Modeling the Response of Canopy Stomatal Conductance to Humidity

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ABSTRACT

Humidity of air is a key environmental variable in controlling the stomatal conductance \((g)\) of plant leaves. The stomatal conductance–humidity relationships employed in the Ball–Woodrow–Berry (BWB) model and the Leuning model have been widely used in the last decade. Results of independent evaluations of the two models vary greatly. In this study, the authors develop a new diagnostic parameter that is based on canopy water vapor and CO\(_2\) fluxes to assess the response of canopy \(g\) to humidity. Using eddy-covariance flux measurements at three boreal forest sites in Canada, they critically examine the performance of the BWB and the Leuning models. The results show that the BWB model, which employs a linear relationship between \(g\) and relative humidity \((h_s)\), leads to large underestimates of \(g\) when the air is wet. The Leuning model, which employs a nonlinear function of water vapor pressure deficit \((D_s)\), reduced this bias, but it still could not adequately capture the significant increase of \(g\) under the wet conditions. New models are proposed to improve the prediction of canopy \(g\) to humidity. The best performance was obtained by the model that employs a power function of \(D_s\), followed by the model that employs a power function of relative humidity deficit \((1 - h_s)\). The results also indicate that models based on water vapor pressure deficit generally performed better than those based on relative humidity. This is consistent with the hypothesis that the stomatal aperture responds to leaf water loss because water vapor pressure deficit rather than relative humidity directly affects the transpiration rate of canopy leaves.

1. Introduction

Stomatal conductance \((g)\) controls CO\(_2\) and water vapor exchanges between plant leaves and the atmosphere. These two fluxes largely determine the ecosystem carbon and water cycles when vegetation cover is high (Kljun et al. 2006; Wang 2008). As such, understanding stomatal conductance and mechanism has been a key area in ecological and climate studies. The magnitude of stomatal conductance varies greatly with plant species and environmental conditions, which can be from 0 when stomata are closed to several hundred mmol(CO\(_2\)) m\(^{-2}\) s\(^{-1}\) [where mmol(CO\(_2\)) is millimoles of carbon dioxide] when stomata open to the maximal width (Larcher 1995). Stomata respond to many environmental factors in a complex way. There is a general consensus that stomata have developed sophisticated physiological-controlling mechanisms that tend to maximize leaf carbon gain while minimizing water loss through transpiration, or the optimization theory first proposed by Cowan (1977) and Cowan and Farquhar (1977). However, these mechanisms are not yet fully understood. As a matter of fact, the calculation of stomatal conductance has been

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one of the most challenging subjects in vegetated land surface modeling. The modeling of stomatal conductance began in the 1970s with the multiplicative algorithm that adjusts a reference value according to changes in environmental variables, such as radiation, air temperature and humidity, soil water content, among others. It can be written as

\[ g = g_{\text{max}} \prod_i f_i(X_i), \]

where \( g_{\text{max}} \) is the maximum \( g \) and \( f_i(X_i) \) is a dimensionless scaling factor varying between 0 and 1 and representing the impact of environmental variable \( X_i \) on \( g \). The Jarvis (1976) model is a typical representation of this approach. This kind of model assumes that environmental variables act independently in controlling \( g \). The theoretical weakness is obvious, as it ignores the linkage between leaf physiology and stomatal conductance. It poorly represents the dynamic interactions among stomatal conductance, transpiration, internal CO2, and leaf water potential as widely observed (Farquhar and Raschke 1978; Jones 1983; Sperry et al. 1998; Oren et al. 1999; Maseda and Fernández 2006). Moreover, the integrated affect of the environmental variables on \( g \) is complex and may not be multiplicative. In practice, the model requires a number of coefficients in \( f_i(X_i) \), which results in a considerable amount of tuning and calibration to yield reasonable carbon and water fluxes.

Advances in ecophysiological theory have lead to an alternative approach that links leaf net photosynthesis \( A \) to \( g \) as proposed by Ball et al. (1987):

\[ g = m h_s A / C_s + g_0, \]

where \( h_s \) (dimensionless) and \( C_s \) (\( \mu \text{mol mol}^{-1} \)) are the relative humidity and CO2 concentration at the leaf surface, respectively; \( g_0 \) is the leaf minimum (residual) \( g \) (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)) as \( A \) (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)) reaches 0; and \( m \) is a dimensionless parameter. Equation (2) [hereafter Ball–Woodrow–Berry (BWB) model] provides us with an algorithm that can calculate how stomatal conductance correlates with leaf physiological functioning in CO2 assimilation. The BWB model requires only one key parameter \( m \) (\( g_0 \) is deemed less critical when \( A \) is not extremely low), and there is an accumulating body of evidence showing that \( m \) has a constrained value when a plant is free of water stress: it centers around nine for C3 plants and four for C4 plants, which makes it easy for applications (Leuning 1990; Collatz et al. 1991; Harley and Tenhunen 1991; Sellers et al. 1997; Wang et al. 2002a).

Some investigators have criticized the BWB model by arguing that stomatal conductance responds more closely to water vapor pressure deficit (\( D_s \)) than relative humidity because \( D_s \) directly drives leaf water loss which, together with plant hydraulics, controls leaf water potential and leaf turgor pressure (Aphalo and Jarvis 1991; Leuning 1995; Mott and Parkhurst 1991; Monteith 1995; Meinzer et al. 1997; Addington et al. 2004). Leuning (1995) modified the BWB model by replacing \( h_s \) with \( D_s \) at the leaf surface:

\[ g = a_1 A [(C_s - \Gamma)(1 + D_s / D_0)] + g_0, \]

where \( a_1 \) (dimensionless) and \( D_0 \) (Pa) are empirical coefficients, and \( \Gamma \) (\( \mu \text{mol mol}^{-1} \)) represents the CO2 compensation point. The inclusion of \( \Gamma \) improves the model performance at low values of \( C_s \). The Leuning model involves two main parameters \( (a_1 \) and \( D_0 \)), thus adding complexity to model parameterization. Results of independent evaluations on the BWB model and the Leuning model are not always in agreement. While some investigators indicated that the Leuning model performs better (e.g., Van Wijk et al. 2000; Mo and Liu 2001; Arora 2003), other studies showed that it yields no distinguishable improvements, or it performs even worse than the BWB model (e.g., Cox et al. 1998; Betts et al. 1999; Gutschick and Simonneau 2002; Gutschick 2007; J. Wang et al. 2007). Whether \( g \) correlates better with \( h_s \) or \( D_s \) is still debated, and there is no compelling evidence in favor of either approach. Both the BWB model and the Leuning model were originally derived from direct measurement of \( g \) in laboratory-controlled environments. These environments are to some degree artificial and do not capture the diversity or complexity of real-world influences. The models need to be validated using in situ ecosystem measurements. Furthermore, these models were developed based on data measured at the leaf level. In applications, such as hydrological or climate modeling, \( g \) at canopy level is required. Because of the complex structure of canopies, heterogeneity of leaf physiological features, and spatial variations in canopy microclimate, \( g \) varies significantly among plant leaves, which makes it difficult to accurately derive the canopy values from the leaf-level measurements. Models for leaf-to-canopy up-scaling of \( g \) inevitably involve substantial simplifications and assumptions that could lead to large uncertainties. Studies have used the inversion of the Penman–Monteith equation (e.g., Wu et al. 2000; Blanken and Black 2004) or sap flux measurements (e.g., Ewers and Oren 2000; Oren et al. 2001) to estimate \( g \) at the canopy or stand level.

In this study, we developed a new diagnostic parameter to assess the response of canopy-level stomatal conductance to humidity. The parameter is mainly based on the ratio of canopy fluxes of water vapor and CO2. By
using the tower flux measurements made at three boreal forest sites of the Fluxnet Canada Research Network, we critically examined the performance of the BWB model and the Leuning model. We also proposed model improvements to more accurately represent the observed response of stomatal conductance to humidity.

2. Method

The main difference between the BWB model and the Leuning model [Eq. (3)] is the formulation of humidity ($H$). Both models can be rearranged in the form of

$$f(H) = (C_s - \Gamma)(g - g_0)/A,$$  

(4)

where $f(H)$ is a dimensionless function representing the response of $g$ to the humidity of air at the leaf surface. The $f(H)$ is equal to $m h_i$ in the BWB model and $a/(1 + D_j/D_0)$ in the Leuning model. Note that $\Gamma$ is also included in the BWB model in this study to make the later comparisons consistent. Deriving $f(H)$ directly using Eq. (4) requires measurements of $g$. In field conditions, measuring leaf $g$ is tedious and costly. It is even more challenging to obtain canopy $g$ from leaf-level measurements as a result of the heterogeneities in both canopy and environmental conditions, as discussed earlier. To eliminate $g$, we introduce the following equation for calculating canopy latent heat exchange $LE_{can}$ (W m$^{-2}$) due to transpiration:

$$LE_{can} = L \rho_s [q_{sat}(r_c) - q_s] g_{H2O},$$  

(5)

where $L$ (J kg$^{-1}$) is the latent heat of vaporization of water; $\rho_s$ (kg m$^{-3}$) and $q_s$ (kg kg$^{-1}$) are the density and specific humidity of the air at leaf surface, respectively; $q_{sat}(r_c)$ (kg kg$^{-1}$) is the saturated specific humidity at leaf temperature $T_c$ (°C); and $g_{H2O}$ (m s$^{-1}$) is the canopy $g$ to water vapor. By coupling Eq. (4) with Eq. (5) (Note that $g_{H2O} = \delta g$, where $\delta$ is a parameter accounting for the difference of stomatal conductance to water vapor and to CO$_2$), we can remove $g$ and obtain

$$f(H) = (C_s - \Gamma)LE_{can}/v \delta L \rho_s [q_{sat}(r_c) - q_s] A - (C_s - \Gamma)g_0/A,$$  

(6)

where $v$ is the volume of gas per mole, calculated using the gas law as $v = RT_c/P$, where $R$ is universal gas constant; and $P$ is the atmospheric pressure.

The values of $f(H)$ obtained by Eq. (6) were used as diagnostic parameters to examine the response of canopy $g$ to humidity and to test various stomatal conductance models. Details of the $f(H)$ calculations are given in appendix. In brief, 30-min values of $LE_{can}$ and $A$ were estimated by correcting the ecosystem flux measurements of latent heat ($F_{le}$) and CO$_2$ ($F_{CO2}$) by the ground-surface latent heat flux ($LE_{soil}$) and ecosystem respiration ($R$) simulated by the ecosystem model Ecological Assimilation of Land and Climate Observations [EALCO, Eq. (A1) and (A2)]. The 30-min values of leaf surface variables required to derive $f(H)$ and its analyses (i.e., $C_s$, $q_{so}$, $P$, $T_c$, $h_i$, and $D_j$) were also obtained from the EALCO model [Eqs. (A3)–(A5)]. Variables required in Eqs. (A3)–(A5) were obtained through the numerical solution of the coupled canopy energy–water–CO$_2$ dynamic transfer equations (Wang 2008). Details of the EALCO model references are summarized in appendix.

3. Study sites and data

This study includes three boreal forest sites in Canada that are known as Southern Old Aspen (SOA), Southern Old Black Spruce (SOBS), and Southern Old Jack Pine (SOJP). Table 1 lists the main ecosystem features of these sites. Measurements at the sites were initiated as part of the Boreal Ecosystem–Atmosphere Study (BOREAS; available online at http://daac.ornl.gov/BOREAS/boreas_home_page.html) and have continued under the Boreal Ecosystem Research and Monitoring Sites program (BERMS; available online at http://berms.ccrp.ec.gc.ca) and the Fluxnet Canada Research Network (FCRN; http://www.fluxnet-canada.ca/). A primary goal of the measurement programs is to improve our understanding of the atmosphere–ecosystem interactions and to characterize the critical climatic controls on the energy, water, and carbon cycles of Canadian forests.

The three sites are located near the southern boreal treeline. SOA is approximately 80 km west-southwest of SOBS, and SOJP is about 30 km east-southeast of SOBS. The annual mean air temperature in the area is 0.4°C, with a maximum monthly mean in July (16.2°C) and a minimum monthly mean in January (−17.9°C). The annual precipitation is 467 mm, with nearly 50% of it falling during the three summer months (June–August; Griffis et al. 2004). The forest types of the three sites are mostly popular in the boreal biome. In general, trembling aspen grows in well-drained soils with good water-holding capacity, and it dominates the southern periphery of the boreal forest. Black spruce is commonly found in organic soils with persistently occurring high water tables. Jack pine is well adapted to dry sandy or gravelly soils where other tree species do not survive.

Eddy-covariance (EC) fluxes and surface meteorology were measured at the three sites from scaffold towers. In this study, the 30-min fluxes of ecosystem CO$_2$ and latent
heat refer to the storage-corrected EC measurements above the canopy. The 30-min observations of down-
ward shortwave and longwave radiation, air temperature, humidity, CO₂ concentration, wind speed, precipitation,
and atmospheric pressure were used to drive the EALCO model to simulate the variables required in
calculating EALCO model to simulate the variables required in
the measured ecosystem CO₂ and latent heat fluxes,
since the affect of uncertainties in

4. Results

4a. Analyses of diagnostic parameter f(H) calculations

The values of the diagnostic parameter f(H) using Eq.

(6) are mainly determined by the ratio of LE_{can}/A.

Because LE_{can} and A were obtained by correcting the
measured ecosystem-level latent heat and CO₂ fluxes
using modeled LE_{soil} and R [see Eqs. (A1) and (A2)],
we first analyzed the relative magnitudes of LE_{soil} versus
LE_{can} and R versus A to evaluate the affect of errors
in the modeled LE_{soil} and R on the accuracy of f(H).

Figures 1a–1c show the 30-min values of CO₂ and latent
heat flux components over five consecutive days during
the midgrowing season in 2001 at SOA, SOBS, and SOJP,
respectively. It can be seen that the relative magnitudes of
the flux components varied among the three study
sites. At SOA (Fig. 1a), LE_{can} reached above 400 W
m⁻², which was remarkably higher than LE_{soil}, which
was typically below 20 W m⁻². The value of A exceeded
35 μmol m⁻² s⁻¹ and was several times higher than R,
which was typically below 10 μmol m⁻² s⁻¹. In compar-
ison, both LE_{can} and A were substantially smaller
at SOBS than SOA (Fig. 1b); however, LE_{soil} and R
were both slightly larger, resulting in higher ratios of
LE_{soil}/LE_{can} and R/A at SOBS than at SOA. At SOJP (Fig.
1c), both LE_{can} and A were the lowest among the
three study sites. While R was slightly lower than those
at the other two sites, LE_{soil} was the highest among the
three study sites. These resulted in its highest propor-
tions of LE_{soil} in LE_{can} and R in A among the three
sites. Another feature observed in Figs. 1a–1c is the
presence of high-frequency fluctuations in the mea-
sured F_{LE} and F_{CO₂}. In contrast, the variations of

<table>
<thead>
<tr>
<th>Site</th>
<th>Location</th>
<th>Elevation (MSL)</th>
<th>Dominant species (overstory/understory)</th>
<th>Std age (2000)</th>
<th>Std density (ha⁻¹)</th>
<th>Std height (m)</th>
<th>Max LAI (m² m⁻²)</th>
<th>Soil texture</th>
<th>Soil drainage</th>
<th>Soil carbon (kg m⁻²)</th>
<th>Sensor height (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SOA</td>
<td>53.63°N, 106.20°W</td>
<td>601</td>
<td>Trembling aspen (Populus tremuloides Michx.) /Hazelnut (Corylus cornuta Marsh.)</td>
<td>73</td>
<td>830</td>
<td>21.5</td>
<td>4.4</td>
<td>Loam to clay-loam</td>
<td>Moderate</td>
<td>6.7</td>
<td>39</td>
</tr>
<tr>
<td>SOBS</td>
<td>53.99°N, 105.12°W</td>
<td>629</td>
<td>Black spruce (Picea mariana Mill.)/Sphagnum (Sphagnum fuscum Schimp.) Feathermoss (Pleurozium spp.)</td>
<td>121</td>
<td>5900</td>
<td>7.2</td>
<td>4.2</td>
<td>Sand and clay</td>
<td>Poor</td>
<td>39.2</td>
<td>25</td>
</tr>
<tr>
<td>SOJP</td>
<td>53.92°N, 104.69°W</td>
<td>579</td>
<td>Jack pine (Pinus banksiana Lamb)/Reindeer lichen (Cladina mitis Sandst.) Green alder (Alnus crispa Ait.)</td>
<td>71</td>
<td>1190</td>
<td>12.7</td>
<td>2.5</td>
<td>Coarse sand</td>
<td>Well</td>
<td>3.4</td>
<td>28</td>
</tr>
</tbody>
</table>
LE_{soil} and R are much smoother. As a result, LE_{can} and A display the high-frequency harmonics of the measured \( F_{LE} \) and \( F_{CO2} \) in computing \( f(H) \). In this study, the residual stomatal conductance \( g_0 \) was assigned the general value for C3 plants (0.01 mol m\(^{-2}\) s\(^{-1}\)). The second item in Eq. (6) is about two orders of magnitude less than the first item, so it has little effect on our analyses.

The relative magnitudes of the flux components varied with time of the day (Fig. 2). Because of the large diurnal variations of A and small variations of R, the ratio of R to A was smaller around noontime than in the early morning or late afternoon. On the contrary, the ratio of LE_{soil}/LE_{can} was larger around noontime than in the early morning or late afternoon, especially at SOJP. This is mainly caused by the higher penetration of radiation through canopy to the ground surface at higher solar zenith angles (S. Wang et al. 2007). SOJP had the smallest leaf area index (LAI), which resulted in the largest diurnal variations. Overall, during the study period over the five years, the ratios of total LE_{soil} to total LE_{can} were 0.05, 0.14, and 0.34, and the ratios of total R to total A were 0.32, 0.51, and 0.53 at SOA, SOBS, and SOJP, respectively.
The modeled LE_{soil} and R were compared with results from other studies. Measurements of LE_{soil} at SOA were conducted using thin-walled plastic lysimeters (15 cm diameter by 15 cm deep) during a 15-day rain-free period in midsummer of 1994 (Blanken et al. 2001; Blanken and Black 2004). The mean ratio of LE_{soil} to LE_{can} estimated from this measurement was 0.05. It compares well with the EALCO simulation discussed above. The 30-min values of R were also estimated at the three sites using conventional gap-filling and CO2 flux partitioning approaches (Amiro et al. 2006; Kljun et al. 2006; Barr et al. 2007). These estimates were mainly based on empirical relationships established between soil temperature and nighttime CO2 flux. Their values are shown in Figs. 1a–1c. The R simulated by EALCO showed good agreement with these estimates. A model validation study showed that the errors in EALCO-simulated ecosystem latent heat flux are within 10% (Wang 2008). Given the LE_{soil}/LE_{can} and R/A ratios stated above, errors of 10% in modeled LE_{soil} and R will result in the estimate error of f(H) less than 4%, 7%, and 9% at SOA, SOBS, and SOJP sites, respectively.

b. Evaluations of the BWB model and the Leuning model

Evaluations of the BWB model and the Leuning model [Eq. (3)] were conducted using the diagnostic parameter f(H) [Eq. (6)]. In each test, the corresponding stomatal conductance model was employed in EALCO to simulate the variables required in f(H) calculations. Parameters in both models were finely tuned to ensure that the simulated total evapotranspiration during the study period in the five years was equal to its measured value. This approach was also used in the tests of new models proposed in section 4c.

Figure 3 shows the test results of the BWB model at SOBS. For h_s < 0.7, the BWB model (line) represented the relationship between f(H) and h_s fairly well. However, for higher values of h_s, the linear BWB model substantially underestimated the nonlinear response of g to humidity. To compensate for the bias (underestimation) of the BWB model at high h_s values, the parameter m had to be overestimated in the mid-to-low range of h_s to ensure that the simulated total transpiration was correct. This overestimation was found relatively small because (i) most data were located in the mid-to-low range of h_s, and (ii) high transpiration rates usually occurred around noontime when h_s was relatively low. Nevertheless, our results show that the BWB model is unable to capture the significant increase in canopy g under conditions of high humidity. Similar results were also obtained at SOA and SOJP. Table 2 compares the statistical results of the model performance at the three sites. In general, the f(H) values at SOA were less scattered than those at SOBS, with a higher correlation coefficient (r) and a smaller standard deviation (σ). In contrast, the f(H) values at SOJP were more scattered than those at SOBS, with a lower r and a larger σ.

Figure 4 shows the test results of the Leuning model at SOBS. The parameterization of the Leuning model is more complicated than the BWB model because it...
involves two parameters that are negatively correlated. Leuning (1995) found that a value for $D_0$ of 350 Pa provided the best fit to most of the data, with $D_0$ values of up to 1500 Pa for some datasets. In this study, we tested $D_0$ in the range of 350–1500 Pa at an interval of 230 Pa. The parameter $a_1$ in Eq. (3) was then fine-tuned for each value of $D_0$ to meet the parameterization criterion mentioned earlier. The obtained $(D_0, a_1)$ pair that gave the best fit (least square error) to the observed $f(H)$ was used in our model evaluation, as reported in Table 2 and shown in Fig. 4 (curve). It can be seen that the Leuning model showed similar differences among the three sites to those obtained by the BWB model: SOA had the highest $r$ and smallest $\sigma$, whereas SOJP had the lowest $r$ and largest $\sigma$.

Both the BWB model and the Leuning model showed a large bias in simulating canopy $g$ when humidity was high, although this bias was smaller for the Leuning model. The direct affect of this bias on ecosystem simulations is, therefore, expected to depend on the humidity characteristics of the site. In addition, errors in stomatal conductance at high humidity would be more relevant to the simulation of CO$_2$ flux than water vapor flux because transpiration would be small as a result of the weak driving force in this case. Figures 5 and 6 show frequency distributions of $h_s$ and $D_s$, respectively, during growing season daytime periods. The $h_s$ remained above 70% and $D_s$ remained under 500 Pa approximately 25% of the time, when the BWB model and the Leuning model poorly represent the relationships between canopy $g$ and humidity. Further model improvements are required to capture the response of canopy $g$ to the actual range of humidity variations.

![Fig. 4](image-url)  
**Fig. 4.** The response of canopy stomatal conductance to leaf surface water vapor pressure deficit at SOBS. The data points represent the 30-min values of $f(H)$ calculated by Eq. (6). The curve represents the Leuning model, which was used in the EALCO model for this calculation.

![Fig. 5](image-url)  
**Fig. 5.** Frequency distributions of relative humidity during the study periods in the five years of 2000–04. Values are the average of the three study sites.
c. New models for calculating canopy stomatal conductance

The $f(H)$ values obtained at SOBS (Figs. 3 and 4) clearly showed strong nonlinear relationships between canopy $g$ and humidity. To improve the simulation of this relationship, we propose the following models, which are based on the power function of relative humidity deficit at leaf surface $(1 - h_s)$:

$$f(H) = a(1.0 - h_s)^b,$$  
(7)

with the corresponding canopy stomatal conductance model of

$$g = a(1.0 - h_s)^b A/(C_s - \Gamma) + g_0,$$  
(7a)

and the power function of $D_s$

$$f(H) = a D_s^b,$$  
(8)

with the corresponding canopy stomatal conductance model of

$$g = a D_s^b A/(C_s - \Gamma) + g_0.$$  
(8a)

Parameters $a$ and $b$ in Eqs. (7) and (8) are fit independently and, therefore, have different values.

Equations (7) and (8) were tested separately using the diagnostic parameter $f(H)$. In each test, the corresponding model given above was employed in EALCO, and $a$ and $b$ were determined similarly to Leuning model parameters. Their values are listed in Table 2. Equation (7) (represented by the curve in Fig. 7) substantially improved the estimation of canopy $g$ for the high humidity values. It also largely removed the bias of the BWB model and the Leuning model, Eq. (7) consistently achieved higher $r$ and lower $\sigma$ (Table 2) at all the study sites. Figure 8 shows the test results by using Eq. (8). Compared with the other three models discussed above [i.e., BWB, Leuning, and Eq. (7)], Eq. (8) performed the best in predicting the response of canopy $g$ to humidity. It achieved the highest $r$ and lowest $\sigma$ (Table 2) at the three study sites.

The new models proposed above involve two parameters. We also tested the reciprocal functions of $f(H) = a/(1.0 - h_s)$ and $f(H) = a/D_s$, which contain only one parameter. The stomatal conductance models corresponding to these two reciprocal functions were employed in EALCO, and the parameter $a$ was calibrated...
similarly to the procedures when the BWB model was used. Table 2 summarized the model test results at the three study sites. For the model of \( f(H) = a/(1.0 - h_s) \), the performance only slightly degraded from its corresponding model of Eq. (7). This is mainly because the \( \beta \) values in Eq. (7) were close to \(-1.0\) (particularly at SOBS where \( \beta = -1.0 \)). For the model of \( f(H) = a/D_s \), the degradation of the model performance was the largest at SOA and smallest at SOJP because the \( \beta \) value in Eq. (8) at SOA (\(-0.65\)) was deviated more from \(-1.0\) than that at SOJP (\(-0.75\)). Overall, the model using reciprocal functions of \((1.0 - h_s)\) performed better than the BWB model and the Leuning model at all three sites. The model using reciprocal functions of \( D_s \) performed better at SOJP but worse at SOA than the BWB model and the Leuning model. At SOBS, it performed better than the BWB model but worse than the Leuning model. It is worth mention that the parameter values in the various stomatal conductance models tested in this study were obtained to yield the correct grand totals of canopy water flux rather than to best fit the observed \( f(H) \) data, as used in some other studies (e.g., Blanken and Black 2004). The latter approach will give higher \( r \) and lower \( \alpha \), but it excludes the fact of different weightings of \( g \) in transpiration.

5. Discussion and conclusions

The response of canopy stomatal conductance to humidity was studied by developing a new diagnostic parameter \([f(H)\) in Eq. (6)] derived from coupling the canopy transpiration equation with photosynthesis-based stomatal models. Our approach is based on the ratio of canopy water vapor and \( \text{CO}_2 \) fluxes rather than their real quantities. This reduces the affect of uncertainties in measurement accuracies and the energy closure problems that existed in flux measurements using the eddy-covariance method (Barr et al. 2006). It also reduces the effects of high-frequency noise in the 30-min EC flux data, which sometimes can be hardly explained by the corresponding environmental variables. The method enables us to evaluate the response of \( g \) to humidity without requiring \( g \) measurements. The method works at the canopy level, which is beneficial for most land surface and hydrology schemes as they operate at canopy level. Moreover, it provides the opportunity to take advantage of the large volume of EC flux measurements accumulated over various biomes around the world in the last two decades for studying the \( g \) and humidity relationships. During our selected study period, the number of data points used for model tests at each site was greater than 6000 or 7000 (Table 2). The method relies on the corrections of measured ecosystem water and \( \text{CO}_2 \) fluxes to their corresponding canopy fluxes. As such, when reliable data are not available for the corrections, the method has higher confidence when applied for ecosystems with higher canopy closures.

Our results showed that the BWB model resulted in large underestimates in \( g \) when \( h_s > 70\% \). The Leuning model reduced this bias, but it still did not adequately capture the increase of \( g \) when \( D_s < 500 \text{ Pa} \). Note that the difference in \( g \) predictions between the two models cannot be directly interpreted as the difference in energy and mass flux modeling because the weightings of \( g \) in controlling leaf transpiration and \( \text{CO}_2 \) influx vary with environmental conditions. For example, the same errors in \( g \) estimation would have a much larger impact on transpiration simulations under low humidity than under high humidity. Because the largest bias of the two models are in the high values of humidity, their effect on flux simulations may, therefore, be reduced. It also implies that the differences of the model performances depend on the humidity conditions of the site. This partially explains the variations in the existing evaluation results of the two models, as mentioned earlier.

The model that employs the power function of \( D_s \) [Eq. (8)] substantially improved the accuracies in predicting the canopy stomatal response to humidity. The model that employs the power function of \( 1 - h_s \) (Eq. 7) also performed fairly well. The model comparison results are consistent among the three study sites. It implies that the new models proposed are independent of site measurements and ecosystems characteristics. Experiments on model parameterizations show that the parameters in the new models are relatively stable among the three study sites. Our results are in general agreement with those in Blanken and Black (2004), Wu et al. (2000), and Lloyd (1991), in which better results in predicting \( g \) were obtained when the linear function of \( h_s \) in the BWB model was replaced by the reciprocal function of \( D_s \). In other studies, Berninger and Hari (1993) obtained a mathematical solution of stomatal sensitivity to the square root of \( D_s \) based on the optimization theory. Oren et al. (1999, 2001) used a logarithm function of \( D_s \) to model the response of \( g \) and analyzed data from a variety of sources employing both porometric and sap flux measurements of \( g \). They found that stomatal sensitivity is proportional to the magnitude of \( g \) at low \( D_s \). All these models permit a much higher rise in \( g \) with increasing humidity than those used in the BWB and Leuning models. It is worth mentioning that measurement errors at high humidity can have a large influence on the estimate of stomatal sensitivity. This can be seen from the large scattering of \( f(H) \) values at high humidity in Figs. 3, 4, 7, and 8, as the difference between \( q_{\text{sat}}(r_s) \) and \( q_s \) in Eq. (6) became very small.
Ewers and Oren (2000) analyzed the errors in the calculation of $g$ from sap flux measurements and suggested that, given the uncertainties in sap flux and humidity measurements, estimates of $g$ should be limited to conditions in which $D_s \geq 0.6$ kPa to keep errors in $g$ estimates less than 10%.

Our results from best curve-fitting excises of the observed $f(H)$ data (not shown) indicate that models based on water vapor pressure deficits generally yielded higher $r$ and smaller $\sigma$ than those based on relative humidity at the three study sites. This can also be seen by the scattering of fewer $f(H)$ versus $D_s$ distributions in Figs. 4 and 8 than that of the $f(H)$ versus $h_s$ distributions in Figs. 3 and 7. This finding is consistent with the hypothesis that stomatal aperture responds to the leaf water loss because water vapor pressure deficit rather than relative humidity directly drives the transpiration rate of canopy leaves.

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APPENDIX

Calculations of Variables in Eq. (6)

The latent heat exchange due to canopy transpiration ($\text{LE}_{\text{can}}$) and the canopy CO$_2$ assimilation rate ($A$) were obtained by modifying the eddy covariance (EC) flux measurements using

$$\text{LE}_{\text{can}} = F_{\text{LE}} - \text{LE}_{\text{soil}} - \text{LE}_{\text{Ecan}}, \quad \text{and} \quad A = F_{\text{CO}_2} + R, \quad \text{(A1)}$$

where $F_{\text{LE}}$ and $F_{\text{CO}_2}$ are the EC-measured ecosystem latent heat and CO$_2$ fluxes (storage corrected), respectively; $\text{LE}_{\text{soil}}$ and $R$ are the soil latent heat exchange and ecosystem respiration simulated by the EALCO model, respectively; and $\text{LE}_{\text{Ecan}}$ is the latent heat exchange due to the evaporation of canopy intercepted precipitation or dew on the canopy. Note that in our study, data with $\text{LE}_{\text{can}} > 0$ were filtered out. All the items in Eqs. (A1) and (A2) are in 30-min time step.

The CO$_2$ concentration at leaf surface $C_i$ ($\mu$mol mol$^{-1}$) was calculated as

$$C_i = (C_{a}g_{h} + C_{i}g)/(g_{h} + g), \quad \text{(A3)}$$

where $C_i$ is the atmospheric CO$_2$ concentration measured above the canopy, $C_{a}$ is the leaf intercellular CO$_2$ concentration, $g_{h}$ is aerodynamic conductance, and $g$ is the canopy stomatal conductance. While $C_{a}$ was available from field measurements, other variables were simulated using the EALCO model at 30-min time step.

The specific humidity of the air at leaf surface $q_s$ (kg kg$^{-1}$) was obtained similarly using

$$q_s = [q_{a}g_{h} + q_{\text{sat} (T_c)}g]/(g_{h} + g), \quad \text{(A4)}$$

where $q_s$ is the specific humidity of the air measured above the canopy, and $q_{\text{sat} (T_c)}$ is the saturated specific humidity at leaf temperature $T_c$. The $q_{\text{sat} (T_c)}$ was assumed to represent the specific humidity of the air in the leaf intercellular space. While $q_s$ was available from the field measurements, other variables were simulated using the EALCO model at 30-min time step. Water vapor pressure deficit and relative humidity at leaf surface, $D_s$ and $h_s$, respectively, can then be calculated after $q_s$ is known.

The air density $\rho_a$ was calculated in EALCO using

$$\rho_a = P_{\text{dry}}/R_{\text{air}}T_c + e_a/(R_{\text{vap}}T_c), \quad \text{(A5)}$$

where $e_a$ is the water vapor pressure, $P_{\text{dry}}$ is the dry atmosphere pressure calculated as the difference between atmosphere pressure $P$ and $e_a$, and $R_{\text{air}}$ and $R_{\text{vap}}$ are the gas constants for dry air and for water vapor, respectively.

The canopy variables in Eq. (A1) (i.e., $\text{LE}_{\text{can}}$) and in Eqs. (A3)–(A5) were obtained in the EALCO model through numerically solving the coupled canopy energy–water–CO$_2$ dynamic transfer equations, as detailed in S. Wang et al. (2007) and Wang (2005, 2008). The soil-surface latent heat exchange in Eq. (A1) was obtained in the EALCO model through solving the ground-surface energy balance equation, as detailed in Zhang et al. (2008). The ecosystem respiration in the EALCO model includes soil heterotrophic respiration and plant autotrophic respiration. The former is controlled by the soil carbon quantity and quality, as well as soil environmental conditions including soil temperature, moisture, and nutrients. A six-layer soil scheme was used in this study. The latter is composed of plant growth respiration, which is determined by the plant growth rates, and maintenance respiration, which is controlled by the living biomass amount and the temperatures of
the soil (for belowground plant tissue respiration) and the canopy (for aboveground plant tissue respiration). Three plant carbon pools representing foliage, sapwood, and fine roots were recognized for the calculations of autotrophic respiration in this study. Detailed algorithms for the plant and soil respiration simulations can be found in Wang et al. (2001, 2002b).

REFERENCES


