (Pothier *et al.*, 1989b); however, such increases may be accompanied by altered $A_1:A_s$ (Espinosa Bancalari *et al.*, 1987; Coyea and Margolis, 1992) such that g_s is unaffected. Here, $A_1:A_s$ was unaffected by the rate of basal area increment ($P > 0.05$), and the increase in L with rate of basal area increment was associated with a concurrent increase in g_s (Fig. 6). Thus, even in an even-aged plantation and in the absence of defoliation, water loss rate per unit leaf area showed a dependency on plant growth rate. Although no direct relationship between L and g_s was found ($P > 0.05$), this may be due to the high degree of variation in g_s during the single preharvest sampling interval. As both parameters were calculated from the same J_s values, a more representative comparison of L and G_s could not be made due to autocorrelation.

Studies relating g_s and L suggest that stomatal adjustments to hydraulic conductance serve to prevent xylem embolism by maintaining ψ_1 above critical values (Jones and Sutherland, 1991; Hacke and Sauter, 1995; Cochard *et al.*, 1996), so that g_s and L may be related. However, as proposed mechanisms of such responses include both chemical (Meinzer *et al.*, 1991) and hydraulic signals (Teskey *et al.*, 1983; Sperry *et al.*, 1993), additional studies of underlying causal relationships are required.

Causal mechanisms must account for both rapid responses to defoliation, which is often associated with herbivory or mechanical, wind-related leaf loss, and long-term effects of growth rate and plant size which have been observed. However, in analysing field measurements, as has been illustrated, caution must be exercised in quantifying short- and long-term effects of leaf area on g_s without regard to degree of canopy development.

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