

# Canopy conductance of *Pinus taeda*, *Liquidambar styraciflua* and *Quercus phellos* under varying atmospheric and soil water conditions

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**Summary** Sap flow, and atmospheric and soil water data were collected in closed-top chambers under conditions of high soil water potential for saplings of *Liquidambar styraciflua* L., *Quercus phellos* L. and *Pinus taeda* L., three co-occurring species in the southeastern USA. Responses of canopy stomatal conductance ( $g_t$ ) to water stress induced by high atmospheric water vapor demand or transpiration rate were evaluated at two temporal scales. On a diurnal scale, the ratio of canopy stomatal conductance to maximum conductance ( $g_t/g_{t,max}$ ) was related to vapor pressure deficit ( $D$ ), and transpiration rate per unit leaf area ( $E_t$ ). High  $D$  or  $E_t$  caused large reductions in  $g_t/g_{t,max}$  in *L. styraciflua* and *P. taeda*. The response of  $g_t/g_{t,max}$  to  $E_t$  was light dependent in *L. styraciflua*, with higher  $g_t/g_{t,max}$  on sunny days than on cloudy days. In both *L. styraciflua* and *Q. phellos*,  $g_t/g_{t,max}$  decreased linearly with increasing  $D$  (indicative of a feed-forward mechanism of stomatal control), whereas  $g_t/g_{t,max}$  of *P. taeda* declined linearly with increasing  $E_t$  (indicative of a feedback mechanism of stomatal control). Longer-term responses to depletion of soil water were observed as reductions in mean midday  $g_t/g_{t,max}$ , but the reductions did not differ significantly between species. Thus, species that employ contrasting methods of stomatal control may show similar responses to soil water depletion in the long term.

**Keywords:** canopy stomatal conductance, feedback, feed forward, loblolly pine, sap flow, sweetgum, transpiration, willow oak.

## Introduction

Canopy conductance ( $g_c$ ) is an important parameter in ecological, meteorological, and air quality models (Shukla and Mintz 1982, Running and Coughlan 1988). To estimate conductance and water vapor flux over large, heterogeneous spatial scales, a mechanistic understanding of the responses of a species to multiple environmental variables is essential. Stomatal responses to highly covarying atmospheric temperature, humidity and incident radiation differ among species (Kozlowski et al. 1991). Responses at diurnal and daily scales are likely to be influenced mainly by atmospheric conditions, whereas longer-term responses are likely to be controlled by variation in soil water content and rooting characteristics (Schulze 1986). Thus, the contribution of individual species to stand

transpiration may change over a range of temporal scales. Therefore, to model canopy conductance in natural stands, water use must be quantified over a range of atmospheric and soil water conditions. In this study we estimated tree canopy conductance from sap flow data in order to quantify and compare responses of three co-occurring species to environmental variables.

*Pinus taeda* L. and *Liquidambar styraciflua* L. are major associates in forests of southeastern USA, co-occurring in many habitats, including wet, poorly drained sites. In these areas, *Quercus phellos* L. is a minor associate (Fowells 1965, Harlow and Harrar 1969). During drought periods, varying reductions in both transpiration rate per unit leaf area ( $E_t$ ) and stomatal conductance ( $g_s$ ) have been observed for *P. taeda*, *L. styraciflua*, and various *Quercus* species (Jarvis and Jarvis 1963, Pezeshki and Chambers 1986, Teskey et al. 1987, Abrams 1988, Abrams 1990, Ni and Pallardy 1990). In *L. styraciflua* there is a large reduction in sap flow rate in response to short-term drought, whereas *P. taeda* and *Quercus* species maintain high rates of sap flow during short drought periods (Pezeshki and Chambers 1986, Oren et al. 1994).

Tree size, rooting depth, and heterogeneity in soil water availability introduce variability into the rate of water uptake of trees in a forest and may obscure species differences in the relationship between atmospheric variables and transpiration. Therefore, we measured transpiration of saplings in closed-top chambers where ambient atmospheric and soil water conditions could be intensively measured.

## Materials and methods

### Study site

The site is located at the Global Climate Change Research Site 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 site is approximately 130 m above sea level, with a mean annual temperature of 15.5 °C and a mean annual precipitation of 1140 mm. The soil type is an Appling Sandy Loam of the Helena series that has been homogenized by rotor-tilling. A slight gradient in depth resulting from a shallow layer of hard clay was found in two coordinate directions.

Nine closed-top chambers were established at the site. Chamber dimensions were 3.1 m in diameter and 4.5 m in height. The experimental design was a complete randomized block with three blocks and one replicate of each species per block. The saplings were planted at a spacing of 60 × 60 cm and were three years old at the time of the experiment.

#### Instrumentation and measurements

Each chamber contained a quantum sensor (Model 190SB, Li-Cor, Inc., Lincoln, NE) to measure incident overstory photosynthetically active radiation ( $I_o$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and a Vaisala temperature and relative humidity probe (Model HMP 35C, Campbell Scientific, Logan, UT) to determine vapor pressure deficit ( $D$ , kPa) as described by Landsberg (1986). Temperature, humidity and quantum sensors were connected to a data logger equipped with a 16-channel multiplexer (Model 21X, Campbell Scientific). Measurements were made throughout the study period.

Because it is necessary to obtain whole-tree estimates of  $E_i$  to calculate  $g_c$ , we quantified sap flux ( $J_s$ ,  $\text{kg H}_2\text{O m}^{-2}$  stem area  $\text{s}^{-1}$ ) by measuring stem sap flow of each sapling. Although there is a time lag between stomatal activity in the canopy and stem sap flow response because of changes in stem storage, these lags are minimal in saplings (Carlson and Lynn 1991), allowing  $J_s$  to be substituted for  $E_i$ .

One sapling in each chamber was equipped with a sap flow gauge (Dynamax, Inc., Houston, TX) at the base of the stem. Data were available for only two of the three *L. styraciflua* chambers because of technical problems in the third chamber. For *Q. phellos* and *P. taeda*,  $n = 3$  for the duration of the experiment. Saplings in three of the chambers (Chamber 1: *L. styraciflua*), (Chamber 4: *Q. phellos*), and (Chamber 7: *P. taeda*) contained an additional sap flow gauge in the middle of the crown.

In some cases, branches were removed to allow placement of the gauge. For these individuals, branches were clipped and sanded until the cut area was flush with the stem surface. Gauges were placed around the affected area several days later so that sap exudate would not interfere with gauge operation. For the *P. taeda* seedlings, the bark was sanded to a thin layer to allow sufficient contact with the heater and thermocouples. In all cases, a thin film of silicon grease was applied to the stem to promote contact and prevent water infiltration. The stem and sap flow gauges were shielded with aluminum foil to minimize stem thermal gradients as described by Gutierrez et al. (1994). Although the gauges were periodically removed and refitted during the growing season, restriction of radial growth was apparent on all saplings at the point of measurement, and although it had no effect on measurements of whole-plant transpiration, such reductions probably affected sap flux at the constriction point. All sap flow gauges were connected to a data logger (DL2, Delta-T Devices Ltd., Cambridge, U.K.). Data were sampled at 30-s intervals and the mean taken over 30-min periods from June 1–18, 1995.

To make meaningful comparisons between chambers varying in leaf area, canopy conductance,  $g_c$ , was expressed on a leaf area basis rather than a ground area basis, and hereafter

termed canopy stomatal conductance,  $g_t$  ( $\text{mmol m}^{-2} \text{s}^{-1}$ ), and was obtained with the equation:

$$g_t = \frac{g_c}{A_1} = \frac{\gamma \lambda J_s}{\rho c_p D A_1 / A_b} \quad (1)$$

where  $A_1$  is leaf area ( $\text{m}^2$ ),  $\gamma$  is the psychrometric constant (kPa  $\text{K}^{-1}$ ),  $\lambda$  is the latent heat of vaporization ( $\text{J kg}^{-1}$ ),  $\rho$  is the density of moist air ( $\text{kg m}^{-3}$ ),  $c_p$  is the volumetric heat capacity of moist air at constant pressure ( $\text{J kg}^{-1} \text{K}^{-1}$ ),  $D$  is vapor pressure deficit (kPa), and  $A_1/A_b$  is the ratio of leaf area to cross-sectional stem area (Monteith and Unsworth 1990). Because  $D$  was measured above the canopy in all chambers, boundary layer and aerodynamic conductance are included in this estimation of  $g_t$ . However, where boundary layer conductance ( $g_b$ ) is large relative to stomatal conductance, leaf temperature does not deviate significantly from air temperature, thus allowing the use of  $D$  as a proxy for the leaf-to-air vapor pressure difference ( $\delta w$ ). Under such conditions,  $g_t$  closely approximates the mean stomatal conductance of the canopy.

Leaf water potential ( $\Psi_1$ , MPa) was measured in Chambers 1, 4 and 7 at 0500 and 1200 h EST from June 1 to 8 with a Scholander pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA). At each measurement time, three to five leaves or fascicles were collected within 5 min from the middle of each sapling crown, excluding saplings at the periphery of the chambers. Because of the small size of *Q. phellos* leaves, small shoots containing three to five leaves were measured. Samples were sealed in a plastic bag and refrigerated at 4 °C for a maximum of 5 min before  $\Psi_1$  was measured. There was no measurable decrease in  $\Psi_1$  with storage time.

#### Leaf area estimates

To express transpiration and canopy stomatal conductance on a leaf area basis, leaves of the measurement trees in Chambers 1, 4 and 7 were harvested and separated into three vertical canopy layers of approximately 0–90 cm, 90–150 cm, and greater than 150 cm. Ten sample leaves were chosen from each layer to represent a range of leaf ages and sizes. For the hardwood species, the 30 leaves were photocopied and the silhouettes cut out and weighed to estimate the area of each leaf. The area of the *P. taeda* fascicles was estimated optically (DIAS II Digital Image Analysis System, Decagon Devices, Inc., Pullman, WA). Leaf area values are reported as projected or one-sided leaf area. All leaves were oven dried for 48 h at 70 °C to obtain specific leaf area ( $A_1/M_1$ ,  $\text{cm}^2$  leaf area  $\text{g}^{-1}$  dry mass) for each crown layer. The leaf area of each measurement tree was estimated after drying and weighing the remaining leaves from each layer.

To estimate the leaf area index (LAI) of each chamber, leaves of eight saplings per chamber were harvested and divided into three canopy layers. For each canopy layer, the areas of 10 leaves were measured optically (DIAS II, Decagon Devices, Inc.) and their leaf mass determined after drying for 48 h at 70 °C. Leaf area of each sapling was calculated by summing the products of  $A_1/M_1$  and dry mass of the remaining leaves in each layer. A ratio of sapling leaf area to stem

cross-sectional area ( $A_l/A_b$ ) was developed to give the total chamber leaf area.

#### Calculations of water relations parameters

Hydraulic conductance ( $L_c$ ,  $\text{g m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ ) from the soil to the leaves was calculated by dividing the flux,  $J_s$ , by the water potential difference between the soil ( $\Psi_s$ ) and transpiring leaves ( $\Psi_l$ ) (Loustau and Granier 1993):

$$L_c = \frac{J_s}{\Psi_s - \Psi_l} \quad (2)$$

Because our calculation of  $g_t$  uses both  $J_s$  and  $D$  (Equation 1), modeling stomatal response to these variables, or any highly correlated variables such as humidity and  $I_o$ , will result in autocorrelation. Monteith (1995) proposed expressing  $g_t$  as a proportion of the extrapolated maximum conductance  $g_{t,\max}$  obtained as a coefficient in the relationship between  $1/E$  and  $1/D$  and direct measurements of either  $E$  or  $D$ . In this manner,  $g_t/g_{t,\max}$  may be calculated from one variable and regressed on the other variable without incurring autocorrelation error:

$$\frac{g_t}{g_{t,\max}} = 1 - \frac{E_l}{E_m} \quad (3a)$$

$$\frac{g_t}{g_{t,\max}} = \frac{1}{1 + \frac{g_{t,\max} D}{E_m}} \quad (3b)$$

where  $E_m$  is the extrapolated maximum transpiration rate.

This approach was used to evaluate differences among species in diurnal decreases in  $g_t$  in a feed-forward response to  $D$  or as a feedback response to  $E_l$ .

Use of  $g_t$  instead of  $g_s$  in Equation 3 is based on the assumption that boundary layer conductance ( $g_{bl}$ ) is large relative to  $g_s$ . To calculate  $g_{bl}$ , longitudinal wind velocity at sapling height in the center of the chamber was estimated. Measurements of longitudinal air velocity near the inflow ports gave a value of  $7.8 \text{ m s}^{-1}$ . Jetten (1992) found that, in an empty chamber of similar design, wind velocity decreased with distance from the inflow ports as:

$$u = u_o e^{(-0.8d)} \quad (4)$$

where  $u_o$  ( $\text{m s}^{-1}$ ) is the initial velocity at the inlet ports and  $u$  ( $\text{m s}^{-1}$ ) is the velocity at distance  $d$  (m) from the ports in the absence of vegetation. Because the decrease in wind velocity will be greater in a chamber containing saplings than in an empty chamber, we estimated the wind velocity in the middle of the chamber as a reduction to the fourth power of the distance, or  $u_o e^{(-1.13d)}$ . Thus, longitudinal wind velocity in the center of the chamber was calculated to be approximately  $1.35 \text{ m s}^{-1}$ . At such speeds, leaves in the chamber were in constant motion, and boundary layer conductance is likely to be large (Grace 1989). Boundary layer conductance was then estimated as:

$$g_{bl} = 306.7 \sqrt{u/d_l} \quad (5)$$

where  $d_l$  is leaf dimension (m), and  $u$  is wind speed ( $\text{m s}^{-1}$ ) (Jones 1992). Based on a wind speed of  $1.35 \text{ m s}^{-1}$  and leaf dimensions of 0.03, 0.01 and 0.002 m for *L. styraciflua*, *Q. phellos* and *P. taeda*, respectively,  $g_{bl}$  was calculated as 2057, 3563, and 7968  $\text{mmol m}^{-2} \text{s}^{-1}$  for the three species, respectively.

The error incurred by substituting  $D$  for  $\delta w$  in calculations of  $g_t$  as a proxy of  $g_s$  decreases with increasing  $g_{bl}$ . These parameters are related as follows (Whitehead and Jarvis 1981):

$$\frac{1}{g_{bl}} = 1 / \left( \frac{1}{g_t} - \frac{1}{g_s} \right) \quad (6)$$

From Equations 1 and 6,  $g_s$  can be calculated as  $95.5 \text{ mmol m}^{-2} \text{s}^{-1}$  for sweetgum compared with  $g_t$  of  $91.3 \text{ mmol m}^{-2} \text{s}^{-1}$ . Similarly, for oak  $g_s = 48.2 \text{ mmol m}^{-2} \text{s}^{-1}$ , whereas  $g_t = 47.6 \text{ mmol m}^{-2} \text{s}^{-1}$ , and for loblolly pine  $g_s = 88.4 \text{ mmol m}^{-2} \text{s}^{-1}$  and  $g_t = 87.4 \text{ mmol m}^{-2} \text{s}^{-1}$ . Given that  $g_{bl}$  is higher than  $g_t$ , it is not surprising that  $g_t$  is similar to  $g_s$ . Consequently, because of the high  $g_{bl}$ , leaf to air temperature difference ( $\Delta T$ ) should be small. We measured leaf and air temperatures at midday for four days during the first week of the experiment. Two days were cloudless, one was partially cloudy, and one was overcast. Mean  $\Delta T$  was  $0.38 \pm 0.29 \text{ }^\circ\text{C}$  for *L. styraciflua*,  $0.44 \pm 0.19 \text{ }^\circ\text{C}$  for *P. taeda*, and  $-0.14 \pm 0.17 \text{ }^\circ\text{C}$  for *Q. phellos*. Using the upper limit of  $\Delta T$  obtained for *L. styraciflua*,  $0.67 \text{ }^\circ\text{C}$  causes a 7% error in substituting  $D$  for  $\delta w$  at an air temperature of  $30 \text{ }^\circ\text{C}$  and a relative humidity of 50%. Thus, we concluded that  $D$  could serve as a reasonable approximation of  $\delta w$ .

#### Statistical analyses

Sap flow and environmental data were analyzed with SAS statistical software (SAS Institute, Cary, NC). Because of the small number of spatial replicates, data from different days were incorporated into least significant difference comparisons among means with experiment day as a repeated measurement in a randomized complete block design. Differences between regression slopes were tested with pairwise *t*-tests according to Steele and Torrie (1980). An assumption of regression analysis is that data are independently measured; it should be noted that this assumption is violated with the use of time series data.

#### Results

There were eight rain events during the study, delivering a total of 97.2 mm of precipitation between June 3 and 13. The chambers were not irrigated during the experiment, but there was some lateral movement of water into the chambers following a rain event (Todd 1995). There was no precipitation during the last week of the study, June 13–18. In a concurrent study at this site, mean  $\Psi_s$  did not drop below  $-0.07 \text{ MPa}$  in any chamber at soil depths of 10, 20, and 30 cm (Todd 1995).

Maximum daily mean  $J_s$  calculated in relation to the cross-sectional stem area below the gauges is reported in Table 1.

Representative diurnal patterns of  $D$  and  $J_s$  are presented in Figure 1. There were no significant differences between species in maximum daily mean values of  $J_s$  across chambers, because of high variability between individuals of the same species (Table 1). Therefore maximum daily mean  $E_1$  is presented only for the measured saplings for which  $A_1/A_b$  was determined directly. Among the species,  $E_1$  was highest in *L. styraciflua*, although *P. taeda* exhibited the highest  $J_s$  ( $P < 0.05$ ).

#### Canopy structure

Specific leaf area,  $A_1/M_1$ , increased with depth from the top of the canopy in all species ( $P < 0.05$ ). Predicted specific leaf area of the measurement trees was within the range determined for the harvested saplings. The leaf to basal area relationship ( $A_1/A_b$ ) for each species ( $P = 0.0001$ ,  $r^2 = 0.94-0.98$ ) (Table 1) was used to calculate LAI (Table 2) from the measured diameters of all individuals in each chamber (Waring et al. 1977, Waring et al. 1982, Oren et al. 1986).

#### Daily transpiration and conductance

The relationship between mean daily  $J_s$  and mean daily  $D$  standardized by the number of hours when  $I_0$  was  $> 10 \mu\text{mol m}^{-2} \text{s}^{-1}$  ( $D_z = (\text{daytime sum of } D)/(\text{number of light hours}/24)$ ), for each species is shown in Figure 2. Because of the large variation in  $J_s$  among individuals and the small sample size ( $n \leq 3$ ),  $J_s$  values for each chamber were converted to a ratio of the maximum observed value within the chamber thus permitting comparison of  $J_s$  responses to environmental variables among species.

The response of mean daily  $J_s$  to  $D_z$  was nonlinear. When  $D_z$  was small, the slope of the regression of  $J_s$  on  $D_z$  (with zero intercept) approximated daily  $g_t$ . With increasing  $D_z$ ,  $\Delta J_s$  approached zero as the relationship became curvilinear, particularly for *P. taeda* and *L. styraciflua* (Figure 2). Data were fitted with a second-order polynomial to describe this curvilinear response, which is indicative of reduced daily  $g_t$  at high  $D_z$ .

To quantify the change in  $g_t$  with increasing  $D_z$ , first-order regression coefficients were obtained for the linear portion of the data where  $D_z < 0.5$  kPa. The regression line was then extrapolated to higher values of  $D_z$  to represent potential  $J_s$ , defined here as the maximum flux that would occur for a given

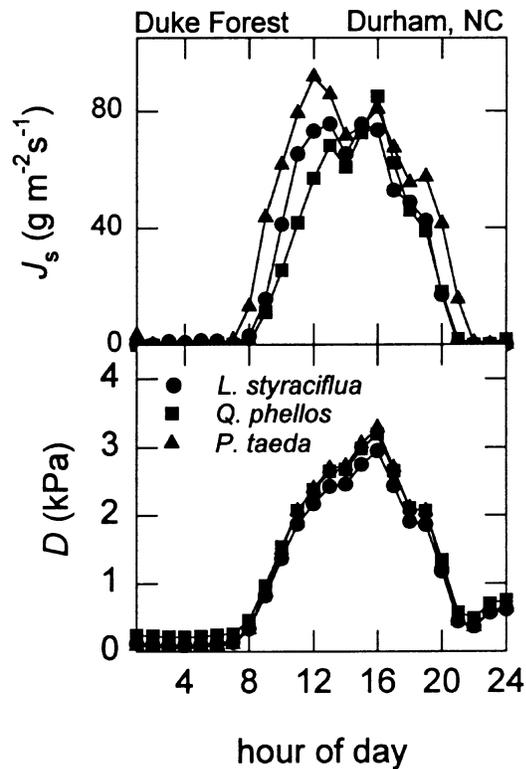


Figure 1. Diurnal sap flux ( $J_s$ ) and vapor pressure deficit ( $D$ ) in the study chambers on June 7, 1995.

Table 2. Leaf area index (LAI), mean basal area ( $A_b^*$ ), and basal area of the measurement tree ( $A_b$ ) for the eight sampled chambers.

Chamber no. and species	LAI ( $\text{m}^2 \text{m}^{-2}$ )	$A_b^*$ ( $\text{cm}^2$ )	$A_b$ ( $\text{cm}^2$ )
1. <i>L. styraciflua</i>	3.22	3.59 (0.38) <sup>1</sup>	3.83
2. <i>L. styraciflua</i>	1.72	1.84 (0.18)	1.01
3. <i>Q. phellos</i>	2.50	2.61 (0.26)	2.29
4. <i>Q. phellos</i>	2.13	2.10 (0.21)	2.64
5. <i>Q. phellos</i>	2.39	2.36 (0.26)	1.34
6. <i>P. taeda</i>	5.76	7.06 (0.49)	4.52
7. <i>P. taeda</i>	6.29	8.39 (0.59)	8.77
8. <i>P. taeda</i>	6.74	9.99 (0.73)	1.33

<sup>1</sup> The standard error is given in parentheses.

Table 1. Maximum daily mean sap flux ( $J_s$ ) in the main study chambers, maximum daily mean sap flux across all chambers ( $J_s^*$ ), maximum daily mean transpiration rate per unit leaf area ( $E_1$ ), canopy stomatal conductance ( $g_t$ ), mean specific leaf area ( $A_1/M_1$ ), and leaf area to stem cross-sectional area ratio ( $A_1/A_b$ )<sup>1</sup>.

Species	$J_s^2$ ( $\text{g m}^{-2} \text{s}^{-1}$ )	$J_s^*$ ( $\text{g m}^{-2} \text{s}^{-1}$ )	$E_1$ ( $\text{mmol m}^{-2} \text{s}^{-1}$ )	$g_t$ ( $\text{mmol m}^{-2} \text{s}^{-1}$ )	$A_1/M_1$ ( $\text{cm}^2 \text{g}^{-1}$ )	$A_1/A_b$ ( $\text{m}^2 \text{cm}^{-2}$ )
<i>L. styraciflua</i>	53.56 a	152.24 a (102.17) <sup>3</sup>	1.62 a	91.3 a	152.0 a (6.4)	0.27 (0.01)
<i>Q. phellos</i>	57.49 a	74.71 a (19.48)	1.26 b	47.6 b	104.8 b (4.0)	0.27 (0.01)
<i>P. taeda</i>	73.93 b	103.23 a (23.45)	1.09 b	87.4 a	75.1 c (6.4)	0.37 (0.02)

<sup>1</sup> Letters represent significant differences between species over the experimental period as tested by LSD ( $\alpha = 0.05$ ). ANOVAS included chambers, if present, as replicates, and experimental day as a repeated measure.

<sup>2</sup> Maximum twelve hour means (0700 to 1900 h EST) recorded during the experimental period for  $J_s$ ,  $J_s^*$ ,  $E_1$ , and  $g_t$ .

<sup>3</sup> The standard error is given in parentheses.

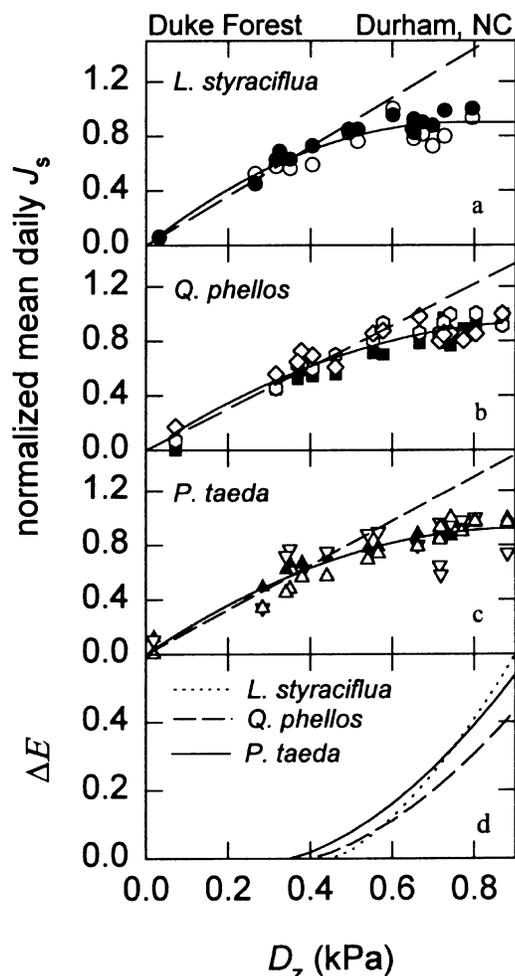


Figure 2. Normalized mean daily sap flux ( $J_s$ ) for each species (a–c) against increasing mean daily vapor pressure deficit standardized to the number of hours when  $I_o > 10 \mu\text{mol m}^{-2} \text{s}^{-1}$  ( $D_z$ ). Data represented by a second-order polynomial and by a linear regression for  $D_z < 0.5$  kPa are indicated by a solid and a dashed line, respectively. Chambers are distinguished by symbols; closed symbols represent data from main study chambers for each species. The modeled difference between first- and second-order predictions (Panel d) is presented as an index of reduced flux, or increased resistance,  $\Delta E$ , with increasing  $D_z$ .

set of environmental conditions at constant  $g_t$  and non-limiting soil water. Values of predicted  $J_s$  from the second-order regression representing actual data were subtracted from values of  $J_s$  represented by the linear extrapolation to obtain a measure of deviations from potential  $E_1$ . This parameter,  $\Delta E$ , was modeled over the measured range of mean daily  $D_z$  to evaluate species differences in reduced  $J_s$  as an index of decreasing mean  $g_t$ , or increasing resistance, as follows:

$$\Delta E = J_p - J_s, \quad (7)$$

where  $J_p$  is the potential sap flux for a given species represented by the linear extrapolation and  $J_s$  is the actual flux described by the second-order polynomial. There were larger increases in  $\Delta E$  with increasing  $D_z$  in *L. styraciflua* and

*P. taeda* than in *Q. phellos* and a more rapid increase in  $\Delta E$  in *L. styraciflua* than in *P. taeda* (Figure 2).

#### Diurnal transpiration and conductance

To develop relationships between  $g_t$  and  $D$  or  $E_1$ ,  $g_{t,\text{max}}$  and  $E_m$  were obtained from regression analysis as described by Monteith (1995). For this analysis,  $D$  and  $E_1$  data were restricted to periods when  $1/E_1$  and  $1/D$  were linearly related ("Regime A" in Monteith 1995). For *L. styraciflua* and *P. taeda*, this period was 1000 to 1400 h EST, after which hysteresis was commonly observed with declining  $D$ . Data for *Q. phellos* were obtained between 1100 and 1500 h EST because plots of  $1/E_1$  versus  $1/D$  were curvilinear in the early morning, as a result of a linear response of  $E_1$  to  $D$  similar to that observed for the integrated daily values (Figure 2). Coefficients from each regression are presented in Table 3.

The effects of  $E_1$  and  $D$  on  $g_t/g_{t,\text{max}}$  are shown in Figure 3 for the overlapping time periods 1100 to 1400 h. To explain the large variability in the responses of  $g_t/g_{t,\text{max}}$  to  $E_1$  and  $D$ , which was particularly noticeable in *L. styraciflua*, data were grouped into days of high mean  $I_o$  ( $\geq 900 \mu\text{mol m}^{-2} \text{s}^{-1}$  from 0800 to 1500 h EST) and low mean  $I_o$  ( $< 900 \mu\text{mol m}^{-2} \text{s}^{-1}$  from 0800 to 1500 h EST). A multivariate regression model indicated that, for *L. styraciflua*,  $g_t/g_{t,\text{max}}$  was significantly higher when regressed on  $D$  on days of high  $I_o$  than on days of low  $I_o$ . For all species,  $g_t/g_{t,\text{max}}$  was significantly lower when regressed on  $E_1$  on days of high  $I_o$  than on days of low  $I_o$  ( $P < 0.05$ ). On days of high  $I_o$ , the relationship between  $g_t/g_{t,\text{max}}$  and  $E_1$  was curvilinear for *Q. phellos* and *L. styraciflua*, such that  $g_t/g_{t,\text{max}}$  was not reduced at high values of  $E_1$ . Independently of  $I_o$ ,  $g_t/g_{t,\text{max}}$  in *P. taeda* was curvilinearly related to  $D$  ( $P < 0.05$ ).

For days of high  $I_o$ ,  $g_t/g_{t,\text{max}}$  tended to decline during the last week of the study as the soil dried from June 13 to June 17. The mean of  $g_t/g_{t,\text{max}}$  for the period 1100 to 1400 h EST was regressed against cumulative daily soil water extraction (mm) as calculated by  $E_1$  scaled to the stand by LAI. This daily mean  $g_t/g_{t,\text{max}}$  tended to decline with soil water depletion for all species ( $P > 0.05$ , Figure 4), but the magnitude of the decline, as represented by the slope of the regression, was not significantly different between species ( $P > 0.05$ ).

Values of  $E_1$  for *P. taeda* and *L. styraciflua* were comparable to those reported by Tolley and Strain (1985) and Dalton and Messina (1995). Similarly, absolute  $g_t$  values calculated from sap flow measurements in the three intensively measured chambers fell within the range of previously recorded stomatal

Table 3. Maximum conductance ( $g_{t,\text{max}}$ ,  $\text{mmol m}^{-2} \text{s}^{-1} \text{kPa}^{-1}$ ) and maximum transpiration ( $E_m$ ,  $\text{mmol m}^{-2} \text{s}^{-1}$ ) as obtained by regression of  $1/E_1$  and  $1/D$  after Monteith (1995)<sup>1</sup>.

Species	$r^2$	$g_{t,\text{max}}$	$E_m$
<i>L. styraciflua</i>	0.76	1.58	3.11
<i>Q. phellos</i>	0.81	0.57	8.6
<i>P. taeda</i>	0.88	3.13	5.80

<sup>1</sup> All models are significant at  $P = 0.0001$ .

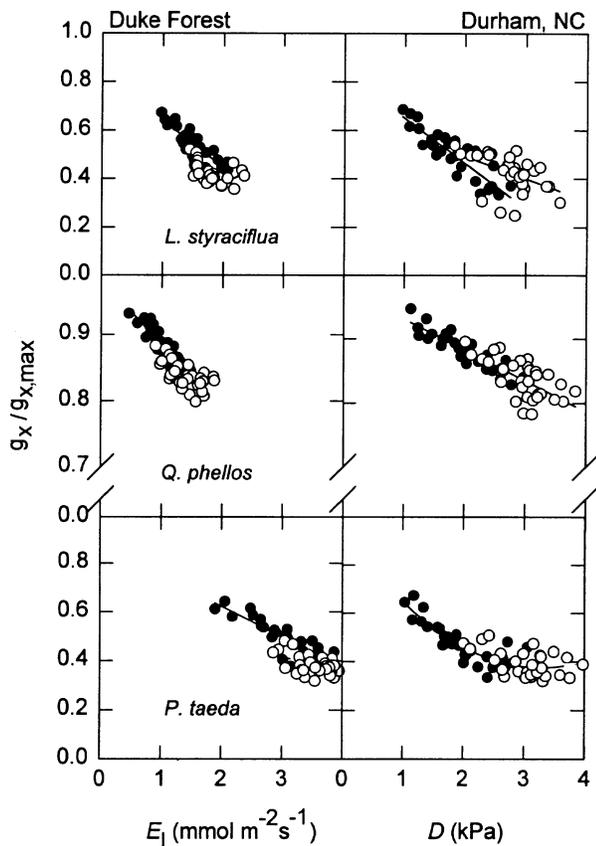


Figure 3. Changes in ratio of canopy stomatal conductance  $g_t$  to maximum conductance  $g_{t,max}$  in response to increasing transpiration ( $E_i$ ) and vapor pressure deficit ( $D$ ). Calculations are based on Monteith (1995). Data are given for days when mean  $I_o \geq 900 \mu\text{mol m}^{-2} \text{s}^{-1}$  (open symbols) and for days when mean  $I_o < 900 \mu\text{mol m}^{-2} \text{s}^{-1}$  (closed symbols). When significant ( $P < 0.05$ ), data are represented by separate or curvilinear regressions.

conductance values for *L. styraciflua*, *P. taeda*, and various *Quercus* species (Gresham 1975, Black 1984, Tolley and Strain 1985, Pezeshki and Chambers 1986, Abrams 1988, Dalton and Messina 1995, Ren and Sucoff 1995).

#### Within-canopy variability

Sap flow data were obtained at two canopy positions in one sapling of each species. The upper sap flow sensor recorded flow rates associated with 66% of the leaf area in *L. styraciflua* and 22% in *Q. phellos*. The high LAI and rapid growth of *P. taeda* resulted in self-shading and subsequent loss of lower crown foliage from the time of sensor installation to the initiation of the experiment, and as a result the upper sensor was associated with 91% of leaf area of the *P. taeda* individual. Fluxes measured at the two canopy levels were not significantly different ( $P > 0.005$ ). In *Q. phellos* the upper 22% of canopy LAI was responsible for  $58 \pm 7\%$  of the midday (1200–1400 h EST) transpiration, whereas the upper 66% of the *L. styraciflua* canopy LAI produced  $87 \pm 5\%$  of the midday transpiration.

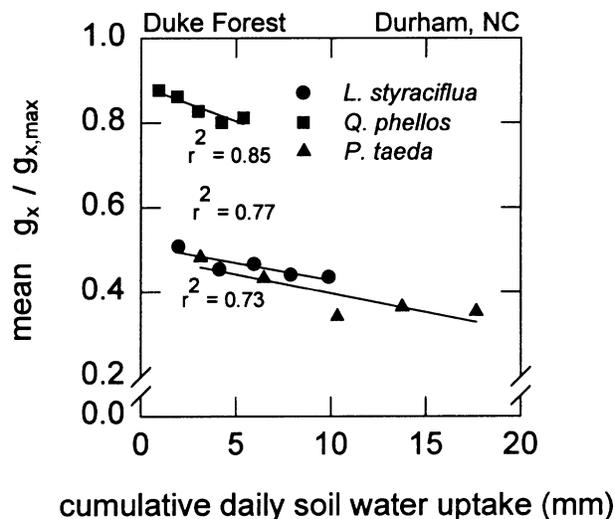


Figure 4. Mean  $g_t/g_{t,max}$  (1100–1400 h EST) versus cumulative soil water uptake for *P. taeda*, *Q. phellos*, and *L. styraciflua*. Differences among the slopes are not significant ( $P > 0.1$ ).

In both broadleaf species,  $g_t$  was low in the lower canopy of both broadleaf species, and midday values remained fairly constant during the entire study period, although  $g_t$  increased slightly with increasing  $I_o$  in *Q. phellos*. Upper canopy  $g_t$  was 8- and 4-fold higher than lower canopy  $g_t$  in *Q. phellos* and *L. styraciflua*, respectively. In both species, upper canopy  $g_t$  decreased with increasing  $I_o$ . The decrease was a result of the high correlation between midday  $I_o$  and  $D$  causing autocorrelation between  $g_s$  and  $D$  that was noticeable at high  $g_t$ . To distinguish between the effects of  $I_o$  and  $D$ , we chose a narrow range of  $D$  ( $2.5 \pm 0.2$  kPa) that was associated with a broad range of  $I_o$  (400 to  $1400 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Under these conditions, only  $g_t$  of *L. styraciflua* increased with increasing  $I_o$  ( $P < 0.001$ , Figure 5;  $P > 0.1$  for *Q. phellos* and *P. taeda*).

#### Hydraulic conductance

Species differences were also apparent in hydraulic conductance ( $L_c$ ). Values of  $L_c$  were higher in *L. styraciflua* than in *Q. phellos* or *P. taeda* ( $P < 0.05$ , Table 4), although sap flux density was similar in the three species (Figure 1).

#### Discussion

Species differences in daily whole-plant transpiration were observed in response to changes in mean daily  $D$ . Relative to potential daily transpiration, the reductions driven by  $D_z$ ,  $\Delta E$ , indicated higher proportional reductions in conductance, or larger increases in resistance, at high  $D$ , for *L. styraciflua* and *P. taeda* than in *Q. phellos* (Figure 3). *Liquidambar styraciflua* showed a more rapid increase in resistance than the other two species. In *Q. phellos*, the smaller increase in resistance with increasing  $D_z$  corresponded to the small reductions in  $g_t/g_{t,max}$  observed over the range of  $D$  occurring on a diurnal time scale (Figure 4). The small increase in resistance may be a reflection

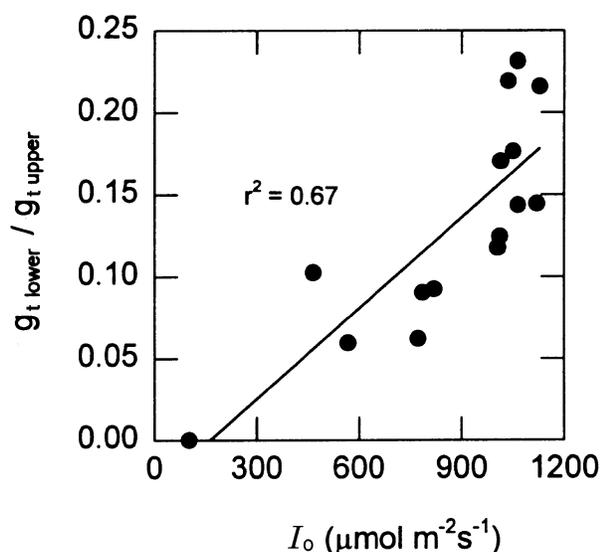


Figure 5. Relationship between canopy stomatal conductance ( $g_t$ ) and canopy radiation ( $I_o$ ) for *L. styraciflua* ( $P = 0.001$ ). Data were restricted to periods when  $D = 2.5 \pm 0.2$  kPa.

Table 4. Predawn and midday leaf water potential ( $\Psi_1$ , MPa), midday soil water potential ( $\Psi_s$ , MPa), and hydraulic conductance ( $L_c$ ,  $\text{g m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ ) for three chambers<sup>1</sup>.

Chamber no. and species	$\Psi_1$ predawn	$\Psi_1$ midday	$\Psi_s$ midday	$L_c$
1. <i>L. styraciflua</i>	-0.20 a (0.11)	-0.63 c (0.29)	-0.005 (0.0005)	252.42 c (52.78)
4. <i>Q. phellos</i>	-0.34 ab (0.19)	-1.80 d (0.32)	-0.01 (0.001)	44.57 d (4.40)
7. <i>P. taeda</i>	-0.33 b (0.12)	-1.07 c (0.58)	-0.02 (0.003)	98.62 d (10.55)

<sup>1</sup> Means over the experimental period are reported  $\pm$  the standard error. Letters indicate significant differences between chambers as obtained by LSD ( $\alpha = 0.05$ ). The standard error is given in parentheses.

of the generally low  $g_t$  and transpiration rate displayed by this species, regardless of the driving force. In both broadleaf species, stomatal responses to environmental variables were observed in the upper canopy only, perhaps because  $g_t$  in the lower canopy was generally low. In *Q. phellos*, despite a low transpiration rate, the low  $L_c$  caused the minimal stomatal response to  $D$  to be associated with lower midday  $\Psi_1$  values than in *L. styraciflua* (Table 4). Hydraulic conductance was lower in *Q. phellos* than in *L. styraciflua*, but comparable to literature values for *Quercus* (Bréda et al. 1993). Our estimates of  $L_c$  for *P. taeda* were similar to values reported for *Pinus pinaster* Ait. (Loustau and Granier 1993). Species differences in  $L_c$  cannot be explained by differences in the rooting zone, because root length densities and the vertical distribution of roots were similar for all species (Todd 1995).

On a diurnal scale, the sensitivity of  $g_t$  to variations in  $D$  and

$E_1$  differed among species. On clear days with high  $I_o$ , during which  $D$  typically reached values greater than 3 kPa,  $g_t/g_{t,\max}$  of the two broadleaf species declined linearly with increasing  $D$ . Under similar conditions,  $g_t/g_{t,\max}$  of loblolly pine decreased linearly with increasing  $E_1$ , but showed decreasing sensitivity to  $D$  at high values.

Reductions in  $g_t$  with increasing  $D$  have frequently been observed (Farquhar 1978, Sheriff 1979, Grantz 1990, Aphalo and Jarvis 1991). Peristomatal or epidermal transpiration, which is not associated with reductions in bulk leaf water potential, has been proposed as the mechanism underlying this response, termed feed-forward stomatal behavior (Schulze 1986, Schulze et al. 1987). Evidence of decreasing  $E_1$  with increasing  $D$  has been cited as evidence of such a mechanism, because the decrease cannot be explained by a feedback response to  $\Psi_1$  (Farquhar 1978); however, data showing such behavior are rare (Monteith 1995, Franks et al. 1997). Monteith (1995) has pointed out that studies in which  $g_t$  but not  $E_1$  declined with increasing  $D$  have generally shown curvilinear responses of  $g_t$  to  $D$ . When the same data were analyzed for  $g_t$  as a function of  $E_1$ , linear responses were found, suggesting that a true feed-forward mechanism was not operating.

On both clear and overcast days,  $g_t/g_{t,\max}$  of *P. taeda* decreased linearly with increasing  $E_1$ , whereas the response to  $D$  was curvilinear, suggesting a direct stomatal response to  $E_1$  (cf. Mott and Parkhurst 1991). At low  $I_o$ , both broadleaf species showed a linear reduction in  $g_t/g_{t,\max}$  with increasing  $E_1$  or  $D$ . However, on clear days, the response of  $g_t/g_{t,\max}$  to increasing  $D$  remained linear, whereas  $g_t/g_{t,\max}$  exhibited a decreasing sensitivity to increasing  $E_1$ , until increases in  $E_1$  did not result in additional decreases in  $g_t/g_{t,\max}$ . Under such conditions, a physiological mechanism associated with a direct response of  $g_t$  to  $E_1$ , as proposed by Mott and Parkhurst (1991), is difficult to invoke. However, because the criterion of decreasing  $E_1$  with increasing  $D$  was not met, and  $E_1$  continued to increase, midday  $\Psi_1$  declined significantly from predawn values for both broadleaf species, reaching a mean midday value of  $-1.8$  MPa in *Q. phellos* (Table 4). Thus, our data do not support a traditional feed-forward model in which low  $\Psi_1$  is avoided. Our finding of large species differences in the behavior of  $g_t$  to increasing  $D$ , emphasizes that current models of  $g_t$  behavior do not adequately explain its physiological control under commonly observed conditions; that is, when  $E_1$  does not decrease in response to increasing  $D$ .

Although a feed-forward mechanism of stomatal control appears to underlie the response of  $g_t$  to  $D$  on a short temporal scale in *L. styraciflua* and *Q. phellos*, other control mechanisms of stomatal response must be involved for longer time scales such as days and even hours. The sensitivity of  $g_t/g_{t,\max}$  to soil water content at the root surface is readily discernible if water in the active rooting zone is not replenished within several days. Despite only a slight decrease in bulk soil  $\Psi_s$  (Todd 1995), mean  $g_t/g_{t,\max}$  of all species decreased during soil water depletion (Figure 4), indicating that even in moist soils, depletion of water is sufficient to reduce  $g_s$  (Bates and Hall 1981, Barataud et al. 1995).

Soil-root resistance may increase in response to only a few hours of high  $E_1$ . In all species,  $g_t/g_{t,\max}$  at the same  $E_1$  was lower

at low  $I_0$  than at high  $I_0$ . Days with high  $I_0$  are associated with high  $D$ , which causes  $E_1$  to increase in the morning. Over several hours, high  $E_1$  can deplete water in the soil volume immediately adjacent to fine roots (Katul et al. 1997), causing a decrease in  $g_t/g_{t,max}$  as a result of a feedback mechanism, even when the bulk soil is moist (Figure 4).

*Quercus phellos* and *P. taeda* showed similar  $g_t/g_{t,max}$  responses at a given  $D$  regardless of  $I_0$ . In contrast,  $g_t/g_{t,max}$  of *L. styraciflua* increased with increasing  $I_0$  at the same  $D$ . Other studies suggest that the stomata of *P. taeda* are relatively unresponsive to  $I_0$  above a certain value (Gresham 1975), compared with the stomata of *L. styraciflua* (Tolley 1982).

In summary, species differences in  $g_t$  responses were apparent at several temporal scales. At hourly time steps, the broad-leaf species exhibited feed-forward stomatal control, whereas *P. taeda* exhibited feedback stomatal control (Figure 3), and *L. styraciflua* showed an additional sensitivity to  $I_0$  (Figure 5). Over time steps of several hours, however, feedback behavior was evident in all three species on days when soil water depletion was high. On a daily time scale, a comparison of the responses of  $J_s$  to  $D_z$  in the three species indicated that fluxes were lower in *Q. phellos* at low  $D$  because of low  $L_c$ , but fluxes were higher during periods of high  $D_z$  because of the decreased sensitivity of  $g_t/g_{t,max}$  (Figure 2). During periods between rain events, decreases in canopy stomatal conductance were similar for all species (Figure 4). Consequently, the species with high canopy stomatal conductance on moist soils will contribute proportionally more to total stand transpiration as soil water decreases between rain events than species with low canopy stomatal conductance on moist soils. Thus, to estimate canopy conductance accurately even in areas receiving frequent precipitation during the growing season, it is necessary to quantify the response of each species to variations in atmospheric conditions and soil water availability.

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