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## Sensitivity of mean canopy stomatal conductance to vapor pressure deficit in a flooded *Taxodium distichum* L. forest: hydraulic and non-hydraulic effects

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**Abstract** We measured the xylem sap flux in 64-year-old *Taxodium distichum* (L.) Richard trees growing in a flooded forest using Granier-type sensors to estimate mean canopy stomatal conductance of the stand ( $G_S$ ). Temporal variations in  $G_S$  were investigated in relation to variation in vapor pressure deficit ( $D$ ), photosynthetic photon flux density ( $Q_o$ ), and the transpiration rate per unit of leaf area ( $E_L$ ), the latter variable serving as a proxy for plant water potential. We found that  $G_S$  was only weakly related to  $Q_o$  below 500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  ( $r^2=0.29$ ), but unrelated to  $Q_o$  above this value. Above  $Q_o=500 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $D=0.6$  kPa,  $G_S$  decreased linearly with increasing  $E_L$  with a poor fit ( $r^2=0.31$ ), and linearly with  $\ln D$  with a much better fit ( $r^2=0.81$ ). The decrease of  $G_S$  with  $\ln D$  was at a rate predicted based on a simple hydraulic model in which stomata regulate the minimum leaf water potential. Based on the hydraulic model, stomatal sensitivity to  $D$  is proportional to stomatal conductance at low  $D$ . A hurricane caused an ~41% reduction in leaf area. This resulted in a 28% increase in  $G_S$  at  $D=1$  kPa ( $G_{S\text{ref}}$ ), indicating only partial compensation. As predicted, the increase in  $G_{S\text{ref}}$  after the hurricane was accompanied by a similar increase in stomatal sensitivity to  $D$  (29%). At night,  $G_{S\text{ref}}$  was ~20% of the daytime value under non-limiting light ( $Q_o>500 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). However, stomatal sensitivity to  $D$  decreased only to ~46% (both reductions referenced to prehurricane daytime values), thus having more than twice the sensitivity expected based on hydraulic consid-

erations alone. Therefore, non-hydraulic processes must cause heightened nighttime stomatal sensitivity to  $D$ .

**Keywords** Canopy stomatal conductance · Cypress swamp · Hurricane effect · Light · Nighttime conductance · *Taxodium distichum* · Transpiration · Vapor pressure deficit · Xylem sap flux

### Introduction

The regulation of stomatal conductance ( $g_s$ ) by biological and environmental variables has been the subject of intensive research. The relative importance of various control mechanisms is difficult to quantify. In the field, stomatal responses to diurnal changes in photosynthetically active radiation ( $Q_o$ ), vapor pressure deficit ( $D$ ), leaf temperature, hydraulic conductance within the plant, and soil moisture near the roots are confounded (Sandford and Jarvis 1986). Diurnally,  $D$  generally follows the pattern displayed by  $Q_o$ , but with a lag. At the same time, plant and rhizosphere hydraulic conductance tend to decrease, and then slowly increase, mirroring the diurnal patterns of water potential and associated cavitation in the xylem (McCully et al. 1998), and moisture depletion in the soil near roots (Aylmore 1993). In addition, the environment in which plants were grown, and in which measurements are made (e.g., laboratory vs field conditions; Bunce 1998), affects stomatal sensitivity to environmental factors. For example, controlled experiments have been argued to highlight mechanisms of stomatal regulation that may be less important to plants growing in the field (Kramer 1988; Boyer 1989).

Analyzing data collected under moist soil conditions, where soil and soil-root interface resistance are assumed to be small and constant relative to the resistance in other parts of the soil-plant-atmosphere pathway, simplifies analyses of environmental regulation of mean canopy stomatal conductance for water vapor ( $G_S$ ). This allows variation in stomatal conductance to be evaluated solely based on variability in  $Q_o$ ,  $D$  (Cienciala and

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Lindroth 1995; Granier and Bréda 1996), and transpiration (Mott and Parkhurst 1991; Monteith 1995), which correlates with bulk plant water potential (Jarvis 1976; Hinckley et al. 1978). However, even under these conditions, resistance to water movement in the rhizosphere increases diurnally in direct relation to the transpiration rate and soil properties, both of which control how fast moisture is depleted near the roots (Kramer 1983; see also Aylmore 1993). This is reflected in the tendency of models to overestimate stomatal conductance in the afternoon (Martin et al. 1997), and the need to use time-of-day as a variable to account for the overestimation (Körner 1993). As a result, the assumption of small and constant root-soil resistance is only partially correct, even under conditions of low transpiration rates, or where plants with high root-to-leaf surface area ratios are monitored while absorbing water from moist, fine soils (Carbon et al. 1980; Sperry et al. 1998). However, under flooded conditions, the assumption of invariable resistance to water uptake from the soil is satisfied.

Flood-tolerant species grow well under flooded conditions, and avoid the adverse consequences of an anaerobic rooting zone mostly by producing adventitious roots into the water above the soil (Sena Gomes and Kozłowski 1980; Pezeshki and Anderson 1997). *Taxodium distichum* (L.) Richard is a highly flood-tolerant species (see Brown and Montz 1986; Megonigal et al. 1997), with transpiration that proceeds at high rates under continuous flooding (Brown 1981; Oren et al. 1999a). Thus, monitoring *T. distichum* under flooded conditions, where there are no diurnal changes in soil resistance to water flow, can supply the necessary data to quantify more accurately stomatal responses to variations in  $Q_o$ ,  $D$ , and transpiration rate.

We investigated the regulation of water use in a 64-year-old stand of *T. distichum* growing on a nearly continuously flooded site. Our primary goal was to quantify the effects of  $D$  within the canopy, and  $Q_o$  above the canopy, on mean  $G_s$  under conditions of constant, near-zero soil water potential ( $\Psi_s$ ). We hypothesized that *T. distichum* will show significant reductions in  $G_s$  as a direct response to increasing transpiration, and indirect response to increasing  $\ln(D)$  (see Oren et al. 1999b). During the study, a hurricane reduced the leaf area ( $A_L$ ) in the stand by ~45% (Oren et al. 1999a). Although damage to needle surfaces caused by high wind speed can increase epidermal conductance (i.e., the sum of cuticular and stomatal conductance; van Gardingen et al. 1991), the minimum epidermal conductance of damaged needles is less than a tenth of typical stomatal conductance of *T. distichum*. This allowed us to test an additional hypothesis that stomata can compensate completely for an abrupt natural defoliation of such magnitude.

Under light-saturating conditions and high  $D$ , most plants exhibit a reduction of  $G_s$  which limits the rate of water loss and development of potentially damaging low leaf water potential ( $\Psi_L$ ). The adaptive advantage of this response may in part be the avoidance of dehydrative damage associated with critically low  $\Psi_L$  (Meinzer

1993). For example, several studies have suggested that the absence of stomatal regulation would cause excessive xylem cavitation and failure of water transport (Tyree and Sperry 1988; Sperry et al. 1993; Tyree et al. 1993; Saliendra et al. 1995; Cochard et al. 1996; Lu et al. 1996). This “hydraulic constraint” may be particularly important for species adapted to constant and high  $\Psi_s$  (Sperry et al. 1998), such as *T. distichum*.

If one goal of stomatal action under light-saturating conditions is the regulation of  $\Psi_L$ , predictions can be made for the response of  $G_s$  to  $D$  and  $A_L$ . The interaction between  $\Psi_L$ ,  $G_s$ , and  $A_L$  in response to  $D$  and  $\Psi_s$  can be summarized at steady-state (and infinite boundary layer conductance,  $g_{bl}$ ) by the function (modified from Sperry 1995):

$$\Psi_L = \Psi_s - (G_s \times D) \times \left( \frac{A_L}{k} \right) \quad (1)$$

where  $k$  is the soil-to-leaf hydraulic conductance, and the ratio  $k/A_L$  is the corresponding leaf-specific hydraulic conductance. If we assume constant  $\Psi_s$ ,  $\Psi_L$ , and  $k$ , this relationship predicts that trees with higher  $G_s$  at low  $D$  will exhibit a proportionally more sensitive stomatal closure with increasing  $D$  (see theory in Oren et al. 1999b). It also predicts a perfect compensatory response of  $G_s$  in response to reduced  $A_L$ , as has been demonstrated in experimental leaf area reduction in a nearby pine stand (Pataki et al. 1998). These predictions are evaluated in light of our observations from *T. distichum*.

## Materials and methods

The study was conducted at the Lost Shoe Swamp, Duke Forest, Durham, North Carolina (35°52' N, 79°59' W), where mean annual temperature is 15.5°C, and mean annual precipitation is 1,140 mm. Seedlings of *T. distichum* were planted in 1933 in an impoundment at an elevation of about 130 m above sea level. Although 1996 was dry relative to the mean, the soil in the study area was continuously flooded to about 0.5 m with slowly flowing water.

In a circular plot of 25 m radius positioned in the middle of the stand, a minor component of *Fraxinus pennsylvanica* (Marsh.) was present in the sub-canopy [56 trees ha<sup>-1</sup> with a basal area at breast height (1.3 m above soil surface) of 4.8 m<sup>2</sup> ha<sup>-1</sup>], with crowns mostly of epicormic branches. Small individuals of *T. distichum* are healthy and support a normal crown. At age 64, *T. distichum* in the plot ranged in diameter from 0.18 to 0.56 m, and reached a height of about 27 m. *T. distichum* was fairly uniformly planted, and has a current density of 722 trees ha<sup>-1</sup>, with a basal area of 73.6 m<sup>2</sup> ha<sup>-1</sup>. Hydroactive xylem (i.e., sapwood) depth was measured on cores taken from ten trees representing the range in diameter. Sapwood depth varied from 20 to 70 mm (mean=47.5 mm, SE 4.6) but showed only a weak tendency to increase with diameter ( $P=0.12$ ,  $r^2=0.25$ ). Using the mean sapwood depth from the sampled trees and the diameter of all individuals in the plot, sapwood area was 31.7 m<sup>2</sup> ha<sup>-1</sup>. Leaf area index (LAI; estimated with the Canopy Area Analyzer, LAI2000; Li-Cor, Lincoln, Neb.) was 2.2, thus producing a ratio of sapwood area at breast height to leaf area,  $A_s:A_L=0.0014$  m<sup>2</sup> m<sup>-2</sup> (Oren et al. 1999a, 1999b).

The study was performed on 22–27 August 1996 when data were collected to evaluate the effect of  $Q_o$  and  $D$  on  $G_s$ . On 8–14 September, we resumed measurements to test the hypothesis that the  $G_s$  behavior quantified in August was not altered by a considerable stand-wide defoliation caused by hurricane Fran on 5 September (sustained winds of 35 m s<sup>-1</sup>; Wurman and Winslow 1998).

Measured sap flux ( $J_s$ , kg H<sub>2</sub>O m<sup>-2</sup> sapwood s<sup>-1</sup>) in the xylem of trees is increasingly used to estimate  $G_s$  (Köstner et al. 1992; Granier and Loustau 1994; Granier et al. 1996; Phillips and Oren 1998; Oren et al. 1998a, 1998b), based on the assumption that  $J_s$  scaled by  $A_s:A_L$  is equal to transpiration rate per unit of leaf area ( $E_L$ ). Thus,  $G_s$  for conifers or other species with small leaves (Landsberg 1986; Phillips and Oren 1998; Ewers and Oren 2000) can be calculated using the function (modified from Monteith and Unsworth 1990):

$$G_s = \frac{\gamma \times \lambda}{\rho \times c_p \times D} \times \frac{J_s \times A_s}{A_L} \quad (2)$$

where  $G_s$  is the canopy stomatal conductance for water vapour (m s<sup>-1</sup>),  $\gamma$  is the psychrometric constant (kPa·K<sup>-1</sup>),  $\lambda$  is the latent heat of vaporization (J·kg<sup>-1</sup>),  $\rho$  is the density of air (kg·m<sup>-3</sup>),  $c_p$  is the specific heat of air at constant pressure (J·kg<sup>-1</sup> K<sup>-1</sup>), and  $D$  is the vapor pressure deficit (kPa).  $G_s$  can then be converted to molar units (Pearcy et al. 1989). In Eq. 2,  $\frac{J_s \times A_s}{A_L}$ , equals  $E_L$  only if  $J_s$

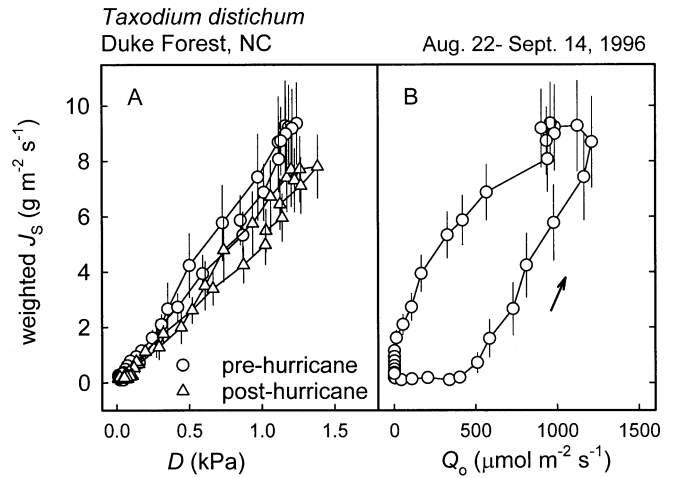
represents the spatially weighted mean flux (Oren et al. 1998a).

Sap flux density was measured with a Granier-type sensor composed of a heated (constant heat flow) and unheated thermocouple pair connected in opposition to measure temperature difference, as described by Granier (1987). The 20-mm-long sensors were installed in the outer sapwood band of ten trees within 15 m of the plot center at 1.3 m above the soil surface. In five of the trees, a Granier-type sensor was installed in the outer 20 mm of the sapwood. In the other five trees, the modified Granier-Phillips type (Phillips et al. 1996) was used. This sensor measures sap flux separately in the outer 20 mm sapwood and the next 20-mm band of xylem (20–40 mm from the cambium), and uses a single unheated reference thermocouple in the sapwood 10–30 mm from the cambium, after verifying that diurnal radial temperature gradients over these depth ranges were insignificant. In addition, we verified the absence of potential error-causing thermal gradients (Oren et al. 1999a).  $J_s$  is calculated from the temperature difference, relative to the maximum difference occurring at times of zero flow. Complete information on sensor installation and flux calculations can be found in Granier (1987) and Phillips et al. (1996).

$J_s$  may be used to estimate  $G_s$  only after it is converted to a spatially weighted mean flux. A weighted mean  $J_s$  was calculated for each tree using the results of an additional study in this stand which evaluated spatial variation in  $J_s$  (Oren et al. 1999a). In that study, (1)  $J_s$  of small-diameter individuals (mean diameter=0.24 m) was 0.70 that of trees with diameter 0.30 m or greater, and (2)  $J_s$  in the northern third of the tree circumference was 0.64 of that in the other two-thirds. Using these ratios, and the relationships between  $J_s$  at sapwood depth of 20–40 mm from the cambium and that in the outer 20 mm of the sapwood (which represent a constant ratio of 0.4),  $J_s$  measured in each tree was scaled to total flow by the tree, and divided by the sapwood area of the tree to obtain weighted mean  $J_s$ . The flow beyond 40 mm in the sapwood was assumed to equal the flow in the 20- to 40-mm depth. Once the mean flux in each tree was obtained, a population mean  $J_s$  at half-hourly temporal scale was calculated, and multiplied by the population mean of  $A_s:A_L$  to estimate  $E_L$ , and  $G_s$  (Eq. 2), at the canopy scale.

To calculate  $D$  (kPa), air relative humidity and temperature were measured (HMP 35C probe; Vaisala, Finland) at 20 m above-ground, corresponding to 0.67 of the canopy length from the bottom. In addition, before the hurricane,  $Q_o$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was measured above the canopy (LI-190S; Li-Cor) by attaching the sensor to the end of a pole, and extending the telescoping pole above the canopy. Light measurements were unavailable after the hurricane due to sensor failure. The xylem flux and micro-meteorological data were sampled with a multi-channel data logger (Delta-T Devices, Cambridge, UK) at 30-s intervals, averaged and recorded every 30 min.

Three important assumptions in using Eq. 2 for calculating conductance are: (1)  $E_L$  is directly related to  $J_s$  measured at the lower stem, i.e., the stem hydraulic capacitance is negligible (Jarvis 1976; Phillips and Oren 1998); (2) leaf boundary layer



**Fig. 1** Diurnal relationships between ensemble mean sap flux density ( $J_s$ ), weighted for the entire sapwood area, and vapor pressure deficit ( $D$ ) in the pre- and post-hurricane period (A), and photosynthetic photon flux density ( $Q_o$ ) in the pre-hurricane period (B). Vertical lines represent 1 SE of the mean ( $n=10$  trees) of the ensemble means. Arrow represents the direction of the hysteresis

conductance ( $g_{bl}$ ) is large relative to leaf stomatal conductance ( $g_s$ ; Whitehead and Jarvis 1981), and (3)  $D$  is uniform throughout the canopy volume, requiring only one measurement point.

In interpreting the diurnal relationship of  $J_s$  and  $D$ , a counter-clockwise hysteresis indicates hydraulic capacitance (Doley 1967; Schulze et al. 1985; Meinzer et al. 1997), in proportion to the width of the hysteresis (Jarvis 1976; Hinckley et al. 1978). The absence of such a hysteresis (Fig. 1A) provides strong support for the first assumption, justifying the use of  $J_s$  for estimating  $G_s$ . The counter-clockwise hysteresis seen in the relationship between weighted  $J_s$  and  $Q_o$  (Fig. 1B) indicates that although stomata may open with light, transpiration, as reflected in xylem flux rate, is too low to measure as long as  $D$  is very low. Thus, assumption 1 is met in this study.

Assumption 2 is generally considered true for narrow leaves (Whitehead and Jarvis 1981; Landsberg 1986). This assumption is reflected in Eq. 2, where the energy term is neglected, because  $D$  is considered approximately equal to leaf-to-air vapor pressure difference, and is calculated from measurements within the canopy volume but outside the leaf boundary layer. Boundary layer conductance,  $g_{bl}$  ( $\text{mmol m}^{-2} \text{s}^{-1}$  at 25°C), can be estimated using Jones (1992):

$$g_{bl} = 304.4 \times \sqrt{\frac{u}{d_L}} \quad (3)$$

where  $u$  is mean windspeed (m s<sup>-1</sup>), and  $d_L$  is a characteristic leaf dimension (m). Based on the dimension of either a single needle-leaf of *T. distichum* ( $d_L < 0.002$  m) or of the lateral branchlets ( $d_L < 0.03$  m; Brown and Montz 1986), it is possible to solve for the windspeed that will result in  $g_{bl}/g_s=10$ , a condition in which the conductance calculated from  $J_s$  is dominated by the stomata rather than the boundary layer (Whitehead and Jarvis 1981). Using a typical stomatal conductance of *T. distichum* seedlings (ca 100  $\text{mmol m}^{-2} \text{s}^{-1}$ ; Pezeshki and Anderson 1997), the windspeed necessary to create this condition is 0.02 and 0.32 m s<sup>-1</sup> for the leaf and branchlet, respectively. In our region, such rates prevail (>90% of the daytime shows windspeed >0.4 m s<sup>-1</sup>, the lowest resolution of a typical cup anemometer). Furthermore, both rates are probably somewhat overestimated because seedlings have higher stomatal conductance than mature, taller individuals of the same species (Friend 1993; Saliendra et al. 1995), and Eq. 3 tends to underestimate  $g_{bl}$  (Grace 1989). Thus, in this stand, high  $g_{bl}$  predominates because it can be attained with low windspeeds,



and because wind can penetrate with little obstruction into the relatively open stand.

Although  $D$  must vary somewhat with height because  $D \approx 0$  near the water surface, given the low LAI and the prevailing wind conditions, the air within the canopy can be considered well mixed with the air above the canopy (Jarvis 1976; Parker 1995). This supports the third assumption that  $D$  measured at one point, at 2/3 canopy height, represents  $D$  in the entire canopy zone (6–27 m aboveground; e.g., Sullivan et al. 1996).

All statistical analyses were performed using SAS software (SAS Institute, Cary, N.C.).

## Results and discussion

Ensemble means for the pre- and post-hurricane periods show that the rate of water uptake at half-hourly resolution increased linearly with  $D$  before the hurricane, but followed a lower trajectory with a tendency to saturate in the post-hurricane period (Fig. 1A). Although the relationship between weighted  $J_S$  and  $D$  did not include a hysteresis commonly seen when lag occurs between  $D$ -driven transpiration and water uptake, a large hysteresis was seen with  $Q_o$  in the pre-hurricane period (Fig. 1B). Thus, uptake begins about 0.5–1.5 h after dawn, when  $D$  begins to increase, and continues into the night, until  $D$  reaches zero. Variation among trees in lags between  $J_S$  and  $Q_o$  were unrelated to tree size ( $P > 0.05$ ). Furthermore, unlike nearby *Pinus taeda*, which showed stomatal closure at night thus using water uptake for recharge (Phillips et al. 1996), water taken up at night by *T. distichum* is immediately transpired. This behavior was especially clear on 13 September when nighttime flux, mostly in the outer sapwood, accompanied a nighttime surge in  $D$  to 0.6 kPa (Oren et al. 1999a). Thus, use and replenishment of water stored in this species is not large, allowing  $G_S$  to be calculated from  $J_S$  on half-hourly time scales without accounting for modulation by storage. Half-hourly means of  $G_S$  under sufficient light and low  $D$  were within the range of instantaneous  $g_S$  reported for seedlings (Pezeshki et al. 1995; Pezeshki and Anderson 1997). Nevertheless, caution must be used when interpreting early morning data, when  $J_S$  and  $D$  are often immeasurable, but  $G_S$  may be high.

### Daytime responses of $G_S$ to $E_L$ , $Q_o$ , and $D$

To address the primary objective of this study, it was necessary to relate  $G_S$  to  $E_L$ ,  $Q_o$ , and  $D$ . Empirical relationships between  $g_S$  and  $Q_o$  or  $D$  provide a convenient approach to describing the response of stomatal conductance to varying atmospheric conditions (Jarvis 1976; Sandford and Jarvis 1986; Whitehead 1998). An exponential rise to a maximum is the form commonly used to describe stomatal response to light (Jarvis 1976). Many forms of non-linear functions have been used to describe the decrease in  $G_S$  with increases in  $D$  (see Lohammar et al. 1980; Massman and Kaufmann 1991; McNaughton and Jarvis 1991; Granier and Loustau 1994; McCaughey and Iacobelli 1994; Monteith 1995; Dang et al. 1997;

Martin et al. 1997). Models use these functions to generate a multiplier, one of several used in multiple-constraint functions, to reduce maximum  $g_S$  or  $G_S$  to estimates of actual conductance (see Schulze et al. 1994); maximum conductance is determined for each species under non-limiting environmental conditions (e.g., high irradiance without water limitation; Dai et al. 1992).

In analyzing the effect of environmental variables on  $G_S$ , we used an empirical non-linear multiple regression model (Bréda et al. 1993; Granier and Bréda 1996) after Lohammar et al. (1980) to quantify the effects of  $D$  and  $Q_o$  on  $G_S$ . The model is modified from the original by replacing global radiation with  $Q_o$ :

$$G_S = \left[ \frac{Q_o}{Q_o + a} \right] \times [b + (m \times \ln D)] \quad (4)$$

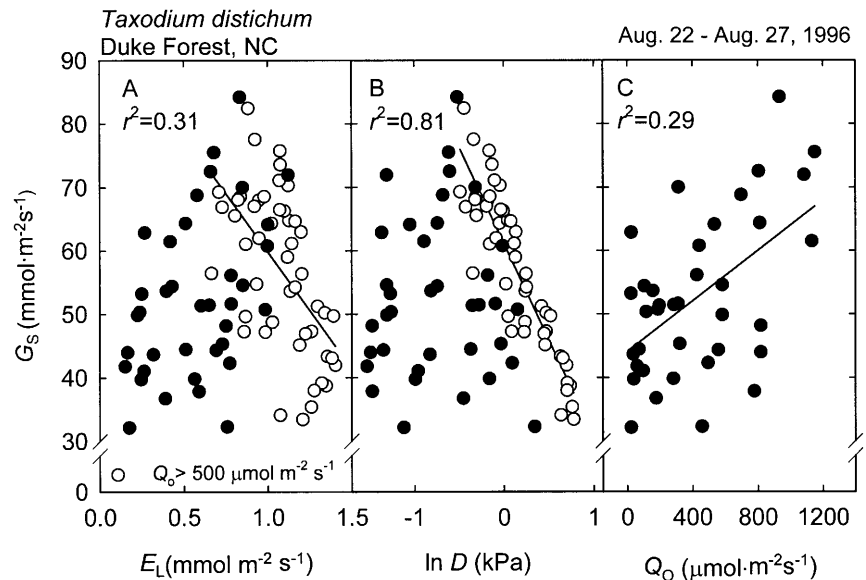
where  $a$ ,  $b$ , and  $m$  are empirically fitted coefficients.

This empirical model performs as well as biophysically based functions (Massmann and Kaufmann 1991), and may have a better theoretical justification than certain of the other empirical functions in that (1) it is consistent with the assumption that  $g_S$  decreases linearly with  $E_L$  (Leuning 1995; Monteith 1995), indicating a mechanism designed to minimize although not eliminate changes in bulk leaf water potential (Sandford and Jarvis 1986), and (2) it accounts for the effect of the initial maximal value of  $g_S$  on the sensitivity of  $g_S$  to  $D$  (McNaughton and Jarvis 1991). The relationship between  $G_S$  and  $\ln D$  provides the coefficient  $b$ , which can serve as a reference  $G_S$  ( $G_{S_{ref}}$  at  $D=1$  kPa), which is especially convenient because it falls within the range of typically available data, thus not requiring extrapolation.

The half-hourly values of  $G_S$  were analyzed based on Eq. 4. The model accounted well ( $r^2=0.77$ ,  $P < 0.0001$ ) for variation in pre-hurricane  $G_S$  (while  $Q_o$  was available and before  $A_S:A_L$  increased), yielding the coefficient estimates  $a=121.3$  (SE 35.2),  $b=70.6$  (SE 14.6), and  $m=35.5$  (SE 11.0).

We partitioned the data into two parts in which interactive effects of increasing light and vapor pressure deficit on  $G_S$  are minimized in order to test the hypothesized effects of  $E_L$  and  $D$  on  $G_S$ . Transpiration of a *T. distichum* sapling was unrelated to  $Q_o$  above 200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Steinberg et al. 1990). Given the low LAI in this, as in many other *T. distichum* stands (Brown 1981), light at the bottom of the canopy is about 260  $\mu\text{mol m}^{-2} \text{s}^{-1}$  when  $Q_o=500 \mu\text{mol m}^{-2} \text{s}^{-1}$ . After selecting data representing  $Q_o > 500 \mu\text{mol m}^{-2} \text{s}^{-1}$ , which effectively removed data for  $D < 0.6$  kPa, the model (Eq. 4) results were significantly improved ( $r^2=0.86$ ,  $P < 0.0001$ ). For the selected data,  $G_S$  decreased significantly with increasing  $E_L$  ( $P < 0.001$ ; Fig. 2A, open symbols), but the response was significantly better correlated to increasing  $\ln D$  ( $P < 0.0001$ ; Fig. 2B, open symbols). An approach to remove the effect of auto-correlation between  $G_S$ ,  $E_L$ , and  $D$ , proposed by Monteith (1995), yielded the same outcome.  $G_S$  for the rest of the data (i.e.,  $Q_o < 500 \mu\text{mol m}^{-2} \text{s}^{-1}$  or  $D < 0.6$  kPa) was weakly related to  $Q_o$  ( $P < 0.005$ ; Fig. 2C), but not to  $E_L$  or  $D$ .

**Fig. 2** Relationship between mean canopy stomatal conductance ( $G_S$ ) and transpiration rate per unit of leaf area ( $E_L$ ) (A), vapor pressure deficit ( $D$ ) (B), and photosynthetic photon flux density ( $Q_o$ ) (C) (open symbols represent  $Q_o > 500 \mu\text{mol m}^{-2} \text{s}^{-1}$ , filled symbols represent the remaining data)

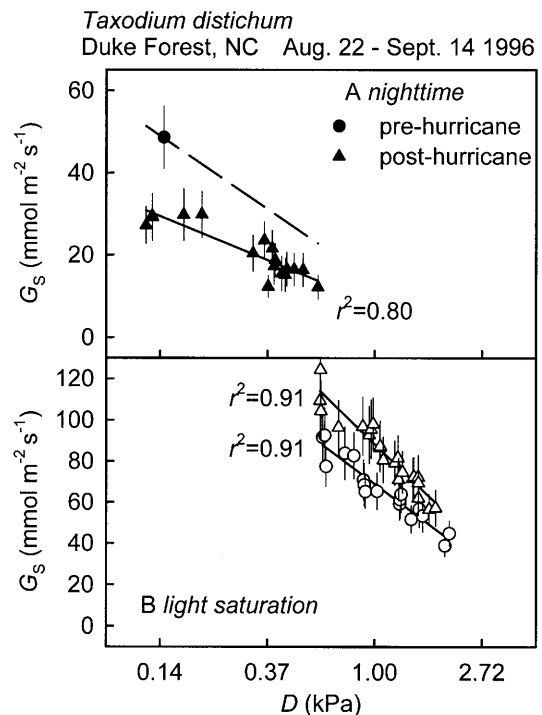


Based on these results, in the absence of limits to water availability, variability in  $G_S$  of *T. distichum* is mostly related to  $D$  at  $Q_o > 500 \mu\text{mol m}^{-2} \text{s}^{-1}$ , a value of  $Q_o$  that may reflect non-limiting light throughout the canopy. At  $Q_o < 500 \mu\text{mol m}^{-2} \text{s}^{-1}$ , a more detailed approach may be necessary to describe the variability in  $G_S$ , e.g., one that estimates the weighted mean light as a function of leaf area density distribution and light attenuation (Campbell and Norman 1998).

#### Response to defoliation

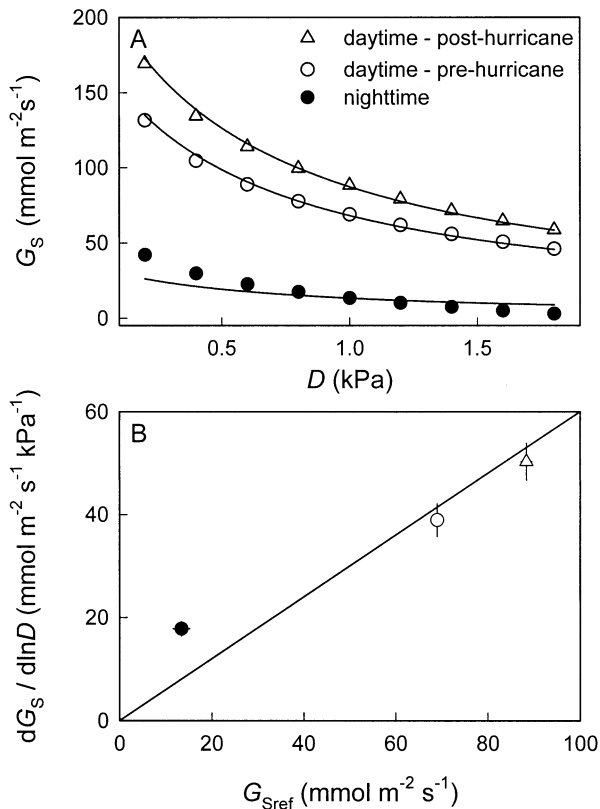
Hurricanes in *T. distichum* stands tend to strip foliage and branches (Putz and Sharitz 1991), causing an abrupt reduction in  $A_L$ . The reduction in  $A_L$  in this stand by hurricane Fran was estimated at ~45% (Oren et al. 1999a). We confirmed this estimate by using conductance values obtained at night. At very low  $D$  at nighttime (e.g., 0.14 kPa), stomata were probably as open after the hurricane as before it. Thus, the difference in  $G_S$  (Fig. 3A) between the two nighttime data sets at  $D=0.14$  kPa (48.6 vs 28.7  $\text{mmol m}^{-2} \text{s}^{-1}$  for pre- and post-hurricane, respectively) is due to not accounting for leaf loss in the calculations of post-hurricane  $G_S$ . To match the post-hurricane  $G_S$  with the pre-hurricane value required a 41% reduction in  $A_L$  to reflect leaf loss ( $A_S:A_L$  increase from 0.0014 to 0.0024  $\text{m}^2 \text{m}^{-2}$ ), remarkably similar to the estimate based on leaf fall (45%).

A 41% reduction in  $A_L$  will cause an inversely proportional increase (69%) in the leaf-specific hydraulic conductivity ( $k/A_L$ ) assuming no change in  $k$ . If we further assume a constant  $\Psi_L$ , all else being equal, Eq. 1 predicts that a 69% increase in  $k/A_L$  will cause (1) a 69% increase in  $G_S$ . Furthermore, we have recently shown that under a given set of environmental conditions, stomatal conductance sensitivity to  $D$ , quantified as  $dG_S/d\ln D$ , increases proportionally to stomatal conduc-



**Fig. 3A–C** Mean canopy stomatal conductance ( $G_S$ ) in relation to the natural logarithm of vapor pressure deficit ( $D$ ). **A** Nighttime values for the post-hurricane period are shown uncorrected for leaf loss as symbols, and a least-square fit to the corrected data is shown as a dashed line that matches the limited nighttime data in the pre-hurricane period. **B** Daytime response of  $G_S$  to  $D$  as in **A**, selected for non-limiting light conditions based on a boundary line analysis (see text). Post-hurricane values are corrected for leaf loss (see text). Vertical lines represent 1 SE ( $n=10$ )

tance at low  $D$ , e.g., at  $0.6 G_{S\text{ref}}$  (Oren et al. 1999b). Thus, if  $G_{S\text{ref}}$  under non-limiting light increases by 69%, (2) stomatal response to  $\ln D$  is predicted to also increase by 69%. Finally, (3) stand transpiration would be the same before and after the hurricane. Such a response was



**Fig. 4** **A** The response of mean canopy stomatal conductance ( $G_S$ ) to vapor pressure deficit ( $D$ ) during nighttime and during pre- and post-hurricane daytime hours. The symbols represent the least-square fit to the data in Fig. 3A, B, and the lines represent a stomatal response predicted based on a simple hydraulic model and  $G_S$  at  $D=1$  kPa ( $=G_{S\text{ref}}$ ) (see text). **B** The sensitivity of  $G_S$  to increasing  $D$  as a function of  $G_{S\text{ref}}$  representing the slope and intercept of the relationship  $G_S=(m \times \ln D)+b$ , respectively. The diagonal line is the theoretical relationship between the two parameters, and symbols are as in **A**, where a filled symbol is a nighttime value (1 SE for both coefficients is shown for each datum; in some cases it is smaller than the symbol)

indeed seen for a neighboring *P. taeda* L. stand over a 45% reduction in  $A_L$  (Pataki et al. 1998). These are the predictions for a perfect compensatory response of  $G_S$  to partial defoliation.

To facilitate a comparison of  $G_S$  response to  $D$  between the pre- and post-hurricane period, an evaluation of all predictions was made on data selected from scatterplots of  $G_S$  versus  $D$ , based on a boundary line analysis (Martin et al. 1997; Schäfer et al. 2000). This was necessary because light measurements were not available for a conditional sampling of data in the post-hurricane period. There was no difference in the pre-hurricane period between the relationships obtained using  $Q_o > 500 \mu\text{mol m}^{-1} \text{s}^{-1}$  and the boundary line analysis, reflecting the lack of sensitivity of *T. distichum* to light above the selected threshold. In addition, post-hurricane  $G_S$  was calculated based on a 41% leaf loss.

Both  $G_{S\text{ref}}$  and the stomatal sensitivity to  $D$  ( $dG_S/d\ln D$ ) increased following the hurricane (Fig. 3B;  $G_{S\text{ref}}=69.0$  and  $88.4 \text{ mmol m}^{-2} \text{s}^{-1}$  for pre- and post-

hurricane, respectively, paired Student *t*-test  $P=0.03$ ;  $dG_S/d\ln D=-38.9$  and  $-50.3 \text{ mmol m}^{-2} \text{s}^{-1} \text{kPa}^{-1}$  for pre- and post-hurricane, respectively,  $P=0.02$ ). As predicted (2), the increase in both parameters was approximately proportional (28 and 29% increase in  $G_{S\text{ref}}$  and  $dG_S/d\ln D$ , respectively). The least-square fit to the data in Fig. 3B, shown as symbols in Fig. 4A (note that  $D$  in Fig. 4A is not transformed), matched closely the predictions based on the hydraulic constraint whereby  $dG_S/d\ln D \approx -0.60 \times G_{S\text{ref}}$  (Oren et al. 1999b), shown as lines in Fig. 4A. Thus, the consequence of defoliation by the hurricane was to increase both the conductance at low  $D$  and stomatal sensitivity to  $D$  along a theoretical line representing stomatal regulation of leaf water potential (Fig. 4B).

The  $\sim 30\%$  increase in  $G_{S\text{ref}}$  and  $dG_S/d\ln D$  fell short of the 69% increase predicted for a perfect compensatory response (1). Thus, contrary to prediction 3, stand transpiration decreased by 18% rather than staying constant (Oren et al. 1999a). The reduction in stand transpiration is close to the 24% reduction predicted from the 41% loss of leaf area, compensated by an only 28% increase in  $G_{S\text{ref}}$ , which, according to Eq. 1 (for constant  $k$  and  $\Psi_L$ ) and Fig. 4A, B, would apply to  $G_S$  at all  $D$ . Possible reasons that, singly or in combination, could account for the lack of a perfect compensatory response by *T. distichum* stomata include (1) a 24% reduction in either  $k$  or  $\Delta\Psi$  caused by the hurricane, and (2) a maximum possible  $G_S$  set by stomatal density and maximum aperture that is lower than the increase in  $G_{S\text{ref}}$  required to compensate for the loss of foliage.

#### Nighttime responses of $G_S$ to $D$

Some species keep their stomata open at night, and transpire in response to  $D$  (Green et al. 1989; Becker 1998; Benyon 1999). In species that keep stomata open at night, nighttime sensitivity of  $G_S$  to  $D$  can first be predicted based on hydraulic considerations alone (Eq. 1, and Oren et al. 1999b). Then, using a departure from the predicted response, non-hydraulic regulation of  $G_S$  sensitivity to  $D$  can be inferred. In a stand of *Salix viminalis* L.,  $G_S$  at nighttime was in fact nearly equal to  $G_S$  at daytime (global radiation  $>400 \text{ W m}^{-2}$ ) when compared at  $D=0.1$  kPa (calculated from Iritz and Lindroth 1994). However, at  $D=0.5$  kPa, nighttime  $G_S$  was only 15% of daytime values thus showing a disproportionate increase in nighttime sensitivity to  $D$ . A similar increase in sensitivity to  $D$  at night was found in a stand of *Populus tremuloides* Michx. (Hogg and Hurdle 1997). These findings indicate that stomatal sensitivity to  $D$  at night increases more than would be predicted based on hydraulic considerations regarding the role of stomata in regulating leaf water potential.

Nighttime transpiration in a solitary sapling of *T. distichum* has been shown to have a similar pattern as air temperature, and thus  $D$  (Steinberg et al. 1990). We therefore searched the nighttime record for data that



could be used to evaluate whether nighttime stomatal sensitivity to  $D$  is higher than can be expected based simply on hydraulic constraints.

We extrapolated daytime  $G_S$  to  $D=0.14$  kPa under non-limiting light, using the pre-hurricane relationship (Fig. 3B), and compared to the night values obtained during the pre-hurricane period at the same  $D$  (Fig. 3A).  $G_S$  of *T. distichum* at night averaged about 40% of that in the daytime at  $D=0.14$  kPa (Student- $t$   $P<0.01$ ). Cuticular conductance in several conifers (Hadley and Smith 1990) was at least three orders of magnitude smaller than the nighttime  $G_S$  found here, and does not respond to  $D$ , and so could not corrupt the analysis of nighttime  $G_S$ . Because  $G_S$  at a given  $D$  is lower at night, based on Eq. 1, stomatal regulation of  $E_L$  with increasing  $D$  does not need to be as strict to prevent  $\Psi_L$  from reaching damaging (e.g., cavitation-inducing) values (Oren et al. 1999b). Thus, based on hydraulic considerations, we predicted that  $G_S$  at nighttime would show 40% of the daytime sensitivity to  $D$ . This prediction was evaluated with post-hurricane data (full line in Fig. 3A) corrected for leaf loss (dashed line in Fig. 3A).

Comparing the nighttime  $G_S$  response to  $D$  [ $G_S=13.4-(17.8 \times \ln D)$ ; dashed line in Fig. 3A] with the pre-hurricane daytime response [ $G_S=69.0-(38.9 \times \ln D)$ ; circles in Fig. 3B] shows that the hydraulically based proportionality ( $\sim 0.6$ ; Oren et al. 1999b) between  $dG_S/d \ln D$  (the slope in the equations above) and  $G_{Sref}$  (the intercept) is kept during the daytime ( $=0.56$ ) but is far exceeded at night ( $=1.33$ ). This is clearly demonstrated in that the least-square fit to the nighttime data (depicted as full circles in Fig. 4A) shows a greater stomatal sensitivity to  $D$  than is predicted by the hydraulic model (the respective line in Fig. 4A), which uses  $0.6 \times G_{Sref}$  as a proportionality for the  $D$  sensitivity of  $G_S$ . This contrasts with the good correspondence between the least-square fit and model predictions during daytime both before and after the hurricane (Fig. 4A). Thus, the nighttime  $G_S$  of *T. distichum* decreased from 40% of daytime values at  $D=0.14$  kPa to about 30% at  $D=0.5$  kPa, and is projected to reach zero at  $D=2.1$  kPa. This stomatal behavior of *T. distichum* shows a sensitivity to  $D$  at nighttime that is twice the sensitivity predicted based on hydraulic considerations, as is demonstrated by the position of the nighttime  $G_S$  datum above the theoretical hydraulically controlled response (full circle in Fig. 4B;  $P<0.001$ ).

The three species, *T. distichum*, *S. viminalis* and *P. tremuloides* function and grow well in moist soils, and keeping stomata open when soil moisture is not limiting may simply reflect the absence of a need to conserve moisture. When light becomes available in the morning, these mesic and hydric species may, more than other species, avoid the commonly observed lag between enhanced assimilation and increased stomatal conductance (Körner 1993; Pearcy et al. 1994). The tendency of *T. distichum* to form stands of low LAI, thereby having stomata reaching maximum conductance at low  $Q_o$  even in low canopy layers, would result in high early morning conductance and mute stomatal response to a further in-

crease in light (Fig. 2C; Roden and Pearcy 1993; Allen and Pearcy 2000). However, enhanced stomatal sensitivity to  $D$  at night keeps water potential high to sustain growth (Landsberg 1986) at a time that low conductance has no impact on carbon uptake.

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