Correlations of stomatal conductance with hydraulic and chemical factors in several deciduous tree species in a natural habitat

ROBERT M. AUGÉ*, CRAIG D. GREEN, ANN J. W. STODOLA, ARNOLD M. SAXTON, JOSHUA B. OLINICK and RICHARD M. EVANS

Institute of Agriculture, Tennessee Agricultural Experiment Station, University of Tennessee, P.O. Box 1071, Knoxville, TN 37901–1071 USA

Received 7 June 1999; accepted 5 November 1999

SUMMARY

Recent research in whole-plant stomatal physiology, conducted largely with potted plants in controlled environments, suggests that stomatal conductance ($g_s$) might be more closely linked to plant chemical variables than to hydraulic variables. To test this in a field situation, seasonal $g_s$ was examined in relation to a number of plant and environmental variables in 11 temperate, deciduous forest tree species. Stomatal conductance was generally better correlated with environmental variables (air temperature, vapor pressure deficit, PPFD) than with plant variables, and slightly better correlated with plant hydraulic variables (shoot water and osmotic potentials) than with plant chemical variables (xylem sap ABA concentration, xylem sap pH). We examined a model, developed previously for maize, which describes regulation of $g_s$ by xylem sap ABA concentration with leaf water status acting to modify stomatal sensitivity to the ABA signal. This model explained slightly more variation in seasonal $g_s$ in the forest trees than did single plant variables but not more variation than most single environmental variables. Response surface models, especially those incorporating environmental variables, were more consistently successful at explaining $g_s$ across species.

Key words: abscisic acid, maples, oaks, pH of xylem sap, stomatal conductance, temperate trees, water potential.

INTRODUCTION

Stomata regulate plant carbon gain, water loss and other physiological determinants of forest productivity. Our ability to assess impacts of environmental changes on forest ecosystems relies heavily, therefore, on understanding stomatal function and control. The traditional view is that stomatal conductance ($g_s$) is controlled chiefly via leaf water status. It now appears that stomata, at least of plants in drying soil, might also be regulated by root-to-shoot movement of chemical factors (Zhang et al., 1987; Davies et al., 1994; Tardieu et al., 1996; Wilkinson & Davies, 1997). Moreover, chemical root signals, such as abscisic acid concentrations ([ABA]) or pH changes in xylem fluid, have been postulated to exert a predominant influence, with leaf water status acting to modify stomatal sensitivity to the chemical signal (Tardieu & Davies, 1993; Tardieu et al., 1993). Strong correlations between $g_s$ and xylem sap [ABA] have been reported under many conditions for several species, including trees (e.g. Liang et al., 1996; Loewenstein & Pallardy, 1998a,b).

The theory of whole-plant stomatal regulation by root-sourced, nonhydraulic factors has been advanced on the basis of a few field studies (Loveys, 1984; Wartinger et al., 1990; Tardieu et al., 1991) but mostly by work with potted plants in controlled conditions. There are indications that $g_s$ and xylem sap [ABA] might be correlated in trees in field conditions (Loewenstein & Pallardy, 1998b) but additional work is needed to corroborate or refute the idea that $g_s$ of woody species in the field is typically better correlated with chemical rather than with hydraulic plant variables. Our objectives were to: characterize seasonal $g_s$, shoot water relations, xylem sap [ABA] and xylem sap pH of several...
Materials and Methods

Experimental site

Field data were collected between May and September, 1997, on saplings and trees of 11 species growing outdoors at the University of Tennessee Forestry Experiment Station and Arboretum (36° 1' N and 84° 13' W; c. 890 ha) in Oak Ridge, TN, USA. Long-term mean annual precipitation (30 yr normals, 1967–96) at the arboretum is 1385 mm rainfall, and mean temperature is 14.0°C. Trees on two sites with different soil characteristics were examined. The Chestnut Ridge site has strong acidic, moderately permeable forest soils classified as Fullerton cherty silt loams and in the taxonomic class of Clayey, mixed, thermic Typic Paleudults. Soils on the Pine Ridge site are primarily Armuchee sandy silty clay loam in the taxonomic class of Clayey, mixed, thermic Ochreptic Hapludults and are typified as being strongly acid, eroded, infertile and low in available water capacity.

On the Chestnut Ridge site, we measured Acer rubrum L. (red maple), Acer saccharum Marsh. (sugar maple), Cornus florida L. (flowering dogwood), Liriodendron tulipifera L. (tulip poplar), Nyssa sylvatica Marsh. (black gum), Oxydendrum arboreum (L.) D. C. (sourwood), Quercus alba L. (white oak), Quercus prinus L. (chestnut oak), Quercus rubra L. (red oak). On the Pine Ridge site, Liquidambar styaciflua L. (sweet gum) and Quercus muehlenbergii Willd. (chinquapin oak) were measured. The same trees were tagged and measured throughout the season. Replicates of each species were located close to one another, to facilitate sampling and minimize microhabitat-induced variability in measured variables. For each species, we selected locations offering relatively high irradiance wherever possible. Tree size varied with species, with trunk diameters 1.25 m above the soil surface ranging from 1 to 17 cm. All the tree species had been growing in the ground at their current location for several years, from planted seedlings (Q. rubra) or from naturally distributed seed (all other species). We selected trees that were as large as possible but whose foliage was accessible to investigators standing on the ground or on the vehicle used to transport equipment and personnel.

Plant measurements

Six to eight replicates of each species were sampled weekly throughout most of the growing season. Two to three investigators worked together in making plant and environmental measurements for each replicate of each species. All measurements for each replicate were made on one terminal shoot, consisting of c. 8–12 leaves. Preliminary, diurnal gs measurements of trees of each species were recorded at the start of the season to determine the time of day during which gs was reasonably constant, and during which gs was subsequently measured throughout the study (c. 09.30–15.30 hours US Eastern Standard Time). The following data were collected for each shoot. Stomatal conductance and leaf temperature were measured with diffusion porometers (AP4, Delta-T Devices, Cambridge, UK) on four leaves from each shoot, avoiding the two or three most recently expanded, still maturing leaves, as well as any leaves showing insect or other damage. The width (at its widest point) of each sampled leaf was recorded. Immediately following gs measurements, two of the leaves were excised, sealed in separate 3-ml syringes and placed in liquid nitrogen for later measurement of bulk leaf osmotic potential (Ψw).

The entire shoot was then severed and its Ψ immediately estimated with a pressure chamber (Soilmoisture Equipment Corp., Santa Barbara, CA, USA). Immediately following measurement of shoot Ψ, the phloem was stripped from the cut end of the stem protruding from the pressure chamber to avoid contamination of xylem sap by ABA exuding from phloem tissues. A piece of surgical tubing was then placed over the stem and into a microfuge tube; the pressure was raised 0.2–0.3 MPa above the balance pressure until 100–200 μl of xylem sap had been collected from each shoot. Previously, this over-pressure has not artificially altered [ABA] in xylem sap (e.g. Duan et al., 1996; Ebel et al., 1997). The initial 50 μl of sap extracted from each shoot was discarded to avoid contamination from cells at the cut surface. Sap samples were sealed in the tubes and immediately frozen in liquid N2. At the end of each day, syringes containing leaf samples and microfuge tubes containing xylem sap samples were transported back to the laboratory in liquid N2 and placed in a −80°C freezer, for later analysis of pH (MI-410, Microelectrodes Inc., Londonderry, NH, USA) and [ABA].

Turgor potential (Ψs) was computed as Ψ —Ψw. Transpiration was calculated for each leaf as (ρsv —ρsv)/r1r2 (Campbell, 1977): ρsv, the vapor density of the evaporative leaf surface (estimated from shoot Ψ and leaf temperature); ρsv, the ambient vapor density of the air surrounding the shoot; r1, the leaf
resistance to water vapor (inverse of $g_s$, measured as already described); $r_s$, the boundary layer resistance to water vapor diffusion. Boundary layer resistance was calculated as $\delta^b/D_wv; \delta^b$, boundary layer thickness; $D_wv$, the diffusion coefficient of water vapor (Nobel, 1991). $\delta^b = 4.0[(l/r)^{0.5}]; l$, leaf length in the downwind direction (we used leaf dimension at its widest point); $r$, the ambient wind speed within the shoot. $D_wv = [2.42 + (0.015) \text{(leaf temperature in } ^{\circ}C - 20)](10^{-5} \text{ m}^2 \text{ s}^{-1})$.

Syringes were removed from the freezer and allowed to thaw until no longer cold to the touch (10–15 min) before measuring $\Psi_s$ with a vapor pressure osmometer (Model 5500 XR, Wescor Inc., Logan, UT, USA). The osmometer was calibrated with a vapor pressure osmometer (Model 5500 XR, Wescor Inc., Logan, UT, USA). The osmometer was calibrated (10–15 min) before measuring $\Psi_s$ allowing to thaw until no longer cold to the touch.

Xylem sap [ABA] was measured by an indirect ELISA (Walker-Simmons, 1987) using monoclonal antibody to ABA (Agdia, Elkhart, IN, USA) and (+) ABA as a standard, as described previously (Duan et al., 1996). Validation of the ELISA assay for use with unpurified xylem exudate was confirmed by dilution and spike recovery tests for each species for nonspecific interference (Walker-Simmons & Abrams, 1991). Comparison of plots of undiluted, standard ABA with plots for standard ABA diluted by xylem sap (four incremental dilutions) indicated only negligible nonspecific interference. As a further check, three serial dilutions were assayed for every xylem sap sample in the experiment, to ensure that each dilution gave similar final values to undiluted sap. Duplicate ABA standards were assayed for each plate. Fluxes of ABA in stems were calculated as $[\text{ABA}] \times E$.

Predawn shoot $\Psi$ was measured with a pressure chamber.

Environmental measurements

Air temperature (platinum resistor; model RH-20C, Omega Engineering Inc., Stanford, CT, USA), relative humidity (dielectric sensor; model RH-20C, Omega Engineering Inc.) and wind speed (hot wire anemometer; model 100-VT, Davis Instruments, Hayward, CA, USA) were measured within each shoot, during each set of $g_s$ measurements. PPFD was measured with a quantum sensor (LI-COR, Lincoln, NE, USA) on each leaf at the time of $g_s$ measurement. Vapor pressure deficit (vapor pressure difference between leaf and air) was calculated from leaf and air relative humidities and temperatures (Campbell, 1977).

Statistical analysis

Various models were fitted to each species subset of the $g_s$ data, using single and multiple independent variables ($X$). Linear models, with $c_1$ to $c_8$ representing various model parameters (e.g. intercepts and slopes), included simple linear regression $g_s = c_1 + c_2X + \epsilon$

and response surface

$g_s = c_1 + c_2X_1 + c_3X_2 + c_4X_1^2 + c_5X_2^2 + c_6X_1X_2 + \epsilon$

Non-linear models included the double exponential explored by Tardieu & Davies (1993) and Tardieu et al. (1993)

$g_s = c_1 \exp(c_2X_1 \exp(c_4X_2)) + \epsilon$

a sum of exponentials

$g_s = c_1 \exp(c_2X_1) + c_3 \exp(c_4X_2) + \epsilon$

exponential response surface

$g_s = c_1 + c_2 \exp(c_1 + c_2X_1 + c_3X_2 + c_4X_1^2 + c_5X_2^2 + c_6X_1X_2) + \epsilon$

and the hyperbolic

$g_s = (c_1 + c_2X_1)/(c_1 + c_2X_1) + 1/(c_3X_2) + \epsilon$

In all these models (except simple linear regression), many combinations of the independent variables were tested. In addition, preliminary multiple regression analyses were run on the $g_s$ data, using various environmental measures as explanatory variables. Residuals from these analyses were then fitted to the above models to see whether controlling these factors would improve the fit of the models of interest. Little difference was found between the fit of adjusted and unadjusted $g_s$, so the simpler models without adjustment were focused on. $R$-square values were calculated for all models by model sums of squares divided by corrected total sums of squares. This penalizes the non-linear models without an explicit intercept (‘correction factor’), but was carried out to make all models comparable and to make the results show how well models fit beyond just an overall mean.

RESULTS

Seasonal behavior

Soils gradually dried throughout the season on both the Chestnut Ridge and Pine Ridge sites, as estimated by predawn shoot $\Psi$ (Fig. 1). At the end of June, predawn shoot $\Psi$ was near $-0.1 \text{ MPa}$ or above for all species except A. saccharum. Subsequent declines were subtle in Liq.stylaricia, N. sylvestica, O. arboreum, Q. muehlenbergii and Q. prinus (to c. $-0.2 \text{ MPa}$), moderate in Q. rubra and Q. alba (to c. $-0.3 \text{ MPa}$ in the latter part of the season), and most
pronounced in *A. rubrum*, *A. saccharum*, *C. florida* and *Lir. tulipifera* (declining to $-0.4$ to $-0.6$ MPa). Environmental conditions around the shoots during sampling of water status are depicted in Fig. 2.

Stomatal conductances remained mostly $<200$ mmol m$^{-2}$ s$^{-1}$ throughout the season in the two maples, *C. florida* and *O. arboreum* (Fig. 3). In *Q. muehlenbergii* and *Q. rubra*, $g_s$ ranged between 100 and 300 mmol m$^{-2}$ s$^{-1}$. In the remaining species, $g_s$ oscillated between c. 100 and 400 mmol m$^{-2}$ s$^{-1}$. Across species, $g_s$ was generally lower at the start and end of the season (May and Aug/Sept) than during June and July. Typically, changes in transpiration (Fig. 4) and $g_s$ were not closely related. Xylem sap [ABA] were lowest in *A. rubrum*, *A. saccharum*, *C. florida*, *Liq. styraciflua*, *O. arboreum* and *Q. muehlenbergii*, remaining $<600$ nM during the season (Fig. 5). Except for the first sampling date in May, [ABA] also remained $<600$ nM in *Q. alba*. [ABA] was somewhat higher (c. 1000 nM) in *N. sylvatica*, *Q. prinus* and *Q. rubra*, and $>2000$ nM during the first half of the season in *Lir. tulipifera*. These xylem sap [ABA] are within the ranges observed previously in these and other, well watered or moderately droughted, tree species (Wartinger *et al.*, 1990; Jackson *et al.*, 1995; Loewenstein & Pallardy, 1998a,b): for example 50 to c. 500 nM for *Quercus*...
Fig. 3. Seasonal stomatal conductance ($g_s$) in 11 tree species. Symbols represent weekly means ± 1 SE ($n = 6–8$ trees, four leaves per shoot, one shoot per tree).

Fig. 4. Seasonal transpiration rates at the time of $g_s$ measurements in 11 tree species. Symbols represent weekly means ± 1 SE ($n = 6–8$ trees, four leaves per shoot, one shoot per tree).

species (Triboulot et al., 1996; Fort et al., 1997; Loewenstein & Pallardy, 1998a,b) and 65–185 nM in sugar maple (Loewenstein & Pallardy, 1998a,b). In most species, xylem sap [ABA] was higher in May than later in the season. Fluxes of ABA remained <10 pmol m$^{-2}$ s$^{-1}$ in $A$. rubrum, $A$. saccharum, $C$. florida and $O$. arboreum (Fig. 6), but were somewhat higher in $N$. sylvatica, $Q$. muehlenbergii and $Q$. rubra ($\leq$ 30 pmol m$^{-2}$ s$^{-1}$). ABA fluxes were also in this range for $Liq$. styraciflua, $Q$. alba, and $Q$. prinus, except for higher values in May or the beginning of June. Fluxes of ABA were consistently highest in $Lir$. tulipifera (100–120 pmol m$^{-2}$ s$^{-1}$) for the first half of the season.

Xylem sap pH varied during the season; ranging from 6.0 to 7.0 in $A$. rubrum, $A$. saccharum, $Liq$. styraciflua, $N$. sylvatica, $Q$. muehlenbergii and $Q$. rubra; from 6.0 to 6.5 in $Q$. prinus; from 5.5 to 6.5 in $C$. florida, $Lir$. tulipifera and $Q$. alba; and from 5.0 to 5.5 in $O$. arboreum (Fig. 7). In many species, xylem sap was slightly more alkaline at the end than at the start of the season.

Mean shoot $\Psi$ decreased c. 1 MPa during the season in $A$. rubrum, $A$. saccharum, $Q$. alba, $Q$. muehlenbergii and $Q$. prinus, from c. –1.0 MPa early in the season to –2.0 MPa or just below by the end of August (Fig. 8). Declines in shoot $\Psi$ of c. 0.5 MPa were observed in $Liq$. styraciflua and $N$. sylvatica during the course of the season, and declines of c. 0.8 MPa were observed in $O$. arboreum from June until the end of the season. These changes are mostly consistent with declines in predawn shoot $\Psi$ during that time. Shoot $\Psi_p$ was relatively low in May for $Q$. alba, $Q$. muehlenbergii and $Q$. prinus, increasing in the latter two species during June and then falling again (in all three species) by the end of the season (Fig. 9). For $A$. rubrum and $A$. saccharum, $\Psi_p$ values appeared unreliable and were therefore not reported.
Shoot \( \Psi \) and \( \Psi_s \) remained mostly constant during much of the season in *C. florida*, *Lir. tulipifera* and *Q. rubra*, and did not reflect the declines in predawn shoot \( \Psi \) observed in these species. Fluctuations in shoot \( \Psi_s \) were relatively small in all species during the season (Fig. 10). Shoot \( \Psi_s \) remained relatively constant throughout the season in *C. florida*, *Liq. styraciflua*, *Lir. tulipifera* and *N. sylvatica*. Other species did show seasonal declines in shoot \( \Psi_s \), of c. 0.3–0.5 MPa.

Mean PPFD and VPD during porometry are shown in Figs 11 and 12.

**Correlations of \( g_s \) with hydraulic and chemical variables**

Table 1 is a multiple variable model including all the variables listed. It summarizes how much of the variability in \( g_s \) can be explained by plant and environment effects. It serves as a ‘control’ model with which to compare the models described subsequently. Table 1 also serves as a source for some chosen variables (e.g. temperature and VPD), and it indicates which physical variables were important.

**Single variable regression analyses**

Single variable regression analyses of \( g_s \) and several plant and environmental variables are summarized in Table 2, with some examples depicted in Fig. 13. Stomatal conductance was generally better correlated with environmental variables than with plant variables. Mean correlation coefficients (\( R \) values) of \( g_s \) with air temperature, VPD and PPFD across species were 0.29, 0.25 and 0.20, respectively, each higher than mean correlation coefficients of \( g_s \) with shoot \( \Psi \), shoot \( \Psi_s \) and [ABA] and pH of xylem sap. Stomatal...
Stomatal conductance was also significantly correlated with environmental variables for more species than for plant variables. Stomatal conductance was significantly correlated with air temperature, VPD and PPFD for seven, six and five species, respectively, while \( g_s \) was significantly correlated for no more than four species with any of the five plant variables. Significant correlations between \( g_s \) and each environmental variable were positive in every instance. Among environmental variables, \( g_s \) was best correlated with air temperature and least well correlated with air velocity, in terms of mean \( R \) value across species and number of species showing significant correlations. Transpiration was much better correlated with PPFD than was \( g_s \) (Table 2).

Among plant variables, \( g_s \) was best correlated with shoot \( \Psi_s \) and least well correlated with pH of xylem sap, as characterized by the mean \( R \) value across species and number of species showing significant correlations with \( g_s \). Stomatal conductance was somewhat better correlated with each of the plant hydraulic variables (shoot \( \Psi_s \), shoot \( \Psi_p \) and total shoot \( \Psi \)) than with either of the plant chemical variables ([ABA] or pH of xylem sap), in terms of mean \( R \) values across species. Between plant chemical variables, \( g_s \) was better correlated with xylem sap [ABA] than with xylem sap pH, both in terms of mean \( R \) value and number of species showing significant correlations. The one species in which \( g_s \) was significantly correlated with xylem pH, \( O. \) arboreum, had the lowest xylem pH and a relatively stable pH throughout the season. The relationship was negative: \( g_s \) declined as pH increased.

Significant single-variable correlations between each \( \Psi \) component and \( g_s \), and between xylem sap [ABA] and \( g_s \), were positive for some species and negative for others. Stomatal conductance was significantly correlated with xylem [ABA] for four of
Fig. 9. Seasonal shoot turgor potential ($\Psi_p$) at time of $g_s$ measurements in 11 tree species. Symbols represent weekly means ± 1 SE (n = 6–8 trees, and determinations on two leaf samples per tree).

The 11 species. Viewed throughout the season, increases in xylem [ABA] were correlated with decreases in $g_s$ for *N. sylvatica, Q. alba* and *Q. prinus*, as indicated by negative correlation coefficients. Xylem [ABA] was positively, significantly correlated with $g_s$ in *Lir. tulipifera*.

Stomatal conductance was significantly correlated with shoot $\Psi$ for four of the 11 species. Stomatal conductance declined as shoot $\Psi$ declined in *A. rubrum* and *Liq. styraciflua*, and shoot $\Psi$ declined as $g_s$ increased in *O. arboreum* and *Q. rubra*. The latter relationship suggests that high $g_s$ and transpiration were driving shoot $\Psi$ in *O. arboreum* and *Q. rubra*, rather than vice versa, which is reasonable as shoot $\Psi$ remained above −1.5 MPa in these species (above levels that would evoke much drought response).

The best $g_s$ correlations for individual species were with air temperature in *Q. prinus* ($R^2 = 0.52$) and *Q. alba* ($R^2 = 0.49$). The best correlation of $g_s$ with a plant variable was for shoot $\Psi_s$ in *Liq. styraciflua* ($R^2 = 0.46$).

Multiple variable regression analyses. A model developed for maize relating $g_s$ to xylem sap [ABA] and leaf $\Psi$ (Tardieu & Davies, 1993; Tardieu et al., 1993 see the Materials and Methods section for equation) did not account for as much variation in $g_s$ (Table 3) as most of the single environmental variable linear regressions (Table 2). The Tardieu model explained a significant amount of seasonal variation in $g_s$ in four of the 11 tree species, whereas air temperature, for example, explained a significant amount of seasonal variation in $g_s$ in seven of the 11 tree species. The Tardieu model was fairly successful in accounting for variation in $g_s$ for *Liq. styraciflua* and *Q. prinus* ($R = 0.45$ for each); $c_1$ ($g_{s\text{ min}}$) was removed from the Tardieu model, as values of $R$ were higher without it.

Other variables were just as successful as [ABA] and shoot $\Psi$ when substituted into the Tardieu double exponential equation (data not shown). Modifying sensitivity of $g_s$ to [ABA] by shoot $\Psi_s$ rather than shoot $\Psi$, for example, gave an $R$ of 0.29 averaged across species, versus the mean $R$ of 0.25 for the [ABA]:shoot $\Psi$ relation. The pH:shoot $\Psi$ double exponential model gave a mean $R$ value of 0.22. Modifying stomatal sensitivity to either [ABA] or pH by VPD, PPFD or air temperature gave
higher $R$ values than modifying stomatal sensitivity to [ABA] or pH by shoot $\Psi$. PPFD:VPD gave the highest mean $R$ value for the double exponential model (0.36), with nine species showing significant correlations.

Other multiple variable models were also tested with the same combinations of variables as for the double exponential. All non-linear models performed no better than the double exponential, with $R$ values being generally low and only occasionally significant (data not shown). It became apparent that the variability in the data (e.g. Fig. 13) could not be explained by a model with only a few parameters. Therefore, the more flexible response-surface models were tried. The exponential response surface gave no better performance than the linear response surface, so the latter models were focused on.

Correlation coefficients for the [ABA]:shoot $\Psi$ response surface (mean of 0.36 across species) and the pH:shoot $\Psi$ response surface (mean of 0.34) were higher than corresponding $R$ values for the Tardieu models based on those variables (0.25 and 0.22, respectively). Again, substituting shoot $\Psi_p$ for shoot $\Psi$ improved the correlation of $g_s$ with [ABA] and one $\Psi$ component. As in the double exponential models and the single-variable models, response surfaces based on the environmental variables accounted for the greatest variation in $g_s$ (columns 6–9 of Table 3; $R$ (averaged across species) = 0.44–0.46). The response surface showing a significant correlation for the most number of species (10 of the 11 species) was the shoot $\Psi_p$:air temperature model, which incorporated the best single plant predictor (shoot $\Psi_p$) and the best single environmental predictor (air temperature).

The response surface giving the highest correlation coefficient for $g_s$ within an individual species
Table 1. Regression analyses for stomatal conductance using plant and environmental variables

<table>
<thead>
<tr>
<th>Species</th>
<th>Leaf size</th>
<th>Trunk diameter</th>
<th>Time of day</th>
<th>Air temperature</th>
<th>Leaf temperature</th>
<th>Air velocity</th>
<th>VPD</th>
<th>PPFD</th>
<th>Model $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer rubrum</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.34</td>
</tr>
<tr>
<td>Acer saccharum</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.17</td>
</tr>
<tr>
<td>Cornus florida</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.37</td>
</tr>
<tr>
<td>Liquidambur styraciflua</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Liriodendron tulipifera</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>*0.27</td>
</tr>
<tr>
<td>Nyssa sylvatica</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.23</td>
</tr>
<tr>
<td>Oxycodendrum arboreum</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.31</td>
</tr>
<tr>
<td>Quercus alba</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.50</td>
</tr>
<tr>
<td>Quercus muehlenbergii</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.30</td>
</tr>
<tr>
<td>Quercus prinus</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.55</td>
</tr>
<tr>
<td>Quercus rubra</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.23</td>
</tr>
</tbody>
</table>

* Models included all variables listed, and significant variables are indicated by *($P < 0.05$). Date of sampling was also examined but not included in regression analyses as it was not significant for any species given the other variables.

Discussion

Seasonal fluctuations in plant variables are summarized in the Results section to give a sense of tree response to the environmental conditions of 1997, which proved to be a reasonable year to test our hypotheses. There were no dramatic climatic extremes, yet there was sufficient variability in precipitation and soil moisture to provide a range in values of $g_s$ and other plant and environmental variables.

The recent discovery of non-hydraulic, root-sourced stress signals is changing our understanding of the way in which plants ‘sense’, and stomata respond to, fluctuations in soil moisture. Previously, it had been widely held that $g_s$ was hydraulically regulated by leaf $\Psi$ or turgor (Kramer & Boyer, 1995), at least in anisohydric plants (Tardieu et al., 1996; Tardieu & Simmoneau, 1998). However, there have been several reports of instances where $g_s$ was inhibited in drying soils even in the absence of perturbations in leaf water status (see Davies et al., 1994, for review). Such studies suggest that stomatal closure resulting from soil water depletion is mediated by changes in root water status through effects on the chemical flow of information from root to shoot. The existence of ‘nonhydraulic’ root signals has been demonstrated or suggested in several woody species, including Acer pseudoplatanus (Khali & Grace, 1993), Prunus avium × pseudocerasus (Gowing et al., 1993), Malus × domestica (Gowing et al., 1990), Prunus dulcis (Fußereder et al., 1992), Rosa hybrida (Augé & Duan, 1991), some coniferous species (Jackson et al., 1995) and C. floridica, O. arboresum, L. tulipifera, A. rubrum, Chionanthus virginicus and Halesia carolina (Croker et al., 1998). Much evidence supports the hypothesis that the movement of ABA from roots to shoots in xylem acts as the stress signal (Davies et al., 1994). Other evidence suggests that stomata might be responding to changes in apoplastic pH that occur in response to changes in soil moisture (Hartung et al., 1998). Whether or not the ABA moving to guard cell complexes is predominantly of leaf or root origin (Salindra et al., 1995; Liang et al., 1997; Thompson et al., 1997; Hartung et al., 1998), $g_s$ has often been more closely correlated with concentrations of ABA in leaf and shoot xylem than with leaf $\Psi$ or soil $\Psi$.

Our purpose was to determine if seasonal $g_s$ of forest trees is better correlated with plant chemical factors ([ABA] or pH of xylem fluid), plant hydraulic factors (shoot $\Psi$ components) or environmental factors (PPFD, VPD, air temperature, air velocity). Xylem sap [ABA] was not strongly associated with $g_s$ in the trees studied here. Stomatal conductance:
Fig. 13. Relationship between seasonal stomatal conductance ($g_s$) and some plant and environmental variables, for five representative tree species (*Acer rubrum* (a), *Cornus florida* (b), *Liquidambar styraciflua* (c), *Quercus alba* (d) and *Q. prinus* (e)). $\Psi_p$, osmotic potential; VPD, vapor pressure deficit; [ABA], ABA concentration in xylem sap. Each point represents a sample from one tree and 1 d (mean of four leaves for the tree); $g_s$ was measured from May to September 1997. The dashed line represents the 1–1 line of perfect prediction. Correlation coefficients and significance of correlation for these and other single variable regressions are listed in Table 2.

[ABA] correlation coefficients were mostly higher than those observed previously in large *Quercus* trees under natural conditions (Triboulet et al., 1996) and lower than those observed previously in *Juglans nigra*, *A. saccharum* and *Q. alba* (Loewenstein & Pallardy, 1998b). Averaged across species, $g_s$ correlation coefficients were slightly higher with shoot $\Psi$ than with xylem [ABA], but effectively $g_s$ appeared to be similarly linked with shoot $\Psi$ and xylem [ABA] throughout the season. Strength of the correlation
Table 2. Correlation coefficients (R) for single variable models explaining stomatal conductance

<table>
<thead>
<tr>
<th>Species</th>
<th>Shoot $\Psi$</th>
<th>Shoot $\Psi_w$</th>
<th>Shoot $\Psi_t$</th>
<th>[ABA]</th>
<th>Xylem pH</th>
<th>VPD</th>
<th>PPFD</th>
<th>Air temperature</th>
<th>Air velocity</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Acer rubrum</strong></td>
<td>0.27**</td>
<td>0.16</td>
<td>—</td>
<td>—0.08</td>
<td>—0.03</td>
<td>—0.18</td>
<td>0.24*</td>
<td>0.28**</td>
<td>0.19</td>
</tr>
<tr>
<td><strong>Acer saccharum</strong></td>
<td>0.01</td>
<td>0.17</td>
<td>—</td>
<td>—0.06</td>
<td>0.12</td>
<td>0.25*</td>
<td>0.23*</td>
<td>0.17</td>
<td>0.01</td>
</tr>
<tr>
<td><strong>Cornus florida</strong></td>
<td>-0.17</td>
<td>-0.17</td>
<td>-0.06</td>
<td>0.01</td>
<td>-0.05</td>
<td>0.20</td>
<td>0.17</td>
<td>0.13</td>
<td>0.24*</td>
</tr>
<tr>
<td><strong>Liquidambar styraciflua</strong></td>
<td>0.37**</td>
<td>0.46**</td>
<td>0.21</td>
<td>-0.04</td>
<td>-0.15</td>
<td>0.39**</td>
<td>-0.11</td>
<td>0.39**</td>
<td>0.17</td>
</tr>
<tr>
<td><strong>Liriodendron tulipifera</strong></td>
<td>-0.07</td>
<td>-0.12</td>
<td>-0.00</td>
<td>0.31*</td>
<td>-0.15</td>
<td>0.43**</td>
<td>0.41**</td>
<td>0.33***</td>
<td>0.18</td>
</tr>
<tr>
<td><strong>Nyssa sylvatica</strong></td>
<td>0.14</td>
<td>-0.27*</td>
<td>0.27*</td>
<td>-0.25*</td>
<td>-0.02</td>
<td>0.05</td>
<td>0.28*</td>
<td>0.00*</td>
<td>0.24*</td>
</tr>
<tr>
<td><strong>Oxydendrum arboreum</strong></td>
<td>-0.21*</td>
<td>-0.23*</td>
<td>-0.06</td>
<td>0.17</td>
<td>-0.30**</td>
<td>0.14</td>
<td>0.19</td>
<td>0.37***</td>
<td>0.06</td>
</tr>
<tr>
<td><strong>Quercus alba</strong></td>
<td>-0.02</td>
<td>0.07</td>
<td>-0.16</td>
<td>-0.27*</td>
<td>0.14</td>
<td>0.44**</td>
<td>0.13</td>
<td>0.49**</td>
<td>0.06</td>
</tr>
<tr>
<td><strong>Quercus muehlenbergii</strong></td>
<td>-0.01</td>
<td>-0.23</td>
<td>0.10</td>
<td>0.02</td>
<td>-0.12</td>
<td>0.12</td>
<td>0.01</td>
<td>0.28*</td>
<td>0.23</td>
</tr>
<tr>
<td><strong>Quercus prinus</strong></td>
<td>-0.27</td>
<td>0.31*</td>
<td>-0.34</td>
<td>-0.34**</td>
<td>0.09</td>
<td>0.32**</td>
<td>-0.18</td>
<td>0.52***</td>
<td>0.06</td>
</tr>
<tr>
<td><strong>Quercus rubra</strong></td>
<td>-0.33**</td>
<td>-0.17</td>
<td>-0.26*</td>
<td>-0.02</td>
<td>0.04</td>
<td>0.29**</td>
<td>0.01</td>
<td>0.27</td>
<td>0.11</td>
</tr>
</tbody>
</table>

*Mean, $\mu_c$

†Mean, transpiration

Models were fitted to each species separately, using all data collected during the season.

Asterisks indicate significance of regression ($R^2$) at $P < 0.05$ (*), 0.01 (**) or 0.001 (**). Mean correlation coefficients for $g_c$ across species for each variable were computed from absolute values of species correlation coefficients.

For comparative purposes, mean correlation coefficients across species for each variable were also provided for transpiration. Numbers in parentheses indicate the number of species that showed significant correlation, $P = 0.05$. — indicates regression not computed, as the variable was used in calculating transpiration (or, in the case of shoot $\Psi_w$, shared a variable).
Table 3. Multiple correlation coefficients (R; always positive) for various two-variable models explaining stomatal conductance

<table>
<thead>
<tr>
<th>Species</th>
<th>aTardieu</th>
<th>[ABA]/shoot Ψ</th>
<th>[ABA]/shoot Ψ_a</th>
<th>pH/shoot Ψ</th>
<th>Air temp/PPFD</th>
<th>Air temp/VPD</th>
<th>VPD/PPFD</th>
<th>Shoot Ψ_a/air temp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer rubrum</td>
<td>0.14</td>
<td>b0.52***</td>
<td>0.47***</td>
<td>0.36*</td>
<td>0.53***</td>
<td>0.44**</td>
<td>0.44***</td>
<td>0.37*</td>
</tr>
<tr>
<td>Acer saccharum</td>
<td>0.21</td>
<td>0.22</td>
<td>0.28</td>
<td>0.30</td>
<td>0.42**</td>
<td>0.28</td>
<td>0.43***</td>
<td>0.35*</td>
</tr>
<tr>
<td>Cornus florida</td>
<td>0.24</td>
<td>0.24</td>
<td>0.26</td>
<td>0.34</td>
<td>0.25</td>
<td>0.25</td>
<td>0.33</td>
<td>0.30</td>
</tr>
<tr>
<td>Liquidambar styraciflua</td>
<td>0.45***</td>
<td>0.47*</td>
<td>0.46*</td>
<td>0.39</td>
<td>0.49**</td>
<td>0.62***</td>
<td>0.61***</td>
<td>0.60***</td>
</tr>
<tr>
<td>Liriodendron tulipifera</td>
<td>0.24</td>
<td>0.32</td>
<td>0.28</td>
<td>0.30</td>
<td>0.55***</td>
<td>0.48***</td>
<td>0.52***</td>
<td>0.38*</td>
</tr>
<tr>
<td>Nyssa sylvatica</td>
<td>0.30*</td>
<td>0.34</td>
<td>0.48**</td>
<td>0.22</td>
<td>0.35</td>
<td>0.26</td>
<td>0.34</td>
<td>0.43*</td>
</tr>
<tr>
<td>Oxydendrum arboreum</td>
<td>0.22</td>
<td>0.29</td>
<td>0.36</td>
<td>0.56***</td>
<td>0.42**</td>
<td>0.44**</td>
<td>0.29</td>
<td>0.42**</td>
</tr>
<tr>
<td>Quercus alba</td>
<td>0.32*</td>
<td>0.42**</td>
<td>0.41**</td>
<td>0.31</td>
<td>0.61***</td>
<td>0.65***</td>
<td>0.57***</td>
<td>0.54***</td>
</tr>
<tr>
<td>Quercus muehlenbergii</td>
<td>0.04</td>
<td>0.30</td>
<td>0.43*</td>
<td>0.35</td>
<td>0.43*</td>
<td>0.49**8</td>
<td>0.47***</td>
<td>0.41*</td>
</tr>
<tr>
<td>Quercus prinus</td>
<td>0.45***</td>
<td>0.46**</td>
<td>0.45**</td>
<td>0.23</td>
<td>0.62***</td>
<td>0.56***</td>
<td>0.48*</td>
<td>0.61***</td>
</tr>
<tr>
<td>Quercus rubra</td>
<td>0.17</td>
<td>0.41*</td>
<td>0.31</td>
<td>0.40*</td>
<td>0.36</td>
<td>0.39*</td>
<td>0.38*</td>
<td>0.39*</td>
</tr>
<tr>
<td>Mean, g_s</td>
<td>0.25</td>
<td>0.36</td>
<td>0.39</td>
<td>0.34</td>
<td>0.46</td>
<td>0.45</td>
<td>0.44</td>
<td>0.44</td>
</tr>
</tbody>
</table>

a Tardieu represents the double exponential model developed for maize (Tardieu et al., 1993; Tardieu & Davies, 1993). All other models are response surfaces. See Materials and Methods section for model descriptions. Models were fitted to each species separately, using all data collected during the season.

b Asterisks indicate significance of regression (R^2) at P < 0.05 (*), 0.01 (**) or 0.001 (***)..

c Mean correlation coefficients across species for each variable were compared from absolute values of species correlation coefficients.
Fig. 14. Relationship between observed seasonal stomatal conductance ($g_s$) and predicted $g_s$, for five representative tree species (Acer rubrum (a), Cornus florida (b), Liquidambar styraciflua (c), Quercus alba (d) and Q. prinus (e)). Each point represents $g_s$ of one tree and 1 d (mean of four leaves for the tree); $g_s$ was measured from May to September 1997. Stomatal conductance was predicted with a double exponential model published for maize (Tardieu & Davies, 1993; Tardieu et al., 1993), and with several response surfaces. The two-variable response surfaces with the best overall correlations that incorporate a plant chemical and plant hydraulic variable ([ABA]:shoot osmotic potential ($\Psi_s$)) and a plant and environmental variable (shoot $\Psi_s$:air temperature), as well as the response surface giving the best correlation among any two plant or environmental variables (air temperature:PPFD) are shown. The dashed line represents the 1–1 line of perfect prediction. Correlation coefficients and significance of correlation for these and other models are listed in Table 3.
varied considerably with tree species, but for individual species the best correlations of \( g_s \) with either \( \Psi \) or \([ABA]\) were similar: 0.37 for \( g_s \); shoot \( \Psi \) in \textit{Ligustrum styraciflua} and 0.34 for \( g_s \); \([ABA]\) in \textit{Q. primus}. Moreover, the same number of species showed significant correlations for \( g_s \); shoot \( \Psi \) and \( g_s \); \([ABA]\). Shoot \( \Psi \) better explained \( g_s \) than either shoot \( \Psi \) or xylem sap \([ABA]\), and xylem pH generally most poorly explained \( g_s \) relative to other plant and environmental variables.

The more easily measured environmental variables were generally better indicators of \( g_s \) than either the plant hydraulic or plant chemical variables. For example, \( g_s \) was significantly correlated with the air temperature surrounding leaves for each of the four species having significant \( g_s \); shoot \( \Psi \) correlations, as well as for an additional three species. More species showed significant \( g_s \) correlations with PPFD and VPD than with either \([ABA]\) or shoot \( \Psi \). Stomatal conductance was significantly correlated with air temperature for more species than with any other single plant or environmental variable. Moreover, the nature of the \( g_s \) correlation was more predictable for environmental than for plant variables. Unlike \([ABA]\) or shoot \( \Psi \) components, higher PPFD, VPD, air temperature and air velocity were always correlated with higher \( g_s \), when correlations were significant. It was found that \( g_s \) was somewhat better related to changes in VPD than PPFD. Transpiration, however, was relatively well correlated with PPFD. Other investigators have observed that VPD explained more variation in transpiration than did PPFD (e.g. Oren et al., 1999).

Many investigators favoring the ideas of either chemical or hydraulic control of \( g_s \) concede that \( g_s \) is probably affected by both factors. In refining their hypotheses of regulation of \( g_s \), Saliendra et al. (1995) noted that an integration of hydraulic and chemical signals controlling \( g_s \) is more likely than control based on chemical signals or water relations alone. In describing the method by which leaf hydration controls \( g_s \), Saliendra et al. (1995) noted that both hydroactive and hydropassive processes are likely to be important and would involve both hormonal and hydraulic mechanisms. Correia & Pereira (1995) and Thomas & Eamus (1999) also noted the likely interaction of both hormonal and hydraulic influences in modulating \( g_s \).

A model of stomatal behavior has been developed, using field-grown corn, which incorporates both hormonal and hydraulic factors, linking \( g_s \) to xylem \([ABA]\) with a sensitivity dependent upon leaf \( \Psi \) (Tardieu & Davies, 1993; Tardieu et al., 1993). This model accounted for more variation in \( g_s \) than either xylem \([ABA]\) or shoot \( \Psi \) alone, in many of the forest trees studied here. Correlation coefficients were not nearly as high as those observed for maize (Tardieu et al., 1993), and we would expect more variation in the model under conditions studied here than under the conditions for which it was developed, for several reasons. In the maize field, Tardieu obtained measurements on genetically similar plants of the same age, over a short time period (3 d), under relatively high illumination. In the forest, we examined plants with much greater genetic variability, of widely different ages, seasonally from May to September, often under non-saturating illumination. Further, Tardieu et al. (1993) were able to correct non-saturating \( g_s \) values to \( g_s \) at light saturation, according to the well known relationship between \( g_s \) and PPFD corroborated for maize (Tardieu & Davies, 1993). We attempted to develop such plots for our tree species, both in the forest and under higher illumination using urban trees, but a strong correlation between \( g_s \) and PPFD was not observed, even within one tree with measurements made over a short time period.

The mechanism by which stomata perceive an ABA signal has yet to be clearly defined, and others have addressed the question of whether the stomatal response is directly linked to xylem \([ABA]\) or to a measure of the amount of ABA entering the leaf. The xylem sap concentration of ABA was evaluated here because most investigators have found that \( g_s \) is better correlated with \([ABA]\) than with flux of ABA to leaves, in both herbaceous plants (e.g. Tardieu et al., 1992, 1993; Tardieu & Davies, 1993; Jia et al., 1996) and trees (Gowing et al., 1993; Liang et al., 1996; Loewenstein & Pallardy, 1998a). Fluxes of ABA were measured here and their seasonal trends were compared with \([ABA]\). \( R \) and \( P \) values are not summarized in Tables 2–3 for models incorporating ABA flux, because auto-correlation effects artificially inflate those values; \( g_s \) was used to compute ABA flux (\( g_s \) in computing transpiration, and transpiration in computing ABA flux).

The double exponential model for \( g_s \) developed by Tardieu combined equations describing the generation and effects of chemical signals and classical equations of water flux (Tardieu & Davies, 1993). We tested numerous models incorporating many environmental and plant variables, both chemical and hydraulic, for the best empirical correlation with \( g_s \) and found that response surfaces provided the best fits. The xylem \([ABA]\); shoot \( \Psi \) response surface was significantly correlated with \( g_s \) in more species than was the Tardieu model, and the mean correlation coefficient across species was higher. However, a response surface that modified stomatal sensitivity to xylem \([ABA]\) by shoot \( \Psi \), rather than by shoot \( \Psi \) accounted for even greater variation. Of all models incorporating a plant variable, the shoot \( \Psi \); air temperature response surface accounted for the most variation in \( g_s \).

The shoot \( \Psi \); air temperature response surface also resulted in significant \( g_s \) correlations in 10 of the 11 species, more than for any other model. As in the double exponential models, using environmental
variables in the response surfaces explained as much or more variation in \( g_s \) than using plant variables.

Two-variable response surfaces incorporating any two of these three environmental variables – air temperature, PPFD, VPD – were equally robust in describing seasonal \( g_s \) and better described \( g_s \) than any two-variable combination of [ABA], pH, shoot \( \Psi \), shoot \( \Psi_s \) or shoot \( \Psi_v \).

Others have suggested that \( g_s \) might be regulated by xylem sap pH (Thompson et al., 1997; Wilkinson 
& Davies, 1997) or that stomatal sensitivity to [ABA] might be modified by xylem sap pH (Jia 
& Zhang, 1997; Zhang et al., 1997; Hartung et al., 1998; Wilkinson et al., 1998): pH gradients in the leaf control ABA distribution in the leaf and ABA concentration at guard cells, and thereby influence stomatal aperture. In the trees in this study, seasonal \( g_s \) was generally not associated with xylem sap pH. Stomatal conductance was significantly correlated with xylem sap pH in only one of the 11 species, and the mean correlation coefficient of \( g_s \) with pH was lower than for the other plant variables, including xylem [ABA]. Stronger correlations of \( g_s \) with [ABA] than with pH of xylem sap have been observed before, in J. nigra, Salix nigra, A. saccharum and O. alba (Loewenstein & Pallardy, 1998a,b). We tested the hypothesis that that xylem sap pH might modify stomatal sensitivity to [ABA] or to shoot \( \Psi \) and found that [ABA]: pH models, shoot \( \Psi \): pH and \( \Psi_v \) component:pH models did not explain seasonal variations in \( g_s \) as well as [ABA]: shoot \( \Psi \) and [ABA]: shoot \( \Psi_v \) models.

Air humidity surrounding leaves can modify \( g_s \) (Lange et al., 1971; Schulze et al., 1987), and in some species \( g_s \) can be well correlated with the difference in absolute humidities between leaf and air (e.g. Assman & Grantz, 1990; Aphalo & Jarvis, 1991). In other species, \( g_s \) is relatively insensitive to VPD (Schulze et al., 1987), perhaps especially in the field (Tardieu 
& Simonneau, 1998). Stomatal conductance of over half of the tree species here showed significant seasonal correlations with VPD, and VPD was one of the best descriptors of seasonal \( g_s \), better than any of the plant variables. Stomatal conductance of large Q alba trees has previously been shown to be better correlated with VPD than with xylem [ABA] (Loewenstein 
& Pallardy, 1988b), as in our study, and we found that among the 11 species, Q. alba had the highest \( g_s \). VPD correlation coefficient. When \( g_s \) is related to VPD (not always the case in woody species, e.g. Turner et al., 1984), the relationship is typically a negative one, \( g_s \) decreasing as VPD increases (e.g. Turner et al., 1984; Ball et al., 1987; Thomas 
& Eamus, 1999). However, in our study, in every case of significant correlation between seasonal \( g_s \) and VPD (A. saccharum, Liq. styraciflua, Lir. tulipifera, Q. alba, Q. prinus and Q. rubra), \( g_s \) increased as VPD increased. Vapor pressure deficit is greatly affected by temperature, and temperature also affects \( g_s \). Sometimes the \( g_s \):air temperature relation is negative, sometimes it is positive, depending on species and temperature range (Wilson, 1948; Meyer 
& Anderson, 1952; Wuenensch 
& Kozlowski, 1971). Stomatal conductance has previously been positively correlated with temperature in sugar maple in the air temperature range of 26–30°C (Pereira 
& Kozlowski, 1977), and we also observed positive correlations between \( g_s \) and air temperature in each of the seven instances for which individual species correlations were significant. It is likely, therefore, that the positive \( g_s \):VPD relationships were driven by the positive \( g_s \):air temperature relationships. Air temperature was the single strongest describer of \( g_s \) among all plant and environmental variables examined.

Tardieu et al. (1993) also tested a model involving [ABA] and VPD and determined that in their maize system leaf \( \Psi \) better described stomatal sensitivity to ABA than did VPD. We found that, overall, VPD better described stomatal sensitivity to [ABA] than did shoot \( \Psi \). Nine tree species showed significant correlations of \( g_s \) with the [ABA]:VPD response surface, versus five species for the [ABA]:shoot \( \Psi \) response surface. Mean correlation coefficients across all 11 species were 0.42 and 0.36 for the [ABA]:VPD and [ABA]: shoot \( \Psi \) response surfaces, respectively. Correlation coefficients were similar for the double exponential (Tardieu) [ABA]:shoot \( \Psi \) and [ABA]:VPD models, each with four species having significant correlations.

The limitations of statistical empirical modeling are recognized. The response surface models were used to identify influential variables among species in this study but not as a means of predicting \( g_s \) in the future. The response surface models used here have many parameters, which allow them to fit almost any data. However, this flexibility has the price of making the results specific to the current data. Thus, while certain variables might be important in explaining \( g_s \), the relationships among the variables, and thus the prediction model, could very well change with field setting. As an illustration, a subset of four plants from each species was fitted with a response surface in shoot \( \Psi_v \) and air temperature, and this equation was used to predict the other plants in that species. The mean \( R \) value was 0.54 in the fitted data, but only 0.22 for predicting other plants. Many of the predicted \( R \) values were negative, indicating data with a reversed relationship compared with the four-plant subset. When this was repeated with [ABA] and shoot \( \Psi \), the mean \( R \) value went from 0.48 to 0.10, suggesting an even less predictable relationship.

Further, the types of models chosen are highly dependent on the types of data used. The biologically-based double exponential model of Tardieu might actually be correct, but only for conditions in which the environment and plant characteristics
have been standardized. In a more variable forest situation, variables such as xylem sap [ABA] might still be operating to influence g_s, but, as we observed, other variables might be more influential. Finding the single best model might be an elusive goal.

ACKNOWLEDGEMENTS

This manuscript is based upon work supported by the Tennessee Agricultural Experiment Station and the US Department of Energy, National Institute for Global Environmental Change, Southeast Regional Center, under Award No. DE-FC03-90ER61010.

REFERENCES


Tardieu F, Simonneau Th. 1998. Variability among species of stomatal control under fluctuating soil water status and


