



**Modeling stomatal
conductance in the
Earth system**

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Modeling stomatal conductance in the Earth system: linking leaf water-use efficiency and water transport along the soil-plant-atmosphere continuum

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Abstract

The empirical Ball–Berry stomatal conductance model is commonly used in Earth system models to simulate biotic regulation of evapotranspiration. However, the dependence of stomatal conductance (g_s) on vapor pressure deficit (D_s) and soil moisture must both be empirically parameterized. We evaluated the Ball–Berry model used in the Community Land Model version 4.5 (CLM4.5) and an alternative stomatal conductance model that links leaf gas exchange, plant hydraulic constraints, and the soil–plant–atmosphere continuum (SPA) to numerically optimize photosynthetic carbon gain per unit water loss while preventing leaf water potential dropping below a critical minimum level. We evaluated two alternative optimization algorithms: intrinsic water-use efficiency ($\Delta A_n/\Delta g_s$, the marginal carbon gain of stomatal opening) and water-use efficiency ($\Delta A_n/\Delta E_l$, the marginal carbon gain of water loss). We implemented the stomatal models in a multi-layer plant canopy model, to resolve profiles of gas exchange, leaf water potential, and plant hydraulics within the canopy, and evaluated the simulations using: (1) leaf analyses; (2) canopy net radiation, sensible heat flux, latent heat flux, and gross primary production at six AmeriFlux sites spanning 51 site–years; and (3) parameter sensitivity analyses. Without soil moisture stress, the performance of the SPA stomatal conductance model was generally comparable to or somewhat better than the Ball–Berry model in flux tower simulations, but was significantly better than the Ball–Berry model when there was soil moisture stress. Functional dependence of g_s on soil moisture emerged from the physiological theory linking leaf water-use efficiency and water flow to and from the leaf along the soil-to-leaf pathway rather than being imposed a priori, as in the Ball–Berry model. Similar functional dependence of g_s on D_s emerged from the water-use efficiency optimization. Sensitivity analyses showed that two parameters (stomatal efficiency and root hydraulic conductivity) minimized errors with the SPA stomatal conductance model. The critical stomatal efficiency for optimization (ι) was estimated from leaf trait datasets and is related to the slope parameter (g_1) of the Ball–Berry model. The optimized parameter value was consistent with this

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estimate. Optimized root hydraulic conductivity was consistent with estimates from literature surveys. The two central concepts embodied in the stomatal model, that plants account for both water-use efficiency and for hydraulic safety in regulating stomatal conductance, imply a notion of optimal plant strategies and provide testable model hypotheses, rather than empirical descriptions of plant behavior.

1 Introduction

The empirical Ball–Berry stomatal conductance model (Ball et al., 1987; Collatz et al., 1991) combined with the Farquhar et al. (1980) photosynthesis model was introduced into the land component of climate models in the mid-1990s (Bonan, 1995; Sellers et al., 1996; Cox et al., 1998). The stomatal conductance model is based on observations showing that for a given relative humidity (h_s), stomatal conductance (g_s) scales with the ratio of assimilation (A_n) to CO_2 concentration (c_s) such that $g_s = g_0 + g_1 h_s A_n / c_s$. It is now commonly used in land surface models for climate simulation.

Part of the scientific debate about the Ball–Berry model has concerned the form of the vapor pressure deficit term. The Ball–Berry model uses a fractional humidity at the leaf surface, $h_s = e_s / e_*(T_l) = 1 - D_s / e_*(T_l)$ with e_s the vapor pressure at the leaf surface, $e_*(T_l)$ the saturation vapor pressure at the leaf temperature, and $D_s = e_*(T_l) - e_s$ the vapor pressure deficit. Leuning (1995) modified the model to replace h_s with $(1 + D_s / D_0)^{-1}$, where D_s is scaled by the empirical parameter D_0 . Medlyn et al. (2011b) presented a form of the model that uses $D_s^{-1/2}$, derived from water-use efficiency optimization theory. Katul et al. (2009) similarly derived a dependence of g_s on $D_s^{-1/2}$ based on water-use efficiency optimization, and such a dependence is common across many plant species and functional types (Oren et al., 1999).

An additional challenge is how to represent stomatal closure as soil moisture declines. The Ball–Berry model is appropriate for well-watered soils. Various empirical

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functions directly impose diffusive limitations in response to soil drying by decreasing the slope parameter (g_1). Other approaches impose biochemical limitations and decrease g_s by reducing A_n as soil water stress increases. Neither method completely replicates observed stomatal response to soil water stress (Egea et al., 2011; De Kauwe et al., 2013).

An alternative approach models g_s directly from optimization theory. This theory assumes that the physiology of stomata has evolved as a compromise to constrain the rate of water loss for a given unit of carbon gain (Cowan, 1977; Cowan and Farquhar, 1977). This optimization can be achieved by assuming that g_s varies to maintain water-use efficiency constant over some time period (e.g., the model time step). The empirical Ball–Berry model, despite not being constructed explicitly as an optimality model, is consistent with this theory; a theoretical form of the model can be derived from water-use efficiency optimization, after some simplifying assumptions (Katul et al., 2010; Medlyn et al., 2011b). For example, Medlyn et al. (2011b) obtained $g_s = g_0 + 1.6(1 + g_1 D^{-1/2}) A_n / c_a$, where here vapor pressure deficit and CO_2 concentration refer to ambient air.

Additional understanding of stomatal behavior comes from the transport of water through the soil–plant–atmosphere continuum. Water flows down potential gradients from the soil matrix to the leaf epidermis, maintained by water loss through the stomata. The rate of flow is proportional to the conductance of the entire soil-to-leaf path, which is a function of soil properties, plant hydraulic architecture, xylem construction, and leaf boundary layer, mesophyll and stomatal conductances. Rates of water loss cannot on average exceed the rate of supply without ultimately resulting in desiccation (Meinzer, 2002). Thus, the collective architecture of the soil and plant hydraulic systems must ultimately control the maximum rate of water use. Air intrusion into either the soil matrix or xylem matrix reduces the conductivity of each medium, and it is widely accepted that there is a limit to the maximum rate of water transport under a given set of hydraulic circumstances. If additional suction beyond this point is applied to the continuum, rates of water supply decline, leading to desiccation in the absence of

stomatal control (Sperry et al., 2002). Significant evidence has accumulated that stomatal conductance and leaf water content are strongly linked to plant and soil hydraulic architecture (Mencuccini, 2003; Choat et al., 2012; Manzoni et al., 2013). Despite this, efforts to account for the physics of water transport in the land surface models used with Earth system models have been limited.

Many models of plant hydraulic architecture exist that explicitly represent the movement of water to and from the leaf (McDowell et al., 2013). Here, we adopted (and modified) the approach used by the soil–plant–atmosphere model (SPA; Williams et al., 1996, 2001a), which combines both instantaneous water-use efficiency and a representation of the dynamics of leaf water potential in the same framework. Stomatal conductance is incremented until further opening does not yield a sufficient carbon gain per unit water loss or further opening causes leaf water potential to decrease below a minimum sustainable leaf water potential. Similar approaches have been adopted by, among others, Tuzet et al. (2003) and Duursma and Medlyn (2012).

We compared the Ball–Berry stomatal conductance model used in the Community Land Model version 4.5 (CLM4.5), the land component of the Community Earth System Model, with the SPA stomatal parameterization. We tested whether the performance of the alternative stomatal conductance models can be distinguished in comparisons of model simulations with eddy covariance flux tower data. The SPA parameterization optimizes intrinsic water-use efficiency ($iWUE$; $\Delta A_n / \Delta g_s$, the marginal carbon gain of stomatal opening). Because this approach has no inherent stomatal response to vapor pressure deficit, we additionally tested an alternative optimization based on water-use efficiency (WUE ; $\Delta A_n / \Delta E_l$, the marginal carbon gain of water loss).

2 Methods

We evaluated the stomatal models in a common canopy modeling framework at 6 AmeriFlux sites comprising a total of 51 site–years. The canopy model was forced with gap-filled tower meteorology from the North American Carbon Program (NACP) site

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synthesis (Schaefer et al., 2012). We compared the simulations with tower net radiation (R_n), sensible heat flux (H), latent heat flux (λE), and gross primary production (GPP). R_n , H , and λE were obtained from the AmeriFlux Level 2 dataset. None of these fluxes were gap-filled. Gross primary production was from the NACP site synthesis (Schaefer et al., 2012). The gap-filled meteorological data and tower fluxes for these six sites were used in the development of CLM4.5 (Oleson et al., 2013).

2.1 Flux tower sites

The 6 AmeriFlux sites represented 3 deciduous broadleaf forests (DBF) and 3 evergreen needleleaf forests (ENF) spanning a range of climates (Table 1). Site descriptions were taken from published literature (Table 2):

1. US-Ha1 is a mixed species temperate deciduous forest located at Harvard Forest in central Massachusetts (Urbanski et al., 2007). The climate is temperate continental with warm summers (Köppen climate Dfb).
2. US-MMS is a mixed species temperate deciduous forest located at the Morgan Monroe State Forest in south-central Indiana (Schmid et al., 2000). The climate is humid subtropical (Köppen climate Cfa).
3. US-UMB is a northern hardwood forest located at the University of Michigan Biological Station (Schmid et al., 2003). The climate is temperate continental with warm summers (Köppen climate Dfb).
4. US-Dk3 is a loblolly pine plantation located at the Duke Forest in North Carolina (Siqueira et al., 2006; Stoy et al., 2006). The climate is humid subtropical (Köppen climate Cfa). The years 2001 and 2002 had mild and severe drought, respectively.
5. US-Ho1 is an evergreen needleleaf forest located at Howland Forest in Maine (Hollinger et al., 1999). The climate is temperate continental with warm summers (Köppen climate Dfb).

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6. US-Me2 is the *Metolius* intermediate aged ponderosa pine forest in central Oregon (Thomas et al., 2009). The climate is dry-summer subtropical (Köppen climate Csb). The years 2002–2003 were anomalously dry and 2006 was anomalously wet.

2.2 Model formulation

Leaf assimilation, stomatal conductance, and leaf water potential can have strong vertical gradients within the canopy. Many of the sites used in this study have high leaf area indices ($> 3 \text{ m}^2 \text{ m}^{-2}$) and highly contrasting radiative environments through the canopy. The SPA optimization is numerical, and cannot be resolved arithmetically in the manner of a “big leaf” approximation. Therefore, we simulated the leaf water potential state and all other related fluxes at multiple layers through the canopy.

We used a multi-layer canopy model (Fig. 1), similar to CANVEG (Baldocchi and Meyers, 1998; Baldocchi and Wilson, 2001; Baldocchi et al., 2002) and SPA (Williams et al., 1996, 2001a) but adapted for CLM4.5, to evaluate the stomatal models. The multi-layer model combines information about plant canopy structure, radiative transfer, leaf physiology and gas exchange, and the canopy microenvironment to simulate scalar flux exchanges with the atmosphere. It builds upon the canopy model of Bonan et al. (2011, 2012), but also utilizes the functionality of CLM4.5 (for canopy turbulence and model parameter values; Oleson et al., 2013). Within this model structure, we implemented the Ball–Berry and SPA stomatal parameterizations.

The canopy is divided into multiple leaf layers, each with a sunlit and shaded fraction. Radiative transfer of visible, near-infrared, and longwave radiation is calculated at each layer, accounting for scattering within the canopy (Fig. 1a). Photosynthesis, stomatal conductance, leaf temperature, and the leaf energy balance are coupled at each layer (Fig. 1b). The Ball–Berry model requires an iterative calculation of g_s and A_n (Fig. 2a). The SPA stomatal optimization, in contrast, calculates g_s for each canopy layer to maximize A_n within the limitations imposed by plant water storage, soil-to-leaf water transport, and their combined impact on leaf water status (Fig. 2b). Stomata conductance

is incremented at each time step until either further opening does not yield a sufficient carbon gain per unit water loss (defined by a stomatal efficiency parameter) or further opening causes leaf water potential (ψ_l) to decrease below a minimum value (ψ_{lmin}). The SPA model defines the critical stomata efficiency based on intrinsic water-use efficiency (i_* ; $\Delta A_n / \Delta g_s$). An alternative stomatal efficiency can be defined by water-use efficiency (i ; $\Delta A_n / \Delta E_l$). We tested both optimizations, designated SPA-iWUE and SPA-WUE, respectively. Leaf water potential and water supply to foliage are calculated from soil–plant–atmosphere continuum theory based on leaf transpiration rate (E_l), soil water potential (ψ_s), plant capacitance (C_p), and the hydraulic conductance of the soil-to-leaf pathway (k_L). This conductance integrates in series the aboveground stem conductance (k_p) and the belowground conductance defined by a soil-to-root conductance (k_s) and a root-to-stem conductance (k_r) within each soil layer (Fig. 1c). Plant conductances are static, but the soil-to-root conductance is a function of soil hydraulic conductivity and the density of the root matrix. The full model is described in Appendix A.

2.3 Model parameters

Table 3 lists parameters specified by plant functional type, and Table 4 lists site-specific parameters. Plant functional type parameters are from CLM4.5, except for the SPA stomatal optimization model. A key parameter is the maximum carboxylation rate at 25 °C ($V_{c_{max25}}$). We used values from Kattge et al. (2009), also used in the simulations of Bonan et al. (2011, 2012), which are generally consistent with site-specific estimates calculated from observed foliage nitrogen (Table 5). The largest deviation is for US-UMB and US-Me2, where the model $V_{c_{max25}}$ is larger than the observationally-based estimate. Values for additional photosynthetic metabolic parameters (J_{max25} , T_{p25} , and R_{d25}) are proportional to $V_{c_{max25}}$ (Bonan et al., 2011, 2012). The SPA stomatal optimization requires four additional parameters that describe plant water relations and four parameters for fine roots.

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2.3.1 Minimum leaf water potential

Minimum leaf water potential values are related to xylem function (Choat et al., 2012) and can be observed directly. For this study, we used a moderate value of $\psi_{\min} = -2$ MPa. This is similar to values used in previous SPA simulations for arctic ecosystems and black spruce boreal forest (-1.5 MPa; Williams et al., 2000; Hill et al., 2011), ponderosa pine (-1.7 to -2.0 MPa; Williams et al., 2001a, b; Schwarz et al., 2004), deciduous forest (-2.5 MPa; Williams et al., 1996), tropical rainforest (-2.5 MPa; Williams et al., 1998; Fisher et al., 2007), and Australian woodland (-2.8 MPa; Zeppel et al., 2008).

2.3.2 Plant capacitance

Plant capacitance controls the timing of plant water use throughout the day. High values mean that there is a large buffer at the beginning of the day, before (in dry soils) water use is eventually limited to the rate of supply directly from the soil. Capacitance can be measured directly using paired sap flow observations (e.g., Goldstein et al., 1998). We used $C_p = 2500 \text{ mmol H}_2\text{O m}^{-2} \text{ leaf area MPa}^{-1}$. Previous SPA simulations used a range of values for black spruce boreal forest (2000; Hill et al., 2011), tropical rainforest (2300; Fisher et al., 2007; derived from Goldstein et al., 1998), Australian woodland (5000; Zeppel et al., 2008), and deciduous and tropical forest (8000; Williams et al., 1996, 1998).

2.3.3 Plant hydraulic conductance

The SPA model assumes a constant plant conductance to water. This is a simplification compared to more complex models that diagnose changes in conductance caused by xylem embolism under tension (Sperry et al., 2002; McDowell et al., 2013). However, previous analyses suggest that the majority of soil-to-leaf resistance is belowground (Fisher et al., 2007) and also that the soil-to-root conductance provides an adequate ex-

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planation of the variability in observed soil-to-leaf conductance (Williams et al., 2001a; Zeppel et al., 2008). Previous SPA simulations used stem hydraulic conductivity (not conductance) with a range of values of 3.5–100 mmol H₂O m⁻¹ s⁻¹ MPa⁻¹ (Williams et al., 1996, 1998, 2001a, b; Schwarz et al., 2004; Zeppel et al., 2008; Hill et al., 2011).

5 In contrast, we used a leaf-specific stem hydraulic conductance $k_p = 4 \text{ mmol H}_2\text{O m}^{-2} \text{ leaf area s}^{-1} \text{ MPa}^{-1}$, estimated from stem, root, and whole-plant conductance reported in the literature.

Several studies have estimated the stem portion of whole-plant conductance. Such estimates of stem conductance vary with stem diameter or branch location. 10 Yang and Tyree (1994) reported leaf-specific stem conductance values of 1.4–2.8 mmol H₂O m⁻² s⁻¹ MPa⁻¹ for large maple trees (*Acer saccharum*, *Acer rubrum*). Tyree et al. (1991) reported whole-shoot leaf-specific conductivity (not conductance) of approximately 50 mmol H₂O m⁻¹ s⁻¹ MPa⁻¹ for large maple stems, which converts to 2.5–5 mmol H₂O m⁻² s⁻¹ MPa⁻¹ for 20 m and 10 m tall trees, respectively. Tyree et al. (1998) reported 1–4 mmol H₂O m⁻² s⁻¹ MPa⁻¹ for tropical tree seedlings. Tyree et al. (1993) found a value of 7 mmol H₂O m⁻² s⁻¹ MPa⁻¹ for walnut (*Juglans regia*) saplings.

Few studies report the root portion of whole-plant conductance. A study of *Betula occidentalis* in the field estimated the root and stem conductances to be 8 and 20 22 mmol H₂O m⁻² leaf area s⁻¹ MPa⁻¹, respectively (i.e., the root resistance is approximately 75% of the whole-plant resistance) (Saliendra et al., 1995). Other studies of walnut (Tyree et al., 1994) and tropical tree seedlings (Tyree et al., 1998) found approximately equal root and stem conductances. Federer et al. (2003) assumed equal root and stem conductances in their model.

25 If root and stem conductances are equal, a leaf-specific stem conductance $k_p = 4 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ gives a leaf-specific whole-plant conductance $k_L = 2 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$. Duursma and Medlyn (2012) also used this value for k_L in MAESPA, and it is also consistent with field estimates. Various whole-plant

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(soil-to-leaf) estimates of leaf-specific conductance (k_L) reported in the literature are: 1.1 mmol H₂O m⁻² s⁻¹ MPa⁻¹ for loblolly pine (*Pinus taeda*) in North Carolina (Ewers et al., 2000); on the order of 0.5–1 for aspen (*Populus tremuloides*) and black spruce (*Picea mariana*) and 6–11 for jack pine (*Pinus banksiana*) boreal forest in Manitoba, Canada (Ewers et al., 2005); 1–10 for tropical trees (Meinzer et al., 1995); and 6 for *Betula occidentalis* in the field (Saliendra et al., 1995).

2.3.4 Stomatal efficiency

The stomatal efficiency parameter (ι_* or ι , $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$) defines the water-use strategy (Williams et al., 1996). Low values, where a small increase in assimilation allows a unit of stomatal opening, optimize at high A_n , high g_s , and high E_i ; plant water storage can be depleted, causing stomata to close in early-afternoon. Higher values, with a larger marginal return, define a more conservative strategy. Optimization is achieved at lower g_s , so that A_n and E_i are also lower. This reduces afternoon water stress, but restricts daily GPP.

We tested two alternative definitions of stomatal efficiency: ι_* , based on intrinsic water-use efficiency ($\Delta A_n / \Delta g_s$); and ι , based on water-use efficiency ($\Delta A_n / \Delta E_i$). We estimated ι_* to match observed relationships between A_n and g_s in the Glopnet leaf trait database (Wright et al., 2004). ι is related to ι_* by vapor pressure deficit ($\iota_* = \iota D_s$), as given by Eq. (A17). We estimated ι assuming $D_s = 0.01 \text{ mol mol}^{-1}$ ($\sim 1 \text{ kPa}$) for the Glopnet data (the Glopnet data report maximum A_n and g_s , which we assumed occurred with humid air). Given this assumption, baseline values are $\iota_* = 7.5$ and $\iota = 750 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$. For evergreen needleleaf forest, we tested a more conservative water-use strategy, $\iota_* = 15$ and $\iota = 1500 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$.

2.3.5 Root conductance

Hydraulic conductivity of the soil-to-root pathway requires an estimate of root length density (mm^{-3}) as a vertical profile. To estimate this, the model uses root biomass, root

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radius and root density as inputs. We estimated fine root (≤ 2 mm diameter) biomass, radius, and density from the Jackson et al. (1997) literature survey. Live fine root biomass in temperate deciduous and coniferous forests averages 440 and 500 gm^{-2} , respectively. We used $M_T = 500 \text{ gm}^{-2}$. This is comparable to values of 400 – 1000 gm^{-2} used in previous SPA simulations (Williams et al., 2001a; Schwarz et al., 2004; Fisher et al., 2007; Hill et al., 2011). The mean fine root radius of trees is $r_r = 0.29$ mm and the specific root length is 12.2 mg^{-1} (Jackson et al., 1997), so that the specific root density is $r_d^{-1} = 12.2 \text{ mg}^{-1} \times \pi r_r^2 = 0.31 \text{ gcm}^{-3}$. Williams et al. (2001a) used $r_r = 0.50$ mm and $r_d = 0.50 \text{ gcm}^{-3}$ in ponderosa pine simulations, and Zeppel et al. (2008) used $r_r = 0.10$ mm in Australian woodland simulations.

We used root hydraulic resistivity $R_r^* = 25 \text{ MPa s g mmol}^{-1} \text{ H}_2\text{O}$. Shimizu et al. (2005) reported root hydraulic resistivity values $< 5 \text{ MPa s gmmol}^{-1}$ for saplings of six tropical tree species. Tyree et al. (1998) reported values of 5 – $36 \text{ MPa s gmmol}^{-1}$ for seedlings of five tropical tree species. Rieger and Litvin (1999) reported root hydraulic conductivity (per unit length) of several woody plant species ranges from about 0.55 – $5.5 \times 10^{-3} \text{ mmolm}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$, equivalent to a resistivity of 15 – $150 \text{ MPa s gmmol}^{-1}$ with a specific root length of 12.2 mg^{-1} . Other SPA simulations used values of 3 – $400 \text{ MPa s gmmol}^{-1}$ (Williams et al., 2001a, b; Schwarz et al., 2004; Zeppel et al., 2008). With fine root biomass $M_T = 500 \text{ gm}^{-2}$, $R_r^* = 25 \text{ MPa s gmmol}^{-1}$ gives a total root conductance of $20 \text{ mmolm}^{-2} \text{ ground area s}^{-1} \text{ MPa}^{-1}$, or $4 \text{ mmolm}^{-2} \text{ leaf area s}^{-1} \text{ MPa}^{-1}$ in a forest with a leaf area index of $5 \text{ m}^2 \text{ m}^{-2}$. This is equal to our leaf-specific stem conductance, consistent with our notion of equal stem and root conductance and our whole-plant leaf-specific conductance $k_L = 2 \text{ mmolm}^{-2} \text{ leaf area s}^{-1} \text{ MPa}^{-1}$. For evergreen needleleaf forest, we additionally tested $R_r^* = 75 \text{ MPa s gmmol}^{-1}$, obtained from parameter optimization analysis. In this case, $k_L = 1 \text{ mmolm}^{-2} \text{ leaf area s}^{-1} \text{ MPa}^{-1}$.

2.4 Model simulations and evaluation

2.4.1 Canopy-scale simulations

We used meteorological observations at the flux tower sites to drive the canopy model and eddy covariance observations from those same towers to evaluate the model. The gap-filled tower meteorology was available at either 30 min or 60 min frequency depending on site (Table 4). Similar simulations were performed to evaluate CLM4.5. Those simulations specified CO₂ concentration at 367 μmol mol⁻¹, which we also used. We only used data for the month of July to evaluate the simulations, to constrain the model without seasonal changes in leaf area or soil water. Our intent was to use the SPA stomatal conductance model to diagnose deficiencies in the performance of the CLM4.5 canopy flux parameterization given specified soil water. Soil temperature was initialized from a spin-up simulation that repeated the July forcing data. Soil moisture inputs were obtained from CLM4.5 simulations for the tower sites, with the same forcing. The canopy model additionally used the tower height, canopy height, plant functional type, leaf area index, and soil texture at each tower site.

Vegetation and soil parameters were from CLM4.5, based on the vegetation and soil texture of each tower site (Oleson et al., 2013). A single plant functional type (broadleaf deciduous tree or needleleaf evergreen tree) was used for each site. Canopy top height (h_{top}) was specified from the tower canopy height, and the bottom height (h_{bot}) was obtained using the CLM4.5 ratio of top and bottom heights (evergreen needleleaf tree, 17/8.5 m; deciduous broadleaf tree, 20/11.5 m). Roughness length (z_0) and displacement height (d) were specified in proportion to canopy height as in CLM4.5 ($z_0 = 0.055h_{\text{top}}$ and $d = 0.67h_{\text{top}}$). We used the same leaf area index as in CLM4.5 for the flux tower sites (Table 5). Those values, obtained from high resolution CLM4.5 surface datasets, are comparable to values reported for July in site syntheses (Table 2) as well as the AmeriFlux Level 2 dataset and Ollinger et al. (2008). The $V_{\text{C,max}25}$ values are comparable to values estimated from observed foliage nitrogen at each site (Table 5).

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The largest discrepancy is for US-Me2, where leaf area index is 36 % too high and $V_{c_{\max}25}$ is 30 % too high.

We evaluated the canopy model using flux tower estimates of R_n , H , λE , and GPP. We did not correct the data for systematic errors due to failure in energy balance closure. Other model–data comparisons have forced energy balance closure (e.g., Stöckli et al., 2008), but the reasons for lack of closure are still being debated and include methodological concerns, failure to account for storage terms, and landscape heterogeneity (Foken, 2008; Hendricks Franssen et al., 2010; Leuning et al., 2012; Stoy et al., 2013). We estimated random errors using the empirical relationships of Richardson et al. (2006, 2012). The probability distribution of random flux errors is described by a double-exponential, or Laplace, distribution. About 76 % of the values drawn from a double-exponential distribution fall within ± 1 standard deviation of the mean and 94 % fall within ± 2 standard deviations. Richardson et al. (2006, 2012) showed that the standard deviation of the random error, $\sigma(\varepsilon)$, scales with the magnitude of the flux (Table 6).

For each of the 51 sites–years, we performed simulations with baseline parameter values (Table 3) and additionally performed three sets of parameter sensitivity analyses to assess parameter optimization for the Ball–Berry model and the SPA-WUE optimization model. (1) For the Ball–Berry model, we simultaneously varied the intercept g_0 (0.001–0.1 mol H₂O m⁻² s⁻¹) and the slope parameter g_1 (3–15). (2) For the SPA-WUE model, we simultaneously varied four parameters that affect aboveground plant hydraulics: ψ_{\min} (–2 to –4 MPa), k_p (1–20 mmol H₂O m⁻² s⁻¹ MPa⁻¹), C_p (1000–10 000 mmol H₂O m⁻² MPa⁻¹), and ι (500–1500 μ mol CO₂ mol⁻¹ H₂O). (3) In a separate set of simulations with the SPA-WUE model, we simultaneously varied four parameters that govern belowground root conductance: M_r (400–1000 g m⁻²), r_r (0.1–0.5 mm), r_d (200–500 kg m⁻³), and R_r^* (10–500 MPa s g mmol⁻¹ H₂O). We used latin hypercube sampling to generate a collection of random parameter values with a sample size of $m = 500$ points with $n = 2$ (Ball–Berry) or $n = 4$ (SPA-WUE) variables.

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2. We used the same forcing data as (1) to derive the dependence of g_s on vapor pressure deficit (D_s). Simulations calculated g_s for the SPA-iWUE and SPA-WUE optimization over a range of relative humidity from 5–100 %.
3. We compared relationships between A_n and g_s simulated using the SPA-iWUE and SPA-WUE optimization with observations from the Glopnet leaf trait database (Wright et al., 2004). That database provides maximum A_n and g_s measured at high light, moist soil, and ambient CO_2 . For C_3 plants, A_n ranged from 0.1–35 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, and g_s varied from < 0.05 to $> 1 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$. This reflects a range in photosynthetic capacity, seen in leaf nitrogen concentration that varied from 0.5 % to > 4 % (by mass). We generated similar model data for 100 theoretical leaves that differed in photosynthetic capacity, specified by varying $V_{c_{\text{max}}25}$ from 1.5–150 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. Simulations were for a sunlit leaf at the top of the canopy, at midday (high irradiance), and without water stress ($\psi_l > \psi_{l\text{min}}$). Six different time slices of forcing data were used to sample a range of meteorological conditions. The range of conditions was: $T_{\text{ref}} = 22.5\text{--}27.5^\circ\text{C}$, $u_{\text{ref}} = 1.1\text{--}2.3 \text{ m s}^{-1}$, relative humidity = 44–51 %, $S \downarrow = 852\text{--}895 \text{ W m}^{-2}$, $L \downarrow = 387\text{--}406 \text{ W m}^{-2}$, $P_{\text{ref}} = 976\text{--}985 \text{ hPa}$, and $c_{\text{ref}} = 367 \mu\text{mol mol}^{-1}$. We repeated these simulations for a range of stomatal efficiency parameters ($\iota_* = 5\text{--}15 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ for iWUE optimization; $\iota = 500\text{--}1500 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ for WUE optimization).
4. We compared g_s simulated by the SPA-iWUE and SPA-WUE optimization with the Ball–Berry stomatal index ($A_n/c_s h_s$; Ball et al., 1987) and with the Medlyn et al. (2011b) stomatal index ($A_n/c_s D_s^{-1/2}$). Analyses used results for the sunlit leaf at the top of the canopy, obtained from simulations for the entire month of July 2003. We performed these simulations using 11 values of ι_* (5–15 $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$) for iWUE optimization and 11 values of ι (500–1500 $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$) for WUE optimization.

3 Results

3.1 Leaf-scale analyses

Figure 3 illustrates the SPA stomatal optimization and the role of stomatal efficiency in determining the optimal g_s , A_n , and E_l under well-watered conditions. In these calculations, g_s was specified, and A_n and E_l were calculated for that conductance. The calculated A_n and E_l increase with higher g_s . For both iWUE and WUE optimization, higher values of stomatal efficiency result in both lower A_n , E_l , and g_s at optimization (denoted by open and closed circles in the figure) and higher water-use efficiency. Consider, for example, the iWUE optimization (Fig. 3a): $A_n/E_l = 3.8 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ with $\iota_* = 5$, whereas $A_n/E_l = 5.1 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ with $\iota_* = 15$ (both at 75 % relative humidity). Similar behavior occurs at 45 % relative humidity, and with WUE optimization (Fig. 3b). The two optimization algorithms differ, however, in their response to changes in vapor pressure deficit. With iWUE optimization, the optimal g_s and A_n are nearly insensitive to lower relative humidity (Fig. 3a). With WUE optimization, the optimal g_s and A_n both decrease substantially with lower relative humidity (Fig. 3b).

Simulated g_s does have minor dependence on vapor pressure deficit (D_s) with iWUE optimization (not shown). This dependence arises indirectly, because of changes in leaf temperature and associated changes in A_n . In contrast, WUE optimization produces a sharp reduction in g_s as D_s increases (Fig. 4). The decrease follows the relationship $g_s/g_{s\text{ref}} = 1 - m \ln D_s$, expected from water-use efficiency optimization theory (Katul et al., 2009), and the slope (0.5) is consistent with observations ($m = 0.5\text{--}0.6$) for over 40 species of grasses, deciduous trees, and evergreen trees (Oren et al., 1999; Katul et al., 2009). Simulations using several different values of stomatal efficiency show that over the range $\iota = 500\text{--}1250 \text{ } \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$, $g_{s\text{ref}}$ decreases from 0.41 to $0.24 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$, but m is conserved in the range 0.58–0.48, consistent with observations (Oren et al., 1999; Katul et al., 2009). The relationship $1 - 0.5 \ln D_s$ is itself an approximation of $D_s^{-1/2}$ for $D_s = 0.5\text{--}2.0 \text{ kPa}$ (Katul et al., 2009).

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The iWUE and WUE optimization are both consistent with the range of observations of $A_n - g_s$ from the Glopnet leaf trait database (Fig. 5). The observed measurements reflect maximum rates obtained for high light, moist soils, and ambient CO_2 . For similar conditions, the stomatal optimization simulates comparable increases in A_n with higher g_s as are seen in the observations. With iWUE optimization, the slope of the simulated $A_n - g_s$ relationship increases with larger values of ι_* (i.e., larger ι_* produces higher A_n for a given g_s). Values of ι_* equal to 7.5 and $10 \mu\text{molCO}_2 \text{mol}^{-1} \text{H}_2\text{O}$ generally bracket the empirical relationship, while 5 and $15 \mu\text{molCO}_2 \text{mol}^{-1} \text{H}_2\text{O}$ are biased low and high, respectively (Fig. 5a). Similarly for WUE optimization, ι equal to 750 and $1000 \mu\text{molCO}_2 \text{mol}^{-1} \text{H}_2\text{O}$ replicate the observations, while 500 and $1500 \mu\text{molCO}_2 \text{mol}^{-1} \text{H}_2\text{O}$ are biased low and high, respectively (Fig. 5b). The WUE simulations (with dependence of vapor pressure deficit) have a curvilinear response; the iWUE simulations (without vapor pressure deficit) have a linear response.

The iWUE and WUE optimizations are consistent with empirical and theoretical stomatal conductance models. Stomatal conductance simulated with iWUE optimization is significantly correlated with the Ball–Berry stomatal index ($A_n/c_s h_s$); the correlation with the Medlyn et al. (2011b) stomatal index ($A_n/c_s D_s^{-1/2}$) is weaker (Fig. 6a and b). Stomatal conductance simulated with WUE optimization is well-described by both stomatal indices (Fig. 6c and d). Analyses similar to Fig. 6 but using data simulated with 11 different values of ι_* (5– $15 \mu\text{molCO}_2 \text{mol}^{-1} \text{H}_2\text{O}$) and ι (500– $1500 \mu\text{molCO}_2 \text{mol}^{-1} \text{H}_2\text{O}$) show that the effective slope parameter (g_1) of these relationships decreases with higher stomatal efficiency (Fig. 7). For iWUE (using $A_n/c_s h_s$): $g_1 = 7.55 + 8.20 \exp(-0.1315 \iota_*)$, $R^2 = 0.99$. For WUE (using $A_n/c_s D_s^{-1/2}$): $g_1 = 3.24 + 7.65 \exp(-0.0013 \iota)$, $R^2 = 0.99$. The dependence of g_1 on ι closely approximates $\iota^{-1/2}$, as expected from theory (Medlyn et al., 2011b). The same is not true for iWUE and ι_* .

3.2 Canopy-scale analyses

Figure 8 compares observed and simulated fluxes for US-Ha1 during July 2001. Net radiation is biased low at high radiation for each model. Sensible heat flux is comparable among models. Each equally well replicates the observations, and model fluxes fall within the random error of the observed fluxes. The Ball–Berry model underestimates latent heat flux at high values, but simulated fluxes fall within the random error of the observed fluxes for each model. Gross primary production is similarly comparable among the models. These conclusions are also seen in the average diurnal cycle for the month (Fig. 9). Net radiation is biased low at mid-day, but sensible heat flux, latent heat flux, and GPP are comparable among models.

Taylor diagrams show these results are common across the years 1992–2006 (Fig. 10). Sensible heat flux simulated by the multi-layer canopy model with the Ball–Berry stomata is improved relative to CLM4.5. The SPA-iWUE and SPA-WUE stomatal optimizations are improved compared with Ball–Berry, but are both similar. The Ball–Berry multi-layer canopy model simulates latent heat flux comparable to CLM4.5; the SPA optimizations are improved compared with Ball–Berry. Gross primary production simulated with the multi-layer Ball–Berry stomata is improved compared with CLM4.5, and the SPA optimizations better match the observations.

Similar results are seen at other sites (Fig. 11). The skill of the multi-layer canopy model is generally similar to or improved relative to CLM4.5 for sensible heat flux, latent heat flux, and GPP across sites. The SPA optimization models generally have similar or slightly improved skill compared with the Ball–Berry model. Large improvements in sensible heat flux, latent heat flux, and GPP are seen at US-Me2 with the multi-layer model compared with CLM4.5 and with the SPA optimization models compared with the Ball–Berry model.

At US-Me2, CLM4.5 overestimates the variance of sensible heat flux compared with the observations (Fig. 12a). The multi-layer canopy reduces the variance, and the SPA optimization models are improved relative to the Ball–Berry model. CLM4.5 and the

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multi-layer Ball–Berry model underestimate latent heat flux variance; the SPA-iWUE optimization overestimates the variance; and the SPA-WUE optimization is closer to the observations (Fig. 12b). Marked differences among models are seen in GPP (Fig. 12c). CLM4.5 underestimates the variance and has low correlation with the observations.

5 The multi-layer canopy model performs better. The Ball–Berry multi-layer canopy has higher correlation than CLM4.5, and the SPA-iWUE and SPA-WUE optimizations have still higher correlation and variance comparable to the observations.

The improvements with the SPA optimization models compared with the Ball–Berry model are related to the simulation of soil moisture stress in the stomatal models. The year 2002 had a persistent drought throughout the month of July (Fig. 13). The CLM4.5 soil wetness factor (β_t) used in the Ball–Berry model is low and decreases during the month. The leaf specific hydraulic conductance used in the SPA-WUE optimization is similarly low and decreases during the month. The Ball–Berry model underestimates some high mid-day peak latent heat flux seen in the observations and systematically underestimates GPP. In contrast, the SPA-WUE optimization better replicates latent heat flux and GPP. These differences among stomatal models are evident in scatter plots of observed and simulated fluxes (Fig. 14). The Ball–Berry model overestimates sensible heat flux and underestimates latent heat flux and GPP. The SPA-iWUE optimization overestimates latent heat flux and GPP. The SPA-WUE optimization is somewhat improved compared with the SPA-iWUE optimization. The failure of the Ball–Berry model is related to the implementation of soil moisture stress. Increasing the soil wetness factor (β_t) by 0.3 increases latent heat flux and GPP and improves the simulation (Fig. 14m–p).

10 In 2005, drought developed at US-Me2 in the later two-thirds of the month (Fig. 15). The Ball–Berry and SPA-WUE optimization models both replicate the observed latent heat flux, especially the decline in evapotranspiration as soil moisture stress increases. The Ball–Berry model matches the observed GPP prior to development of soil moisture stress, but as the water stress progresses GPP is biased low. The SPA-WUE optimization simulates GPP consistent with the observations throughout the month. Increasing

the soil wetness factor (β_i) by 0.3 improves GPP for the Ball–Berry model without substantially degrading latent heat flux (not shown).

The SPA optimization simulations for US-Ho1 and US-Me2 used a higher stomatal efficiency ($\iota_* = 15$ and $\iota = 1500 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$) than the other sites ($\iota_* = 7.5$ and $\iota = 750 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$). The higher stomatal efficiency improved the skill of sensible heat flux, latent heat flux, and GPP compared with the lower value, for both the iWUE and WUE optimizations (Fig. 16). Similar or improved results were also obtained with higher root resistivity ($R_r^* = 75 \text{ MPa s g mmol}^{-1} \text{ H}_2\text{O}$). Both parameters decreased maximum latent heat flux and GPP compared with the lower parameter values. At US-Dk3, however, the higher parameter values degraded the model skill, particularly for the WUE optimization.

3.3 Parameter sensitivity analyses

Latin hypercube parameter sampling showed that model error varies to some extent with g_0 and g_1 in the Ball–Berry model (not shown), but failed to distinguish optimal parameter values that minimized model error. This is illustrated in Fig. 17 for US-Ha1 during July 2001. The 50 simulations with the lowest RMSE (i.e., the lowest 10% of the 500 parameter tries) have comparable RMSE with the baseline simulation shown in Fig. 8. Values of $g_0 > 0.05 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ were discriminated against, but values $< 0.01 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ also gave low RMSE (Fig. 17a). Values of g_1 in the 50 simulations with the lowest RMSE ranged from 6–12 (Fig. 17b). This is because there is a negative correlation between g_0 and g_1 in the simulations with low model error (Fig. 18). Similar results occur across other sites and years.

Well-defined values of stomatal efficiency and root resistivity minimized model error for the SPA-WUE optimization (Fig. 19). Optimal parameter values varied from about 600–950 $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ for ι and 25–100 $\text{MPa s g mmol}^{-1} \text{ H}_2\text{O}$ for R_r^* . The baseline parameter values (Table 3) are within this range. Other aboveground and belowground parameters did not differentiate between prior and posterior values. This is

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because ι explains 97% of the variation in RMSE in the simulations that varied the four aboveground plant parameters (Fig. 20a). Root resistivity explains 85% of the variation in RMSE in the simulations that varied the four belowground root parameters (Fig. 20b). The scatter about the regression line in Fig. 20b arises from an additional dependence with fine root biomass (M_T), in which RMSE decreases as M_T increases after accounting for R_r^* . Similar results occur across other sites and years.

4 Discussion

The multi-layer canopy model simulates sensible heat flux and latent heat flux across sites and years that are comparable to or improved relative to CLM4.5; GPP is significantly improved (compare CLM4.5 and the Ball–Berry multi-layer canopy, Fig. 11). CLM4.5 uses a big-leaf canopy parameterization (with sunlit and shaded fractions). A steep decline in leaf nitrogen with depth in the canopy ($K_n = 0.3$) is needed to decrease photosynthetic capacity ($V_{c_{\max 25}}$) and compensate for inadequacies in the absorption of diffuse radiation by shaded leaves in the big-leaf parameterization (Bonan et al., 2012). Co-limitation among the Rubisco-, RuBP, and product-limited rates of assimilation, used in the CLM4.5 big-leaf canopy, also reduces GPP. The multi-layer canopy model uses a more gradual decline in leaf nitrogen, based on observations across many forests (Lloyd et al., 2010), and does not invoke co-limitation.

The SPA-WUE optimization performs significantly better than the Ball–Berry model when there is soil moisture stress (Fig. 13, Fig. 15). In the stomatal optimization, soil moisture control of latent heat flux and GPP is an outcome of plant hydraulic constraints on leaf water-use efficiency optimization, whereas the similar dependence on soil moisture is specified in the Ball–Berry model by adjusting the intercept (g_0) and A_n (through $V_{c_{\max 25}}$) for soil moisture (β_i). The exact form of this soil moisture stress function is unknown, and other approaches adjust the slope (g_1) (Egea et al., 2011; De Kauwe et al., 2013). In our simulations, higher β_i improves the Ball–Berry model (Fig. 14). In contrast, the soil moisture stress emerges from the SPA optimization as a result of root

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uptake, water transport through the stem, and leaf water-use efficiency. Duursma and Medlyn (2012) also implemented the SPA plant hydraulics in the MAESTRA model, with improvement for simulation of drought stress.

At sites without soil moisture stress, improvements with the SPA stomatal optimization are not as evident (Fig. 11). For deciduous broadleaf forests, the skill of latent heat flux and GPP compared with the Ball–Berry model improves slightly at US-Ha1 and more so at US-MMS and US-UMB. All models perform comparably at US-Ho1, an evergreen needleleaf forest. Differences between intrinsic water-use efficiency optimization ($\Delta A_n/\Delta g_s$) and water-use efficiency optimization ($\Delta A_n/\Delta E_l$) are not clear at the canopy scale.

The outcome of the stomatal optimization is much more evident at the leaf scale. The relationship of g_s with vapor pressure deficit (D_s) emerges from the optimization theory, as does the Ball–Berry model and variants, and does not require a priori relationships. The water-use efficiency optimization directly predicts a relationship in which g_s varies in relation to $D_s^{-1/2}$ (Fig. 4), consistent with observations and theory (Oren et al., 1999; Katul et al., 2009, 2010; Medlyn et al., 2011b). Moreover, the functional form of the stomatal model, i.e., $g_s = g_0 + g_1 h_s A_n / c_s$ (Ball et al., 1987) or $g_s = g_0 + 1.6(1 + g_1 D^{-1/2}) A_n / c_a$ (Medlyn et al., 2011b), emerges from the optimization (Fig. 6).

A key parameter in the SPA stomatal optimization is the stomatal efficiency. The stomatal efficiency can be estimated from leaf trait databases of maximum g_s and A_n (Fig. 5). Moreover, it relates closely to the slope (g_1) of the Ball–Berry model and its variants (Fig. 7). Medlyn et al. (2011b) showed that g_1 varies in relation to $(\Gamma_* \lambda)^{1/2}$, where λ is the marginal water cost of carbon gain (the inverse of stomatal efficiency) and Γ_* is the CO_2 compensation point. The intrinsic water-use efficiency optimization does not follow this scaling, but g_1 obtained with water-use efficiency optimization scales with $\iota^{-1/2}$, as expected from theory. Medlyn et al. (2011b) also found that values for g_1 increase with growth temperature (through the temperature

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dependence of Γ_*), are lower in gymnosperms than in angiosperms, and vary in relation to plant water-use strategy. Such variation also manifests in stomatal efficiency, where we found that a higher value (more conservative water-use strategy) minimized model errors at the evergreen needleleaf forest US-Ho1 and US-Me2 (we used $\iota = 1500 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ for these sites, but not US-Dk3) compared with the lower value for deciduous broadleaf forest ($\iota = 750 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$).

Two parameters (ι , stomatal efficiency; and R_r^* , root hydraulic conductivity) minimized errors in the SPA water-use efficiency stomatal optimization model (Fig. 20). Functional relationships among photosynthetic capacity, stomatal conductance, and plant hydraulics may help constrain these and other model parameters. For example, higher stomatal efficiency or high root resistivity both improved simulations at US-Ho1 and US-Me2 (Fig. 16). In fact, it is likely that both traits co-vary with plant carbon–water economics. This suggests a need to include a concept of plant hydraulic architecture in the definition of functional types, noted also by Medlyn et al. (2011b).

5 Conclusion

Stomatal control of energy, water, and CO_2 fluxes is a key component of land–atmosphere coupling in Earth system models. Here, we outline a framework for modeling stomatal conductance that is new to Earth system models. This framework links leaf gas exchange, plant hydraulic constraints, and the soil–plant–atmosphere continuum to numerically optimize photosynthetic carbon gain per unit water loss while avoiding desiccation through low leaf water potential. Thus, we extend the water-use efficiency hypothesis inherent in the Ball–Berry stomatal model (Katul et al., 2010; Medlyn et al., 2011b) with a model that also considers whether the rates of water transport and water use are physiologically plausible. The two concepts, that plants account for both water-use efficiency and for hydraulic safety in their stomatal regulatory physiology, imply a notion of optimal plant strategies, and thus provide testable model hypotheses, rather than empirical descriptions of plant behavior.

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The plant canopy model used in this study provides a complete description of leaf physiology, plant hydraulic architecture, and canopy biometeorology from leaf to canopy scales. The functional form of stomatal responses to vapor pressure deficit and soil moisture stress emerges from theory rather than being imposed a priori, as does the form of the equivalent empirical stomatal conductance model. The discrimination among stomatal models at the leaf scale is seen also at the canopy scale in improved skill of the SPA stomatal optimization.

Credible simulations of land–atmosphere feedbacks in Earth system models require that models be characterized in terms of process parameterizations and assumptions in order to correctly interpret the projections of a future Earth (Medlyn et al., 2011a). The development and evaluation of the land component of Earth system models must embrace a synergy of ecological observations (herein, leaf and canopy fluxes), theory to explain the observations (herein, plant carbon–water economics), numerical parameterizations to mathematically describe that theory, and simulations to evaluate the parameterizations across scales, from leaf to canopy, and ultimately global. The canopy model described here represents a necessary approach to rigorously and comprehensively evaluate process parameterizations for consistency with observations and theory prior to implementation in a full Earth system model. The model code is available upon request from the first author.

Appendix A

A1 Canopy structure and photosynthetic capacity

The canopy is divided into n layers each with leaf area index $\Delta L = 0.1 \text{ m}^2 \text{ m}^{-2}$. The leaf area is evenly distributed between the canopy top and bottom heights. Foliage nitrogen and photosynthetic capacity are distributed with depth in the canopy as in CLM4.5

(Bonan et al., 2012). Foliage nitrogen concentration (per unit leaf area) declines exponentially with greater cumulative leaf area from the canopy top, defined by a decay coefficient (K_n). Photosynthetic parameters ($V_{C_{\max}}$, J_{\max} , T_p , and R_d) scale directly with leaf nitrogen and similarly decrease with depth in the canopy. For example, $V_{C_{\max}}$ at cumulative leaf area index x from the canopy top is given by the equation,

$$V_{C_{\max}}(x) = V_{C_{\max}}(0)e^{-K_n x} \quad (A1)$$

where $V_{C_{\max}}(0)$ is defined at the top of the canopy. K_n scales with $V_{C_{\max}}$ at the canopy top following Lloyd et al. (2010),

$$K_n = \exp\left(0.00963V_{C_{\max}} - 2.43\right) \quad (A2)$$

A2 Radiative transfer

Radiative transfer is calculated from Norman (1979) for visible, near-infrared, and longwave radiation, similar to CANVEG and SPA, and accounts for scattering within the canopy based on leaf reflectance (ρ_l), transmittance (τ_l), and leaf orientation (χ_l) (Fig. 1a). Solar radiation incident on the canopy is partitioned as 50 % visible and 50 % near-infrared. The two shortwave bands are divided into direct and diffuse streams, as in CLM4.5. The canopy is partitioned into sunlit and shaded fractions at each layer, with the sunlit fraction given by,

$$f_{\text{sun}}(x) = e^{-K_b x} \quad (A3)$$

where K_b is the extinction coefficient for direct beam. Shaded leaves receive only diffuse radiation while sunlit leaves receive diffuse and direct beam radiation. Soil albedo is calculated as in CLM4.5 and varies with soil color class and water content of the first soil layer. Leaf emissivity is $\varepsilon_l = 0.98$, and soil emissivity is $\varepsilon_g = 0.96$.

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A3 Leaf model

A3.1 Leaf temperature and energy balance

The leaf model couples photosynthesis, stomatal conductance, leaf temperature, and the leaf energy balance at each layer in the canopy (Fig. 1b). Sensible heat (H_l , W m^{-2}) is exchanged between the leaf with temperature T_l (K) and canopy air with temperature T_a (K),

$$H_l = 2c_p(T_l - T_a)g_{bh} \quad (\text{A4})$$

where c_p is the specific heat of air at constant pressure ($\text{J mol}^{-1} \text{K}^{-1}$) and g_{bh} is the boundary layer conductance for heat ($\text{mol m}^{-2} \text{s}^{-1}$). Latent heat flux (λE_l , W m^{-2}) is linearized about saturation vapor pressure,

$$\lambda E_l = \frac{c_p}{\gamma} [e_*(T_a) + s(T_l - T_a) - e_a] / (g_s^{-1} + g_{bv}^{-1}) \quad (\text{A5})$$

Here, $e_*(T_a)$ is the saturation vapor pressure (Pa) at air temperature, e_a is the vapor pressure (Pa) within the canopy, and s (Pa K^{-1}) is the slope of the saturation vapor pressure function with respect to temperature. The term $\gamma = c_p P_{\text{ref}} / \lambda$ is the psychrometric constant (Pa K^{-1}), with P_{ref} atmospheric pressure (Pa) and λ latent heat of vaporization (J mol^{-1}). The term $g_v = 1 / (g_s^{-1} + g_{bv}^{-1})$ is the total leaf conductance for water vapor ($\text{mol m}^{-2} \text{s}^{-1}$) from stomata (g_s) and the boundary layer (g_{bv}) in series. Leaf temperature is calculated from the energy balance equation,

$$R_{nl} = H_l + \lambda E_l \quad (\text{A6})$$

and

$$T_l - T_a = \frac{R_{nl} - \frac{c_p}{\gamma} [e_*(T_a) - e_a] g_v}{2c_p g_{bh} + \frac{c_p}{\gamma} s g_v} \quad (\text{A7})$$

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with R_{nl} the net radiation for the canopy layer. Leaf boundary layer conductances (g_{bh} and g_{bv}) vary with leaf dimension (d_l) and wind speed (u_a).

A3.2 Photosynthesis

Leaf carbon assimilation is calculated as in CLM4.5, using the Farquhar et al. (1980) photosynthesis model described by Bonan et al. (2012), with the addition of temperature acclimation (Kattge and Knorr, 2007). Net leaf CO_2 assimilation (A_n , $\mu\text{mol}CO_2\text{m}^{-2}\text{s}^{-1}$) is the lesser of three rates,

$$A_n = \min(A_c, A_j, A_p) - R_d \quad (\text{A8})$$

where the rubisco-limited rate is,

$$A_c = \frac{V_{c_{\max}}(c_i - \Gamma_*)}{c_i + K_c(1 + o_i/K_o)} \quad (\text{A9})$$

the RuBP-limited rate is,

$$A_j = \frac{J(c_i - \Gamma_*)}{4c_i + 8\Gamma_*} \quad (\text{A10})$$

and the product-limited rate is,

$$A_p = 3T_p \quad (\text{A11})$$

In these equations, c_i ($\mu\text{mol mol}^{-1}$) is the intercellular CO_2 , Γ_* ($\mu\text{mol mol}^{-1}$) is the CO_2 compensation point, K_c ($\mu\text{mol mol}^{-1}$) and K_o (mmol mol^{-1}) are the Michaelis–Menten constants, and $o_i = 209 \text{ mmol mol}^{-1}$ is the O_2 concentration. The electron transport rate (J , $\mu\text{mol m}^{-2}\text{s}^{-1}$) varies with absorbed photosynthetically active radiation with a maximum rate J_{\max} . The maximum rate of carboxylation ($V_{c_{\max}}$, $\mu\text{mol m}^{-2}\text{s}^{-1}$), maximum

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rate of electron transport (J_{\max} , $\mu\text{mol m}^{-2} \text{s}^{-1}$), triose phosphate utilization rate (T_p , $\mu\text{mol m}^{-2} \text{s}^{-1}$), and leaf respiration rate (R_d , $\mu\text{mol m}^{-2} \text{s}^{-1}$) scale directly with leaf nitrogen concentration according to Eq. (A1). The product-limited rate (A_p) is not relevant for the simulations reported here.

5 A3.3 Stomatal conductance

The Ball–Berry stomatal conductance model (Ball et al., 1987; Collatz et al., 1991) is,

$$g_s = g_0 + g_1 A_n \frac{h_s}{c_s} \quad (\text{A12})$$

10 where g_0 is the minimum conductance ($\text{mol m}^{-2} \text{s}^{-1}$), g_1 is the slope parameter, h_s is the fractional relative humidity at the leaf surface, and c_s ($\mu\text{mol mol}^{-1}$) is the leaf surface CO_2 concentration. The system of equations is solved for the c_i that balances the metabolic assimilation rate, given by Eq. (A8), and the diffusive rate given by,

$$A_n = \frac{g_{bv}}{1.4} (c_a - c_s) = \frac{g_s}{1.6} (c_s - c_i) = \frac{(c_a - c_i)}{1.4g_{bv}^{-1} + 1.6g_s^{-1}} \quad (\text{A13})$$

15 with c_a the CO_2 concentration of air ($\mu\text{mol mol}^{-1}$). This requires an iterative calculation of g_s and A_n , and because the metabolic parameters ($V_{c_{\max}}$, J_{\max} , T_p , R_d , Γ_* , K_c and K_o) that govern assimilation depend on leaf temperature, the entire calculation is iterated until leaf temperature converges within some specified tolerance (Fig. 2a).

20 In this implementation, as in CLM4.5, soil water influences stomatal conductance directly by multiplying g_0 by a soil moisture stress function β_t (with values 0–1) and also indirectly by multiplying $V_{c_{\max}}$ by β_t . Soil moisture stress is calculated for each soil layer and summed, weighted by the relative root fraction of the soil layer (Δf_j). For

unfrozen soil,

$$\beta_t = \sum_j \frac{\psi_c - \psi_j}{\psi_c - \psi_o} \Delta f_j \quad (\text{A14})$$

where ψ_j is the soil water potential of layer j , and ψ_c and ψ_o are the soil water potential at which stomata are fully closed or open, respectively.

The stomatal optimization calculates g_s for each canopy layer to maximize A_n within limitations imposed by plant water storage and soil-to-leaf water transport (Fig. 2b). Stomata conductance is incremented until further opening does not yield a sufficient carbon gain per unit water loss (defined by a stomatal efficiency parameter) or further opening causes leaf water potential to decrease below the minimum sustainable leaf water potential that prevents xylem cavitation (defined by the parameter ψ_{imin}).

We tested two alternative definitions of stomatal efficiency: ι_* , based on intrinsic water-use efficiency (iWUE; $\Delta A_n / \Delta g_s$); and ι , based on water-use efficiency (WUE; $\Delta A_n / \Delta E_l$). These are related by the equations,

$$\frac{A_n}{g_s} = \frac{c_s(1 - c_i/c_s)}{1.6} \quad (\text{A15})$$

and

$$E_l = \frac{(e_i - e_s)}{P_{\text{ref}}} g_s = D_s g_s \quad (\text{A16})$$

where $D_s = (e_i - e_s) / P_{\text{ref}}$ is the vapor pressure deficit at the leaf surface (mol mol^{-1}) and $e_i = e_*(T_i)$ is the vapor pressure in the stomatal cavity. Combining equations gives,

$$\frac{A_n}{E_l} = \frac{c_s(1 - c_i/c_s)}{1.6 D_s} = \frac{A_n}{g_s} \frac{1}{D_s} \quad (\text{A17})$$

For iWUE optimization, g_s is incremented by a small amount ($\Delta g_s = 1 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) until $\Delta A_n \leq \iota_* \Delta g_s$. The same procedure applies to WUE optimization, but with $\Delta A_n \leq \iota D_s \Delta g_s$.

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A4 Plant hydraulics

A4.1 Leaf water potential

The change in leaf water potential (ψ_l , MPa) of each canopy layer is governed by the equation,

$$5 \quad \frac{d\psi_l}{dt} = \frac{k_L (\bar{\psi}_s - \rho_w g h 10^{-6}) - 1000E_l - k_L \psi_l}{C_p} \quad (\text{A18})$$

$\bar{\psi}_s$ is soil water potential (MPa), and $\rho_w g h 10^{-6}$ is the gravitational potential (MPa) for a water column with height h (m), density ρ_w (kg m^{-3}), and gravitational acceleration g (m s^{-2}). k_L is the hydraulic conductance of the soil-to-leaf pathway per unit leaf area (leaf-specific conductance, $\text{mmol H}_2\text{O m}^{-2} \text{ leaf area s}^{-1} \text{ MPa}^{-1}$), composed of a below-ground (R_b) and aboveground plant (R_a) resistance ($\text{MPa sm}^2 \text{ leaf area mmol}^{-1} \text{ H}_2\text{O}$) in series. $1000E_l$ is the transpiration loss for the layer ($\text{mmol H}_2\text{O m}^{-2} \text{ leaf area s}^{-1}$). C_p is plant capacitance ($\text{mmol H}_2\text{O m}^{-2} \text{ leaf area MPa}^{-1}$), defined as the ratio of the change in plant water content to the change in water potential. Equation (A18) is solved for each canopy layer. The change in leaf water potential over a model timestep (Δt , s) is,

$$15 \quad \Delta\psi_l = (a - \psi_0)(1 - e^{-\Delta t/b}) \quad (\text{A19})$$

ψ_0 is the leaf water potential at the beginning of the timestep, $a = \bar{\psi}_s - \rho_w g h 10^{-6} - 1000E_l/k_L$, and $b = C_p/k_L$.

A4.2 Leaf-specific hydraulic conductance

The leaf-specific hydraulic conductance of the soil-to-leaf pathway integrates the hydraulic conductance of roots, stems, and branches and is given by a belowground (R_b)

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and aboveground plant (R_a) resistance in series,

$$\frac{1}{k_L} = R_b + R_a \quad (\text{A20})$$

The aboveground plant resistance governing flow through stems to leaves is,

$$R_a = \frac{1}{k_p} \quad (\text{A21})$$

where k_p ($\text{mmol H}_2\text{O m}^{-2} \text{ leaf area s}^{-1} \text{ MPa}^{-1}$) is the leaf-specific stem hydraulic conductance (i.e., the stem-to-leaf path).

The belowground resistance is the resistance to water uptake imposed by water movement in the soil and by fine roots (≤ 2 mm diameter). It is represented by multiple soil layers connected in parallel with a soil-to-root conductance (k_s) and a root-to-stem conductance (k_r) within each layer (Fig. 1c), as described by Williams et al. (2001a). The conductance of the soil-to-root path is based on Williams et al. (2001a), used also in MAESPA (Duursma and Medlyn, 2012), which builds upon the theoretical framework of Gardner (1960) and Newman (1969). For soil layer j , it depends on the soil hydraulic conductivity of the layer (G_j , $\text{mmol H}_2\text{O m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$), which varies with soil water content and texture, and the characteristics of the rooting system given by the equation,

$$k_{s,j} = \frac{2\pi L_{r,j} \Delta z_j G_j}{\ln(r_{s,j}/r_r)} \quad (\text{A22})$$

where $L_{r,j}$ is the root length per unit volume of soil (root length density, m m^{-3}), $L_{r,j} \Delta z_j$ is the root length per unit area of soil (root length index, m m^{-2}) in a layer with thickness Δz_j (m), and r_r is the mean fine root radius (m). The term $r_{s,j} = (\pi L_{r,j})^{-1/2}$ is one-half the distance between roots (m), calculated with the assumption of uniform root spacing and assuming the soil is divided into cylinders with the root along the middle axis.

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The conductance of the root-to-stem path is calculated from root resistivity (R_r^* , MPa s g mmol⁻¹ H₂O) and root biomass per unit soil volume ($M_{r,j}$, root biomass density, g m⁻³),

$$k_{r,j} = \frac{M_{r,j} \Delta z_j}{R_r^*} \quad (\text{A23})$$

The total belowground resistance is obtained assuming the layers are arranged in parallel,

$$R_b = \left(\sum_j \frac{1}{k_{s,j}^{-1} + k_{r,j}^{-1}} \right)^{-1} L_T \quad (\text{A24})$$

Multiplication of the belowground resistance by the canopy leaf area index (L_T) arises because the belowground resistance is calculated on a ground area basis; multiplying by L_T converts to leaf area. This assumes that each canopy layer is connected to each soil layer, so that the roots in each soil layer supply water to each canopy layer, and that the fraction of roots supplying each canopy layer is the same as the leaf area in that layer. In a wet soil, soil hydraulic conductivity is large, and most of the belowground resistance is from the roots (k_r). As the soil becomes drier, hydraulic conductivity decreases and k_s contributes more to the total resistance.

The total canopy transpiration can be partitioned to each soil layer. The maximum water uptake rate for a soil layer is determined by the difference between soil water potential ($\psi_{s,j}$, MPa) and the minimum leaf water potential,

$$E_{\max,j} = \frac{\psi_{s,j} - \psi_{l\min}}{k_{s,j}^{-1} + k_{r,j}^{-1}} \quad (\text{A25})$$

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The fractional of transpiration supplied by an individual soil layer is,

$$f_{t, j} = E_{\max, j} / \sum_j E_{\max, j} \quad (\text{A26})$$

and the weighted soil water potential for Eq. (A18) is,

$$\bar{\psi}_s = \sum_j \psi_{s, j} f_{t, j} \quad (\text{A27})$$

A5 Root profile

The root system is described by live fine root biomass (M_T , g m^{-2}) and its distribution with depth in the soil. The root biomass density ($M_{r, j}$, root biomass per unit soil volume, g m^{-3}) in a soil layer Δz_j (m) thick that contains Δf_j of the total root biomass (specified as in CLM4.5, Eq. 8.30 using the root distribution parameters r_a and r_b ; Oleson et al., 2013) is,

$$M_{r, j} = M_T \Delta f_j / \Delta z_j \quad (\text{A28})$$

The root length density ($L_{r, j}$, root length per unit volume of soil, m m^{-3}) is,

$$L_{r, j} = \frac{M_{r, j}}{r_d \pi r_r^2} \quad (\text{A29})$$

where r_d is the specific root density ($\text{g biomass perm}^3 \text{ root}$) and πr_r^2 is the root cross-sectional area (m^2) calculated from mean fine root radius (r_r , m).

A6 Soil temperature and energy balance

The ground surface temperature is the temperature that balances the net radiation, sensible heat flux, latent heat flux, and soil heat flux at the soil surface,

$$R_{\text{ng}} = H_g + \lambda E_g + G_{\text{soil}} \quad (\text{A30})$$

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Net radiation (R_{ng}) at the soil surface is calculated as part of the canopy radiative transfer. Sensible heat is exchanged between the soil surface with temperature T_g (K) and canopy air with temperature T_a (K),

$$H_g = c_p(T_g - T_a)g'_{ah} \quad (A31)$$

where g'_{ah} is the aerodynamic conductance within the canopy ($\text{mol m}^{-2} \text{s}^{-1}$). Latent heat flux is similarly exchanged between the soil surface and canopy (e_a),

$$\lambda E_g = \frac{c_p}{\gamma} [h_g e_*(T_g) - e_a] g_v \quad (A32)$$

$h_g = \exp[gM_w\psi_{s1}/(\mathcal{R}T_{s1})]$ is the fractional humidity at the soil surface, with g gravitational acceleration (ms^{-2}), M_w the molecular mass of water (kg mol^{-1}), \mathcal{R} the universal gas constant ($\text{JK}^{-1} \text{mol}^{-1}$), ψ_{s1} the matric potential of the first soil layer (here with units m), and T_{s1} the temperature of the first soil layer (K). $g_v = 1/(g_{soil}^{-1} + g'_{ah}{}^{-1})$ is the total conductance for water vapor ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$) from the soil surface (g_{soil}) and within-canopy aerodynamics (g'_{ah}) in series. In this study, $g_{soil} = 0.002\hat{\rho}$, where $\hat{\rho} = P_{ref}/\mathcal{R}T_{ref}$ is the molar density (mol m^{-3}), i.e., the surface resistance is 500 s m^{-1} . This formulation of surface fluxes is based on CLM4.5, but additionally uses a ground surface conductance (g_{soil}) to represent the effects of diffusion constraints on soil evaporation.

The soil heat flux between the surface and the first soil layer with temperature T_{s1} (K), thermal conductivity κ_1 ($\text{W m}^{-1} \text{K}^{-1}$), and thickness Δz_1 (m) is,

$$G_{soil} = \kappa_1 \frac{(T_g - T_{s1})}{\Delta z_1/2} \quad (A33)$$

Soil temperatures are calculated from the one-dimensional energy conservation equation,

$$\rho c \frac{\partial T_s}{\partial t} = \frac{\partial}{\partial z} \left(\kappa \frac{\partial T_s}{\partial z} \right) \quad (A34)$$

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where ρc is volumetric heat capacity ($\text{J m}^{-3} \text{K}^{-1}$).

A7 Canopy scalars

The calculation of air temperature (T_a), vapor pressure (e_a), and wind speed (u_a) within the canopy follows CLM4.5. With the assumption of negligible capacity to store heat in the canopy air, the total sensible heat flux exchanged with the atmosphere (H) is balanced by the sum of the sensible heat flux from the ground and all canopy layers,

$$H = c_p(T_a - \theta_{\text{ref}})g_{\text{ah}} = H_g + \sum_{i=1}^n [H_{\text{sun},i}f_{\text{sun},i} + H_{\text{shade},i}(1 - f_{\text{sun},i})]\Delta L_i \quad (\text{A35})$$

Here, $H_{\text{sun},i}$ and $H_{\text{shade},i}$ are the leaf fluxes, given by Eq. (A4), for the sunlit leaf and shaded leaf, respectively, at canopy layer i . Similarly, for water vapor flux,

$$E = \frac{1}{P_{\text{ref}}}(e_a - e_{\text{ref}})g_{\text{ah}} = E_g + \sum_{i=1}^n [E_{\text{sun},i}f_{\text{sun},i} + E_{\text{shade},i}(1 - f_{\text{sun},i})]\Delta L_i \quad (\text{A36})$$

with the sunlit and shaded fluxes given by Eq. (A5). The wind speed in the canopy is,

$$u_a = u_{\text{ref}} \left(g_{\text{am}} \hat{\rho}^{-1} / u_{\text{ref}} \right)^{1/2} \quad (\text{A37})$$

θ_{ref} , e_{ref} , u_{ref} , and P_{ref} are the potential temperature ($\theta_{\text{ref}} = T_{\text{ref}} + 0.0098z_{\text{ref}}$, K), vapor pressure (Pa), wind speed (ms^{-1}), and pressure (Pa) at the tower reference height, respectively. g_{am} and g_{ah} ($\text{mol m}^{-2} \text{s}^{-1}$) are aerodynamic conductances for momentum and heat, respectively, calculated from Monin–Obukhov similarity theory between the tower at height z_{ref} and the surface at height $z_0 + d$. The canopy air CO_2 concentration is that of the tower ($c_a = c_{\text{ref}}$).

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Table 1. Site information for the 3 deciduous broadleaf forest (DBF) and 3 evergreen needleleaf forest (ENF) flux towers, including mean annual temperature (MAT) and annual precipitation (Prec).

Site	Forest type	Latitude	Longitude	MAT (°C)	Prec (mm)	Years	Frequency
US-Ha1	DBF	42.54	−72.17	6.6	1071	1992–2006	60 min
US-MMS	DBF	39.32	−86.41	10.8	1032	1999–2006	60 min
US-UMB	DBF	45.56	−84.71	5.8	803	1999–2006	60 min
US-Dk3	ENF	35.98	−79.09	14.4	1170	2000–2004	30 min
US-Ho1	ENF	45.20	−68.74	5.3	1070	1996–2004	30 min
US-Me2	ENF	44.45	−121.56	6.3	523	2002–2007	30 min

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Table 2. Species composition, leaf area index, canopy height, tower height, and soil texture taken from site descriptions of each flux tower.

Tower	Species	Leaf area index (m ² m ⁻²)	Canopy height (m)	Tower height (m)	Soil texture
US-Ha1	Red oak (<i>Quercus rubra</i>), red maple (<i>Acer rubrum</i>)	4.5–5.5	23	30	Loam
US-MMS	Sugar maple (<i>Acer saccharum</i>), tulip poplar (<i>Liriodendron tulipifera</i>), sassafras (<i>Sassafras albidum</i>), white oak (<i>Quercus alba</i>), black oak (<i>Quercus nigra</i>)	4.6	27	48	Clay
US-UMB	Bigtooth aspen (<i>Populus grandidentata</i>) and quaking aspen (<i>Populus tremuloides</i>), with red maple (<i>Acer rubrum</i>), red oak (<i>Quercus rubra</i>), paper birch (<i>Betula papyrifera</i>), and beech (<i>Fagus grandifolia</i>)	4.2	21	46	Sand
US-Dk3	Loblolly pine (<i>Pinus taeda</i>)	4.2	19	22	Sandy loam
US-Ho1	Red spruce (<i>Picea rubens</i>), eastern hemlock (<i>Tsuga canadensis</i>)	5	20	29	Sandy loam
US-Me2	Ponderosa pine (<i>Pinus ponderosa</i>)	2.8	14	32	Sandy loam

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Table 3. Model parameter values for evergreen needleleaf forest (ENF) and deciduous broadleaf forest (DBF) plant functional types. Parameter values are from CLM4.5 (Oleson et al., 2013), except for the stomatal optimization (as described in the text).

Symbol	Description	Units	ENF	DBF
$V_{c_{\max 25}}$	Maximum carboxylation rate at 25 °C	$\mu\text{mol m}^{-2} \text{s}^{-1}$	62.5	57.7
ρ_l	Leaf reflectance (vis, nir)	–	0.07, 0.35	0.10, 0.45
τ_l	Leaf transmittance (vis, nir)	–	0.05, 0.10	0.05, 0.25
χ_l	Departure of leaf angle from spherical orientation	–	0.01	0.25
ε_l	Leaf emissivity	–	0.98	0.98
d_l	Leaf dimension	m	0.04	0.04
r_a	CLM4.5 rooting distribution parameter	m^{-1}	7	6
r_b	CLM4.5 rooting distribution parameter <i>Ball–Berry</i>	m^{-1}	2	2
g_0	Minimum leaf conductance	$\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$	0.01	0.01
g_1	Slope parameter	–	9	9
ψ_c	Soil water potential for stomatal closure	mm	–255 000	–224 000
ψ_0	Soil water potential at which stomata are fully open <i>SPA optimization</i>	mm	–66 000	–35 000
ψ_{\min}	Minimum leaf water potential	MPa	–2	–2
k_p	Leaf-specific stem hydraulic conductance	$\text{mmol H}_2\text{O m}^{-2} (\text{leaf}) \text{s}^{-1} \text{MPa}^{-1}$	4	4
C_p	Plant capacitance	$\text{mmol H}_2\text{O m}^{-2} (\text{leaf}) \text{MPa}^{-1}$	2500	2500
ι_s, ι	Stomatal efficiency ($\Delta A_n / \Delta g_s, \Delta A_n / \Delta E_l$)	$\mu\text{mol CO}_2 \text{ mol}^{-1} \text{H}_2\text{O}$	15, 1500 ^a	7.5, 750
M_T	Fine root biomass	g m^{-2}	500	500
r_r	Fine root radius	m	0.29×10^{-3}	0.29×10^{-3}
r_d	Specific root density (fine root)	$\text{g biomass m}^{-3} \text{root}$	0.31×10^6	0.31×10^6
R_r^*	Fine root hydraulic resistivity	$\text{MPa s g mmol}^{-1} \text{H}_2\text{O}$	25 ^b	25

^a Except for US-Dk3, which used the DBF values.

^b We also tested a value of 75 for evergreen needleleaf forest.

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Table 4. Site-specific model input. The model additionally uses the canopy height, plant functional type, and soil texture at each tower site.

Symbol	Description	Units	Source
Z_{ref}	Tower reference height	m	Tower
T_{ref}	Air temperature	K	Tower
e_{ref}	Vapor pressure	Pa	Tower
u_{ref}	Wind speed	m s^{-1}	Tower
c_{ref}	CO ₂ concentration	$\mu\text{mol mol}^{-1}$	CLM4.5 (367)
P_{ref}	Air pressure	Pa	Tower
$S \downarrow$	Solar radiation	W m^{-2}	Tower
f_{dif}	Diffuse fraction	–	CLM4.5
Z	Solar zenith angle	–	CLM4.5
$L \downarrow$	Longwave radiation	W m^{-2}	Tower
β_t	Soil wetness factor	–	CLM4.5
θ_j	Volumetric soil water	$\text{m}^3 \text{m}^{-3}$	CLM4.5
L_T	Leaf area index	$\text{m}^2 \text{m}^{-2}$	CLM4.5

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Table 5. Site vegetation parameters used in the model simulations.

Site	Foliage N (% by mass)	$V_{c_{\max 25}}$		Leaf area index (LAI)	
		Observed ^c	CLM4.5 ^d	Observed	CLM4.5
US-Ha1	1.97 ^a	50.4	57.7	5.1 ^a	4.9
	1.95 ^b	49.9		4.9 ^b	
US-MMS	2.22 ^a	56.0	57.7	4.6 ^a	4.7
	2.06 ^b	52.4		4.9 ^b	
US-UMB	1.76 ^a	45.6	57.7	4.2 ^a	4.2
US-Dk3	1.19 ^a	59.9	62.5	4.2 ^a	4.7
	1.47 ^b	72.5		4.5 ^b	
US-Ho1	1.06 ^a	54.0	62.5	5.2 ^a	4.6
	1.16 ^b	58.5		5.7 ^b	
US-Me2	0.93 ^a	48.2	62.5	2.8 ^a	3.8

^a Observations from AmeriFlux Level 2 biological, ancillary, disturbance and metadata.

^b Observations from Ollinger et al. (2008).

^c Estimated using empirical relationships between N_{area} and $V_{c_{\max 25}}$ from the TRY leaf trait database (Kattge et al., 2009) with observed foliage N converted from N_{mass} to N_{area} using the mean leaf mass per unit area (LMA) for temperate forest trees reported in the Glonnet leaf trait database (Wright et al., 2004). DBF, $n = 191$, LMA = 76 gm^{-2} . ENF, $n = 18$, LMA = 248 gm^{-2} .

^d Oleson et al. (2013), using the mean values of Kattge et al. (2009).

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Table 6. Standard deviation of the random flux error, $\sigma(\varepsilon)$, for forests. $\sigma(\varepsilon)$ scales with the magnitude of the flux (Richardson et al., 2006, 2012).

	$\sigma(\varepsilon)$	
Flux	Flux ≥ 0	Flux ≤ 0
H	$19.7 + 0.16H$	$10.0 - 0.44H$
λE	$15.3 + 0.23\lambda E$	$6.2 - 1.42\lambda E$

Table B1. List of symbols, their definition, and units.

Canopy variables	
c_a	CO ₂ concentration of canopy air ($\mu\text{mol mol}^{-1}$)
d	Displacement height (m)
e_a	Vapor pressure of canopy air (Pa)
g_{ah}	Aerodynamic conductance for heat, above canopy ($\text{mol m}^{-2} \text{s}^{-1}$)
g_{am}	Aerodynamic conductance for momentum, above canopy ($\text{mol m}^{-2} \text{s}^{-1}$)
g'_{ah}	Aerodynamic conductance, under canopy ($\text{mol m}^{-2} \text{s}^{-1}$)
K_n	Canopy nitrogen decay coefficient (–)
T_a	Canopy air temperature (K)
u_a	Wind speed in canopy (ms^{-1})
z_0	Roughness length (m)
Biometeorological variables	
c_p	Specific heat of air at constant pressure, $c_{pd}(1 + 0.84q_{\text{ref}})M_a$ ($\text{J mol}^{-1} \text{K}^{-1}$)
c_{pd}	Specific heat of dry air at constant pressure ($1005 \text{ J kg}^{-1} \text{K}^{-1}$)
$e_*(T)$	Saturation vapor pressure (Pa) at temperature T
g	Gravitational acceleration (9.80665 ms^{-2})
γ	Psychrometric constant, $c_p P_{\text{ref}} / \lambda$ (Pa K^{-1})
λ	Latent heat of vaporization, $56780.3 - 42.84T_{\text{ref}}$ (J mol^{-1})
M_a	Molecular mass of air, $\rho_a / \hat{\rho}$ (kg mol^{-1})
M_d	Molecular mass of dry air ($0.02897 \text{ kg mol}^{-1}$)
M_w	Molecular mass of water ($0.01802 \text{ kg mol}^{-1}$)
q_{ref}	Specific humidity, $0.622e_{\text{ref}} / (P_{\text{ref}} - 0.378e_{\text{ref}})$ (kg kg^{-1})
\mathcal{R}	Universal gas constant ($8.31446 \text{ J K}^{-1} \text{ mol}^{-1}$)
$\hat{\rho}$	Molar density, $P_{\text{ref}} / \mathcal{R}T_{\text{ref}}$ (mol m^{-3})
ρ_a	Air density, $\hat{\rho}M_d(1 - 0.378e_{\text{ref}}/P_{\text{ref}})$ (kg m^{-3})
ρ_w	Density of water (1000 kg m^{-3})
s	Slope of saturation vapor pressure, $de_*(T)/dT$ (Pa K^{-1})

Table B1. Continued.

Model variables defined at each leaf layer	
A_c	Leaf rubisco-limited assimilation rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
A_j	Leaf RuBP-limited assimilation rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
A_n	Leaf net assimilation ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
A_p	Leaf product-limited assimilation rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
c_i	Leaf intercellular CO_2 concentration ($\mu\text{mol mol}^{-1}$)
c_s	Leaf surface CO_2 concentration ($\mu\text{mol mol}^{-1}$)
D_s	Vapor pressure deficit at leaf surface (Pa, or mol mol^{-1})
e_s	Vapor pressure at leaf surface (Pa)
E_l	Leaf transpiration flux ($\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$)
λE_l	Leaf latent heat flux (W m^{-2})
f_{sun}	Sunlit fraction (–)
g_{bh}	Boundary layer conductance for heat ($\text{mol m}^{-2} \text{ s}^{-1}$)
g_{bv}	Boundary layer conductance for water vapor ($\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$)
g_s	Stomatal conductance ($\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$)
Γ_*	CO_2 compensation point ($\mu\text{mol mol}^{-1}$)
h	Layer height (m)
h_s	Fractional relative humidity at the leaf surface (–)
H_l	Leaf sensible heat flux (W m^{-2})
$I \uparrow_i$	Upward diffuse flux above layer i
$I \downarrow_{i+1}$	Downward diffuse flux onto layer $i + 1$
$I \downarrow_{\text{b},i+1}$	Direct beam flux onto layer $i + 1$
J	Electron transport rate ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
J_{max}	Maximum electron transport rate ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
k_L	Leaf-specific conductance ($\text{mmol H}_2\text{O m}^{-2} \text{ leaf area s}^{-1} \text{ MPa}^{-1}$)
K_b	Extinction coefficient for direct beam (–)
K_c	Michaelis–Menten constant ($\mu\text{mol mol}^{-1}$)
K_o	Michaelis–Menten constant (mmol mol^{-1})
ΔL	Layer leaf area index ($\text{m}^2 \text{ m}^{-2}$)
o_i	O_2 concentration (mmol mol^{-1})

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Table B1. Continued.

Model variables defined at each leaf layer	
R_a	Aboveground plant resistance ($\text{MPa sm}^2 \text{ leaf area mmol}^{-1} \text{H}_2\text{O}$)
R_b	Belowground resistance ($\text{MPa sm}^2 \text{ leaf area mmol}^{-1} \text{H}_2\text{O}$)
R_d	Leaf respiration rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
R_{nl}	Leaf net radiation (W m^{-2})
T_l	Leaf temperature (K)
T_p	Triose phosphate utilization rate ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
τ_b	Direct beam transmittance through a single layer, $\exp(-K_b \Delta L)$ (-)
τ_d	Diffuse transmittance through a single layer (-)
$V_{c_{\max}}$	Maximum carboxylation rate ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
ψ_l	Leaf water potential (MPa)
Soil variables	
λE_g	Ground surface latent heat flux (W m^{-2})
$E_{\max,j}$	Maximum water uptake rate for soil layer ($\text{mmol H}_2\text{O m}^{-2} \text{ ground area s}^{-1}$)
ε_g	Soil emissivity
Δf_j	Fraction of roots in soil layer (-)
$f_{t,j}$	Fraction of transpiration supplied by soil layer (-)
g_{soil}	Soil conductance for water vapor ($\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$)
G_j	Hydraulic conductivity of soil layer ($\text{mmol H}_2\text{O m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$)
G_{soil}	Soil heat flux (W m^{-2})
h_g	Fractional relative humidity at the soil surface (-)
H_g	Ground surface sensible heat flux (W m^{-2})
$k_{r,j}$	Root-to-stem conductance of soil layer ($\text{mmol H}_2\text{O m}^{-2} \text{ ground area s}^{-1} \text{ MPa}^{-1}$)
$k_{s,j}$	Soil-to-root conductance of soil layer ($\text{mmol H}_2\text{O m}^{-2} \text{ ground area s}^{-1} \text{ MPa}^{-1}$)
κ_j	Thermal conductivity of soil layer ($\text{W m}^{-1} \text{ K}^{-1}$)
$L_{r,j}$	Root length density of soil layer ($\text{m root m}^{-3} \text{ soil}$)
$M_{r,j}$	Root biomass density of soil layer ($\text{g biomass m}^{-3} \text{ soil}$)
$r_{s,j}$	One-half the distance between roots in soil layer (m)
R_{ng}	Ground surface net radiation (W m^{-2})
ρc_j	Volumetric heat capacity of soil layer ($\text{J m}^{-3} \text{ K}^{-1}$)
T_g	Ground surface temperature (K)
$T_{s,j}$	Temperature of soil layer (K)
$\psi_{s,j}$	Soil water potential of layer (MPa, or m)
$\bar{\psi}_s$	Weighted soil water potential (MPa)
Δz_j	Thickness of soil layer (m)

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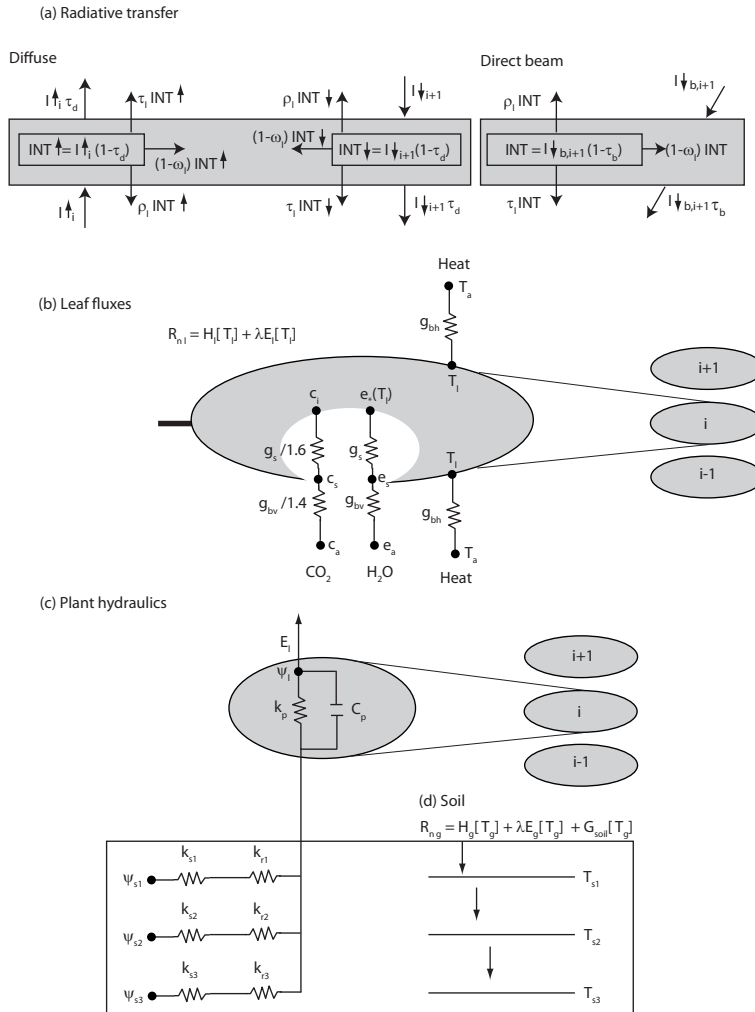
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Fig. 1. Overview of the main processes in the canopy model. The canopy is represented by n leaf layers with layer $i + 1$ above layer i . **(a)** Diffuse and direct solar radiation for layer $i + 1$. Diffuse radiation passes through the layer, proportional to τ_d . The intercepted fraction $(1 - \tau_d)$ is scattered forward (τ_f), scattered backward (ρ_f), or absorbed ($1 - \omega_f$; $\omega_f = \tau_f + \rho_f$). The intercepted direct beam $(1 - \tau_b)$ is similarly absorbed or scattered. Longwave radiation is similar to diffuse radiation, with $\omega_l = 1 - \varepsilon_l$ and the intercepted longwave radiation is reflected ($\rho_l = \omega_l$, $\tau_l = 0$). **(b)** Leaf sensible heat, transpiration, and CO_2 fluxes. Leaf temperature (T_l) is the temperature that balances the energy budget. Sensible heat is exchanged from both sides of the leaf, proportional to the leaf boundary layer conductance (g_{bh}) and the temperature gradient with air ($T_l - T_a$). Water vapor is lost from the stomatal cavity to air, proportional to the vapor pressure deficit ($e_*(T_l) - e_a$) and stomatal (g_s) and boundary layer (g_{bv}) conductances in series. CO_2 similarly diffuses from the canopy air into the stomata, proportional to the gradient $c_a - c_i$. **(c)** Soil water uptake by a canopy layer. Each canopy layer has an aboveground plant stem conductance (k_p) and a capacitance (C_p). Multiple root layers occur in parallel with a conductance comprised of soil (k_s) and root (k_r) components in series. The soil conductance varies with soil water potential (ψ_s). **(d)** Soil energy balance and heat flow. Sensible heat, latent heat, and soil heat fluxes depend on ground temperature (T_g). The soil heat flux is transferred within the soil profile using a Crank–Nicolson formulation with soil heat flux as the upper boundary condition and soil heat capacity and thermal conductivity specified from soil texture, mineralogical properties, and soil water. Appendix A provides the full equation set.

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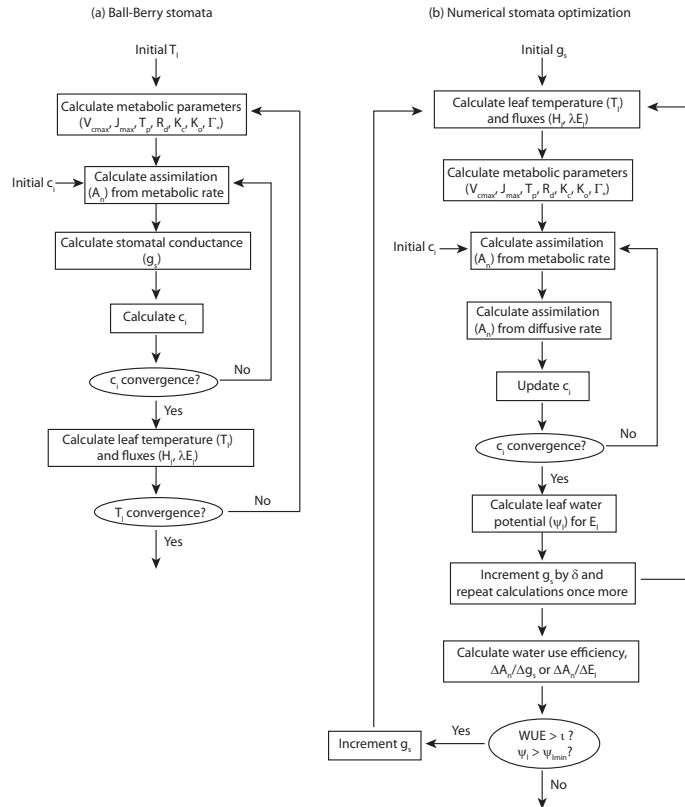


Fig. 2. Flow diagram of leaf flux calculations using **(a)** the Ball–Berry model and **(b)** the SPA stomatal optimization.

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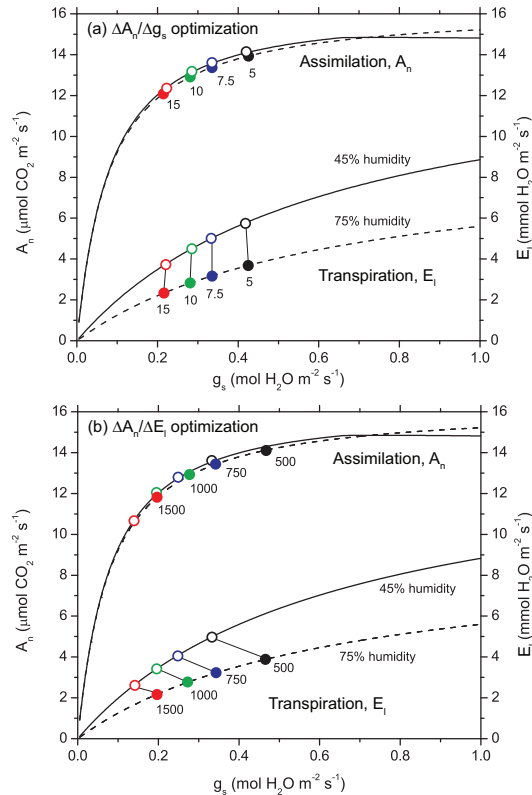


Fig. 3. Leaf assimilation (A_n , left-hand axis) and leaf transpiration (E_l , right-hand axis) in relation to imposed values of stomatal conductance (g_s , bottom axis). Panel **(a)** shows SPA-iWUE optimization and **(b)** shows SPA-WUE optimization. Results are for a warm, sunny day with relative humidity equal to 45 % (solid lines) and 75 % (dashed lines). Circles denote optimized values for A_n , E_l , and g_s at which **(a)** $\iota_* = 5, 7.5, 10,$ and $15 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ (iWUE optimization) and **(b)** $\iota = 500, 750, 1000,$ and $1500 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ (WUE optimization). Open circles are with 45 % relative humidity. Filled circles are with 75 % relative humidity.

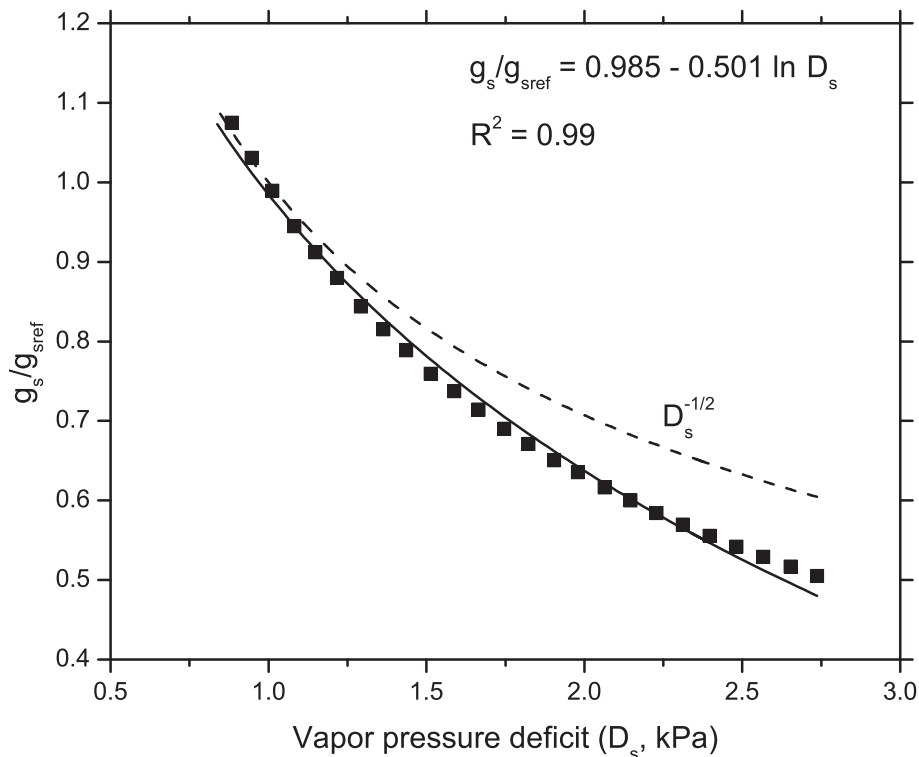


Fig. 4. Relationship between g_s and D_s derived for SPA-WUE optimization. g_{sref} is the stomatal conductance at $D_s = 1$ kPa. The solid line shows the best-fit regression equation using the relationship $g_s/g_{sref} = y_0 + m \ln D_s$ from Katul et al. (2009). The dashed line shows $D_s^{-1/2}$. Calculations used $\iota = 750 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$.

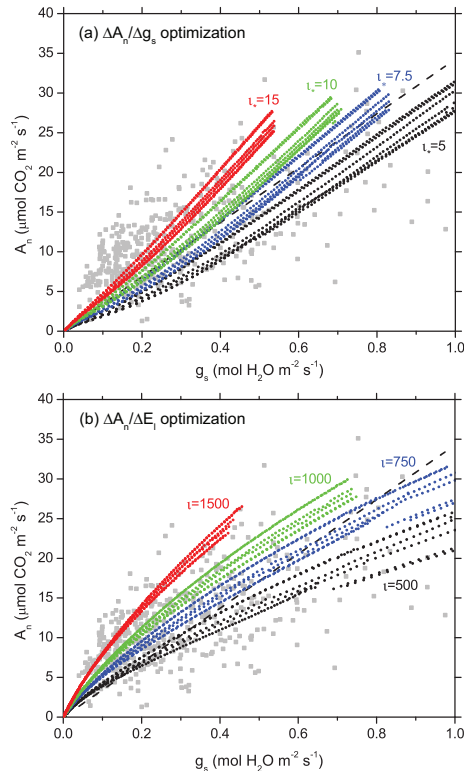


Fig. 5. Observed and simulated relationships between A_n and g_s . Observations (light grey symbols) are from the Glopnet leaf trait database (Wright et al., 2004) for C_3 plants ($n = 421$). The dashed line shows the best-fit regression equation, $A_n = 34.3g_s$. Simulations show optimal A_n and g_s calculated for **(a)** $\iota_* = 5, 7.5, 10,$ and $15 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ (SPA-iWUE optimization) and **(b)** $\iota = 500, 750, 1000,$ and $1500 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ (SPA-WUE optimization). The model simulations used six different meteorological forcings, producing six different A_n – g_s relationships for each value of stomatal efficiency.

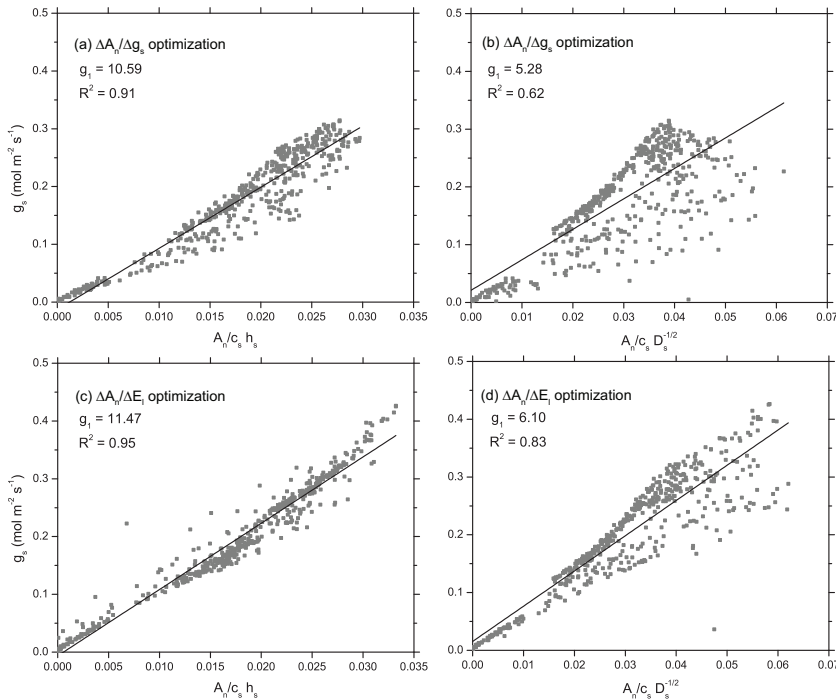


Fig. 6. Simulated stomatal conductance in relation to **(a, c)** $A_n/c_s h_s$ (Ball et al., 1987) and **(b, d)** $A_n/c_s D_s^{-1/2}$ (Medlyn et al., 2011b). Panels **(a, b)** show SPA-iWUE optimization and **(c, d)** show SPA-WUE optimization. Simulations used forcing from US-Ha1 for July 2003, and data are for the sunlit leaf at the top of the canopy. The linear regression line (solid line) is shown, with the slope (g_1) and R^2 . These simulations used $\iota_* = 7.5 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ for iWUE optimization and $\iota = 750 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ for WUE optimization. Environmental conditions were: absorbed photosynthetically active radiation, $7\text{--}1288 \mu\text{mol m}^{-2} \text{ s}^{-1}$; T_1 , $12\text{--}33 \text{ }^\circ\text{C}$; h_s , $0.42\text{--}1.0$; D_s , $0\text{--}2.6 \text{ kPa}$; and A_n , $0\text{--}13 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

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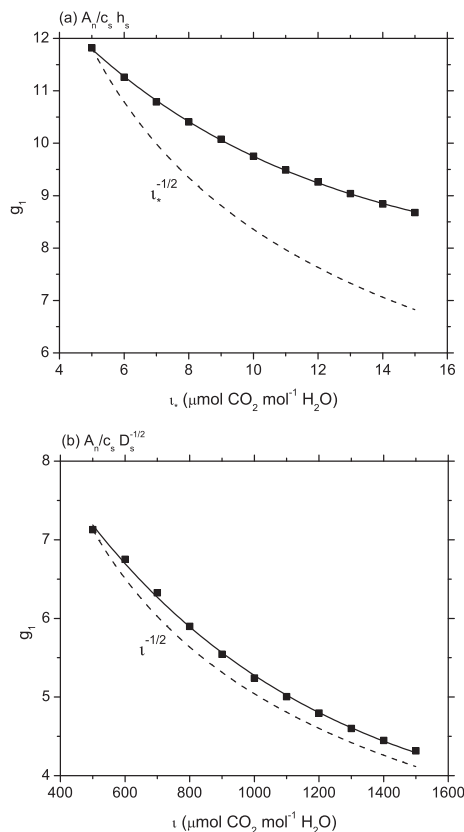


Fig. 7. Slope (g_1) of empirical stomatal models in relation to stomatal efficiency. **(a)** SPA-iWUE optimization with the slope $g_1 A_n/c_s h_s$ (as in Fig. 6a). **(b)** SPA-WUE optimization with the slope $g_1 A_n/c_s D_s^{-1/2}$ (as in Fig. 6d). Dashed lines show $l_*^{-1/2}$ **(a)** and $l^{-1/2}$ **(b)**.

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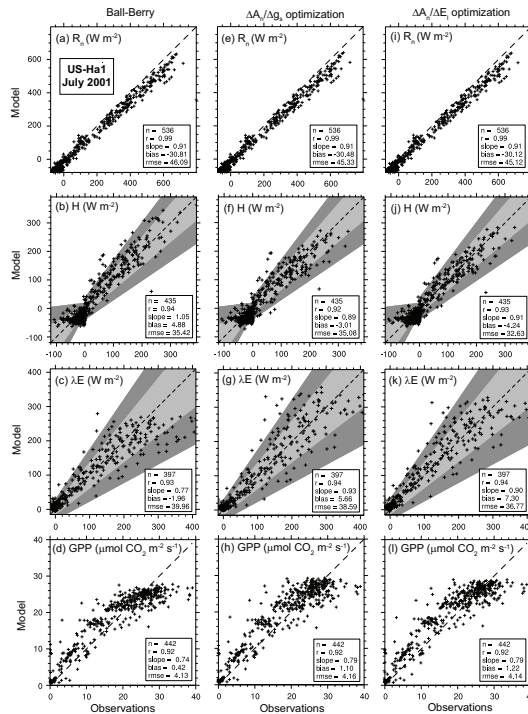


Fig. 8. Canopy flux simulations for US-Ha1, July 2001. Shown are observed and simulated net radiation (R_n), sensible heat flux (H), latent heat flux (λE), and gross primary production (GPP) for the Ball-Berry model (left-hand panels; **a–d**), SPA-iWUE optimization (middle panels; **e–h**) and SPA-WUE optimization (right-hand panels, **i–l**). The dashed line shows the 1 : 1 relationship, with the light and dark shading denoting ± 1 and ± 2 standard deviations, respectively, of the random flux error, $\sigma(\varepsilon)$. Statistics show sample size (n), correlation coefficient (r), slope of the regression line, mean bias, and root mean square error (rmse). Data are shown for periods without rain. GPP is for daylight hours only.

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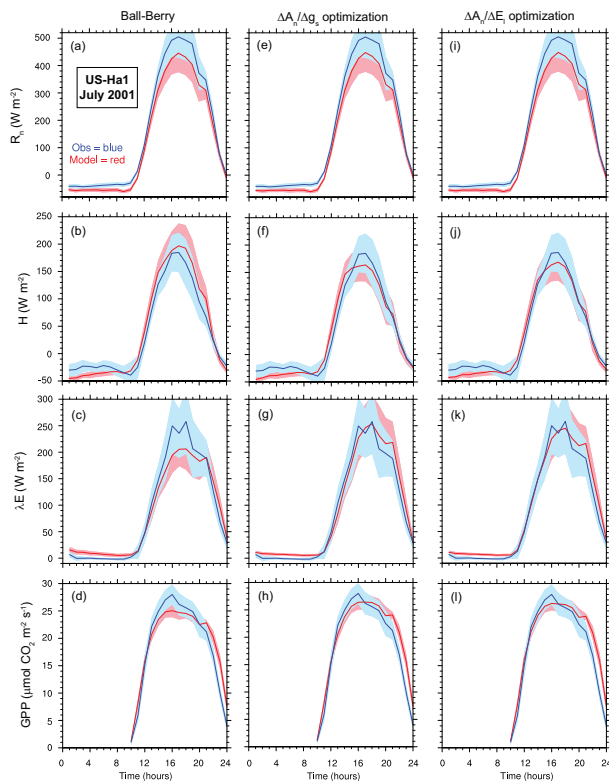


Fig. 9. Average diurnal cycle for US-Ha1, July 2001. Shown are observed and simulated net radiation (R_n), sensible heat flux (H), latent heat flux (λE), and gross primary production (GPP) for the Ball–Berry model (left-hand panels; **a–d**), SPA-iWUE optimization (middle panels; **e–h**) and SPA-WUE optimization (right-hand panels, **i–l**). The shading denotes ± 2 standard error of the mean.

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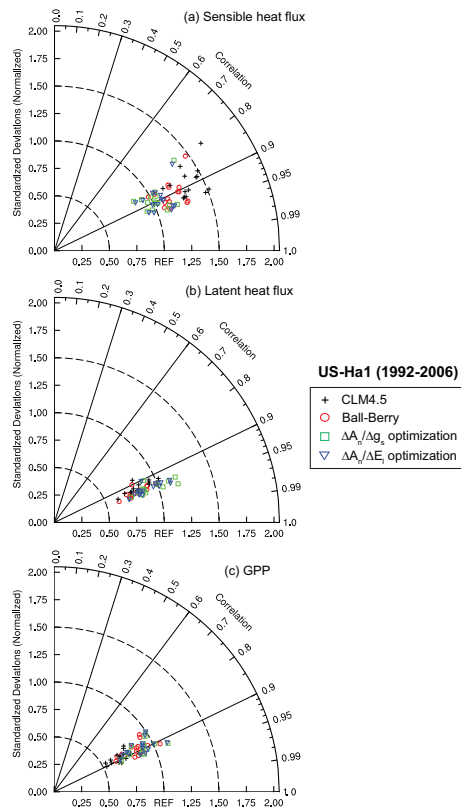


Fig. 10. Taylor diagram of **(a)** sensible heat flux, **(b)** latent heat flux, and **(c)** gross primary production for US-Ha1. Data points are for the years 1992–2006 for CLM4.5 and the multi-layer canopy model with Ball–Berry stomata, SPA-iWUE optimization, and SPA-WUE optimization. Simulations are evaluated by the normalized standard deviation (relative to the observations) and the correlation with the observations.

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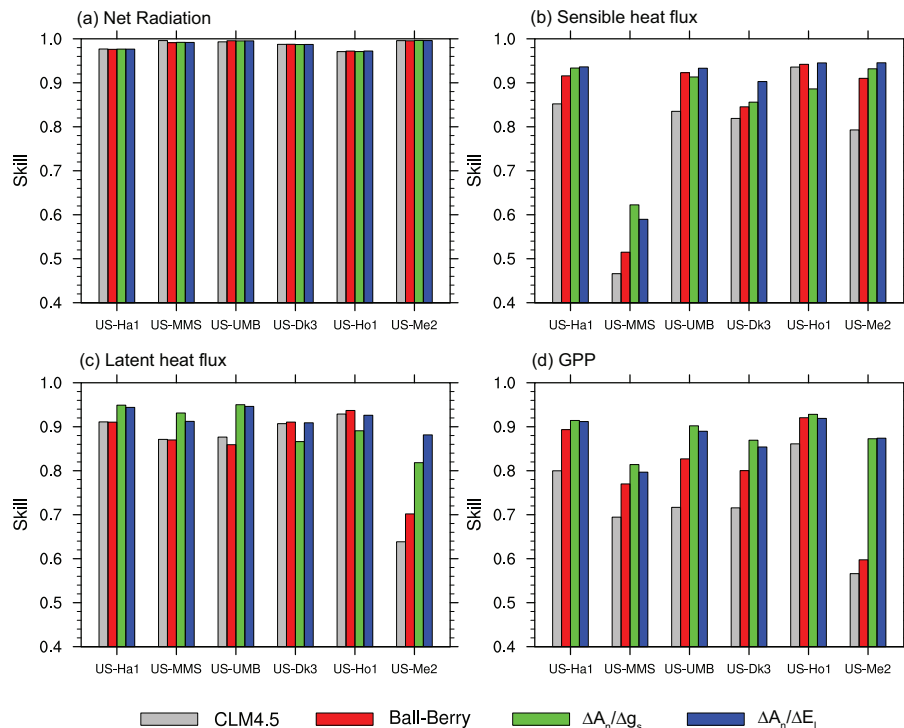


Fig. 11. Average skill across all years for each flux tower site for **(a)** net radiation, **(b)** sensible heat flux, **(c)** latent heat flux, and **(d)** gross primary production. Shown are simulations for CLM4.5 and the multi-layer canopy model with Ball–Berry stomata, SPA-iWUE optimization, and SPA-WUE optimization. Stomatal efficiency is $\iota_* = 15 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ (iWUE optimization) and $\iota = 1500 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ (WUE optimization) for US-Ho1 and US-Me2. All other parameter values are as in Table 3.

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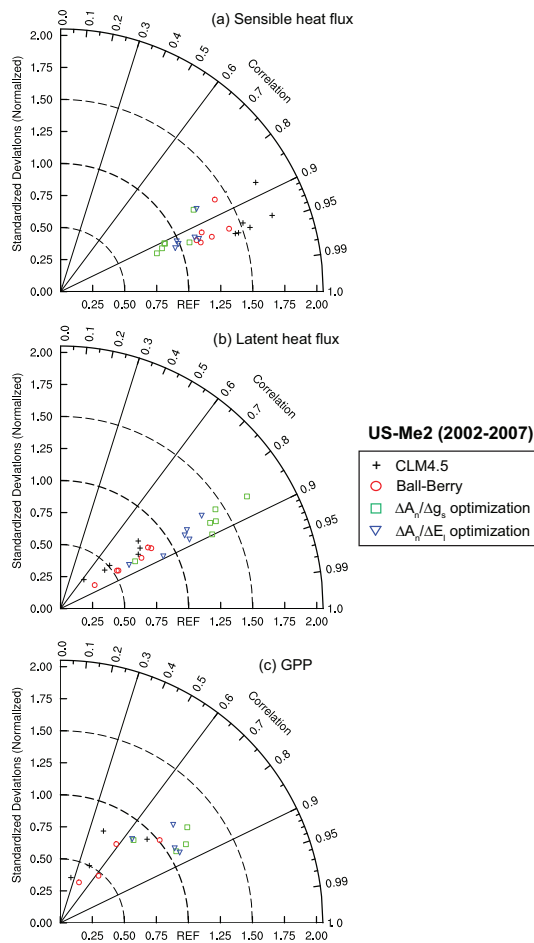


Fig. 12. As in Fig. 10, but for US-Me2 (2002–2007).

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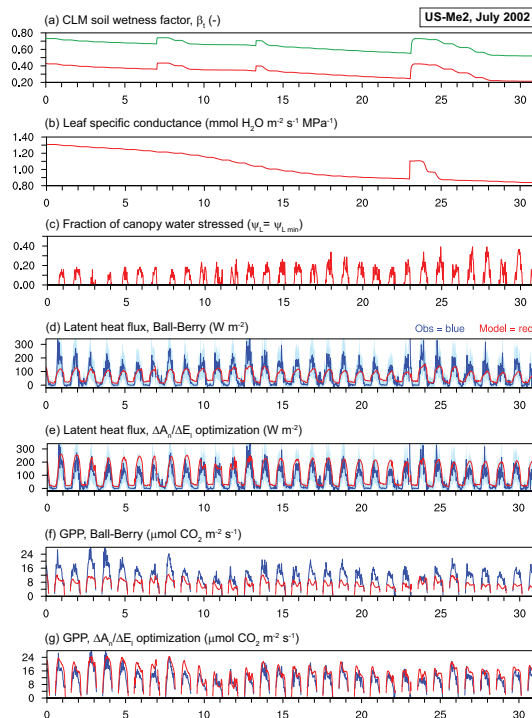


Fig. 13. Simulations for US-Me2 for July 2002 during a prolonged drought. **(a)** CLM4.5 soil wetness factor (β_t). The green line shows β_t increased by 0.3, needed to improve latent heat flux and GPP simulations with the Ball–Berry model. **(b)** Leaf specific conductance (k_l) with SPA-WUE optimization. **(c)** Fraction of canopy that is water stressed with SPA-WUE optimization. **(d, e)** Latent heat flux simulated with the Ball–Berry model and SPA-WUE optimization (red) compared with observations (blue). The light blue shading denotes ± 2 standard deviations of the random flux error, $\sigma(\varepsilon)$. **(f, g)** Gross primary production simulated with the Ball–Berry model and SPA-WUE optimization (red) compared with observations (blue).

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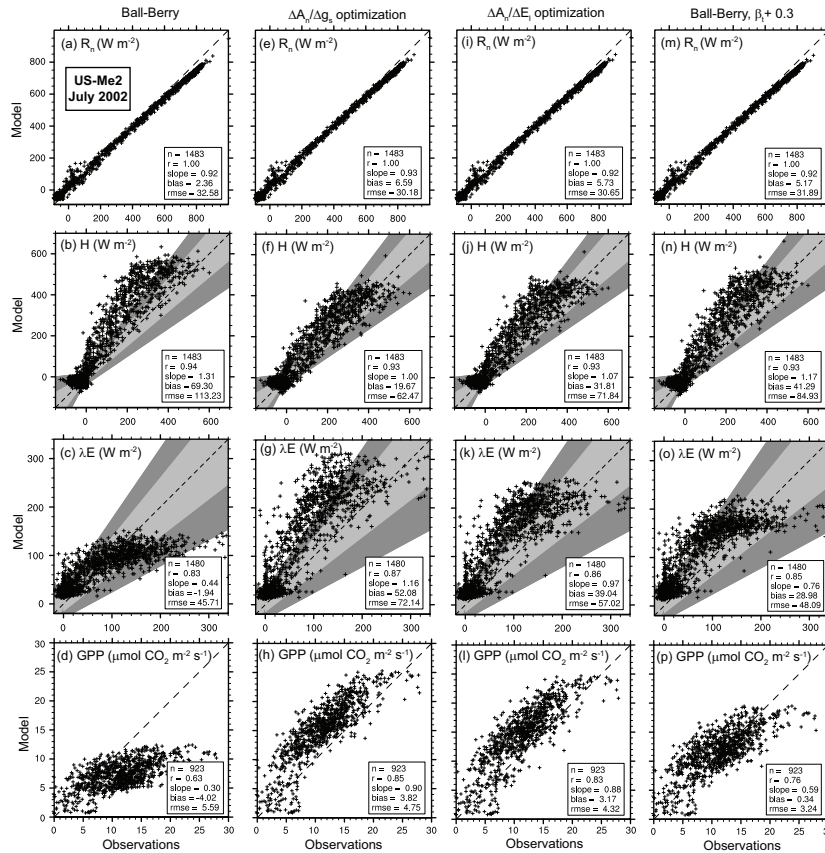


Fig. 14. As in Fig. 8, but for US-Me2, July 2002. Also shown are simulations for the Ball-Berry model with β_t increased by 0.3 (m–p).

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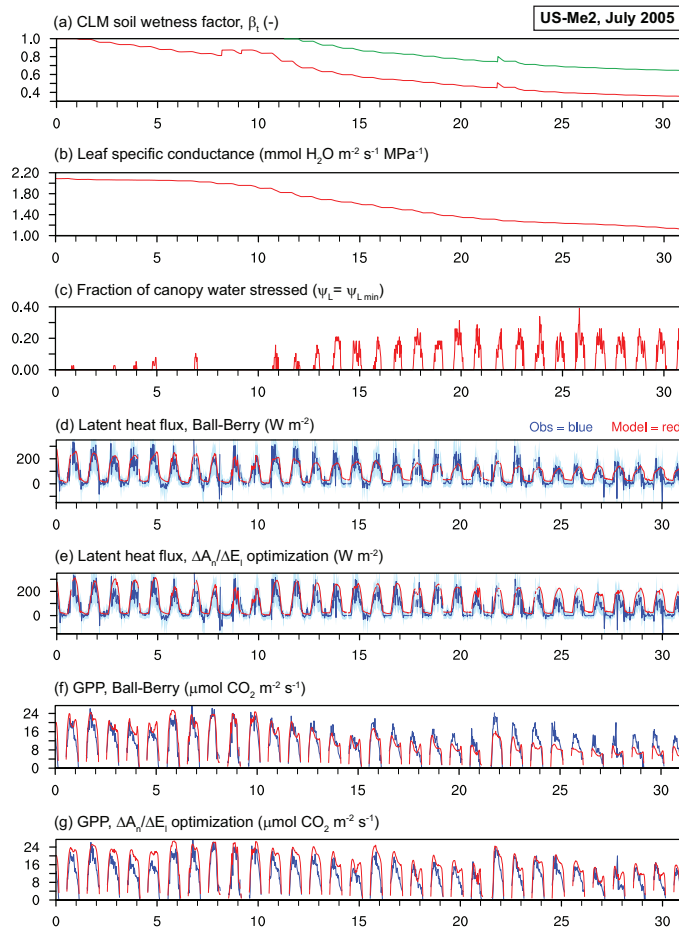


Fig. 15. As in Fig. 13, but for July 2005 during an evolving drought.

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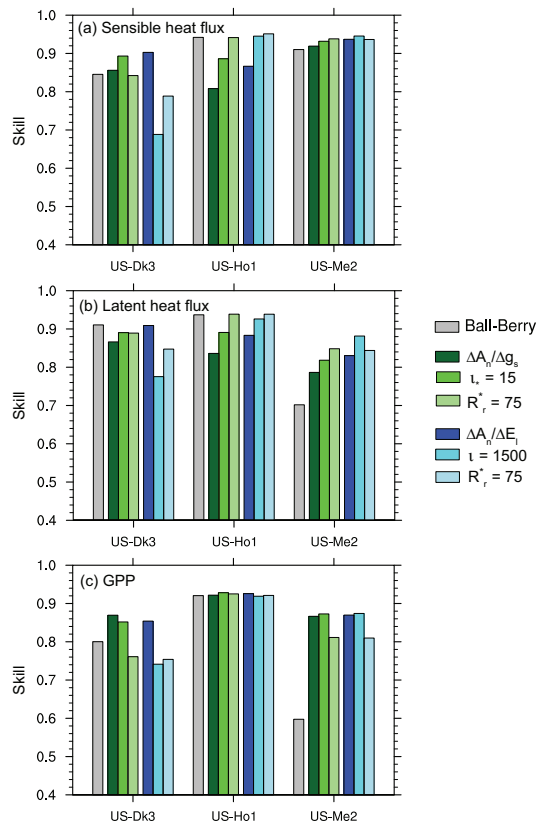


Fig. 16. Average skill across all years for evergreen needleleaf forest tower sites for **(a)** sensible heat flux, **(b)** latent heat flux, and **(c)** gross primary production. Simulations are shown for the Ball–Berry model, SPA-iWUE optimization, and SPA-WUE optimization using baseline parameter values (Table 3). Additional simulations are shown with higher stomatal efficiency ($\iota_* = 15$ and $\iota = 1500 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$) and higher root resistivity ($R_r^* = 75 \text{ MPa s g mmol}^{-1}$).

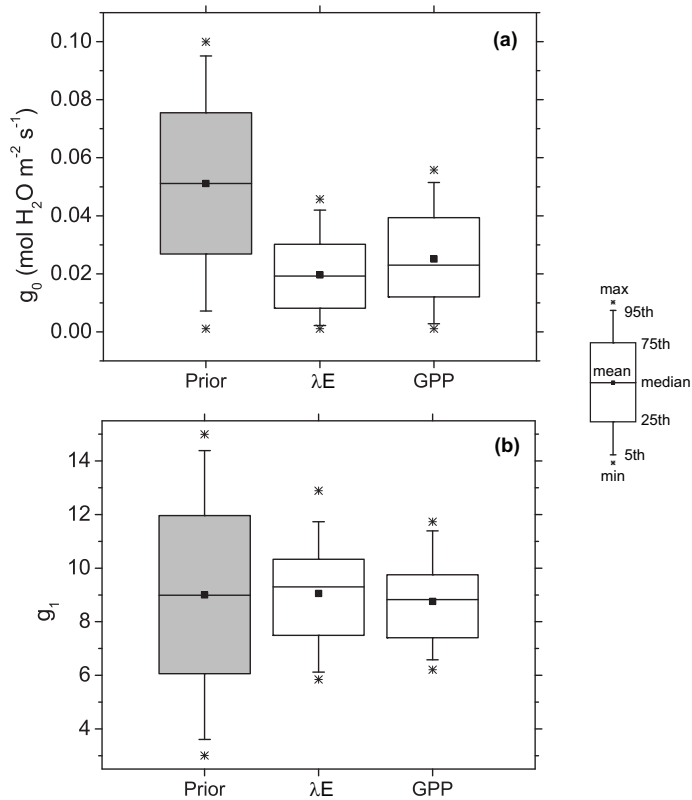


Fig. 17. Parameter optimization of **(a)** g_0 and **(b)** g_1 for the Ball–Berry model using flux data for US–Ha1 (July 2001). Shown are the distributions of prior parameter values from the latin hypercube sampling ($m = 500$ points with $n = 2$ variables) and the parameter values of the 50 simulations with the lowest root mean square error (lowest 10%) for latent heat flux (λE) and gross primary production (GPP). For these 50 simulations, $RMSE = 37\text{--}41 \text{ W m}^{-2}$ and $4.09\text{--}4.15 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

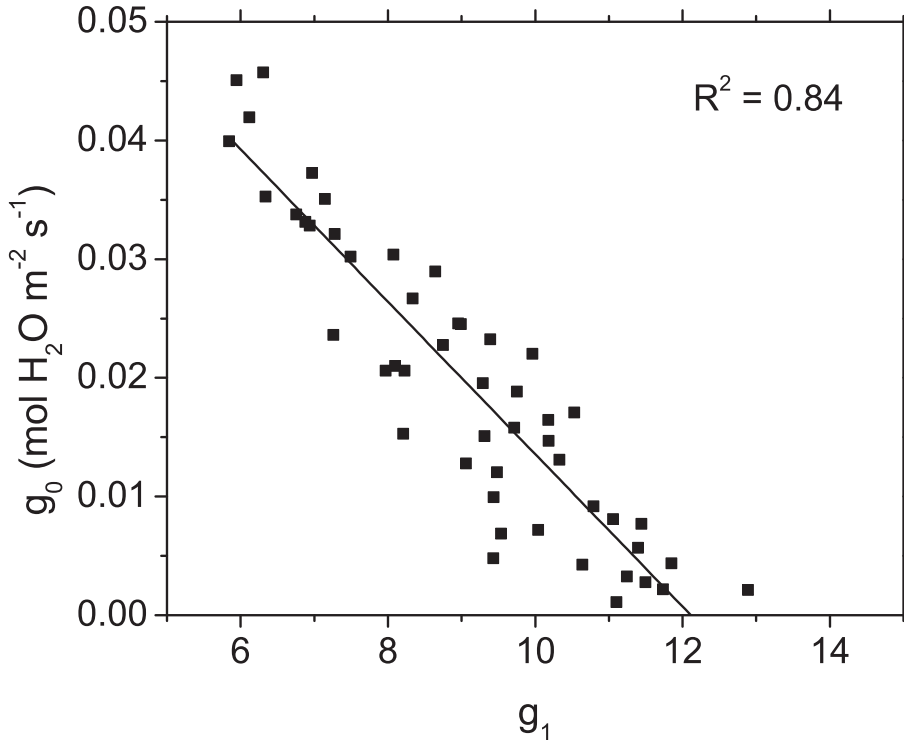


Fig. 18. Relationship between g_0 and g_1 for the 50 simulations with the lowest root mean square error in latent heat flux. Data are from Fig. 17. Analysis of GPP errors shows a similar negative correlation (not shown).

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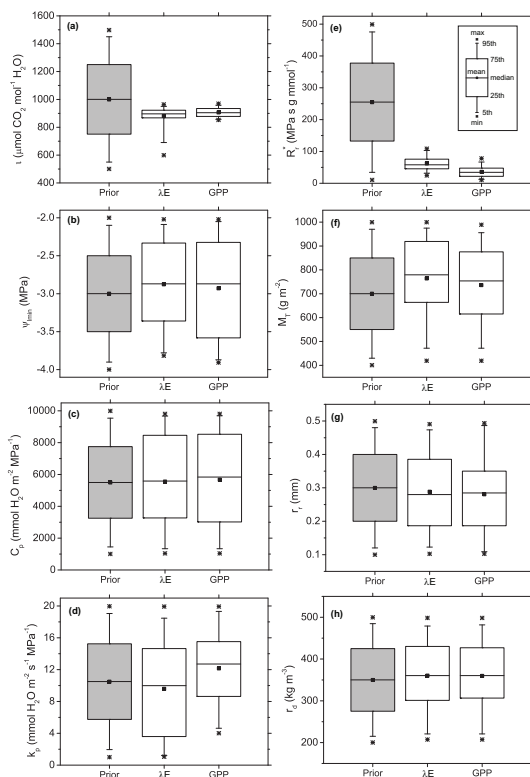


Fig. 19. As in Fig. 17, but for SPA-WUE optimization. Parameters were generated from latin hypercube sampling ($m = 500$ points with $n = 4$ variables). The left-hand panels (a–d) show prior and posterior values of the four aboveground stem and leaf parameters. The right-hand panels (e–h) show values of the four belowground root parameters. For simulations with the lowest 10% error, $\text{RMSE} = 35\text{--}37 \text{ W m}^{-2}$ and $4.08\text{--}4.20 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

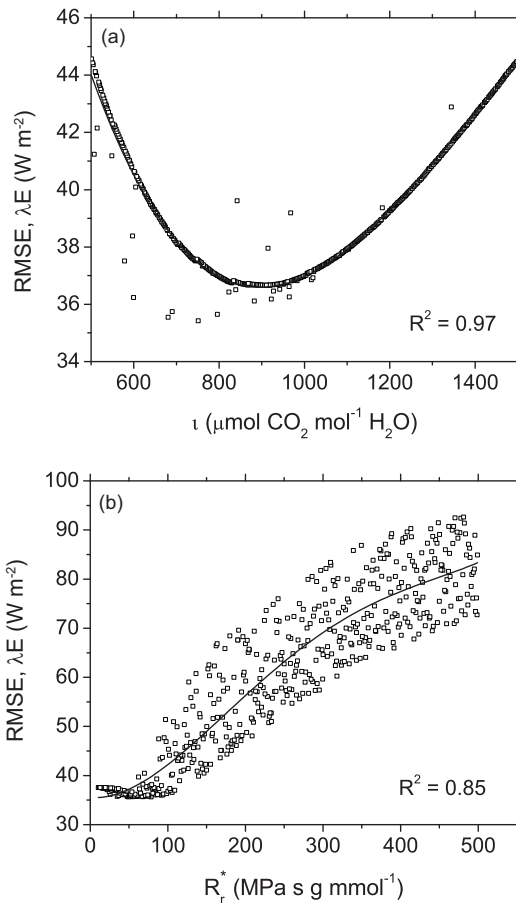


Fig. 20. Root mean square error of latent heat flux from the latin hypcube sampling ($m = 500$ points) in relation to **(a)** ι and **(b)** R_r^* for US-Ha1 (July 2001) using SPA-WUE optimization. The solid lines show the polynomial regression. Analysis of GPP errors shows similar relationships (not shown).