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A comparison of three approaches to modeling leaf gas exchange in annually drought-stressed ponderosa pine forests

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Summary We tested, compared and modified three models of stomatal conductance at the leaf level in a forest ecosystem where drought stress is a major factor controlling forest productivity. The models were tested against 2 years (1999 and 2000) of leaf-level measurements on ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) growing in the Mediterranean climate of California, USA. The Ball, Woodrow and Berry (1987) (BWB) model was modified to account for soil water stress. Among the models, results of the modified BWB model were in the closest agreement with observations ($r^2 = 0.71$). The Jarvis (1976) model showed systematic simulation errors related to vapor pressure deficit ($r^2 = 0.65$). Results of the Williams, Rastetter, Fernandes et al. (1996) (SPA) model showed the poorest correlation with empirical data, but this model has only one calibration parameter ($r^2 = 0.60$). Sensitivity analyses showed that, in all three models, predictions of stomatal conductance were most responsive to photosynthetically active radiation and soil water content. Stomatal conductance showed little sensitivity to vapor pressure deficit in the Jarvis model, whereas in both the BWB and SPA models, vapor pressure deficit (or relative humidity) was the third most important variable. Parameterization of the SPA model was in accordance with the parameterization of the modified BWB model, although the two models differ greatly. Measured and modeled results indicate that stomatal behavior is not water conservative during spring; however, during summer, when soil water content is low and vapor pressure deficit is high, stomatal conductance decreases and, according to the models, intrinsic water-use efficiency increases.

Keywords: models, PAR, soil water content, stomatal conductance, vapor pressure deficit, water-use efficiency.

Introduction

Stomatal behavior is a central topic of ecophysiological research because it affects plant growth, vegetation distribution and ecosystem function. Stomata are the major pathway for the transfer of trace gases between vegetation and the atmosphere, and hence are of major importance in the biological control of the climate system and atmospheric composition. Furthermore, air pollutants such as ozone cause most damage to vegetation when they enter foliage through stomata (Hogsett et al. 1989). The physiological mechanisms controlling the response of stomata to environmental conditions are complex and not fully understood. Models of stomatal conductance can help us to understand and predict changes in land biosphere–atmosphere exchanges of gases, energy and water vapor resulting from predicted global climate changes.

Although stomatal conductance responses to photosynthetic photon flux density, leaf temperature, vapor pressure deficit, internal CO_2 concentration and soil water potential have been reported (Cowan 1977, Jarvis and Morison 1981, Schulze 1986, Zeiger et al. 1987), a mechanistic description of stomatal conductance behavior remains unavailable. Wong et al. (1979) indicated that there is a strong coupling between stomatal conductance and photosynthesis. These observations have led to a wide range of empirical and semi-empirical models. All the approaches have appealing attributes but none of them has escaped criticism. Consequently there is a need to test and compare some of these models in an integrative framework.

The Jarvis (1976) model, which is largely empirical, uses a multiplicative algorithm that adjusts a reference value of stomatal conductance according to changes in environmental conditions and assumes that stomatal conductance is independent of the rate of photosynthesis. Jarvis and Morison (1981) showed that the dependence of stomatal conductance on internal CO_2 concentration can be broken by exposure to blue light. This class of model is currently used in Europe for modeling and predicting ozone pollution at the landscape level (Emberson et al. 2000). The Jarvis algorithm has been shown to perform well across many different forest types (e.g., Massman and Kaufmann 1991, Bosveld and Bouten 2001), including drought-stressed ecosystems (Running and Coughlan 1988, Running 1994).

Another class of model, which can be classified as semi-empirical, is based on evidence that a tight relationship exists between stomatal conductance, internal CO_2 concentration and photosynthesis. The model proposed by Ball et al. (1987), hereafter the BWB model, links stomatal conductance to photosynthesis. The BWB model has been shown to perform well for different species under low to moderate soil water deficits (Leuning 1990, Collatz et al. 1991, Reynolds et al. 1992, de Pury and Farquhar 1997). When water supply decreases, the BWB model needs modification to better account for the effects of drought stress on stomatal conductance (Sala and Tenhunen 1996, Baldocchi 1997).

A third class of models assumes that stomatal aperture is controlled by an optimization mechanism that maximizes carbon gain per unit of water loss (Cowan 1977, Farquhar et al. 1980*a*). Tyree and Sperry (1988) hypothesized that stomata close in response to decreasing leaf water potential in a way that prevents runaway cavitation. Among optimization models, the stomatal conductance algorithm included in the Soil-Plant-Atmosphere (SPA) canopy model is based on the hypothesis that stomatal variation operates to maximize photosynthesis per unit of transpiration, consistent with the avoidance of catastrophic xylem cavitation (Williams et al. 1996). The SPA model has been tested against canopy-level gas exchange (Williams et al. 1996, 2001*a*, Law et al. 2000), but the stomatal conductance algorithm has never been tested at the leaf level (M. Williams, University of Edinburgh, personal communication).

We tested, compared and modified the Jarvis, BWB and SPA models for use in a forest ecosystem where drought stress is a major factor controlling stomatal conductance. The models were tested against 2 years (1999 and 2000) of leaf-level measurements on ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) growing in the Mediterranean climate of California. The wide distribution of this species provides an opportunity to make measurements on trees growing in many different environmental conditions. An earlier paper relates a detailed analysis of the data collected and describes the parameters and some functional relationships needed to drive the models tested in this paper (Panek 2004).

Theory

Jarvis model

Many climate and vegetation–atmosphere models have used the multiplicative empirical model of Jarvis (1976) (e.g., Dickinson et al. 1991). This model assumes that stomatal conductance (g_s) is a function of irradiance (I), with multiplicative limitations imposed by various environmental factors such as temperature (T), humidity deficit (D), leaf water potential (Ψ):

$$g_s = f(I)g(T)h(D)i(\Psi) \tag{1}$$

The model has been modified several times. Most of the equations described here were developed and tested against observations on western coniferous species in Oregon, USA, and then used at a larger spatial scale in the FOREST-BGC model (cf. Running and Coughlan 1988). Leaf g_s to water vapor was computed sequentially as a function of leaf water potential and modified by absolute humidity deficit. We used calculated predawn leaf water potential instead of instantaneous leaf water potential because of the good correlation obtained with soil water content measured at 50 cm depth (see Figure 1a). Stomatal conductance can potentially be limited by low and high temperatures. However, we did not incorporate a temperature response function because: (1) our data did not include freezing or sub-freezing temperatures; (2) temperature data were strongly correlated with absolute humidity deficit; and (3) studies by Massman and Kaufmann (1991) and Granier and Lousteau (1994) show that temperature is of minimal importance in controlling stomatal conductance in the Jarvis model.

Stomatal conductance as a function of predawn leaf water potential was computed as:

$$g_{sw} = g_{smax} - D_w(\Psi_{min} - \Psi_p) \tag{2}$$

where g_{smax} is maximum stomatal conductance (mol m^{-2} s^{-1}), D_w is the slope of the stomatal conductance to leaf water potential (mol m^{-2} s^{-1} MPa^{-1}) relationship, Ψ_p is predawn leaf

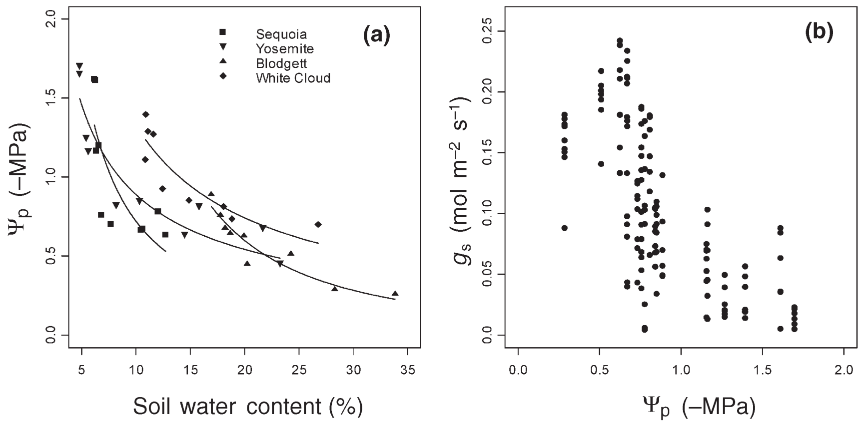

Figure 1. Relationships between (a) soil water content at 50-cm depth and predawn leaf water potential (Ψ_p) and between (b) Ψ_p and stomatal conductance (g_s) at four sites during 1999 and 2000. Lines were calculated with Equation 10, see Table 1.

water potential (MPa), and Ψ_{min} is the leaf water potential at stomatal closure (MPa). We computed D_w (mol m^{-2} s^{-1} MPa^{-1}) as:

$$D_w = \frac{g_{smax}}{\Psi_{min} - \Psi_{max}} \quad (3)$$

where Ψ_{max} is maximum leaf water potential. We then modified g_{sw} (mol m^{-2} s^{-1}) by absolute humidity deficit:

$$g_{sh} = g_{sw}(1 - D_h A_h) \quad (4)$$

where g_{sh} is stomatal conductance with humidity reduction (mol m^{-2} s^{-1}), D_h is the slope between stomatal conductance and absolute humidity deficit, and A_H is absolute humidity deficit (mol m^{-3}). We computed D_h as:

$$D_h = \frac{g_{sw}}{A_{Hmax} - A_{Hmin}} \quad (5)$$

where A_{Hmax} and A_{Hmin} are daily maximum and minimum absolute humidity deficits, respectively (mol m^{-3}).

We used one year of data (1999) to calibrate the model for the parameters g_{smax}, Ψ_{max} and Ψ_{min}. The parameter g_{smax} was calculated as a function of photosynthetically active radiation (PAR) (see below). The second year of data (2000) were used as independent validation data.

BWB model

The BWB model (Ball et al. 1987) links stomatal conductance to net photosynthesis (A_n; μmol m^{-2} s^{-1}), relative humidity (R_H; %) and CO$_2$ concentration at the leaf surface (C_s; ppm):

$$g_s = g_0 + \frac{m A_n R_H}{C_s} \quad (5)$$

where coefficient m is a dimensionless slope, and g_0 is the residual stomatal conductance when A_n tends to zero. Compared with the Jarvis model, the Ball et al. (1987) model requires fewer tuning parameters. Parameter m is constant (10.0 ± 20%) when a plant has an ample supply of soil water (Leuning 1990, Collatz et al. 1991, Harley and Tenhunen 1991). However, under conditions of moderate to severe soil water deficits (Sala and Tenhunen 1996, Baldocchi 1997), or cases involving old trees with decreased hydraulic conductivity (Falge et al. 1996), m has been shown to vary. Nikolov et al. (1995) modified m based on a reduction function related to leaf water potential:

$$m' = \frac{m}{1 + \left(\frac{\Psi_p}{\Psi_0}\right)^n} \quad (6)$$

where m' is the modified value of m, and Ψ_0 and n are fitted parameters.

We tested the ability of Equation 6 and the BWB model to account for the effect of drought stress on stomatal conductance at the leaf level. Predawn leaf water potential was calculated as a function of soil water content at 50-cm depth (see Figure 1a). We used one year of calibration data (1999) to parameterize the model (m, g_0, Ψ_0 and n) and one year of independent data (2000) to test the parameterization.

SPA model

Meinzer and Grantz (1991) hypothesized that stomatal conductance will ideally remain in balance with the hydraulic capacity of the soil and roots to supply leaves with water, avoiding leaf desiccation at one extreme and the unnecessary restriction of CO$_2$ uptake at the other. Williams et al. (1996) translated this explicitly in the SPA canopy model, where plants are assumed to open their stomata until either (1) further opening does not constitute an effective use of stored water in terms of carbon gain per unit water loss, or (2) further opening causes a drop in leaf water potential below the threshold at which severe xylem cavitation begins. The algorithm we tested considers the same mechanisms but is a simplified version of the original method. Among other things, no capacitance was taken into account because sensitivity analysis showed only a small alteration in model response with variation in capacitance (see Williams et al. 1996). The model was formulated as follows. (1) Starting from very low g_s, increment g_s by a small amount (~0.0025 mol m^{-2} s^{-1}). (2) Calculate photosynthesis from the biochemical equations presented below. (3) Calculate transpiration E (mmol m^{-2} s^{-1}) as:

$$E = 1.6 g_s D_s / P_{atm} \quad (7)$$

where 1.6 is the ratio of the diffusion rates of CO$_2$ and water vapor, D_s is the vapor pressure deficit at the leaf surface (Pa), and P_{atm} is atmospheric pressure (Pa). (4) Calculate predawn leaf water potential from soil water content (Figure 1a). (5) Calculate leaf water potential Ψ_l as:

$$\Psi_l = \Psi_s + R_p E \quad (8)$$

where Ψ_s is soil water potential, estimated as being equal to predawn leaf water potential, and R_p is plant hydraulic resistance, fixed at 0.1 MPa s m^2 mmol^{-1} based on our data. (6) Return to step 1 for a further increment of g_s unless either: (a) the previous g_s increment failed to raise assimilation appreciably (see δ below), or (b) Ψ_l has reached its specific cavitation limit (–2 MPa, Hubbard et al. 2001).

The SPA model as described has one calibration parameter:

$$\delta(\%) = \frac{A_i}{A_{(i-1)}} 100 \quad (9)$$

where A_i is assimilation calculated for the ith g_s incremental step and A_{i-1} is assimilation calculated for the previous (i – 1)th g_s incremental step. This parameter defines the limit of increase in assimilation per additional g_s incremental step. It was calibrated on the 1999 data and then tested on the 2000 data.

Photosynthesis model

Evaluation of the BWB and the SPA models depends on a photosynthesis model. Leaf photosynthesis was simulated according to the equations of Farquhar et al. (1980*b*). The enzyme kinetic constants and temperature correction functions were from Woodrow and Berry (1980), Harley and Baldocchi (1995) and de Pury and Farquhar (1997). We used the Boltzman temperature correction function for V_{cmax} as in Harley and Baldocchi (1995). The potential rate of electron transport, J, was calculated as a function of $J_{\max}$ and photosynthetic photon flux density as in de Pury and Farquhar (1997) where $J_{\max}$ was a function of V_{cmax}($J_{\max} = 2.05V_{\mathrm{cmax}}$) as found in an earlier paper that shows the consistencies of this relationship across the different sites and years (Panek 2004). Likewise, the same paper shows a consistent relationship between day respiration R_{d} and V_{cmax} ($R_{\mathrm{d}} = 0.08V_{\mathrm{cmax}}$).

Data

The physiological data collected for this study have been described by Panek (2004) and are only summarized here. Four sites were selected in the Sierra Nevada of California, USA: Sequoia National Park, White Cloud, Yosemite National Park and Blodgett Forest Research Station. The sites span two distinct soil types. Sequoia and Yosemite soils are derived from granitic parent material, and Blodgett and White Cloud soils are andesitic in origin. All sites experience some degree of water stress during the summer (see Figure 1b and Panek 2004). Within each site, six ponderosa pines were selected for physiological measurements. The trees at Sequoia, White Cloud and Yosemite were > 40 years old, and the trees at Blodgett were 9 years old in 1999. Mean diameter at breast height in 1999 was 5.58, 23.4, 22.9 and 40.8 cm for Blodgett, Sequoia, White Cloud and Yosemite, respectively. We used physiological data collected at monthly intervals over the 1999 and 2000 growing seasons of from two fascicles of the 1-year-old age class on the terminal shoot of south-facing branches.

Gas exchanges measurements were made with a Li-Cor LI-6400 (Li-Cor, Lincoln, NE) field-portable infrared gas analysis system. Diurnal trends in gas exchange, including net photosynthesis, stomatal conductance and transpiration, were measured monthly from May (bud break) through September, as trees responded to a typical soil drying cycle (Panek 2004). Response curves of net photosynthesis versus leaf internal CO_2 concentration ($A_{\mathrm{n}}/C_{\mathrm{i}}$ response curves) were measured monthly and were analyzed after the method of D. Ellsworth (Brookhaven National Lab/Duke FACE Experiment, Duke University, Durham, NC). The A_{n}/I response curves and nighttime respiration were measured in June when soil water content was high, and were repeated in August when soil water content was low.

To measure diurnal trends in gas exchange, needle fascicles were enclosed in a 2 × 6 cm chamber providing ambient light, humidity and temperature. These environmental variables were recorded concurrently with gas exchange measurements. Response curves were measured in a 3 × 2 cm chamber with a red/blue light source and the chamber environment modified to maintain relative humidity near maximum (around 50%) and leaf temperature at 25 °C. Nighttime respiration measurements were made between 2100 and 0400 h in a temperature-controlled 2 × 6 cm chamber. Measurements were made at 5 °C intervals, after stabilizing for 5 min at the given temperature. Predawn and midday water potentials were measured on each tree on the day of gas exchange measurement with a pressure chamber (PMS Instruments, Corvallis, OR). Volumetric soil water (CS615, CSI) measurements were made at depths of 10 and 50 cm.

Results

Parameterization

The models each use a calculated value of Ψ_{p}. We found that this variable was tightly related to soil water content at 50-cm depth during both years of measurements at the four experimental sites (Figure 1a). We modeled this relationship as:

$$\Psi_{\mathrm{p}} = a\mathrm{SM}^{b} \tag{10}$$

where SM is soil water content at 50-cm depth (%), and a and b are fitted parameters. Equation 10 was parameterized by a nonlinear algorithm, independently at the four experimental

Table 1. Parameters and coefficient of determination (r^2) of the function (Equation 10) relating predawn leaf water potential to soil water content.

Sites	a	b	r^2
Sequoia	13.35	–1.27	0.63
Yosemite	4.59	–0.71	0.87
Blodgett	151.25	–1.85	0.89
White Clouds	9.15	–0.84	0.79

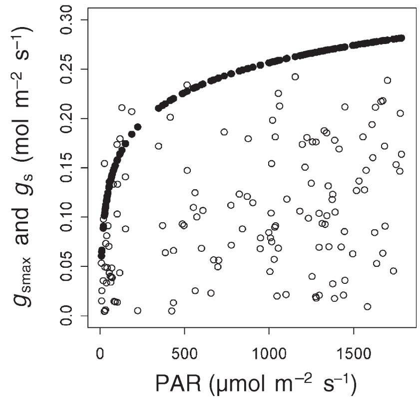

Figure 2. Relationships between photosynthetically active radiation (PAR), measured stomatal conductance (g_{s}, ○) and maximum stomatal conductance (g_{smax}, ●) modeled with the Jarvis model (Equation 11) (1999 data).

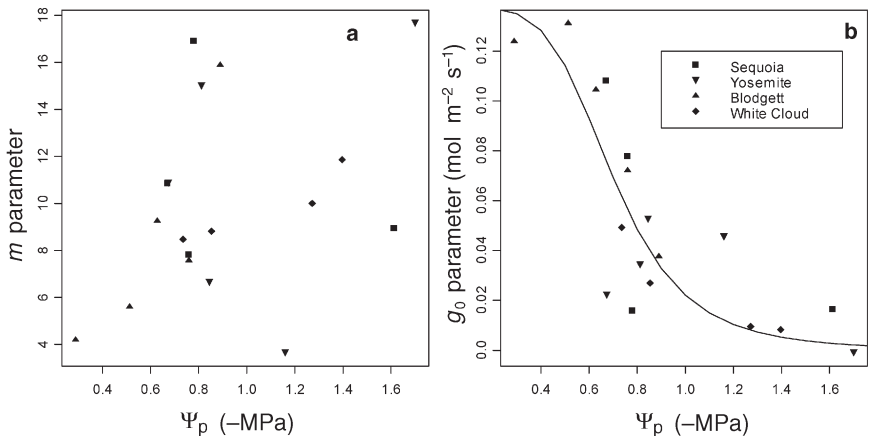

Figure 3. Relationships between parameters m (Figure 3a) and g_0 (Figure 3b) of the BWB model and predawn leaf water potential (Ψ_p) at the four sites during the 1999 period. The line in Figure 3b was calculated with Equation 12 ($r^2 = 0.71$).

sites, with an r^2 varying between 0.63 at Sequoia to 0.89 at Blodgett (Table 1). Blodgett had the highest Ψ_p and soil water content, whereas Sequoia and Yosemite showed the lowest values for both variables (Figure 1a) and White Cloud had a lower predawn leaf water potential for the same soil water content. Equation 10 was used in all models tested.

Some parameters of the Jarvis model were calibrated on the 1999 data. The relationship between g_{smax} and PAR was:

$$g_{\text{smax}} = 0.019\ln(\text{PAR}) - 0.02 \qquad (11)$$

Figure 2 shows the shape of this function, which envelops the cluster of values representing measurements of g_s. The leaf water potential inducing stomatal closure ($\Psi_{\min}$) was fixed at –1.6 MPa (Figure 1b), and $\Psi_{\max}$ was fixed at –0.3 MPa (Figure 1b).

Another parameterization included the values of m and g_0 in the BWB model. To test variability of m over time and possible relationship with drought stress, we calculated the linear regression between g_s and A_nR_H/C_s for each measurement day in 1999. The slope of this regression gave parameter m of the BWB model. The intercept gave g_0, the residual g_s when A_n tends to 0. Figures 3a and 3b show both quantities plotted as a function of Ψ_p in 1999. Parameter m varied significantly over the growing season, ranging from 4 to 18, without showing a consistent relationship with Ψ_p ($r^2 = 0.08$) or any other measured variable (soil water content $r^2 = 0.03$, D_s $r^2 = 0.06$). At Blodgett and White Cloud, m seemed to increase, whereas no relationship was found at Sequoia and Yosemite. On the other hand, parameter g_0, which varied from 0.0 to 0.13, showed a consistent decrease at all sites as a function of decreasing Ψ_p (Figure 3b). This relationship was modeled as ($r^2 = 0.71$):

$$g_0' = \frac{g_0}{1+\left(\frac{\Psi_p}{\Psi_0}\right)^n} \qquad (12)$$

where g_0, Ψ_0 and n are fitted parameters calculated with a nonlinear algorithm ($r^2 = 0.71$, $g_0 = 0.14$, $\Psi_0 = 0.70$ and $n = 4.68$) (Figure 3b). The strong relationship between g_0 and Ψ_p was also observed if parameter m of the BWB model was kept fixed while calculating g_0 (data not shown). Equation 12 was included in the BWB model. Parameter m was fixed at 10.0, which is the mean of the m values calculated for the 1999 data.

The SPA model also required parameterization. In this model, g_s is incremented unless it failed to increase assimilation appreciably. Figure 4 shows the modeled relationship between g_s and A_n in the absence of water stress (leaf water

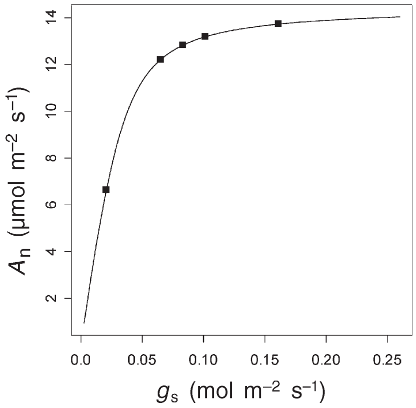

Figure 4. Response of net photosynthesis (A_n) to stomatal conductance (g_s) in the SPA model. The squares show when δ is equal to 10, 1, 0.5, 0.3 and 0.1% (from left to right).

Table 2. Parameters and coefficient of determination (r^2) of the linear regression calculated between the observations (Obs.) and simulations (Sim.) (Obs. = aSim. + b) of stomatal conductance calculated with the SPA model with different δ threshold values.

δ Threshold (%)	a	b	r^2
10	0.06	0.02	0.21
1	0.55	0.03	0.37
0.5	0.70	0.03	0.41
0.3	0.80	0.02	0.44
0.1	0.92	0.02	0.48

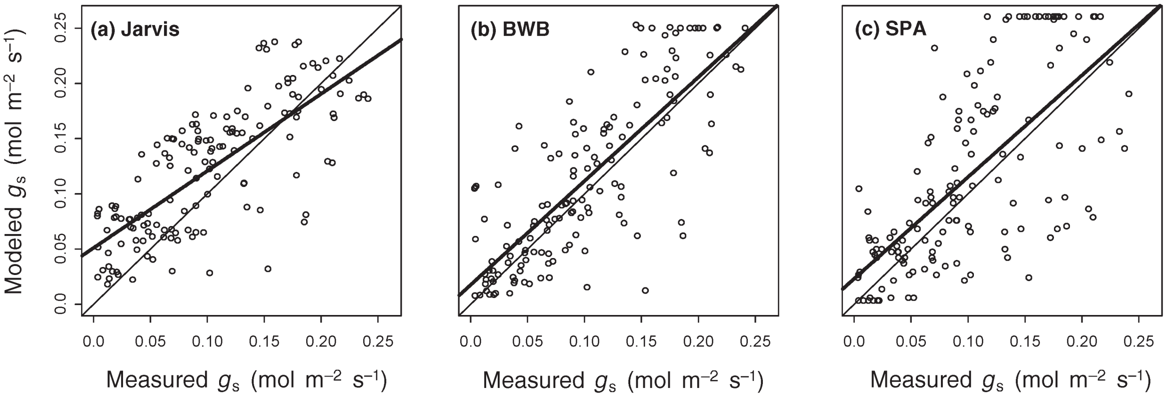

Figure 5. Measured and modeled stomatal conductance (g_S) with the Jarvis, BWB and SPA models for the 1999 calibration period. The thin line is the 1:1 relationship. The thick line is the regression line between observations and simulations (see Table 3).

potential is greater than its specific cavitation limit fixed at –2 MPa) for average environmental conditions. Different values were tested for parameter δ (10.0, 1.0, 0.5, 0.3 and 0.1%). Table 2 shows the regression calculated between observed and simulated stomatal conductance over the calibration period (1999 data) for the different δ thresholds. The 0.1% value gave the best r^2 (0.48) and the best linear regression which almost fit a 1:1 relationship. This value was selected for subsequent model runs.

Predictions of stomatal conductance

The three models showed generally good agreement with observations during the calibration period (1999 data) at the four sites (Figure 5, Table 3). The r^2 between measurements and

Table 3. Parameters and coefficient of determination (r^2) of the linear regression calculated between the observations (Obs.) and simulations (Sim.) (Obs. = *a*Sim. + *b*) of stomatal conductance calculated with the three models over the calibration and validation periods. Mean absolute error (MAE) and root mean square of error (RMSE) are also given (Janssen and Henberger 1995).

Data	Model	*a*	*b*	r^2	MAE	RMSE
Calibration (1999)	Jarvis	0.70	0.051	0.57	0.039	0.048
	BWB	0.94	0.017	0.62	0.036	0.048
	SPA	0.92	0.023	0.48	0.050	0.063
Validation (2000)	Jarvis	0.75	0.035	0.65	0.033	0.043
	BWB	1.01	0.009	0.71	0.035	0.046
	SPA	0.90	0.010	0.60	0.039	0.051

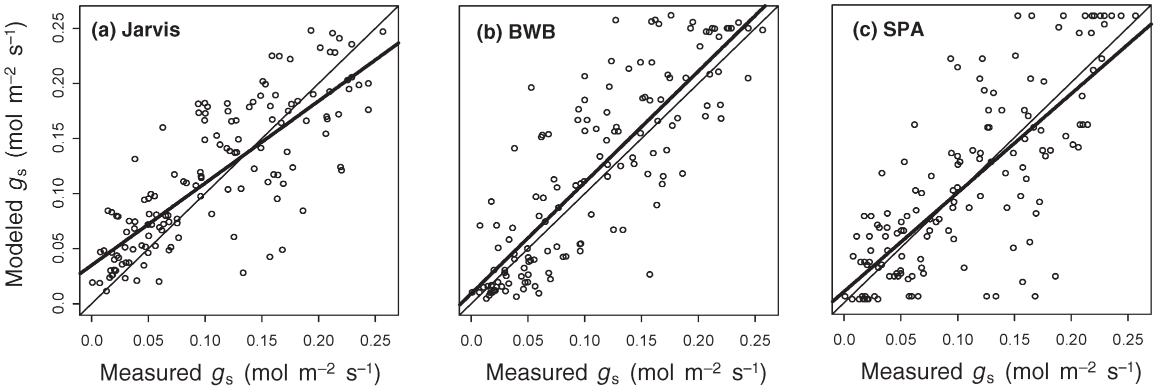

Figure 6. Measured and modeled stomatal conductance (g_S) with the Jarvis, BWB and SPA models for the 2000 validation period. The thin line is the 1:1 relationship. The thick line is the regression line between observations and simulations (see Table 3).

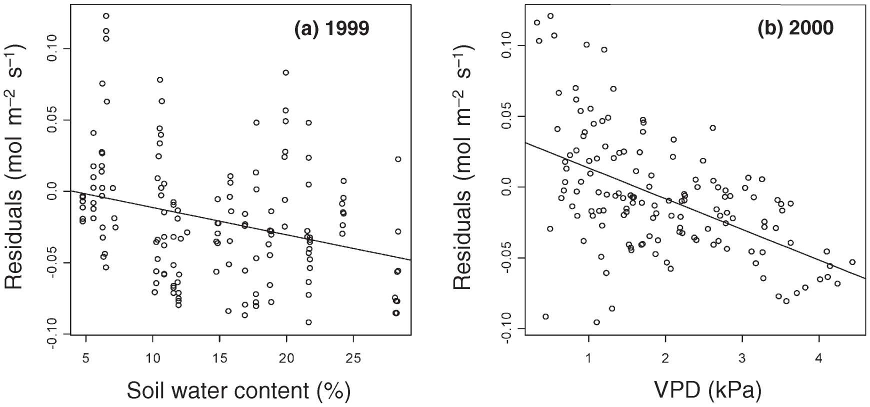

Figure 7. Residuals of the Jarvis model (observed stomatal conductance (g_s) – simulated g_s) as a function of (a) soil water content in 1999 and (b) vapor pressure deficit (VPD) in 2000.

predictions ranged from 0.48 (SPA model) to 0.62 (BWB model). The mean absolute error (MAE) ranged from 0.036 (BWB) to 0.05 (SPA) (Table 3). Linear regressions between measured data and data simulated by both the BWB and the SPA models were close to the 1:1 relationship with a small intercept. The modified BWB model gave the best r^2, with predictions that were closest to the 1:1 relationship with observations. The Jarvis model seemed to overestimate low g_s and

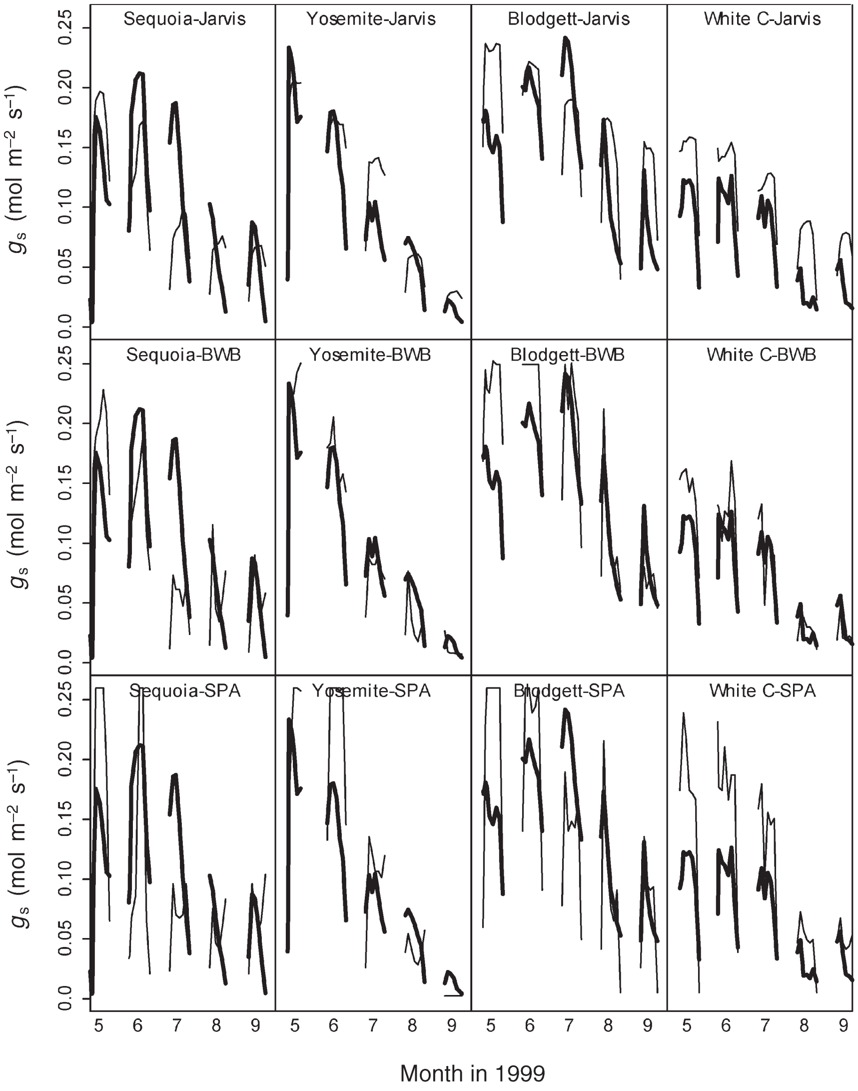

Figure 8. Measured (thick line) and modeled (thin line) stomatal conductance (g_s) with the Jarvis, BWB and SPA models for the four sites during 1999. Measurements were made every 1.5 h throughout the day, once a month during the growing season (Panek 2004).

underestimate high g_s (Figure 5), and the intercept of the relationship between observations and simulations was higher than for the BWB and SPA models (0.051 for Jarvis versus 0.017 and 0.023 for BWB and SPA, respectively) (Table 3). Residuals calculated as the difference between observed g_s and calculated g_s with the Jarvis model showed a relationship with soil water content in 1999, with simulations tending to overestimate measurements at high soil water content (Figure 7a).

Validation runs conducted on an independent data set (2000 datea) gave better r^2 values between measured and modeled data than those from the calibration period (1999 data) (Table 3). The r^2 between measurements and predictions ranged from 0.60 (SPA model) to 0.71 (BWB model), with an improvement of ~10 % compared with the calibration period for the three models tested. The mean absolute error (MAE) also decreased compared with the calibration period, and varied between 0.033 (Jarvis) and 0.039 (SPA) (Table 3). As seen in the calibration data set, the relationship between measured and simulated data was close to the 1:1 relationship with a small intercept for both the BWB and the SPA models (Figure 6). Again, the Jarvis model tended to overestimate low g_s and underestimate high g_s (Figure 6). As seen in the calibration data set, the intercept of the regression between observations and simulations was greater with the Jarvis model than with the other models (0.035 for Jarvis versus 0.009 and 0.010 for BWB and SPA, respectively) (Table 3). The modified BWB model gave the best r^2, with predictions that were closest to the 1:1 relationship with observations. Residuals calculated as the difference between observed g_s and calculated g_s by the Jarvis model showed a relationship with vapor pressure deficit in 2000, with the simulations tending to overestimate measurements at high vapor pressure deficit (Figure 7b).

At the seasonal level, the three models were able to account for the decrease in g_s between the beginning and the end of the vegetation period (Figures 8 and 9), mainly as a function of increasing atmospheric humidity deficit and decreasing soil water content. At Blodgett and Sequoia, the three models overestimated the observations in June 1999 (Figure 8), because the

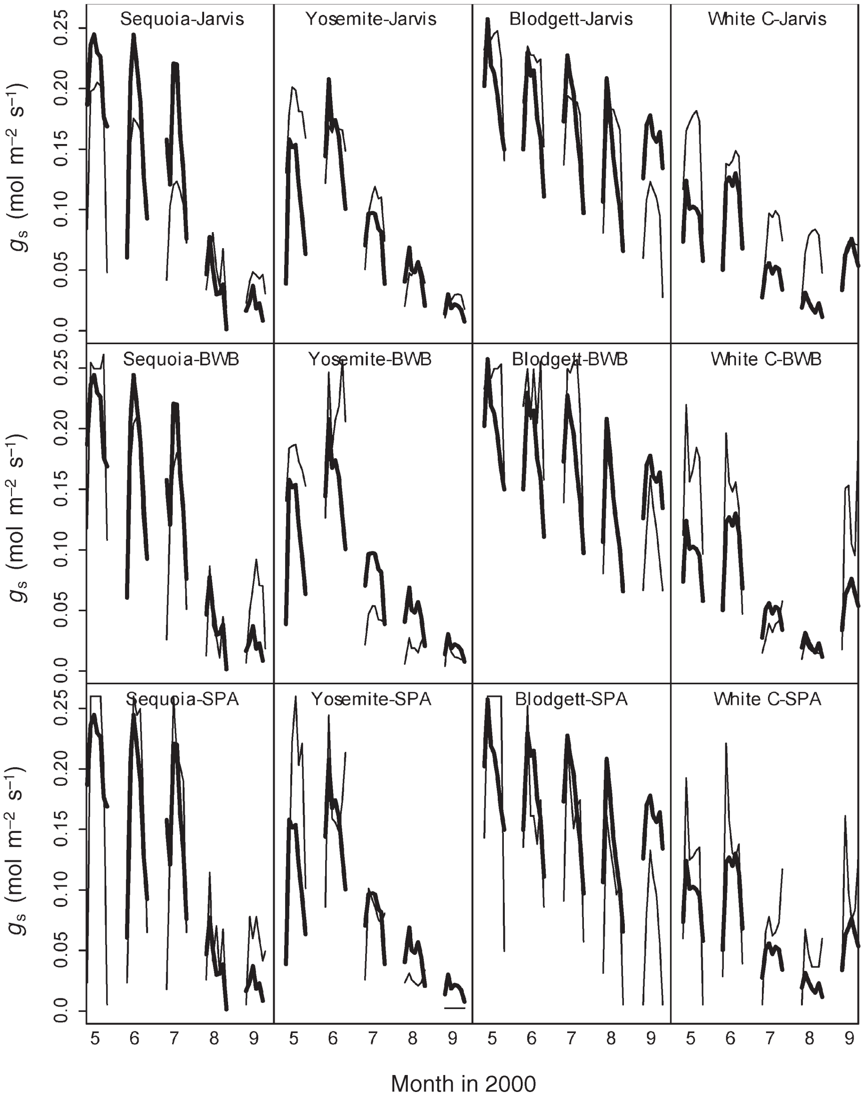

Figure 9. Measured (thick line) and modeled (thin line) stomatal conductance (g_s) with the Jarvis, BWB and SPA models for the four sites during 2000. Measurements were made every 1.5 h throughout the day, once a month during the growing season (Panek 2004).

increase in g_s from May to June at these sites was not accounted for by the models. However, the Jarvis and BWB models predicted values within the range of measurement variability (for clarity the error bars are not shown in Figure 8). On the other hand, the SPA model predictions during the early 1999 season systematically overestimated the observations at the four sites (Figure 8). During 1999 and 2000, the constraint imposed by the δ parameter in the SPA model only operates during early summer, and during the early part and late part of the day during late summer, when increases in g_s caused no decrease in calculated leaf water potential below the limit causing xylem cavitation (–2 MPa) (Figure 10).

Predictions of net photosynthesis

Predictions of net photosynthesis were made with the Farquhar equations coupled to the three stomatal conductance models that we tested. During both the calibration and validation periods, the r^2 between measurements and predictions ranged from 0.7 to 0.81 (Table 4). For the three models, linear regressions between measured and simulated data were close to the 1:1 relationship with a small intercept (Figures 11 and 12, and Table 4).

Model sensitivity to driving variables

The three models were systematically tested for sensitivity of calculated g_s to the driving variables (PAR, temperature, vapor

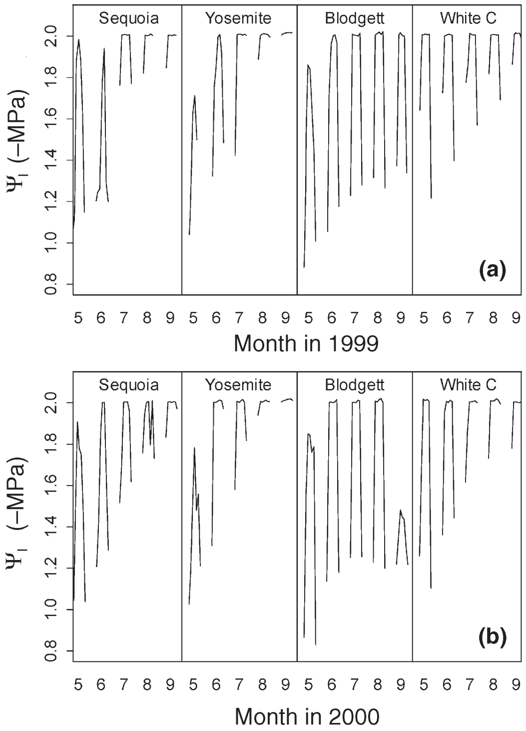

Figure 10. Modeled leaf water potential (Ψ_l) by the SPA model for the four sites during (a) 1999 and (b) 2000. The cavitation limit was set at –2 MPa.

Table 4. Parameters and coefficient of determination (r^2) of the linear regression calculated between the observations (Obs.) and simulations (Sim.) (Obs. = aSim. + b) of net photosynthesis calculated with the Jarvis, BWB and SPA stomatal conductance models and the Farquhar equations over the calibration and validation period. Mean absolute error (MAE) and root mean square of error (RMSE) are also given (Janssen and Henberger 1995).

Data	Model	*a*	*b*	r^2	MAE	RMSE
Calibration	Jarvis	0.91	2.05	0.71	2.19	2.78
(1999)	BWB	1.00	0.35	0.73	1.84	2.40
	SPA	1.00	1.03	0.70	2.18	2.78
Validation	Jarvis	0.97	1.19	0.79	1.75	2.40
(2000)	BWB	1.08	–0.07	0.77	2.01	2.67
	SPA	1.00	0.36	0.81	1.65	2.12

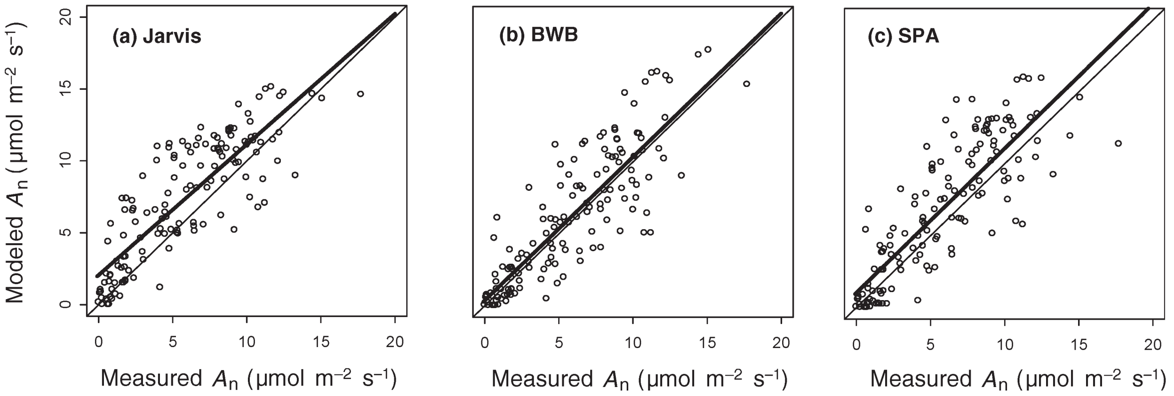

Figure 11. Measured and modeled net photosynthesis (A_n) with the Jarvis, BWB and SPA models for the 1999 calibration period. The thin line is the 1:1 relationship. The thick line is the regression line between observations and simulations (see Table 4).

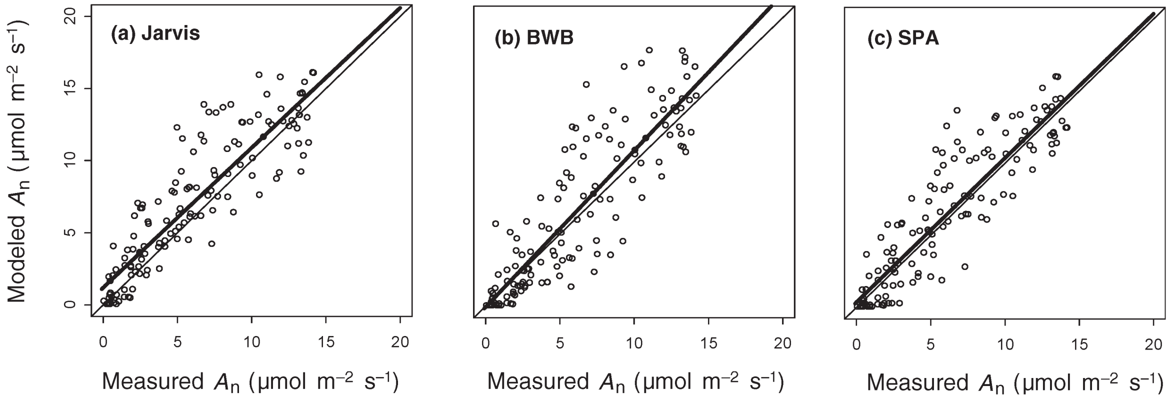

Figure 12. Measured and modeled net photosynthesis (A_n) with the Jarvis, BWB and SPA models for the 2000 validation period. The thin line is the 1:1 relationship. The thick line is the regression line between observations and simulations (see Table 4).

pressure deficit and soil water). Models were run while one of the four driving variables was changed and the other three variables were set at their baseline values. All models were most sensitive to PAR and soil water content (Figure 13). They showed variable responses to temperature and vapor pressure deficit. Overall, the sensitivity of calculated g_s to the driving variables was similar for the SPA and BWB models, whereas, in the Jarvis model, sensitivity was quite different (Figure 13). The Jarvis model as implemented in this study showed no sensitivity to temperature because the function was turned off (see Theory section), and low sensitivity to vapor pressure deficit (Figures 13b and 13c). The response to the driving variables was less smooth with the SPA model than with the BWB model.

Discussion

The annual climate pattern of the Sierra Nevada is characterized by drought from May to October, with soil water content sometimes dropping below 10% (Urban et al. 2000). The trees at all four study sites experienced some water stress at the end of the growing period during both measurement years (Fig-

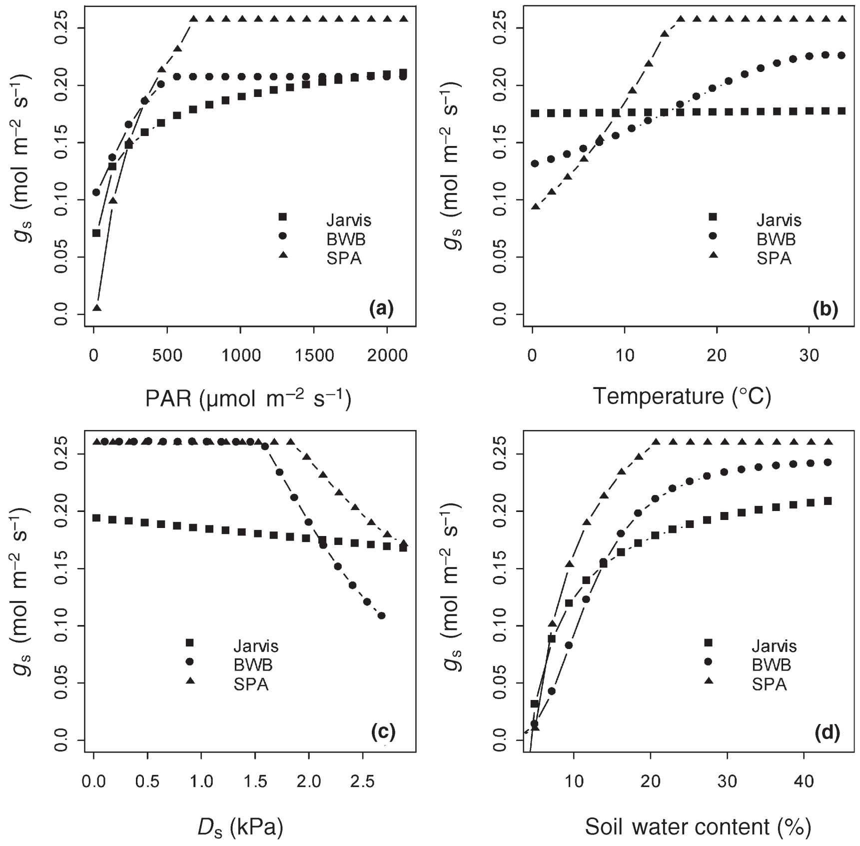

Figure 13. Responses of g_s in the Jarvis, BWB and SPA models to variations in (a) PAR, (b) temperature, (c) D_s and (d) soil water content. Sensitivity was calculated sequentially for each driving variable, with all other variables kept constant at their mean value (PAR = 800 μmol m^{-2} s^{-1}, T = 22 °C, D_s = 1.9 kPa, R_H = 30%, SM = 20%). The response of D_s by the BWB model was simulated by altering the relative humidity from 0 to 100% at constant temperature (Teten 1930). Abbreviations: g_s = stomatal conductance; PAR = photosynthetically active radiation; T = temperature; D_s = vapor pressure deficit at the leaf surface; and R_H = relative humidity.

ure 1b, and Panek 2004). The stomatal conductance models tested were well adapted to this feature as shown by the sensitivity analysis. Nevertheless, modification of the original form of the BWB model was needed to account for soil water stress. Without modifying the intercept of the BWB model as applied in this paper, calculated stomatal conductance did not respond to soil water content and r^2 dropped from 0.62 to 0.25 (with g_0 fixed at 0.05). The inability of the standard BWB model to account for soil water stress has been previously noted (Sala and Tenhunen 1996, Baldocchi 1997, Law et al. 2000).

Of the three models, the modified BWB model gave the best r^2 and regressions between observations and simulations that were closest to the 1:1 relationship. The SPA model had the lowest r^2. However, both the BWB and the Jarvis models had the largest number of calibration parameters (4), whereas the SPA model had only one calibration parameter. Thus, beside large differences in modeling concepts, the higher performance of the BWB and Jarvis models over the SPA model is also associated with their larger number of calibration parameters.

Values of the parameters in the Jarvis model compare well with previous studies (Running 1994), indicating that these parameters may be fairly constant, which facilitates use of the model. This result contradicts other studies showing that the algorithm of the Jarvis model requires a lot of tuning and calibration (Sellers et al. 1986, Baldocchi et al. 1987, Mascart et al. 1991, Baldocchi 1992). However, this algorithm remains diagnostic and mostly empirical because it does not include important feedbacks between g_s, internal CO_2 concentration, transpiration, humidity deficits and leaf water potential.

For the BWB model, the mean value of m is in the range of values reported by others (Harley and Baldocchi 1995, Falge et al. 1996, Sellers et al. 1996, Baldocchi and Meyers 1998, Kosugi et al. 2003). To the best of our knowledge, our study is the first to report large variation in the intercept of the model (g_0) and a tight inverse relationship with predawn leaf water potential (Figure 3b). The variation of intercept with soil water content is unlikely to be a consequence of variation in cuticular conductance because of: (1) the large variation in the intercept (from 0.001 to 0.12 mol m^{-2} s^{-1}); and (2) the low value and variation in cuticular conductance of pine needles (~0.001 mol m^{-2} s^{-1}, see Kerstiens 1996, Anfodillo et al. 2002). Variation in the intercept of the model is more likely to reflect modification in the relationship between photosynthesis and g_s, influenced by soil water content. During spring, soil water content is high and vapor pressure deficit is low. The high intercept of the BWB model suggests that stomatal behavior is not water conservative during this period: g_s is high even when environmental conditions are not optimal for photosynthesis (low irradiance). Later in the season, when soil water content is low and vapor pressure deficit is high, g_s decreases and the model suggests that stomatal behavior is more water conservative. The decrease in the intercept of the BWB model when soil water content becomes limiting implies that intrinsic water-use efficiency (A/g_s ratio) increases with drought stress, which is in accordance with an extensive body of literature (e.g., Cowan and Farquhar 1977, Hall and Schulze 1980, Thomas et al. 1999) and with measurements made at our study sites (Panek 2004).

The parameterization of SPA accords with the parameterization of the modified BWB model, although the two models differ greatly. The low value of δ for which we found the highest r^2 between observations and simulations with SPA implies that when there is no soil water restriction, g_s increases in the model even for low additional calculated photosynthetic rates (up to 0.1%, δ). This non-conservative water use is mainly seen during the spring. During the summer, soil water content is limiting and the behavior of stomatal conductance becomes more water conservative as cavitation risks increase. Of the models we tested, the SPA model is the most mechanistic and is based on well-founded assumptions about the relationship between g_s, photosynthesis and water consumption (Cowan 1977, Meinzer and Grantz 1991, Williams et al. 1996). Sensitivity analyses have shown that the response of g_s calculated with the SPA model is realistic and relatively similar to the BWB model, although the algorithms are very different. Nevertheless, the responses of g_s to the driving variables are less smooth with the SPA model than with the BWB model. This is mainly because the SPA model uses thresholds for defining relationships between g_s, photosynthesis and leaf water potential, whereas the BWB uses continuous functions. Additional data at the leaf level are needed to better understand the behavior of critical parameters such as δ, which defines the relationship between stomatal conductance and photosynthesis. Furthermore, a single cavitation limit for leaf water potential seems too simple for a broad range of ecophysiological conditions (Williams et al. 2001*b*), especially when partial cavitation may occur. Relating soil and xylem hydraulic conductivity to plant water status while g_s is incremented would allow the SPA model to better account for continuous hydraulic limitation of plant water use (Sperry et al. 1998)

Models that link stomatal conductance to photosynthesis such as BWB and SPA are attractive because they make it possible to calculate how stomatal conductance correlates with ecophysiological and biogeochemical factors, such as leaf photosynthetic capacity, nutrition and ambient CO_2 concentration (Schulze et al. 1994, Leuning et al. 1995). Such models offer an integrative framework where stomatal conductance, photosynthesis and water use by the plant are directly linked, and where predictions of these variables can be validated against observations. However this approach has been criticized on the basis that errors associated with calculating photosynthesis become associated with stomatal conductance. Our results contradict this assumption: the sensitivity analysis showed that the response of stomatal conductance to input variables is realistic in the BWB and SPA models, whereas the low response to vapor pressure deficit in our implementation of the Jarvis model is not. This insensitive response explains partly why the Jarvis model sometimes overestimates g_s at low stomatal conductance (at high D_s) and underestimates g_s at high stomatal conductance (at high D_s) as shown by the residual analyses (Figures 7b and 13c).

Conclusion

Our goal was to test, compare and modify three models of stomatal conductance that incorporate the influence of various environmental and physiological factors including drought stress. The most mechanistically based model (SPA), which has never been tested at the leaf level, has only one parameter and did not perform as well as a more empirical model (modified BWB) that has four calibration parameters. In terms of prediction performance and realism, the BWB was the best of the models tested and is now well calibrated and validated for ponderosa pine in the Sierra Nevada. The Jarvis model, as presented in this paper, was found to be unsuitable as a predictive tool because of some simulation errors related to vapor pressure deficit. Beside the ability of the BWB model to serve as tool for prediction, it also provides insights into the ecophysiological processes governing stomatal conductance of ponderosa pine in the Sierra Nevada. In particular, the model shows that ponderosa pine is a non-conservative water user when soil water content is high, that stomatal conductance behavior becomes more water conservative when soil–water content is limiting, and that this change is related to an increase in intrinsic water-use efficiency. The SPA model leads to the same conclusions.

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