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# Stomatal conductance of *Acer rubrum* ecotypes under varying soil and atmospheric water conditions: predicting stomatal responses with an abscisic acid-based model

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**Summary** A multiplicative model of stomatal conductance was developed and tested in two functionally distinct ecotypes of *Acer rubrum* L. (red maple). The model overcomes the main limitation of the commonly used Ball-Berry model (Ball et al. 1987) by accounting for stomatal behavior under soil drying conditions. We combined the Ball-Berry model with an integrated expression of abscisic acid (ABA)-based stomatal response to ABA concentration ([ABA]) in bulk leaf tissue ($g_{fac}$), which coupled physiological changes at the leaf level with those in the root. The factor $g_{fac} = \exp(-\beta[ABA]_L)$ incorporated the stomatal response to [ABA] into the Ball-Berry model by down regulating stomatal conductance ($g_s$) in response to physiological changes in the root. The down regulation of $g_s$ is pertinent under conditions where soil drying may modify the delivery of chemical signals to leaf stomata. Model testing indicated that the multiplicative model was capable of predicting $g_s$ in red maple under wide ranges of soil and atmospheric conditions. Concordance correlation coefficients were high (between 0.59 and 0.94) for the tested ecotypes under three environmental conditions (atmospheric, rhizospheric and minimal stress). The study supported the use of $g_{fac}$ as a gas exchange function that controls water stress effects on $g_s$ and aids in the prediction of $g_s$ responses.

*Keywords: Ball-Berry model, modeling, stomatal sensitivity, vapor pressure deficit.*

## Introduction

Leaf stomatal conductance ($g_s$) responds to both the atmospheric and rhizospheric environments. The atmospheric environment comprises those external variables (temperature, humidity, $CO_2$, light and wind) that directly impact the leaf or its boundary layer. The rhizosphere environment includes those factors that affect root water status and, hence, both xylem water potential and the production of root-sourced chemical signals, particularly the hormone abscisic acid (ABA) (Gutschick and Simonneau 2002).

To date, several empirical models of $g_s$ responses to atmospheric or rhizospheric factors, hereafter referred to as atmospheric and rhizospheric models, respectively, have been created, but few integrate the effects of the atmospheric and rhizospheric environments. Some of the common empirical atmospheric models are those of Jarvis (1976), Ball et al. (1987) and Leuning (1995). Models that incorporate root-sourced signals are not as widely used, but have been tested by Tardieu and Davies (1993), Tardieu et al. (1993) and Tardieu and Simonneau (1998). One of the few models providing an empirical description of the response to both the atmospheric and the rhizospheric environment is that of Tenhunen et al. (1990, 1994). Recently, Gutschick and Simonneau (2002) found that the multiplicative form of an ABA-dependent modified Tenhunen et al. (1994) model gave the best fit when compared with three atmospheric models and an alternative coupling model of stomatal response to the leaf environment in sunflower (*Helianthus annuus* L.). Gutschick and Simonneau (2002) found that the most accurate $g_s$ model of this type was of the combined multiplicative form that incorporated the Ball-Berry model of atmospheric control:

$$g_s = g_{s,BB} g_{fac}([ABA]) \quad (1)$$

where the Ball-Berry term ($g_{s,BB}$), which describes the atmospheric $g_s$ response, is integrated with $g_{fac}([ABA])$, where $g_{fac}([ABA]) = \exp(-\beta[ABA]_L)$, hence changing the stomatal gas exchange limitation. Gutschick and Simonneau (2002) reiterated the conclusions of Whitehead's (1998) review, which found that there is a paucity of data on the importance of ABA-dependent signaling in woody plants. Moreover, with respect to woody plants, the significance of chemical and hydraulic controls in regulating stomatal conductance remains unclear (Whitehead 1998).

Abscisic acid can be synthesized in both root (e.g., Hartung et al. 1994, Zhang and Tardieu 1996, Jeschke et al. 1997) and

leaf tissue (e.g., Cutler and Krochko 1999), and in mycorrhizal and saprophytic fungi (e.g., Hartung and Gimmler 1994). The results of other studies indicate that root-generated ABA, transported to the leaves via the xylem, does not explain the complex signaling in woody plants (Davies and Zhang 1991, Saliendra et al. 1995, Whitehead et al. 1996, Perks et al. 2002). Although considerable evidence in the literature suggests that $g_s$ may be regulated by chemical signals that are independent of hydraulic signals (e.g., Khalil and Grace 1993, Fuchs and Livingston 1996), hydraulic signals are transmitted rapidly (Malone 1993) and evidence suggests that they may regulate $g_s$ (e.g., Meinzer and Grantz 1990, 1991). Alternatively, Saliendra et al. (1995) suggest that hydraulic and leaf ABA mechanisms are interactive in woody plants. Comstock (2002) recently reviewed these chemical and hydraulic interactions. If an important stress detection function exists at the leaf level, where leaf-internal responses to atmospheric stress may be more effective than root-sourced signals in tall trees, it is necessary to investigate ABA accumulation during stomatal closure in response to soil or atmospheric water deficit.

To examine changes in ABA accompanying water stress, induced either by atmospheric or rhizospheric factors, we modeled stomatal water loss in response to ABA-dependent restrictions on gas exchange. We tested the hypothesis that ABA and hydraulic and atmospheric controls on $g_s$ act sequentially. To do so, we tested the dynamic $g_s$ response in two *Acer rubrum* L. (red maple) ecotypes originating from hydrologically contrasting sites (Bauerle et al. 2003). Furthermore, we analyzed agreement between observed and predicted $g_s$ of the two ecotypes under minimal water stress or under water stress imposed by atmospheric or rhizospheric factors. The objectives of our study were to: (1) test a multiplicative combined ABA-based $g_s$ control model in a woody plant system; (2) investigate through simulation whether ecotypes from different hydrological habitats respond similarly; and (3) explore the hypothesis that ABA accumulation in leaf tissue predicts stomatal response to water stress. We discuss the control of $g_s$ by multiple factors in relation to intraspecific divergence in stomatal behavior among ecotypes and the implication to ABA-signaling in tall trees.

## Materials and methods

### *Plant material*

Plant material was collected over 4 years and used in experiments conducted during three growing seasons. In the years 1995–1998, red maple seeds were collected from trees at eight sites. Wet sites had poorly drained soils that are saturated in the spring during seed development (a wetland or swamp), and dry sites had well-drained upland soils. The geographic origin, site descriptions, seedling establishment, ages, stature and initial growth media have been described in detail in Bauerle et al. (2003).

### *Rhizosphere stress response experiment*

The details of plant measurements and design of the rhizosphere stress response experiment are described elsewhere (Bauerle et al. 2003). For the purposes of this study, predawn water potential (estimate of soil water potential), gas exchange and leaf ABA data were used to parameterize, validate and test the multiplicative $g_s$ model described here.

In the rhizosphere stress response experiment, relative humidity, air temperature, wind direction, photosynthetic photon flux (PPF), precipitation and wind speed were measured every 2 min and averaged over 1 h at a weather station (Campbell Scientific, Logan, UT) located ~50 m from the experimental plot.

### *Minimal stress experiment*

An open gas exchange system (Model MPH-1000, Campbell Scientific) was used to measure the response curves of photosynthesis and $g_s$ to light and rhizosphere $CO_2$ concentration at 25 °C and 1.6 ± 0.2 kPa vapor pressure deficit. Additional details concerning measurements and experimental design have been described by Bauerle et al. (2003).

### *Atmospheric stress response experiment*

To investigate responses to atmospheric factors, we conducted an additional experiment in the summer of 2000 in which plants of wet and dry habitats were subjected to a range of atmospheric vapor pressure deficits. Unless otherwise indicated, plant material and growing conditions were as described by Bauerle et al. (2003). In the current study, three Mylar chambers were constructed to control vapor pressure deficit (VPD).

### *Growth chamber conditions*

Plants were grown in two walk-in controlled-environment rooms (Environmental Growth Chamber, Chagrin Falls, OH). Maximum PPF at the top of the plant canopy was 375 μmol $m^{-2}$ $s^{-1}$. Irradiance varied diurnally over the 14-h photoperiod (0600–2000 h). In one growth room (R1), temperature was maintained at 22 °C. Humidity was not controlled, but because of the high humidity of the ambient air, a low VPD (1.2 ± 0.2 kPa) was maintained. A plant chamber ($VPD_C$) with dimensions 1 × 1 × 0.66 $m^3$ was constructed in R1 from polyvinyl chloride (PVC) tubing covered with clear 2-mm Mylar. Relative humidity within the chamber was monitored with a data logger (Model Hobo Pro, Onset Computer, Pocasset, MA), while temperature was monitored at 1-min intervals with an infrared thermocouple (OS36, Omega, Stamford, CT) connected to a remote Campbell Scientific CR21X data logger.

In the other plant growth room (R2), two Mylar chambers, identical to $VPD_C$, were constructed. Temperature in R2 was maintained at 34 °C, which is 4 °C below the thermal carboxylation capacity deactivation temperature in red maple (unpublished data). To impose VPD stress, water vapor was removed from the ambient air entering one of the chambers ($VPD_H$) in R2 by means of a cold-plate condenser and Drierite desiccant. Before entering the chamber, the dehumidified air passed through a plenum, where it was reheated to 34 °C. The air in $VPD_H$ was desiccated further by 7.25 kg of Drierite spread over the chamber floor. Water vapor was

added to the air stream entering the second chamber in R2 ($VPD_M$) by three ultrasonic humidifiers (Sunbeam, Boca Raton, FL) and then reheated to 34 °C, the chamber set point.

Three seedlings from one maple ecotype were placed in each of the Mylar chambers for each 12-h measurement period. The treatments started at 0800 h and leaf gas exchange and bulk leaf tissue ABA concentration ($[ABA]_L$) were measured. Gas exchange data were collected every 2 h from one plant per chamber with a Li-Cor LI-6400 gas analyzer (Li-Cor, Lincoln, NE). The temperature and humidity were adjusted to the chamber conditions over a 0.5 h equilibration period (a Peltier system was used during the first 10 min to aid equilibration with the chamber environment). Immediately after measurement of net photosynthesis ($A_{net}$) and $g_s$, the leaf was excised and enclosed in a plastic bag for later measurement of leaf water potential with a pressure chamber (Soil Moisture, Santa Barbara, CA). The opposite leaf at that branch junction was harvested at the same time and five 1-cm disks per leaf harvested for $ABA_L$ determination. Leaves for ABA analysis were harvested at the same time from the two remaining plants in the chamber. Leaf ABA concentration was determined by enzyme linked immunosorbent assay (ELISA) as described by Alves and Setter (2000) and modified by Bauerle et al. (2003). Once the assay was complete, a 70-µl aliquot was mixed with 400 µl of scintillation fluid (Ecocint H, National Diagnostic, Manville, NJ) and radioactivity measured in a scintillation spectrometer (Model LS 5000 TD, Beckman, Fullerton, CA). Individual ABA values were corrected for losses from the chromatographic clean-up process.

### *Model for ABA-inhibited $g_s$*

To combine the water stress or ABA response of stomata with the stomatal response to the atmospheric environment, we used a combination of the Ball-Berry stomatal control model (Ball et al. 1987) and standard energy balance equations (Gutschick and Simonneau 2002). The equations and their solutions are presented in a Web document (http://biology-web.nmsu.edu/vince/) prepared by V. P. Gutschick (New Mexico State University, Las Cruces, NM) who provided us with an alternative form of the multiplicative model, known as the "model of the minimum." We modified it to operate multiplicatively (Tenhunen et al. 1994, Gutschick and Simonneau 2002). Following Li-Cor's LI-6400 instructions, we estimated boundary layer conductance under cuvette conditions based on partial pressure in the cuvette during gas exchange measurements and leaf temperature.

The environment and physiology of the leaf are specified in the model. The only unknown variable is leaf temperature ($T_L$). Fixed quantities describing the environment and leaf structure are specified and a transcendental equation solves for $T_L$. The Ball-Berry equation of stomatal control is then combined with the response of the leaf to water stress, mediated by ABA:

$$g_s = \left(\frac{g_{fac} m A_{net} h_s}{C_s}\right) + b = \left(\frac{e^{-\beta [ABA]_L} m A_{net} h_s}{C_s}\right) + b \qquad (2)$$

where ABA shifts the Ball-Berry slope downward. The "Ball-Berry" term $g_{sBB}$ is represented by $mA_{net}h_s/C_s + b$, where the slope parameter ($m$), the net rate of $CO_2$ assimilation ($A_{net}$), the relative humidity ($h_s$), the $CO_2$ mixing ratio ($C_s$), and the fitting parameter ($b$) are used so that the equations for $T_L$ and $g_s$ are solved simultaneously. The ABA concentration in the bulk leaf tissue is obtained by maximizing the linear regression $r^2$ between $g_s$ and the new index, $g_{fac}mA_{net}h_s/C_s + b$, so that the optimal value of β is found (Gutschick and Simonneau 2002).

Unlike other studies that use [ABA] in the xylem sap (e.g., Tardieu and Davies (1993), Simonneau et al. (1998), and Gutschick and Simonneau (2002), our model used $[ABA]_L$. To ensure data quality control, we followed the data point exclusion method of Gutschick and Simonneau (2002).

### *Statistical analysis*

Agreement between observed and predicted stomatal conductance of the *Acer* ecotypes under different stress conditions was assessed by concordance correlation analysis. The concordance correlation coefficient ($\rho_c$) provides a measure of reproducibility by evaluating the degree to which pairs of values ($Y_{i1}$,$Y_{i2}$), i = 1, 2, …, n, depart from a 45° line through the origin (Lin 1989) and can be represented by:

$$\rho_c = 2\sigma_{12}/(\sigma_1^2 + \sigma_2^2 + (\mu_1 - \mu_2)^2) \qquad (3)$$

where $\sigma_{12}$ is the covariance of $Y_1$ and $Y_2$, $\sigma_1^2$ is the variance of $Y_1$, $\sigma_2^2$ is the variance of $Y_2$, $\mu_1$ is the mean of $Y_1$, and $\mu_2$ is the mean of $Y_2$. The concordance correlation coefficient contains measures of accuracy and precision and examines the strength of a 1:1 linear relationship between the measured and estimated values of stomatal conductance. Comparisons of concordance correlation coefficients were made with the Fisher transformation (Zar 1996). The 5% error probability level was used for hypothesis testing throughout.

## Results

Measured $g_s$ and $g_s$ predicted by an ABA-based model were compared on the basis of three independent data sets. Parameter values of the model are presented in Table 1. A slope ($m$) of 9.85 fit over 90% of our measurements.

Figure 1 shows $g_s$ as predicted by the combined multiplicative model versus measured $g_s$ in response to rhizospheric, minimal and atmospheric stresses. The combined multiplicative model accurately described $g_s$ and, hence, stomatal behavior for both ecotypes. Although both ecotypes responded in a similar fashion, the wet-site sample estimate of the concordance correlation coefficient ($r_c$) value was closer to 1.0 (perfect concordance correlation) under all three stress conditions than the dry-site $r_c$ values, reflecting higher reproducibility for the wet-site ecotype (Figure 1). Sensitivity of $g_s$ to ABA is lower in dry-site ecotypes (Bauerle et al. 2004) and this was reflected in the modeled sensitivity of $g_s$ to ABA (β) (Table 1). The degree of agreement between measured and predicted $g_s$ ($r_c$) was statistically different for wet- and dry-site ecotypes under each stress condition (Figure 1). Figure 1 further illus-

trates that the combined multiplicative model estimates followed a 45° line through the origin. Regardless of ecotypes, the model performed best when stress was minimal. When there was either rhizospheric or atmospheric stress, the model estimates were in closer agreement with $g_s$ measured on wet sites than on dry sites. The model also appears to work better on environmentally responsive (wet-site) compared with less responsive (dry-site) ecotypes, regardless of the cause of stress (atmospheric or rhizospheric).

Model simulations for wet- and dry-site ecotypes with contrasting ABA sensitivities to soil drying are shown in Figure 2. Simulations were made with the multiplicative model (Equation 2) and the parameters reported in Table 1. Model simulation behaviors were similar to experimental data (Bauerle et al. 2003). Wet-site ecotypes had higher $g_s$ when soil water was not limiting. As soil water deficit increased, wet-site $g_s$ responded more than dry-site $g_s$. The dry-site ecotype $g_s$ response curve, on the other hand, predicts that $g_s$ is higher at lower soil water potentials. Although $g_s$ at the dry-site is lower under well-watered conditions, model simulations predict that, under conditions of soil water deficit, a lower ABA sensitivity to $[ABA]_L$ allows higher values of $g_s$ at the dry site during soil drying.

A potential systematic bias in model estimates of atmospheric stress response was evident. Under rhizosphere water stress conditions, the model underestimated high $g_s$ values. Measured $g_s$ may have been systematically higher because of possible gas exchange boundary layer measurement error, in which case the underestimation of $g_s$ by the multiplicative model may be an artifact of $g_s$ measurement and not of model bias (Gutschick and Simonneau 2002). In their outdoor rhizosphere stress experiment, Gutschick and Simonneau (2002) demonstrated that the quadratic $g_s$ response to humidity was responsible for the divergence from linearity. Our minimal and atmospheric data sets did not show this departure. However, growth chamber conditions in the minimal and atmospheric stress experiments provided more stable humidity in contrast to our outdoor rhizosphere stress experiment. Humidity fluctuation may introduce systematic bias when stomata are more open and stomatal limitation is lower. Such fluctuation would directly influence vapor pressure deficit and potentially increase $g_s$.

## Discussion

Soil water availability and atmospheric demand interact with plant physiological controls to regulate forest transpiration. The drought-induced limitations on stomatal opening that regulate transpiration may result from hydraulic or chemical signals, or an interaction of the two signals. The underlying physiological integration of these processes remains unclear (Whitehead 1998). Our model, which extends the Gutschick and Simonneau (2002) model to include leaf as well as root chemical signals—by using leaf total ABA concentration instead of xylem sap ABA concentration—demonstrates that models that characterize stomatal behavior can provide a basis for the development of models that combine the regula-

Table 1. Parameters of the multiplicative model. A description by V. P. Gutschick of all model equations and the mathematical method of solution is available at http://biology-web.nmsu.edu/vince/. Superscripts w and d denote wet-site and dry-site ecotype parameters, respectively.

| Parameter | Units | Value | Source |
|---|---|---|---|
| Carboxylation capacity ($V_{cmax}$) | μmol $m^{-2}$ $s^{-1}$ | $77^w$ $60^d$ | Bauerle et al. (2003) |
| Ball-Berry slope ($m$) | – | 9.85 | This study |
| Sensitivity of $g_s$ to ABA (β) | $pM^{-1}$ | $4.8^w$ $1.4^d$ | Bauerle et al. (2004) |
| Photosynthetic photon flux | μmol $m^{-2}$ $s^{-1}$ | Variable | This study |
| Partial pressure of $CO_2$ in air | Pa | Variable | This study |
| Ball-Berry intercept ($b$) | mol $m^{-2}$ $s^{-1}$ | 0.03 | This study |
| Leaf water potential ($\Psi_L$) | MPa | Variable | This study |
| Leaf temperature | °C | Variable | This study |
| Thermal $V_{cmax}$ deactivation ($T_d$) | °C | 38 | Unpublished data |
| ABA amplification response to low $\Psi_L$ | $MPa^{-1}$ | 0 | This study |
| Air temperature | °C | Variable | This study |
| Leaf dimension | m | 0.1 | This study |
| Root mass per ground area ($R_m$) | kg $m^{-2}$ | 0.1608 | Gutschick and Simonneau (2002) |
| Thermal deactivation rate above $T_d$ | $K^{-1}$ | 0.1 | Gutschick and Simonneau (2002) |
| Photosynthetic convexity | – | 0.7 | Bauerle et al. (2003) |
| Leaf absorptivity | – | 0.85 | Estimated |
| Leaf surface humidity | – | Variable | This study |
| Root to leaf hydraulic resistance | MPa $mol^{-1}$ $m^{-2}$ $s^{-1}$ | 18 | Gutschick and Simonneau (2002) |
| Leaf ABA synthesis | pM $MPa^{-1}$ $mol^{-1}$ $m^{-2}$ $s^{-1}$ | 2.25 | Bauerle et al. (2004) |
| Depth of soil in rooting volume | m | 0.3 | This study |
| Partial pressure of water vapor in air | Pa | Variable | This study |
| Wind speed | m $s^{-1}$ | Variable | This study |
| Sky radiative temperature | °C | –10 | Gutschick and Simonneau (2002) |
| Total pressure of ambient air | Pa | Variable | This study |

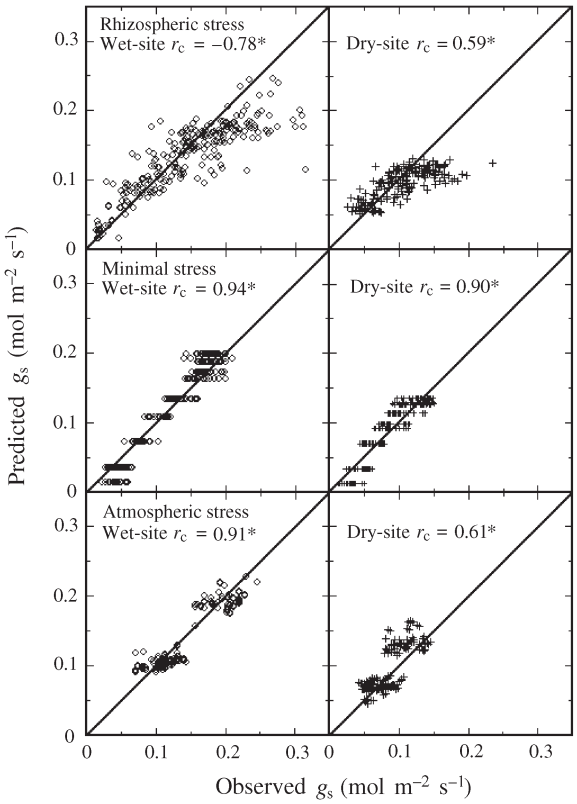


Figure 1. Reproducibility of analyses of stomatal conductance ($g_s$) comparing wet- and dry-site ecotypes under three stress conditions. Sample populations of the wet- and dry-site ecotypes in the three stress conditions were, respectively, rhizospheric stress $n$ = 245 and 180, minimal stress $n$ = 286 and 279 and atmospheric stress $n$ = 158 and 150. Ecotype concordance correlation coefficients ($r_c$) among wet- and dry-sites are reported in each panel along with a 45° line through the origin that represents perfect reproducibility. Significant differences ($P < 0.05$) between wet- and dry-site ecotypes in each stress condition are denoted by an asterisk.

tory roles of leaf hydraulic and chemical signals in woody plants (Dewar 2002).

During drought, ABA biosynthesis occurs in both roots and leaves. In addition, there is a hydraulically propagated change in shoot water potential that could signal stomatal closure (Wilkinson and Davies 2002). Hydraulic or chemical signals that are localized within the leaf have been proposed as a rapid stomatal control mechanism in woody plants (Salleo et al. 2000, Hubbard et al. 2001). In woody species, however, the relevance of root chemical signals as important stomatal regulatory mechanisms has been questioned because of the long distance between roots and shoots (Schulze 1991). Furthermore, ABA transport over long distances, a situation common in tall trees, would require days in the case of normal field conditions, and weeks under drought conditions (Perks et al. 2002). The slow signal transmission time raises the possibility of an additional feed-forward short-term response to soil drying. Furthermore, Triboulot et al. (1996) reported no difference in ABA flux to leaves of field-grown oak, despite a twofold drought-induced increase in xylem [ABA]. Irrespective of the confidence in our $[ABA]_L$ values via the use of [$^3$H] ABA tracking, it is worth noting that our red maple $[ABA]_L$ values are substantially lower than xylem [ABA] reported by others (e.g., Loewenstein and Pallardy 1998). However, others have reported similar $[ABA]_L$ values in leaf tissue of perennial woody plants (e.g., Alves and Setter 2000). The disparity between leaf [ABA] and xylem [ABA] deserves further investigation. Our results indicate that red maple leaves are sensitive to $[ABA]_L$ at pmol concentrations and that ABA synthesis in leaves can occur on a time scale of minutes to hours (Bauerle et al. 2003, 2004).

Newly synthesized ABA, regardless of its site of origin, can increase $[ABA]_L$, filling the symplast reservoir, thus allowing ABA from the xylem stream to penetrate the epidermis. Furthermore, a drop in shoot water potential results in cytoplasmic acidification and the release of symplastic ABA (Wilkinson and Davies 2002). Guard cells in the epidermis are then subject to higher [ABA] in the apoplast, a product of hydraulically induced chemical changes in the leaf. To regulate $g_s$, the guard cells must integrate and process the information from both the shoots and roots. However, no consensus has emerged that explains the regulation of stomatal aperture by internal chemical and hydraulic factors and external meteorological factors (Zweifel et al. 2002). The combined chemical and hydraulic feedback regulation at the leaf level provided a basis to test our combined multiplicative model in two ecotypes that are known to respond differently to drought stress (Bauerle et al. 2003). The combined multiplicative model coupled the Ball-Berry Model with an ABA-based factor ($g_{fac}$). As a result, the slope of the Ball-Berry model was scaled downward in response to drought. This coupling is a practical improvement because it incorporates stomatal responses to soil drought and

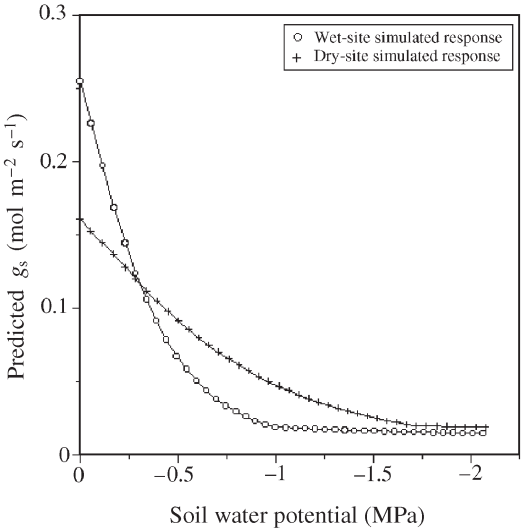


Figure 2. Simulations of the behavior of wet- (○) and dry-site (+) ecotypes with contrasting sensitivity to bulk leaf abscisic acid concentration under soil drying conditions. Model simulations were run at a light-saturating photosynthetic photon flux of 1000 μmol m$^{-2}$ s$^{-1}$ and a leaf temperature of 25 °C. All other parameter values are listed in Table 1.

atmospheric stress in the Ball-Berry model prediction. Moreover, the combined multiplicative model performed well under water stress induced by both rhizospheric and atmospheric factors in maple seedlings. The predictability of the stomatal response, however, differed significantly between wet- and dry-site ecotypes of red maple, which differed in drought tolerance. Nevertheless, characterizing the physiological basis of stomatal chemical and hydraulic signals with a combined response to air and soil environments is an important component in canopy scale models of transpiration.

Tenhunen et al. (1990, 1994) developed and applied $g_{fac}$ to Mediterranean sclerophyll and chaparral shrubs. Recently, Gutschick and Simonneau (2002) successfully incorporated a $g_{fac}$ component that describes the root–shoot signal in a herbaceous plant. Process models are well suited for interpreting physiological differences among perennial plant genotypes (Martin et al. 2001) and the mechanistic-based modeling approach is already a powerful tool for comparing genotypic responses to water deficit (Tardieu 2003). Our simulated curves of $g_s$ response to soil water deficit support the suggestion that species distribution among contrasting habitats is linked to stomatal behavior for optimizing carbon gain (e.g., Fites and Teskey 1988, Tinoco-Ojanhuren and Pearcy 1993*a*, 1993*b*). The ABA explicit model allowed us to aggregate the physiological attributes of red maple ecotypes to the primary level and investigate response to soil water deficits. The multiplicative nature of the model is sufficiently simple that it can be used within larger-scale models that predict forest and species function under different climatic scenarios. Moreover, our results substantiate those of Zweifel et al. (2002), who concluded that stomatal conductance models require both local microclimate and tree water status conditions for accurate predictions. The factor $g_{fac}$ is useful in both quantification of tree water status at the leaf level and, upon spatially explicit integration into canopy models, scaling from leaf responses to the response of a whole plant (Tenhunen et al. 1994). It permits us to capture the essence of such reactions in simulation models that consider time courses of soil water extraction (Tenhunen et al. 1994).

Variation in physiological responses can differ between and among species; therefore, it is necessary for models to represent the response with parameters that are valid under a wide range of conditions. Simulation of these responses to global climatic change relies on the development of stomatal behavior models that can characterize responses under variable atmospheric and soil conditions (Running and Coughlan 1988, Raich et al. 1991). The concordance correlation comparison of the intraspecific variation observed within red maple $g_s$ indicated that ecotypes can be identified while, at the same time, scaling $g_s$ across terrestrial ecosystems. A review of the literature further supports this observation with respect to differences between hydraulic versus chemical signaling among species (e.g., Fuchs and Livingston 1996). Under our experimental conditions, dry-site ecotypes were subjected to a more constant water resource limitation and therefore, their response to atmospheric and rhizospheric stress could not be predicted as accurately as the response of wet-site ecotypes. The higher transpiration of wet-site ecotypes depletes soil water at a higher rate, whereas osmotic adjustment of leaf turgor in dry-site ecotypes could reduce leaf ABA biosynthesis (Bauerle et al. 2003). Overall, wet-site ecotypes are likely more responsive to their environment than dry-site ecotypes because of greater fluctuation in water resource availability.

In conclusion, we identified intraspecific variation in red maple response to stressful and minimally stressed environmental conditions with the use of $g_s$ model predictions that incorporate atmospheric and rhizospheric stress. Although we do not yet fully understand all that there is to know about root and shoot signaling, we are better able to characterize the stomatal behavior under various types and degrees of environmental stress. This may enable us to improve our ability to scale up physiologically important stomatal behavior to estimate stand-level transpiration in simulation models that consider larger-scale ecosystem functioning.

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