Estimating maximum mean canopy stomatal conductance for use in models

B.E. Ewers, R. Oren, K.H. Johnsen, and J.J. Landsberg

Abstract: Fertilized (F) and irrigated and fertilized (IF) stands of *Pinus taeda* L. produced twice the leaf area index of irrigated (I) and control (C) stands. Based on sap flux-scaled mean stomatal conductance (G_S), we found that stomatal conductance in F was half that in other treatments. During the growing season, G_S was related to vapor pressure deficit (D) and soil moisture. During the cooler season, soil moisture was high and light accompanied D in controlling G_S. Under all conditions and treatments, the rate of decrease in G_S with D was proportional to G_S at low D (= 1 kPa). We evaluated whether G_S can be used as an input to growth models and used a simple growth model (3-PG), which also predicts stand transpiration (E_C), to compare with direct E_C measurements in the four stands. Model predictions of monthly E_C based on Penman–Montieth equation parameterized with maximum G_S (G_{Smax}) estimated under highest "native" soil moisture (0.07 $m^3 \cdot m^{-3}$) produced long-term values within 10% of measured E_C. When the model was parameterized with G_{Smax} estimated under experimentally raised soil moisture, or with porometrically measured conductance, E_C values were consistently overpredicted from 12 to 33%. Thus, sap-flux scaled mean canopy stomatal conductance obtained under non limiting light conditions, low D, and highest native soil moisture, is the most appropriate parameter value for certain single-leaf type of models.

Résumé : Des peuplements fertilisés (F) et irrigués et fertilisés (IF) de *Pinus taeda* (L.) ont un indice de surface foliaire équivalent au double de celui de peuplements irrigués (I) et témoins (C). Sur la base d'une conductance stomatique moyenne estimée par flux de sève (G_S), nous avons trouvé que la conductance stomatique du traitement F équivaut à la moitié de celle des autres traitements. Pendant la saison de croissance, la valeur de G_S était corrélée au déficit de pression de vapeur (D) et à l'humidité du sol. Pendant la saison froide, l'humidité du sol était élevée et seuls la lumière et D contrôlaient G_S. Quels que soient les conditions ou les traitements, le taux de décroissance de G_S avec D était proportionnel à G_S pour de faibles valeurs de D (= 1 kPa). Nous avons évalué si G_S peut être utilisée comme intrant de modèles de croissance et nous avons utilisé un modèle de croissance simple (3-PG), qui prédit aussi la transpiration du peuplement (E_C), pour comparer ses prédictions avec les mesures de E_C dans les quatre peuplements. Le modèle prédit la E_C mensuelle à partir de l'équation de Penman–Monteith paramétrée avec une G_S maximale (G_{Smax}). Cette dernière a été estimée pour une humidité de sol observée la plus élevée (0,07 $m^3 \cdot m^{-3}$). Les valeurs prédites à long terme se situent dans un intervalle de 10% autour des valeurs mesurées. Lorsque le modèle est paramétré avec des valeurs de G_{Smax} estimée pour une humidité de sol augmentée expérimentalement ou à partir de valeurs de conductance mesurées par poromètre, les valeurs prédites de E_C sont systématiquement surestimées de 12 à 33%. Par conséquent, la conductance moyenne du couvert obtenue par flux de sève, dans des conditions non limitantes de lumière et lorsque la valeur de D est faible et l'humidité du sol est élevée, représente la valeur la plus appropriée pour paramétrer le type de modèles assimilant la canopée à une feuille.

[Traduit par la Rédaction]

Introduction

Mechanistic models of gas exchange, used in models of tree and stand growth, estimate stomatal conductance based either on linking conductance to assimilation as in the Ball–Berry model (Ball et al. 1987; Leuning 1995) or on empirical responses of stomata to a selected set of environmental variables as proposed by Jarvis (1976). Stomata respond to environmental variables that drive transpiration per unit leaf area E_L (i.e., radiation, and vapor pressure deficit, D), to prevent damagingly low leaf water potential, and to environmental variables that affect CO_2 fixation (i.e., temperature, T, and photosynthetic photon flux density, Q_o), to facilitate photosynthesis. Jarvis (1976) proposed that the response of stomatal conductance (g_S) to each variable can be described by a multiple nonlinear constraint function:

$$[1] \qquad g_S = g_{Smax} f_1(D), f_2(\theta), f_3(T), f_4(Q_o) \; \ldots$$

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where g_{Smax} is maximum g_{S} and θ is soil moisture. Körner (1994) defined g_{Smax} as the highest conductance observed in fully developed leaves, before the onset of senescence, in plants provided with sufficient water and nutrients, under optimal climatic conditions, ambient CO_2 concentration, and sufficient nutrient supply. For $f(D)$, Oren et al. (1999) show that under a given soil moisture and light level:

$$[2] \qquad g_{\mathrm{S}} = b - m \ln D$$

where b is g_{S} at D = 1 kPa, (hereafter, reference g_{S}, g_{SR}) and that m averages ~0.6b for a wide range of conditions and species. The proportionality between g_{SR} and the stomatal sensitivity to D, first proposed by McNaughton and Jarvis (1991), is consistent with the role of stomata in regulating leaf water potential above the level in which catastrophic cavitation occurs (Sperry et al. 1998). Given the g_{S} sensitivity to D, g_{SR} can be used as a surrogate for g_{Smax}. Furthermore, it is possible to use g_{S} measured under sufficiently high light and soil moisture to estimate g_{Smax}, if D at which g_{S} is maximal is known.

Recently, Landsberg and Waring (1997) developed a model (3-PG) that predicts growth and water use on a monthly time step. The model uses the Penman–Monteith equation to calculate E_{C}, with a generic value of g_{Smax}. The model calculates gross primary production from utilizable Q_{o} based on the following dimensionless factors that cause g_{S} to decrease from g_{Smax}: (*i*) increasing D, (*ii*) decreasing θ, and (*iii*) suboptimal T. Several other model parameters partition the gross primary production to respiration and allocate carbon to different growth components. Model predictions of net photosynthesis, and thus growth, as well as E_{C}, are highly sensitive to the choice of g_{Smax}. In this study, we examine a new approach to provide an estimate of g_{Smax} for this class of models (i.e., parameterized with mean canopy stomatal conductance, Landsberg and Waring 1997; Running and Coughlan 1988). Because gross primary production cannot be measured directly as a verification of our approach, and growth prediction is dependent on correct estimation of several other parameters, we will use model predictions of E_{C} to evaluate the approach.

We measured sap flux periodically from 1996 to 1998 in a 11- to 13 year-old *Pinus taeda* L. plantation subjected to fertilization (F), irrigation (I), a combination of both treatments (IF), in addition to untreated control (C), that resulted in a wide range of leaf area indices and stomatal conductance (Albaugh et al. 1998; Ewers et al. 2000). Sap flux was used to estimate mean canopy stomatal conductance (G_{S}; Köstner et al. 1992; Martin et al. 1997; Oren et al. 1998*a*; Pataki et al. 1998) for estimating maximum G_{S} (G_{Smax}) for model parameterization, and E_{C} for model evaluation. Only a small subset of the sap-flux data was used to estimate G_{Smax} for the model. Thus, autocorrelation between model predictions and sap flux scaled E_{C} cannot corrupt the evaluation of model performance with the proposed G_{Smax} parameterization scheme.

Previous work on this sandy site showed that transpiration per unit leaf area (E_{L}) ranks as C = I = IF > F (Ewers et al. 1999). In this study, we first tested the hypothesis that the relationship proposed in eq. 2 holds for G_{S} of all treatments and environmental conditions and that the data from each treatment are consistent with the assumption that there is a strict hydraulic basis for stomatal response to D (Oren et al. 1999). Based on this assumption, treatments and conditions of low G_{S} at low D (= 1 kPa, G_{SR}) have lower G_{S} sensitivity to D. If these responses could be verified, the responses of G_{SR} to θ, Q_{o}, and T could be quantified using a boundary line analysis that selects for the highest values under native conditions. Once the upper boundary G_{SR} value (G_{SRB}) for each treatment was identified, it was projected to G_{Smax}, defined here as G_{S} at 0.6 kPa with saturating light, highest natural soil moisture (i.e., not irrigated), and temperatures higher than those that affect G_{S}. In the sandy soil of the study site, moisture must always exert some limitation on G_{S}. Therefore, we increased soil moisture by continuous irrigation, so we could estimate a value of G_{Smax} closer to the physical limit of conductance and more in line with values typically used as the model parameter. The overall objective of this paper is to compare three approaches for parameterizing maximum stomatal conductance, porometric, sap flux under maximum soil moisture, and sap flux under maximum native soil moisture, in terms of their ability to reproduce stand transpiration estimated by 3-PG-type models.

Materials and methods

Study site and treatments

The Southeast Tree Research and Education Site (SETRES) was established in the Sandhills of North Carolina (35°N, 79°W) on an infertile, well drained, sandy, siliceous, thermic Psammentic Hapludult soil (Wakulla series). Annual precipitation averages 1210 mm with occasional growing season water deficits. The site was planted in 1984 with mixed families of North Carolina Piedmont *Pinus taeda* L. at 2 × 3 m spacing, and sixteen 50 × 50 m treatment plots were established in 1992. Treatments were a 2 × 2 factorial combination of nutrition and water additions replicated four times. Nutrient treatments have been maintained since March 1992 and water addition since April 1993. Nutrient treatments consisted of annual applications designed to achieve optimal nutrition, diagnosed by monthly foliage sampling to check whether nitrogen concentration in upper canopy was maintained at 1.3%, with phosphorus, potassium, calcium, and magnesium balanced with nitrogen levels. Boron was also added to maintain foliar levels greater than 12 ppm. Irrigation kept available soil moisture between field capacity and 40% of available soil water as measured with time-domain reflectometry in the upper 0.50 m of the soil profile, corresponding to 30 mm soil water content in the surface 0.5 m of soil. For details of nutrition and water treatments see Abrahamson et al. (1998), Albaugh et al. (1998), and Murthy et al. (1996).

From July 25 to August 8, 1998, we performed an irrigation experiment designed to maximize soil moisture availability. On this sandy site with saturated hydraulic conductivity of 1.3 $\mathrm{m \cdot day^{-1}}$ (B. Ewers, unpublished data), we were able to ensure maximum moisture availability by continuously irrigating a circular, 5 m diameter area within each plot, raising θ to 0.10 $\mathrm{m^3 \cdot m^{-3}}$ throughout the upper 1.9 m soil profile.

Sap flux measurements and scaling to mean canopy stomatal conductance

We measured sap flux density (J_{S}, g $\mathrm{H_2O \cdot m}$ $\mathrm{sapwood^{-2} \cdot s^{-1}}$) in stem xylem of eight trees with Granier-type sensors (Granier 1987) in a 6 m diameter plot in the buffer zone of one block (Ewers et al. 1999; Ewers and Oren 2000). Measurements were made on the north side of stems (1.4 m above ground) at two depths: the outer 20 mm of the xylem in eight trees and, to account for radial patterns in sap flux, the next 20 mm of the xylem in a subset of five trees. We excluded data from days when temperatures dropped below freezing, causing large uncertainties in base line values and calculated average J_S by weighting the outer J_S by the sapwood area represented in that xylem band and the inner J_S by the sapwood area internal to the outer band (Ewers et al. 1999; Ewers and Oren 2000). This assumes that inner J_S represents the flux inside of 40 mm from the cambium. J_S did not have systematic circumferential variation (Ewers and Oren 2000). Sapwood area was measured on increment cores (Ewers et al. 1999) and leaf area was estimated from allometrics and optical measurements of leaf area index (Albaugh et al. 1998). Scaling J_S to E_L was done with sapwood-to-leaf area ratio (A_S/A_L) as in Oren et al. (1998*b*):

$$[3] \qquad E_L = J_S \frac{A_S}{A_L}$$

G_S was calculated from E_L and D based on the simplified approach suggested by Monteith and Unsworth (1990):

$$[4] \qquad G_S = \frac{K_G(T)E_L}{D}$$

where G_S is the mean canopy stomatal conductance to water vapor ($m \cdot s^{-1}$), K_G is the conductance coefficient ($= 115.8 + 0.4236T$, $kPa \cdot m^3 \cdot kg^{-1}$), which accounts for temperature effects on the psychometric constant, latent heat of vaporization, specific heat of air at constant pressure, and the density of air (Phillips and Oren 1998). This simplification assumes (*i*) that D is close to the leaf-to-air vapor pressure deficit, i.e., boundary layer conductance is high; (*ii*) that there is no vertical gradient of D in the canopy, i.e., aerodynamic coupling between the canopy and the atmosphere is high; and (*iii*) that hydraulic capacitance is low, i.e., transpiration can be inferred from water uptake. Ewers and Oren (2000) showed that all three conditions are met in trees of all treatments at the site. In addition, G_S was calculated only for $D \geq 0.6$ kPa so that measurement errors in G_S are <10% (Ewers and Oren 2000).

Water for irrigation was not amply available at the site, and only a subset of each plot (three of eight trees) received water during the continuous irrigation experiment. Because high tree-to-tree variability was observed during the period before continuous irrigation ensued, a subset of three trees is not likely to represent the entire population well. We normalized the data collected during the continuous irrigation experiment on these three trees in each treatment to facilitate a seamless merging with the rest of the data. For normalizing, we used the very strong cross correlation among trees during the pre-experiment period to establish a relationship between the three irrigated trees within each treatment and the entire group of eight trees. We used the relationship to adjust the mean response to irrigation of the three trees to the probable response of the entire population. For statistical analyses, the error term derived from the three trees was adjusted accordingly, and the number of replicates was kept to three (see Ewers et al. 2000).

Environmental measurements

We calculated D from relative humidity and T based on Goff and Gratch (1946). A relative humidity and temperature probe (Vaisala HMP 35C, Campbell Scientific, Logan, Utah) was positioned at a height of 7 m in the center of each subplot and provided data for calculating D. The θ values were measured using automated time domain reflectometry (TDR) probes with 6 cm long, steel rods (Theta Probe, Delta-T Devices, Cambridge, U.K.) at 0.05, 0.1, 0.25, 0.5, 1.0, and 1.9 m depth. The 1.9 m probe was only available from June to July 1998. Values at this level averaged only 0.002 $m^3 \cdot m^{-3}$ higher than those at 1.0 m, with very little variation, so the 1.0-m value was used to estimate θ at 1.9 m for the entire study period. Xylem flux and all environmental sensors were sampled every 30 s, and 30-min average values were logged (DL2, Delta-T Devices, Cambridge, U.K.).

Biomass measurements

Diameters at sensor height were measured on April 1996, March 1997 and 1998, and January 1999. We estimated projected L using allometric relationships at the beginning of each season (Albaugh et al. 1998), and a leaf area analyzer (LAI-2000, LI-COR, Inc., Lincoln, Nebr.) to correct for seasonal trends (Albaugh et al. 1998; Ewers et al. 1999). Whole tree A_S/A_L was calculated from L and sapwood area determined with cores (Ewers et al. 1999; Ewers and Oren 2000). For branches on which sap flow was measured, A_S/A_L was measured after harvesting (Ewers and Oren 2000).

Roots were excavated in January and February 1998 from 1-m^2 pits in each block of the four treatments ($n = 4$), to incremental depths of 0.15, 0.3, 0.5, 0.7, 0.9, 1.1, 1.3, 1.5, 1.7, and 1.9 m. Roots were sorted into four diameter classes (<1, 1–2, >2–5, and >5 mm), and a fresh subsample from each depth and size class was measured for length, dried at 65°C, and weighed. The ratio of length per unit of dry mass was multiplied by the dry mass within each category to obtain total length. The total surface area (R) was calculated from the total length in each class using the midpoint of the diameter class. We calculated R using roots <5 mm, the size of roots shown to take up water in *P. taeda* seedlings (MacFall et al. 1991).

Determining the soil layer where moisture affects G_S

One of the main goals of this study was to quantify the effect of soil moisture on G_S. However, both soil moisture and root area density profiles were measured only to 1.9 m depth. Therefore, it was important to establish that the amount of water withdrawn from deeper soil was negligible and could not affect G_S responses to moisture in the upper 1.9 m of the soil. We calculated a local water balance (Oren et al. 1998*a*, 1998*b*), limiting it to periods following precipitation events, but after drainage had ceased (Ewers et al. 1999). Decreases in the amount of water stored in the upper 1.9 m of the soil were compared with stand transpiration (E_C, mm) estimated from J_S and sapwood area per unit of ground area (A_S/A_G, Oren et al. 1998*b*).

To obtain independent information about the source of water tapped by the trees, we measured hydrogen isotope ratios (δ^2H) on two different days: a day before the continuous irrigation experiment and the last day of the experiment. Cryogenic vacuum extraction (Ehleringer and Osmond 1989) was performed on stem samples from an increment core and soil samples from a soil core. All δ^2H values were determined on a gas sample generated from pure liquid and measured with an isotope ratio mass spectrometer (dela S, Finnigan, MAT Germany). Values of δ^2H are expressed using the delta notation (‰) where the ratio of the heavy to light isotopes in the sample is determined relative to a standard (V-SMOW; Dawson 1993). Soil samples were taken in the buffer zone of the four plots in the measured block, from the same depths as water content measurements were made. Stem cores were taken from three trees in each plot at predawn to 20 mm depth on the tree nearest the soil measurements. The stem cores were taken from the north, southeast, and southwest sides of the tree and pooled to give one sample. To analyze horizontal spatial patterns, on the day before the experiment we sampled for δ^2H determination soil at 0.05 and 1.9 m and stemwood cores from one tree in each of the four treatment plots in the other three blocks.

Precipitation water for δ^2H determination was taken from throughfall collectors and pooled over all collectors into a single sample. Irrigation water was drawn from a well with water surface at ~30 m, and stored on site in large drums that allow evaporation. During the irrigation experiment, water from these drums was used in the C, F, and IF treatments, whereas the I treatment was irrigated

Table 1. Leaf area index (L, $m^2{\cdot}m^{-2}$) range in March increased linearly from 1996 to 1998, total root surface area (R, $m^2{\cdot}m^{-2}$) for roots <5 mm in diameter in 1998, sapwood/leaf area ratio (A_S/A_L, $cm^2{\cdot}m^{-2}$) and maximum sap flux-scaled canopy stomatal conductance (G_{Smax}, $mmol{\cdot}m^{-2}{\cdot}s^{-1}$) over the three study years at two levels of root weighted soil moisture in the upper 1.9 m of the soil (θ_R, $m^3{\cdot}m^{-3}$) in control, irrigated, fertilized, and irrigated–fertilized (C, I, F, and IF, respectively).

	C	I	F	IF
L	1.3–1.5	1.4–1.6	2.5–2.7	2.8–3.0
R	14.2 (2.1)*a*	12.3 (1.8)*a*	12.5 (1.7)*a*	11.5 (1.0)*a*
A_S/A_L, upper branches	2.3 (0.4)*a*	1.8 (0.3)*a*	1.5 (0.2)*a*	2.6 (0.3)*a*
A_S/A_L, lower branches	16.5 (0.75)*a*	16.7 (1.0)*a*	18.7 (0.71)*a*	21.0 (0.70)*b*
A_S/A_L, stems*	5.0*a*	4.5*a*	4.3*a*	5.8*b*
G_{Smax}, $\theta_R = 0.07$	140.2	135.9	95.7	154.1
G_{Smax}, $\theta_R = 0.10$	193.0	200.8	144.1	243.4
E_C, measured	331.3 (4.0)	325.0 (4.6)	385.0 (6.2)	580.7 (3.2)

Note: Mean annual transpiration (E_C, mm) is based on sap flux measurements, and on 3-PG model predictions (Landsberg and Waring 1997), with G_{Smax} at $\theta_R = 0.07$. Values in parenthesis are SEs ($n = 4$ for R; = 3 for A_S/A_L and E_C). Different letters indicate significant differences at $\alpha = 0.05$.

*Stem A_S/A_L is from Ewers et al. (1999).

directly from the well. δ^2H was determined for both sources of water during the irrigation experiment.

Test of 3-PG model prediction of E_C

We summed daily E_L, obtained from sap flow measurements, and multiplied it by L to obtain E_C to compare with model predictions. Daily E_C was calculated using the sums of E_L of 24-h periods beginning at 05:00, which approximately corresponded to the time of zero flow and, therefore, accounts for nighttime recharge (Phillips and Oren 1998). Because of frequent electrical problems, we had only a few months when collection of the data necessary to test 3-PG model predictions of E_C on a monthly and annual basis was uninterrupted. To fill the gaps, we developed a relationship between daily E_L and D normalized by light hours (D_Z) for each treatment following Oren et al. (1996). D_Z was calculated by averaging daytime D values only, the period in which D affects canopy transpiration (Phillips and Oren 1998), and normalizing by the number of daylight hours (determined as all half-hour intervals in which $Q_o > 0$) divided by 48. E_L was related to D_Z according to

$$[5] \qquad E_L = c(1 - e^{-dD_Z})$$

where c and d are fitting parameters.

Statistical analysis

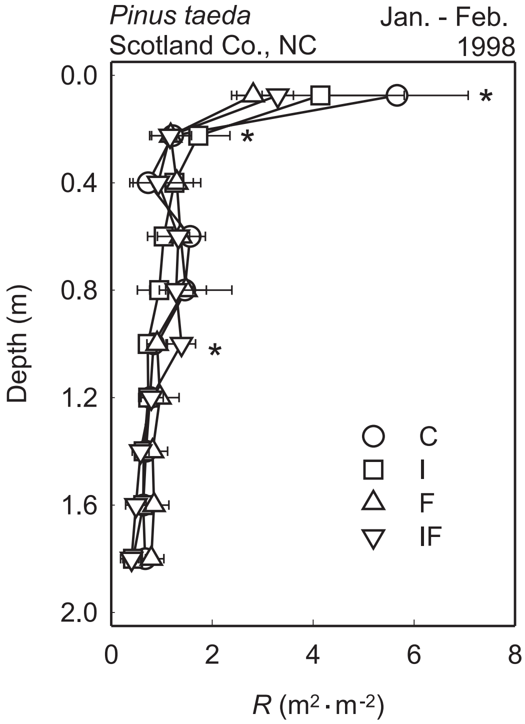
All statistical analyses were performed using SAS general linear methods (GLM) and MIXED procedures (version 6.12, SAS Institute Inc., Cary, N.C.). Non-linear curve fits were performed in SIGMAPLOT (version 4.5, SPSS, Inc., San Rafael, Calif.). Curve fits were performed on individual trees and then parameters were analyzed among treatments based on one-way ANOVA. We used individual tree sap flux measurements, and the resulting scaled variables, as replicates, following the rationale discussed in Ewers et al. (1999). Boundary line analyses were performed using a program based on the methodology described in Schäfer et al. (2000).

Results

Root distribution

To determine the profile of root surface area (R; $m^2{\cdot}m^{-2}$ ground) for estimation of root-weighted soil moisture (θ_R), we measured root biomass and surface area to 1.9 m. In previous work at this site, roots had only been studied to 0.5 m (Albaugh et al. 1998). Our results show that this accounts for approximately 49, 58, 43, and 50% of the total roots in the C, I, F, and IF treatments. Although treatments affected the mass of certain root size classes in a few depth intervals, total R did not differ among them (Table 1), and the profile of R showed only slight differences between treatments (Fig. 1).

Fig. 1. Root area index (R) depth profile in the four treatments (C, control; I, irrigated; F, fertilized; IF, irrigated and fertilized). Asterisks show significant treatment effect ($p < 0.05$).



Environmental impacts on G_S

Over the 3 years, 294 days of data were available for calculations of half-hourly G_S. These data were conditionally sampled to test whether the slope of the relationship be-

Fig. 2. (A) The sensitivity of the stomata to vapor pressure deficit (dG_S/d ln D) vs. stomatal conductance at vapor pressure deficit = 1 kPa (G_{SR}) under high and low soil moisture weighted by root area profile (θ_R) in the four treatments (C, control; I, irrigated, F, fertilized, IF, irrigated and fertilized). (B) dG_S/d ln D vs. G_{SR} under high and low photosynthetic photon flux density (Q_o).

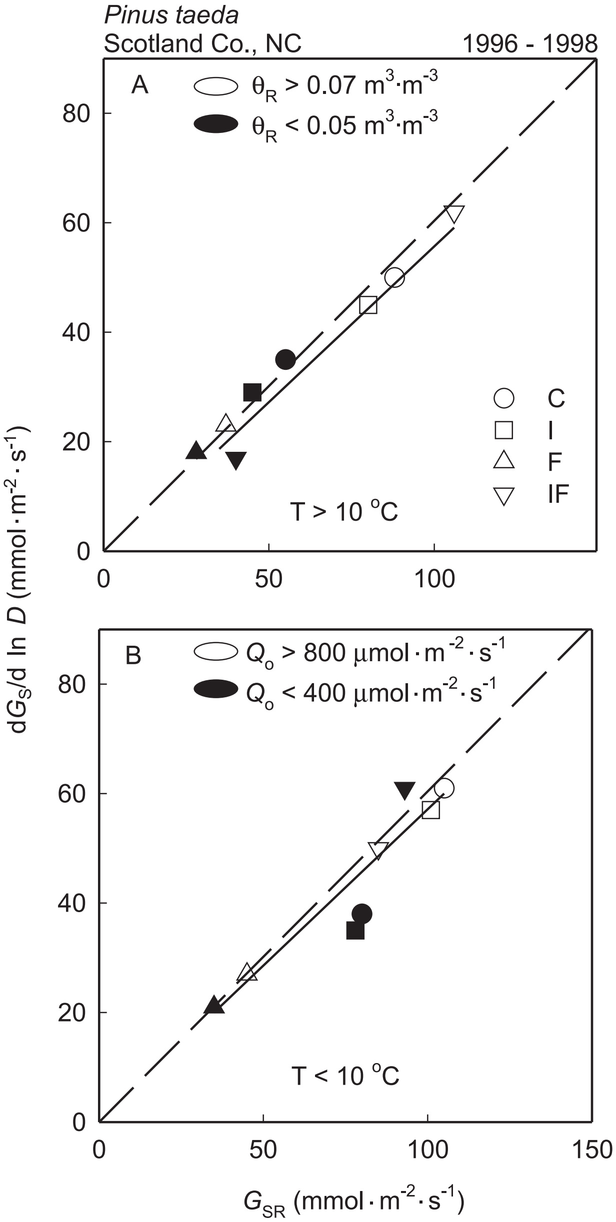
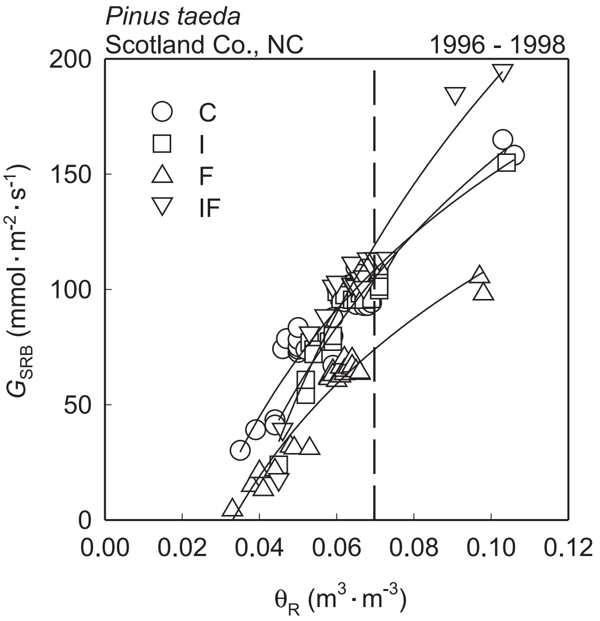


Fig. 3. Boundary line calculated, sap flux-scaled stomatal conductance at vapor pressure deficit = 1 kPa (G_{SRB}) vs. soil moisture weighted by root surface profile (θ_R) in the four treatments (C, control; I, irrigated; F, fertilized; IF, irrigated and fertilized). The curves represent the results of boundary line analyses. The broken line represents maximum θ_R under native conditions. Data to the right of the broken line represent θ_R obtained under continuous irrigation.



tween G_{SR} and dG_S/d ln D (i.e., the slope and intercept in eq. 2) was similar to the mean slope obtained from a large number of species (~0.6; Oren et al. 1999). We also tested whether the slope deviated from the mean slope in any treatment under conditions of high and low θ_R and Q_o. Temperature did not affect G_S ($p > 0.3$), so we partitioned the G_S data into two sets, based on whether nighttime temperatures dropped below 10°C, a temperature that was shown to strongly affect stomatal conductance in *P. taeda* (Ellsworth 2000). When minimum nighttime $T \geq 10$°C, only θ_R had a significant effect on G_{SR} ($p < 0.001$ for all treatments). No other environmental variable and interaction was statistically significant ($p > 0.3$ for all). When minimum $T < 10$°C, only Q_o produced a significant relationship with G_{SR} ($p < 0.01$ for all). No other environmental variable and interaction was statistically significant ($p > 0.4$ for all).

We selected the highest and lowest values of θ_R and Q_o that allowed sufficient data to perform boundary line analyses; the conditional sampling criteria are shown in Fig. 2. In all four treatments, the relationship between G_{SR} and dG_S/d ln D shown by individual tree data was strong (r^2 = 0.70–0.95), and the slope in all comparisons was similar to the mean slope of ~0.6 ($p > 0.3$). For clarity of presentation, each comparison is represented by the mean value of the two parameters (eq. 2) plotted in relation to the mean slope (Fig. 2). The slope of the means of all comparisons was 0.57.

Determination of G_{Smax}

G_S was generally lower when $T < 10$°C. Thus, to determine G_{Smax}, we concentrated only on the effect of θ_R on G_S when $T \geq 10$°C. We determined G_{SRB} over the range in θ_R with a boundary line analysis to avoid the hysteresis that can be expected in the relationship, caused by time lags in recovery from cavitation after soil is rewetted (Hacke et al. 2000). The results are shown in Fig. 3. The data from all four treatments were described best by relationships of the form:

$$[6] \qquad G_{SRB} = j + k \ln \theta_R$$

where j and k are fitted coefficients, the values of which are given in Table 2. Only the intercept of F was significantly lower than that of the other treatments. The broken line in

Table 2. Parameters for eq. 5 ($E_L = c(1 - e^{-dD_Z})$) from data shown in Fig. 4 and eq. 6 ($G_{SRB} = j + k \ln \theta_R$) from data shown in Fig. 3 in control, irrigated, fertilized, and irrigated–fertilized (C, I, F, and IF, respectively).

Equation	C	I	F	IF
5				
c	0.52 (0.06)*a*	0.49 (0.04)*a*	0.26 (0.04)*b*	0.48 (0.04)*a*
d	3.0 (0.4)*a*	2.5 (0.3)*a*	2.4 (0.4)*a*	2.8 (0.3)*a*
6				
j	413.1 (21.4)*a*	479.5 (26.8)*b*	337.4 (13.6)*c*	635.3 (32.6)*d*
k	114.5 (7.5)*a*	140.7 (9.6)*b*	99.0 (4.8)*c*	194.0 (11.9)*d*

Note: Values with different letters are significantly different (α = 0.05).

Table 3. Values of δ^2H in control, irrigated, fertilized, and irrigated–fertilized (C, I, F, and IF, respectively) before and during continuous irrigation experiment.

Water source	Before irrigation				During irrigation			
	C	I	F	IF	C	I	F	IF
Soil	–18.2 (3.0)	–52.4 (6.5)	–17.1 (5.4)	–47.3 (6.3)	–50.1 (5.3)	–38.2 (2.2)	–51.3 (4.3)	–52.3 (4.2)
Irrigation	—	–45.2 (4.5)	—	–45.2 (7.8)	–45.2 (3.5)	–34.9 (1.6)	–45.2 (5.9)	–45.2 (3.2)
Stem	–20.2 (5.4)	–50.3 (6.9)	–18.0 (4.6)	–49.7 (3.3)	–48.2 (6.5)	–37.5 (4.3)	–46.2 (6.1)	–45.9 (7.1)

Note: Values are means with SE in parentheses. For soil, n = 4 before and n = 6 during the experiment. For irrigation water, n = 3 and for stems n = 4 before and n = 3 during the experiment. There was no significant difference in δ^2H within treatments between the irrigation water and soil water in irrigated plots, and between soil water and stem water in all plots.

Fig. 3 represents the maximum "native" moisture conditions (i.e., the highest value after a significant rain), with values to the right of the line attained only under continuous irrigation.

We used eq. 6 to estimate G_{SRB} from θ_R in each treatment (Fig. 3, Table 2) for the highest native value maintained for a whole day in each treatment plot, and for the highest value generated during the irrigation experiment. These two sets of four G_{SRB} values were projected to G_{Smax}, assumed to occur at D = 0.6 kPa, based on the mean slope of ~0.57 (Fig. 2A). The resulting G_{Smax} values for each treatment and θ_R are given in Table 1.

Determining the soil layer where moisture affects G_S

We determined the depth of maximum water uptake for the period when θ was measured at 1.9 m and monthly stand transpiration was at least 90% of maximum in all treatments (June–July 1998) based on the local water balance method. Using the measured profile of θ profile in each treatment, the reduction in soil stored water was calculated for increasing depth intervals from the surface and compared to measured E_C. The decrease in storage in the upper 1.0 m was sufficient to completely balance E_C, in the I and IF treatments, the upper 1.3 m in C, and 1.5 m in F.

Depth of maximum water uptake was evaluated independently by analysis of stable isotopes of hydrogen (Table 3). In all treatments, there was no change in δ^2H down to 1.9 m on both the ambient day and the day during the irrigation experiment ($p > 0.2$). Thus, δ^2H values down the profile were pooled within each treatment. The absence of vertical profile in δ^2H in this soil contrasts results from a study in another sandy soil (Plamboeck et al. 1999). However, the dry surface layer, in which considerable evaporation occurs in sand and which prevents evaporation from below, is less than 0.10 m, and Yamanaka and Yonetami (1999) found no systematic, vertical change in δ^2H below this level despite relatively large changes in θ. Our samples may have integrated over too long a vertical profile (0.15 m) to permit detection of the dry surface layer.

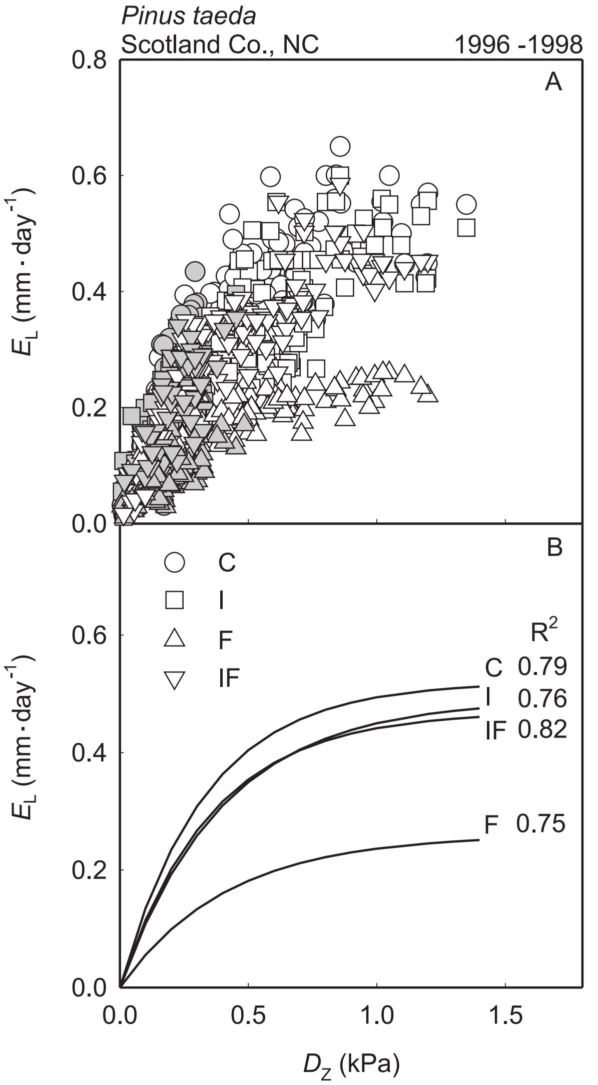
The source δ^2H in the top 1.9 m was similar to the δ^2H in the stem in all treatments ($p > 0.3$; Table 3). Water from the well had a δ^2H value (–37‰) lower than in the soil and stems in the unirrigated plots and higher than in the irrigated plots ($p < 0.001$). When irrigation water was applied directly from the well (i.e., in the I treatment during the continuous irrigation experiment), δ^2H in soil water was higher ($p < 0.001$) than when the water was applied from open storage tanks (i.e., I and IF under normal irrigation regime and C, F, and IF during the irrigation experiment). The δ^2H in stems reflected that of the soil, regardless of whether irrigation was applied or not.

The δ^2H data alone cannot be used to demonstrate that trees were utilizing water from below 1.9 m. However, δ^2H data indicates that the signature of water found in the soil to 1.9 m matches the signature of water in tree stems, supporting the results from the water balance above. The combined information provides a strong support for using soil moisture weighted to 1.9 m as the soil moisture that limits canopy stomatal conductance, even though the root system appears to extend beyond 1.9 m.

Test of 3-PG model prediction of E_C

To test the 3-PG model on an annual basis, gaps in the data were filled based on a relationship between daily E_L and D_Z in each treatment. The available data are shown in Fig. 4A, along with fitted curves based on eq. 5 (Fig. 4B), for which parameter values are given in Table 2. The parameter c for the F treatment was significantly lower than for the

Fig. 4. (A) Daily transpiration per unit leaf area (E_L) vs. daily average vapor pressure deficit normalized by daylight hours (D_Z) in the four treatments (C, control; I, irrigated; F, fertilized; IF, irrigated and fertilized). Open symbols represent conditions when minimum temperature was ≥10°C, and shaded symbols are for days in which minimum temperature was <10°C. (B) Fitted lines to the data in Fig. 4A using eq. 5.

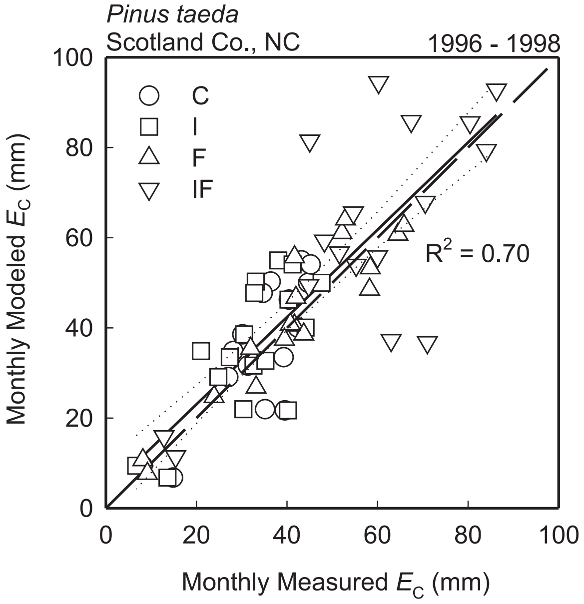


C, I, and IF treatments, but differences in *d* were not significant (Table 2). We found no systematic deviation of the residuals for both minimum T <10°C and ≥10°C.

Using continuous records of relative humidity, T, and Q_o available for the site, D_Z was calculated for each day and used to estimate E_L with eq. 5 and the parameter values in Table 2. Missing daily E_C values were then estimated from daily E_L multiplied by the respective L in each plot. Combined with the measured data, monthly E_C were estimated for testing predictions of 3-PG, and annual values were estimated to provide context with other forests. Thus, monthly E_C estimated is entirely independent of E_C estimated with 3-PG.

We parameterized the 3-PG model for each plot with L measured from 1996 to 1998, G_{Smax} (Fig. 3 and eq. 6) and by adjusting the allometric relations in the model to meet the target L values. All other parameters were from Landsberg and Waring (1997). This parameterization allowed us to evaluate whether our approach to estimating G_{Smax} produces reasonable model predictions of E_C by comparing with measured values.

Fig. 5. Monthly transpiration modeled with 3-PG (E_C modeled) vs. monthly transpiration scaled from sap flux measurements (E_C measured) in the four treatments (C, control; I, irrigated, F, fertilized, IF, irrigated and fertilized). The 1:1 line (broken line) falls within the 95% confidence interval (dotted lines) of the least square fit (solid line).



We compared monthly values of modeled E_C versus measured E_C using G_{Smax} under highest native θ_R conditions (≈0.07 $m^3 \cdot m^{-3}$ in all treatments; based on eq. 6 and Table 2, with results shown in Table 1). From the time the measurements began in August 1996, 50% of the data were missing and were estimated using eq. 5, as described above. To reduce uncertainty in the comparisons of monthly predictions, only those months in which more than 20 days (~70%) of data were available were used. This provided 15 months for comparisons in each treatment. For these months, 3-PG estimated that water shortage did not occur in any month and, thus, did not adjust canopy stomatal conductance to account for limitation on water availability.

The slope of the regression between modeled and observed monthly E_C was not significantly different from one in all treatments (p > 0.2), with r^2 of 0.62, 0.54, 0.86, and 0.52 for the C, I, F, and IF treatments, respectively. Combining all data, the slope of the regression was 0.98, with r^2 = 0.70 (Fig. 5). Both individually and combined, a linear least square fit was unbiased without a pattern in the residuals. A paired t test between measured and modeled monthly E_C were not significant (p > 0.1 for all) with a modeled versus measured value averaging –5, –10, 1, and –6% for C, I F, and IF, respectively. In contrast, using either porometric g_{Smax} or G_{Smax} obtained under experimentally raised soil moisture resulted in a significant overestimation (p < 0.01 for all) of mean monthly E_C of 25, 18, 12, and 33% in the respective treatment stands.

Discussion

Plants with low stomatal conductance have the advantage of smaller absolute reductions in conductance as D increases (Oren et al. 1999). We hypothesized that the relationship described by eq. 2 would hold for all treatments regardless of soil moisture and light conditions. This was shown to be the case; they all showed stomatal conductance responses to D proportional to stomatal conductance at low D for both high and low soil moisture and light conditions (Fig. 2). G_{SR} in trees in the fertilized treatment (F) had lower sensitivity to D than in trees in the other treatments (Fig. 2B; Ewers et al. 2000). Accompanied by lower sensitivity of G_{SR} to θ_R and Q_o in F (Figs. 3 and 4), this translates into lower, but less variable, conductance diurnally and seasonably in F relative to other treatments.

The sandy soil at this site extends to the water table at 30 m, and it seems unlikely to impede roots from reaching water at that depth. Deeper root penetration than that has been shown for several tree species (Canadell et al. 1996), and the vertical profile of root area strongly indicates roots at depths exceeding 1.9 m. However, an earlier study at this site during a wet period, based on a local water balance, indicated that only trees in the F treatment were using water below 1 m (Ewers et al. 1999). A similar analysis for the treatments without irrigation in this study, indicated trees used water to 1.5 m in the F and 1.3 m in the C treatments. Using deuterium measurements to help determine water uptake patterns (see e.g., Dawson and Ehleringer 1991; Thorburn et al. 1993) we found that the δ^2H value of well water was 15–17‰ lower than the stem water in unirrigated plots, and that stem water had similar values to the soil water, indicating that water stored at depth did not account for large proportions of E_C. Uptake from deeper, wetter soil is likely to be important at night, when resistances to water uptake are lower at depth than in upper layers where soil dried out the previous days. This serves to restore xylem water potential and is important for growth during the first part of the following day (Landsberg 1986), but the amounts involved are likely to be small and withing the error terms of water balance or δ^2H. A local water balance in a similar *P. taeda* stand on clay soil showed that >90% of water uptake occurred in the upper 0.35 m of the soil, and stomatal conductance was controlled by the water content in that restricted layer (Oren et al. 1998*a*). Based on the evaluation above, soil water and root surface area within the upper 1.9 m of the sandy soil in this study should control G_{SR}.

Porometric measurements indicated that stomatal conductance in *P. taeda* decreased linearly with daily minimum air temperature below 15°C, and approach zero at 5°C (Ellsworth 2000). Thus, following nights with air temperature reaching below 10°C, stomatal conductance is substantially reduced, and winter conditions of low transpiration and high soil moisture prevail. We have found that temperature was important in separating the data into two groups, one for minimum nighttime $T \geq 10$°C, in which G_{SR} responded to θ_R in the upper 1.9 m, the other for $T < 10$°C in which G_{SR} responded to Q_o (Fig. 2). The apparent lack of response of G_{SR} to Q_o for $T \geq 10$°C is an artifact of the conditional data sampling required to keep measurement errors to <10% in the calculations of G_S (Ewers and Oren 2000). This sampling scheme excludes data for $D < 0.6$ kPa. During the growing season this exclusion encompasses the morning and evening periods when Q_o changes within the range that most likely affects G_S. The lack of response by G_S to θ_R when minimum temperatures were below 10°C was because θ_R remained high during the colder season.

In contrast to other studies in which E_C increased with L (Oren et al. 1986; Meinzer and Grantz 1991; Köstner et al. 1992; Sala et al. 1996), E_C in the fertilized treatment was not a part of the relationship with L (Tables 1 and 2; Ewers et al. 1999). Instead, despite its high L, trees in the F treatment transpired similar amounts annually to those in C and I, and a wide range of European forests, which averaged 333 mm·year^{-1} (Roberts 1983). Fertilized trees at this site showed lower E_L than other treatments (Fig. 4) because their stomatal conductance was lower under all soil moisture conditions (Fig. 2). Although studies with a range of species showed a decrease in root mass or surface area with fertilization (Linder and Axelsson 1982; Gower et al. 1994; Haynes and Gower 1995), trees in F maintained similar root surface area and vertical distribution as in the other treatments (Fig. 1). The similarity in root-to-leaf area ratio in F to IF trees (Table 1) indicates that lower E_L cannot be attributed to a negative effect of soil exploration by roots. A slight increase in E_C (Table 1) and, perhaps rainfall interception with increased L in F (causing the soil there to dry more rapidly and stay dry longer than the soil in the other treatments; data not shown), and a large decrease in the hydraulic conductivity of fine roots (Ewers et al. 2000), which reduces G_{Smax} by reducing maximum leaf specific hydraulic conductivity (Sperry et al. 1998), are probably responsible for decoupling between E_C and L in F.

Application to modeling

Appropriate values of G_{Smax}, hence canopy conductance under a range of conditions, are important for the 3-PG model and any model in which gas exchange, and hence productivity, is mediated by stomatal conductance. As noted earlier, we tested 3-PG in terms of its predictions of transpiration not only because these lead to the water balance and its effects on growth but also because typically transpiration rate is a useful surrogate for CO_2 exchange, and hence productivity. We estimated G_{SRB} from the upper boundary response of G_{SR} to soil moisture weighted by the root area density profile to 1.9 m, the depth within which the local water balance and δ^2H measurements indicated that most transpired water was absorbed. Two G_{SRB} values were estimated for $T \geq 10$°C, one for the highest native θ_R, and one for the maximum θ_R attained during the continuous irrigation experiment. Both values were projected to G_{Smax} based on the proportionality between the sensitivity of stomatal conductance to D and G_{SR} (0.57 for all treatments and conditions; Fig. 3) and assuming that G_S maximizes at D = 0.6 kPa. The 3-PG model, parameterized with estimates of G_{Smax} under highest native θ_R, was used to predict monthly E_C. These predictions were compared with sap flux-scaled monthly E_C estimates, in which missing data (< 30%) were estimated based on L and relationships between E_L and D_Z.

When parameterized with G_{Smax} for highest native θ_R, 3-PG predicted monthly stand transpiration amounts very similar to measured values in all but the IF treatment (Fig. 5).

The 3-PG model predicts long-term transpiration better than monthly E_C because, for simplicity of calculations, the model allows over- and under-predictions of monthly values that "average out" on an annual basis. These errors were particularly noticeable in IF, because this was the only treatment in which soil moisture was frequently recharged with irrigation followed by a strong depletion resulting from the high transpiration rate in this stand. A model that uses monthly average values as input variables is likely to be less accurate at each particular month under such strong fluctuation. Yet, the long-term prediction, a prediction for which the model is aimed, was as accurate in IF (–6%) as in the other treatments when G_{Smax} for highest native θ_R was used.

Accuracy of even the long-term predictions of 3-PG degraded precipitously when G_{Smax} was obtained at maximum θ_R. This estimate of G_{Smax} ranged from 38% higher in C to 58% higher in IF than G_{Smax} at the highest native θ_R (Table 1). Reparameterizing 3-PG with the higher G_{Smax} resulted in overprediction of E_C ranging from 12% in F to 33% in IF. Models based on eq. 1 use porometric g_{Smax} values, often distilled from g_S measured in the upper canopy. These values are generally much higher than the whole canopy G_S, which was more similar to g_S measured in lower branches (B. Ewers, unpublished data). Using maximum g_S from the upper branches in this study would have produced a similar overestimation of E_C by 3-PG as using G_{Smax} obtained under maximum θ_R.

Thus, for models that use spatially averaged stomatal conductance (e.g., 3-PG by Landsberg and Waring (1997) and FOREST-BGC by Running and Coughlan (1988)) rather than the conductance of sunlit foliage adjusted by radiation profile through the canopy (e.g., BIOMASS by McMurtrie et al. (1990) and BEX by Bonan (1991)), G_{Smax}, estimated from the upper boundary of the relationship between G_S and θ_R and scaled to D = 0.6 kPa, may provide the best estimate of conductance. Where 3-PG-type models are applied regionally, the effect of soil hydraulic properties and fertility on G_{Smax} must also be considered in model parameterization.

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