



Combining the [ABA] and net photosynthesis-based model equations of stomatal conductance



Chris Huntingford^{a,*}, D. Mark Smith^{a,b}, William J. Davies^c, Richard Falk^{d,a},
Stephen Sitch^d, Lina M. Mercado^{d,a}

^a Centre for Ecology and Hydrology, Wallingford OX10 8BB, UK

^b International Union for Conservation of Nature, Rue Mauverney 28, 1196 Gland, Switzerland

^c Lancaster Environment Centre, Lancaster University, Bailrigg, Lancaster LA1 4YQ, UK

^d Geography, College of Life and Environmental Sciences, University of Exeter, Rennes Drive, Exeter EX4 4RJ, UK

ARTICLE INFO

Article history:

Received 25 March 2014
Received in revised form 5 January 2015
Accepted 6 January 2015
Available online 28 January 2015

Keywords:

Stomatal conductance
ABA
Soil moisture
Terrestrial carbon cycle
General circulation models
Climate change

ABSTRACT

Stomatal conductance g_s is variously depicted as being dependent on environmental conditions (Jarvis, 1976), transpiration (Monteith, 1995), net photosynthesis (Leuning, 1995) or chemical signalling arriving in the xylem (Tardieu and Davies, 1993). Accurate descriptions of g_s are being increasingly demanded in the large-scale land surface model components of General Circulation Models (GCMs) to predict future land-atmospheric fluxes of water vapour, heat and carbon dioxide. The JULES model, for instance, uses the net photosynthesis description combined with a relatively simple semi-linear dependence on soil moisture content that modulates the photosynthesis dependence (Cox et al., 1998).

Dewar (2002) combines the Leuning (1995) and Tardieu and Davies (1993) models. We revisit that combination, and discuss whether the Vapour Pressure Deficit (VPD) implicit in both components is different or in common. Further, we show a potential re-arrangement of the combined equations reveals that this model for g_s can be considered as being dependent on only four variables: evaporative flux J_w , net photosynthesis a_n , soil moisture content θ and ambient CO_2 concentration c_a . Expressed this way, g_s is influenced by two relatively slowly varying stores of the hydrological and carbon cycles (soil water content and atmospheric CO_2) and two more rapidly fluctuating fluxes from both cycles (evaporation and net photosynthesis).

We consider how the modelling structure and its response to both canopy-level and soil environmental controls may make it suitable for inclusion in GCMs, and what this entails in terms of parameterisation.

© 2015 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Variation in the apertures of stomatal pores in the surface of leaves of terrestrial plants are a key control of both photosynthetic uptake of carbon dioxide and transpirational loss of water by land ecosystems. Their accurate modelling in response to variation in environmental conditions is important for many reasons, including aiding predictability in the role that the land surface plays in the global carbon and water cycles, which themselves may be changing in response to the anthropogenic burning of fossil fuels (IPCC, 2007). Garratt (1993) and Cox et al. (1999), for example, demonstrate the importance of the land surface in global climate simulations. Stomatal control on the partitioning of

available energy into sensible and latent heat (Penman-Monteith equation: Monteith, 1981) also affects meteorological conditions at the regional scale through atmospheric boundary-layer feedbacks. Multiple conceptual models illustrate this feedback (e.g. Jacobs and DeBruin, 1992; Raupach, 1998; Huntingford and Monteith, 1998; and more recently, de Arellano et al., 2012). At an even more local scale, stomata play an important control in influencing water use by crops, along with other vegetation. There is a large interest in predicting the expected future balance, in a carbon dioxide (CO_2)-enriched environment, between altered hydrological conditions (and including potentially detrimental higher evaporation rates that dry soils under crops as a consequence of imposed global warming) and the generally beneficial “ CO_2 -fertilization effect”. Besides physiological changes via stomata, related changes to net primary productivity could also have structural effects for terrestrial ecosystems. This all has implications for future food security (e.g. Long et al., 2006), and especially for regions projected to

* Corresponding author. Tel.: +44 01491 692389.
E-mail address: chg@ceh.ac.uk (C. Huntingford).

have raised risk of major drought, whilst at the global scale these factors control the extent of any future land surface partial “draw-down” of CO₂ emissions. This balance will change should non-CO₂ greenhouse gases also increase significantly, as these will not have fertilization capability (Huntingford et al., 2011).

Laboratory and field experiments confirm strong correlations between stomatal opening and the prevailing environmental conditions, suggesting it may be modelled as a function of five quantities: leaf-level light, temperature, humidity deficit, soil moisture content and atmospheric CO₂ concentration. Jarvis (1976) combines these measurements to model stomatal conductance as a series of multiplicative functions of stomatal response to each of these five environmental variables. This approach is tested successfully by Stewart (1988) against data from a UK pine forest, and subsequently used by others for a range of other vegetation types. Later Huntingford and Cox (1997) are almost able to reproduce such functional responses for the pine forest with an unconstrained neural network fitting procedure. In such studies, inferred stomatal conductance values are found through inversion of the Penman-Monteith equation, where the land-atmosphere energy fluxes are known. The original references used by Jarvis (1976), and which supply details of measurements confirming the five dependences are: Meidner and Mansfield (1968) for light and CO₂, Neilson and Jarvis (1975) for temperature, Lange et al. (1971) for vapour pressure and Stålfelt (1955) for leaf water status.

Alternatively stomatal opening is often modelled as a direct function of the photosynthetic fluxes of carbon dioxide passing through the stomata. Both Ball et al. (1987) and Leuning (1995) propose that stomatal conductance is a linear function of net photosynthesis, along with an additional dependence on VPD. In these descriptions, the stomatal responses to canopy-level temperature, light and atmospheric CO₂ concentration are implicit in the photosynthetic model. These photosynthesis models are frequently modulated directly to capture the influence of the status of soil moisture content (Section 3 and Cox et al., 1998; Clark et al., 2011). This is as opposed to simply adjusting stomatal conductance directly to account for soil moisture influence, and then deriving a new photosynthesis value via impact on internal CO₂ concentration (this is discussed further later). Whichever way this influence is described, it is frequently with a semi-linear dependence on soil moisture content and hence arguably more simplistic than that of the other environmental responses. There is, however, experimental evidence in many species of a more mechanistic link between stomatal closure and soil drying, and that is governed by a chemical signal (Zhang and Davies, 1989). A number of chemical species can potentially contribute to this signalling process, but much research suggests that abscisic acid (ABA) is a central component of the signal. Stomatal opening can decline as the concentration of abscisic acid [ABA] in xylem sap increases (Zhang and Davies, 1990; Khalil and Grace, 1993). Xylem [ABA] is thought to be a function of both the water status of the root and the water flux through the root system (Tardieu et al., 1992), and thereby provides the shoot with a “measure” of the access that the plant root system has to soil water. Further, stomatal sensitivity to [ABA] may co-vary with leaf water potential in some species. As leaf water potential declines, (becoming more negative; for example because of an increase in transpiration), stomata become more responsive to [ABA] (Tardieu and Davies, 1993; Tardieu and Simonneau, 1998). A description of stomatal control that combines these features was developed by Tardieu and Davies (1993).

Dewar (2002) combines the Tardieu and Davies (1993) model of stomatal regulation by ABA with the Leuning (1995)-type model of the dependency of stomatal conductance on net photosynthesis. Here we revisit this, placing a particular emphasis on when all the equations are combined, whether this reveals dependencies on quantities other than the direct surface meteorology. Presented

are a full set of coupled equations, and we discuss required levels of parameterisation. We suggest this framework could be potentially implemented in the land surface models of GCMs, providing a more mechanistic description of soil-plant interactions than presently exists.

2. Methods and results: two models of stomatal response to environmental variables

2.1. Governing equations: hydraulic dependencies

Tardieu and Davies (1993) provide a model for leaf-level stomatal conductance, g_s (m s⁻¹), that responds to drought stress based on both direct hydraulic control and chemical signalling. This is through dependencies on leaf water potential, Ψ_l (MPa), and xylem ABA concentration, c_{ABA} (mol [ABA] (m³ water)⁻¹) respectively. Following Tardieu (1993), stomatal conductance can be given as:

$$g_s = g_{s,\min} + \alpha e^{c_{ABA}\beta e^{\delta\Psi_l}} \quad (1)$$

and where $g_{s,\min}$ (m s⁻¹) is a minimum stomatal conductance, set at 8.93×10^{-4} m s⁻¹ (corresponding to a value of 0.02 mol m⁻² s⁻¹ in physiological units; see typical minimum values of stomatal conductance in Figure 5 of Tardieu et al., 1993). Parameter α can be regarded as the difference between maximum and minimum stomatal conductance; in completely unstressed hydrological conditions Eq. (1) becomes almost exactly $g_s = g_{s,\min} + \alpha$. Tardieu et al. (1993) give a maximum stomatal conductance value of 0.27 mol m⁻² s⁻¹, so α is 0.25 mol m⁻² s⁻¹, which in the units used here, corresponds to 0.0112 m s⁻¹. The other constants are $\beta = -2.69 \times 10^3$ (m³ mol⁻¹) and $\delta = -0.183$ MPa⁻¹ (from Table 1, Tardieu and Davies, 1993, with adjusted units). The ABA concentration itself is modelled as dependent upon the water potential at the root surface Ψ_r (MPa) and total water flux passing from the soil and through the vegetation per unit of land area, J_w (mg m⁻² s⁻¹) thus:

$$c_{ABA} = -\frac{a\Psi_r}{J_w + b}. \quad (2)$$

Here $a = -1.4 \times 10^{-3}$ mol ABA mg m⁻⁵ s⁻¹ MPa⁻¹ and $b = 4.0$ mg m⁻² s⁻¹ (values again from Table 1, Tardieu and Davies, 1993. Also in that table, the last column is the references leading to parameter values used).

Eqs. (1) and (2) can be linked to soil moisture content by a series of hydrological “resistances” and soil properties. Leaf water potential, Ψ_l (MPa), satisfies

$$\Psi_l = \Psi_r - J_w R_p \quad (3)$$

where R_p (MPa m² s mg⁻¹) is a plant resistance which includes both radial resistance within the roots and axial resistance between the roots and leaves. Following Tardieu and Davies (1993), a value of $R_p = 7.2 \times 10^{-3}$ MPa m² s mg⁻¹ is prescribed, which might be a mid-range value for a potato crop (values for a small number of alternative plant types are given in Saugier and Katerji, 1991; Table 5). Additionally Ψ_r (MPa) satisfies

$$\Psi_r = \Psi_s - J_w R_{sp} \quad (4)$$

where Ψ_s (MPa) is the bulk soil water potential between roots, R_{sp} (MPa m² s mg⁻¹) is the resistance between the soil and the root surface. This resistance is calculated using the equation of Newman (1969) as

$$R_{sp} = \frac{1}{4\pi K L_a} \ln \frac{d^2}{r^2} \quad (5)$$

where L_a (m m⁻²) is root length per unit area of ground, d (m) is the half mean distance between roots, r (m) is the mean radius

of the roots and K ($\text{mg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) is soil hydraulic conductivity. Values are prescribed as $L_a = 10^4 \text{ m m}^{-2}$, $r = 5 \times 10^{-4} \text{ m}$ and $d = 5.6 \times 10^{-3} \text{ m}$. Such values are similar to those used by Tardieu and Davies (1993), and correspond to typical values for maize (*Zea mays* L.). These equations can then be linked to soil water (i.e. moisture) content, θ ($\text{m}^3 \text{ water (m}^3 \text{ soil)}^{-1}$) via soil water potential Ψ_s (as required in Eq. (4)) and hydraulic conductivity, K (as required in Eq. (5)), through Clapp and Hornberger (1978) relations thus:

$$\Psi_s = \Psi_{sat} \mu_f^{-b_{CH}}, \quad K = K_{sat} \mu_f^{2b_{CH}+3}. \quad (6)$$

Here $\mu_f = \theta/\theta_{sat}$ and θ_{sat} ($\text{m}^3 \text{ water (m}^3 \text{ soil)}^{-1}$) is the saturated soil moisture content, Ψ_{sat} (MPa) is the saturated soil water potential, K_{sat} ($\text{mg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) is the saturated hydraulic conductivity and b_{CH} is the Clapp–Hornberger coefficient. Values are adopted for a medium soil, as given by Cosby et al. (1984) and in Table 2 of Cox et al. (1999). From these, $\theta_s = 0.458$, $b = 6.63$, and converting to the units of this paper, $\Psi_{sat} = -4.86 \times 10^{-4} \text{ MPa}$ and $K_{sat} = 4.81 \times 10^2 \text{ mg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$. Linking physiological responses to soil water potential has been noted by authors e.g. Lhomme (1998).

Eqs. (1)–(6) may be combined. Elimination of R_{sp} , Ψ_r , Ψ_l , K , Ψ_s and c_{ABA} suggests that this ABA-based model for stomatal conductance reduces to one of water flux and soil moisture content only:

$$g_s = g_s(J_w, \theta). \quad (7)$$

The water flux passes through stomata at different levels throughout a vegetation canopy, and combined these total to J_w . Moving from the top leaves of a canopy downwards, one assumption often made is that all resources (such as light; see also Section 2.2) will decay together through the canopy, and as an exponential in leaf area index above any given point (e.g. Cox et al., 1998). This “big-leaf” assumption allows a canopy stomatal conductance g_c (m s^{-1}) to be defined as

$$g_c = g_s \frac{[1 - e^{-kL_c}]}{k} \quad (8)$$

where L_c ($\text{m}^2 \text{ m}^{-2}$) is total canopy leaf area index, and k is a decay co-efficient, typically taking a value of 0.5. Recently advances have been made highlighting the requirement of more sophisticated in-canopy models (e.g. Mercado et al., 2007, 2009). However if here, to close equations we adopt the more simplistic big-leaf approximation, combined with an assumption that humidity deficit D (kg kg^{-1}) is invariant within a canopy, then the atmospheric demand on evaporation (which will be the same as J_w from earlier) is

$$J_w = \rho_a D g_c 10^{-6}. \quad (9)$$

Here ρ_a (kg m^{-3}) is the density of air. Hence (for a given LAI), eliminating water flux J_w between Eqs. (7) and (9) suggests that the Tardieu and Davies (1993) model can be alternatively expressed as responding to the drivers of soil moisture status and atmospheric humidity demand:

$$g_s = g_s(D, \theta). \quad (10)$$

2.2. Governing equations: photosynthetic dependencies

A strong and direct correlation has often been recorded between photosynthesis and stomatal opening (e.g. Wong et al., 1979). This relation now appears at the centre of many large-scale land surface models, and including JULES (Best et al., 2011; Clark et al., 2011) which is in turn incorporated in to the U.K. Hadley Centre HadGEM2 climate models (Martin et al., 2011; Collins et al., 2011). Based on the work of Ball et al. (1987), Leuning (1995) proposed a model

for stomatal conductance with such an explicit dependence on net assimilation, a_n ($\text{mol CO}_2 [\text{m}^2 \text{ leaf area}]^{-1} \text{s}^{-1}$). This is given by

$$g_s = g_{s,\min} + \frac{\nu a_n}{(c_a - c_*)(1 + (D/D_0))} \quad (11)$$

where ν and D_0 (kg kg^{-1}) are parameters, c_a ($\text{mol CO}_2 (\text{m}^3 \text{ air})^{-1}$) is atmospheric CO_2 concentration and variable c_* ($\text{mol CO}_2 (\text{m}^3 \text{ air})^{-1}$) is the temperature (and atmospheric oxygen)-dependent CO_2 compensation point (Clark et al., 2011) for C_3 plants (value of zero for C_4 plants). Net photosynthesis contains a dependence upon surface temperature, T (K), incoming solar radiation I (W m^{-2}) and intercellular CO_2 concentration, c_i ($\text{mol CO}_2 (\text{m}^3 \text{ air})^{-1}$). The latter is calculated from the flux gradient across the stomata as

$$c_i = c_a - \frac{1.6a_n}{g_s} \quad (12)$$

where the factor of 1.6 is the ratio of the diffusivities of carbon dioxide to water vapour in air. Established models of photosynthesis (e.g. Collatz et al., 1991, 1992) exhibit a peak in temperature response, saturate in incoming photosynthetically active radiation, A_{par} (W m^{-2}) (which itself is almost linear in I) and increase in intercellular CO_2 concentration. Eliminating c_i between Eqs. (11) and (12) with the environmental dependencies of a_n gives

$$g_s = g_s(D, T, I, c_a). \quad (13)$$

The big-leaf assumption (as also applied here) is that all factors affecting a_n remain invariant within a canopy, except for light level which decays exponentially in LAI, causing a similar decay in a_n . For small $g_{s,\min}$, this gives to a good approximation that g_s also decays in this way through the canopy and hence canopy conductance satisfies Eq. (8) (and further under this assumption, and from Eq. (12), c_i is therefore almost invariant in a canopy).

2.3. Potential combining of models of stomatal control

Section 2.1 gives a model in which stomatal control may be interpreted as dependent on soil moisture status and surface specific humidity deficit, whilst Section 2.2 provides equations that can be regarded as giving a dependence on temperature, light intensity, atmospheric CO_2 concentration and again specific humidity deficit. All five of these individual environmental conditions have been identified as influencing stomatal response (e.g. Jarvis, 1976 and Stewart, 1988), and where these authors also find such controlling influences may be expressed multiplicatively. This suggests a combined model may be appropriate, and as has also been suggested by Dewar (2002).

The common variable is D , and in Section 3 we consider whether this is the identical response in both model components, or should effectively appear twice in any combination. To account for both options, then we set a function $f(D)$ as either $f(D) \equiv 1$ or $f(D) = (1 + D/D_0)^{-1}$ and with the parameter D_0 (kg kg^{-1}) as from above. Then a new single model for g_s can be given as

$$g_s = g_{s,\min} + \left(\frac{\kappa f(D) a_n}{c_a - c_*} \right) e^{c_{ABA} \beta e^{\delta \Psi_l}} \quad (14)$$

for some constant κ . The value of κ is selected such that with $f(D) \equiv 1$, and $c_a = 350 \text{ ppm}$ (a value appropriate for early 1990s, allowing use of Tardieu et al., 1993 findings), $T = 303.15 \text{ K}$, $I = 500 \text{ W m}^{-2}$, $\theta = \theta_{sat}$ and $D = 0.0$ (kg kg^{-1}), then $g_s = 0.0121 \text{ ms}^{-1}$ (or $g_s = g_{s,\min} + \alpha = 0.27 \text{ mol m}^{-2} \text{s}^{-1}$). That is, for known near optimal (i.e. maximal) conditions for stomatal opening of high light levels, a mid-range temperature, low water stress and low surface humidity deficit. For these values, the model is normalised to give the maximum values of g_s recorded by Tardieu et al. (1993), which gives a value of $\kappa = 2.34 \times 10^7 \text{ m}^3 \text{ ppm} (\text{mol CO}_2)^{-1}$. For these environmental drivers, then water flux J_w expressed in energy

units is $\lambda E = 384 \text{ W m}^{-2}$ whilst net assimilation in mass units is $1.42 \times 10^{-7} \text{ kg C m}^{-2} \text{ s}^{-1}$. Our description for a_n is identical to that of Cox et al. (1998) and Clark et al. (2011), but here without the direct soil moisture content modulation in those papers.

Fig. 1 presents simulations by Eq. (14), individually varying D , T , I , c_a and θ (and for $f(D) \equiv 1$). In panels (b)–(e), simulations were undertaken for $\theta = 0.3 \text{ m}^3 \text{ water m}^{-3} \text{ soil}$ (corresponding to well-watered soil – green line of Fig. 1) and $\theta = 0.2 \text{ m}^3 \text{ water m}^{-3} \text{ soil}$ (corresponding to partially water stressed vegetation – red line of Fig. 1).

We also undertake calculations, but now with $f(D)$ not equivalent to unity. The exact form we take is $f(D) = (1 - D/D_{q,crit})$, so similarly decreasing for higher D but in keeping with the JULES model (Best et al., 2011); here with $D_{q,crit} = 0.09 \text{ kg kg}^{-1}$. This is done only for the factorial experiment varying D (Fig. 1b), and with these additional simulations shown as dashed lines. Hence the dashed lines of Fig. 1b represent both an implicit dependence on D through that ABA signalling (as indicated in Eq. (10)) and additionally a direct control via a non-unity $f(D)$.

3. Discussion

3.1. Dependency on vapour pressure deficit, D

Dewar (2002) argue that in the linking of approaches, it is incorrect to regard the VPD response of model components of Sections 2.1 and 2.2 as the same entity. That is, this is not a single common component to both model parts. Their argument is based on the finding that some plant types are ABA-deficient or insensitive, yet still retain a direct response to D (Assmann et al., 2000). Further the Tardieu and Davies (1993) model does give a particularly low VPD response for high soil moisture contents (e.g. our nearly flat line of Fig. 1a for $\theta = 0.3$). Hence in the process of model calibration by Leuning (1995), we suggest this may include instances where there is little soil moisture stress, and yet the VPD response remains to give a non-infinite D_0 value – thus supporting the argument of Dewar (2002) of additional direct D dependence. However, the converse argument can also be made. It may also be that during the process of calibration of the parameter D_0 , this will include instances where soil moisture takes values far from saturation, and as such the magnitude of the D_0 parameter may be, in part at least, influenced by invoking an ABA response signalling soil moisture status.

Reduced stomatal sensitivity to D at high soil moisture content is realistic for some species (which might favour $f(D) \equiv 1$). Such behaviour is observed by Tardieu and Simonneau (1998) for maize, sunflower (*Helianthus annuus* L.) and poplar (*Populus euramericana*). Calvet (2000) show further evidence for this response from a re-analysis of published leaf gas exchange measurements. Roberts et al. (1990) show, however, that for tropical rainforest, there is evidence of a sensitivity to surface humidity deficit, even when water is not limited within the soil, which would favour the form of $f(D) = (1 + D/D_0)^{-1}$.

More recently, Medlyn et al. (2011, 2012) provide key insights in to the VPD response by stomatal conductance. Using their model, built from optimisation concepts to maximise photosynthesis for a given water usage, they modulate g_s with a VPD dependence of the form $f(D) = (1 + g_1/\sqrt{D})$. Their observed lowest g_1 value represents a reduction in g_s of around 25% between $D = 0.005 \text{ (kg kg}^{-1}\text{)}$ and $D = 0.015 \text{ (kg kg}^{-1}\text{)}$ (i.e. converting to our VPD units, so allowing comparison to our Fig. 1b) whilst their highest g_1 value approaches a 50% reduction over the same range. The higher g_1 values are for warmer regions, which is found to be in keeping with the optimal hypothesis. Medlyn et al. (2011, 2012) also discuss how other authors adjust g_1 under drought conditions, suggesting they regard

an (unadjusted) non-zero g_1 parameter as applicable without water stress. That conforms to $f(D)$ is not equivalent to unity. However it is also the case that Medlyn et al. (2011, 2012) do find the strongest D dependency (via higher g_1 values) in warmer and thus potentially most drought-stressed regions of the world. Speculation can be made that in those circumstances, any VPD response might be a proxy for a stomatal response to J_w , controlled by ABA signalling, in such drought conditions. That would retain the possibility that any D dependency is not a direct control, favouring more $f(D) \equiv 1$.

As for any proposed introduction of new theory-based physiological descriptions into large-scale land surface models, eventual detailed testing of ability to reproduce measurements from multiple plant types needs to be undertaken. At the field-scale or larger, then databases such as FLUXNET (www.fluxdata.org) are especially valuable, providing simultaneous measurements of water, energy and CO_2 fluxes (for discussion, see e.g. Jung et al., 2009). This can then be used to calibrate land surface models when used in tandem with concurrent meteorological measurements. Routine splitting of datasets into distinct periods where soil water status is expected (or modelled) to be either depleted or fully available may aid in generating a more definitive conclusion as to the form of $f(D)$ in Eq. (14). As an aside, experiments of instantaneous variations in leaf-level humidity have been found to adjust guard cell ABA concentrations simultaneously with altering stomatal opening (Xie et al., 2006); this cannot be a consequence of D influencing J_w and thus [ABA] via our Eq. (2) as that is associated with transmission of signals from the roots, and for which there will always be at least some time delay. Should $f(D)$ be found not equal to unity, and hence direct VPD response at leaf level, then this could represent additional concurrent variations between ABA influence and stomata opening.

3.2. Flux dependencies of combined model

There exists one particularly noteworthy alternative set of potential dependencies, and for the combined model of Eq. (14). The (double) exponential component of Eq. (14), as analysed in Section 2.1, can through Eqs. (1)–(6) be regarded as an implicit function of water flux J_w and soil moisture θ (i.e. leading to Eq. (7)). Additionally, the humidity deficit D response in (14) can be seen instead as a function of J_w (and of g_c itself, and all for given LAI) – i.e. from Eq. (9). This allows the full model in Eq. (14), for a given LAI, to be written as having potential dependencies of only:

$$g_s = g_s(J_w, a_n, \theta, c_a). \quad (15)$$

This constitutes a remarkable set of drivers. It suggests that stomatal opening can be linked, mathematically at least, to be a function of the two land-atmosphere fluxes of the hydrological and carbon cycle, J_w and a_n respectively. The response of g_s to high frequency (sub-diurnal) fluctuations in imposed canopy-level meteorological conditions is through their impact on these fluxes. Then more slowly changing indicators of hydrological and carbon cycle status are contained in what might be regarded as soil and atmospheric store terms of θ and c_a respectively.

We additionally show as two extra panels in Fig. 1 the link between g_s and total water flux J_w (i.e. λE : panel (f)) and the net assimilation a_n (panel (g)). The evaporative flux response is found by changing J_w in Eqs. (1)–(6), decreasing down to different values from its value associated with near optimal conditions outlined above. This provides values for the ABA-based exponential term of Eq. (14), and which is solved for the case of $f(D) \equiv 1$. Similarly the a_n dependence is found again adjusting that quantity only, down from optimal conditions, and again in Eq. (14). In practise, variation in the two quantities might not occur completely independently – a changing water flux J_w will affect g_s , which in turn alters internal

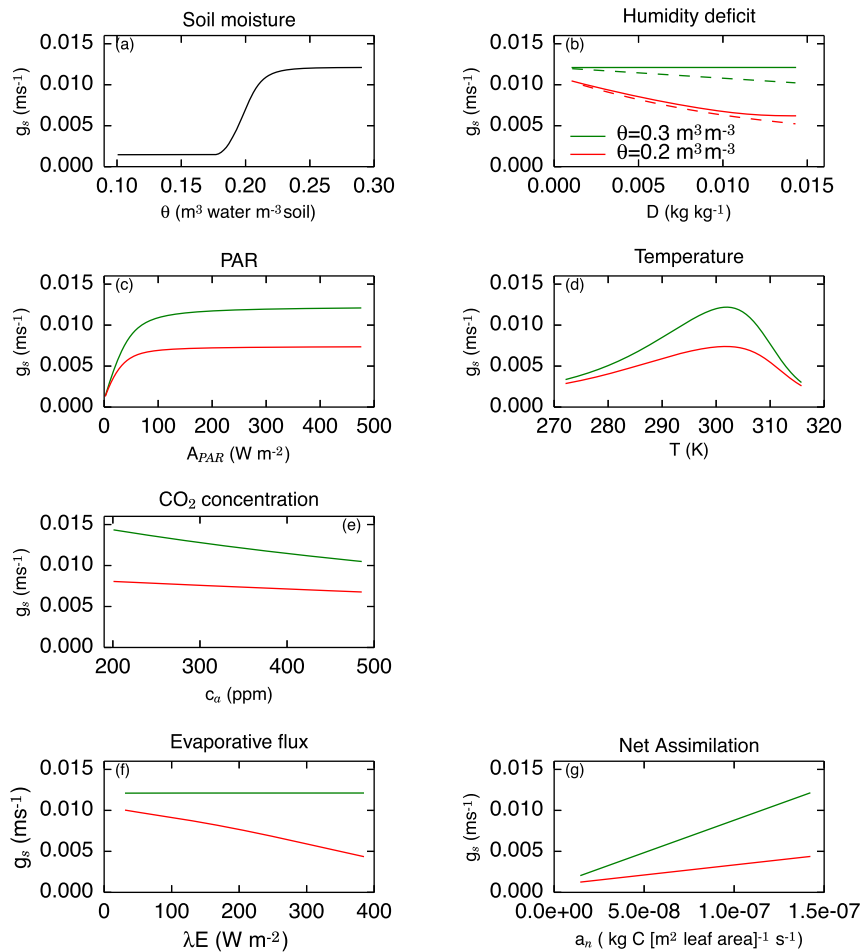


Fig. 1. Predictions of canopy stomatal resistance g_s (m s^{-1}) as a function of (a) soil moisture content, θ , (b) humidity deficit, D , (c) photosynthetically active radiation, I , (d) leaf temperature, T and (e) atmospheric CO_2 concentration, c_a . The control values (except where varied individually) are $\theta = 0.3 \text{ m}^3 \text{ water (m}^3 \text{ soil)}^{-1}$ and $\theta = 0.2 \text{ m}^3 \text{ water (m}^3 \text{ soil)}^{-1}$ (green and red curves respectively), $D = 0.008 \text{ kg kg}^{-1}$, $I = 500 \text{ W m}^{-2}$, $T = 303.15 \text{ K}$ and $c_a = 350 \text{ ppm}$. All simulations are for $f(D) \equiv 1$, except for additional VPD response curves (panel (b), dashed lines) and which correspond to $f(D) = (1 - D/D_{q,\text{crit}})$. Canopy conductance g_c can then be calculated by Eq. (8). Panels (f) and (g) show dependence on evaporative flux and net assimilation respectively (see text for details).

CO_2 concentration c_i , upon which a_n depends. Similarly altering g_s via a_n will also influence J_w via Eq. (9).

We hypothesize that regarding the dependencies in this form may offer an opportunity of comparing understanding of stomatal response more easily to the optimisation hypothesis of Cowan (1977) and Cowan and Farquhar (1977), and as recently updated by Medlyn et al. (2011, 2012). This optimisation concept uses the premise that stomatal conductance operates so as to maximise CO_2 uptake for a given water loss. That is, over a given period, for a prescribed integration of J_w (which will be related to available rainfall) the integral of a_n is maximised. Additionally both Mott and Parkhurst (1991) and Monteith (1995) suggest that the apparent response of stomatal conductance to specific humidity deficit, D , could in fact be a proxy for a dependence upon the water flux. Ignoring temperature, light and CO_2 concentration, Monteith (1995) proposed a linear dependence of the form $g_s = g_{s,\text{min}} + g_{\text{max}}[1 - J_w/J_{w,\text{max}}(\theta)]$ where $J_{w,\text{max}}$ ($\text{mg m}^{-2} \text{ s}^{-1}$) is a maximum water flux, considered to be a function of the soil moisture content. More recently, Jia and Davies (2007) provide experimental evidence of this as a direct dependency. In controlled conditions, with canopy specific humidity deficit held invariant, and by uncoupling vegetation shoots from roots (and hence avoiding any response to J_w along the full root-shoot system), they find that changes in transpiration adjusts sap pH, impacting on [ABA], which then adjusts stomatal opening. This would correspond to

$f(D)$ not being unity although acting as a proxy for an additional (non-root) dependence on water flux J_w in models such as (11).

For carbon fluxes, if any of these model frameworks are extended to include dynamic components that determine vegetation size and structure (i.e. Dynamic Global Vegetation Models; DGVMs), then allometric relations will translate the integration in time of flux a_n to LAI. For one of many examples, Huntingford et al. (2000) present this for the dominant vegetation type in the JULES model.

3.3. Inclusion of the soil moisture dependency

Our combined model of Eq. (14) links soil moisture status with a direct influence on stomatal opening. This influences net photosynthesis, a_n , but indirectly through changes in g_s which in turn affect intercellular CO_2 concentration c_i (via Eq. (12) where a_n depends on c_i). This is in contrast to the analysis of Cox et al. (1998), where for the C_4 vegetation analyzed (Kansas prairie FIFE data; Verma et al., 1992), data suggest that there is a more direct and strong soil moisture control upon a_n . In Cox et al. (1998) a plot for the FIFE data of inferred g_c vs a_n shows the ratio g_c/a_n to be almost constant, and notably including for very low g_c values when soil moisture content is also low. This would be difficult to achieve through changes via c_i alone, given the relative weak influence of c_i changes on a_n . Instead, in Cox et al. (1998), net assimilation is first calculated without water

stress, before this is then multiplied (to give an overall value of a_n) by a semi-linear function that decreases from unity to zero for soil moisture decreasing from its critical value θ_{crit} ($\text{m}^3 \text{ water } (\text{m}^3 \text{ soil})^{-1}$) to a wilting value θ_{wilt} ($\text{m}^3 \text{ water } (\text{m}^3 \text{ soil})^{-1}$). Stomatal opening is then linear in that revised adjusted net assimilation.

To reconcile to our combined model, one possibility is that the behaviour implicit in our equation set and parameters is more non-linear in terms of response to soil moisture content (Fig. 1a), which could elicit a larger response to a_n via changes to g_s and c_i . A second possibility is to retain the approach of Cox et al. (1998), and alternatively regard the exponential dependence on c_{ABA} and Ψ_l in Eq. (14) as instead changing net photosynthesis, a_n . This would give the identical equation for g_s , as in Eq. (14). Where our model would change, compared to the approach outlined above, is that the actual a_n would now include these c_{ABA} and Ψ_l effects directly, rather than just via g_s and c_i . That is a_n would be its value calculated as a function of T , I , c_i , but additionally multiplied by $\exp(c_{ABA}\beta\exp(\delta\Psi_l))$. Of relevance is Zhou et al. (2013), which is a recent and comprehensive assessment of plant responses to drought. Their study observed relationships between both photosynthesis and stomatal conductance, and leaf water potential. They conclude that there is a drought response on both g_s and a_n , suggesting the latter via carboxylation capacity, V_{cmax} . Additionally, they modify the g_1 parameter of Medlyn et al. (2011, 2012) (see above) with a function that is an exponential in pre-dawn leaf water potential, thus having some similarities to our Eq. (1). Further Jarvis and Davies (1998) speculate about a direct influence of soil moisture on net photosynthesis, and potentially involving ABA as the messenger between the two.

3.4. Aspects of implementation in to GCMs and impact models

The model dependences in Eqs. (10) and (13) combine to give what might be regarded as a standard set of five drivers (e.g. Jarvis, 1976) as $g_s = g_s(D, T, I, \theta, c_a)$, and as portrayed in our Fig. 1(a)–(e) and schematic Fig. 2. These are standard leaf-level quantities routinely calculated in most GCMs. Practical aspects of a more commonplace

implementation of ABA-based models in to large-scale land surface models are as follows. GCMs already often contain parameters K , K_{sat} , θ_{sat} , b_{CH} and Ψ_{sat} as part of their soil parameterisation. To implement the [ABA]-based description of Eq. (14) requires additionally prescription of parameter β in Eq. (1), parameters a and b in Eq. (2), parameter R_p in Eq. (3) and parameters L_a , d and r in Eqs. (4) and (5). It requires characterisation of functional form of $f(D)$ (Section 3.1). We assume estimates already exist for α based on existing knowledge of maximum and minimum values of stomata opening. Analysis would be needed to discover whether determination of this higher number of unknowns is possible from, for example, FLUXNET measurements, or if collinearity between parameters is a problem, requiring additional ABA-specific measurements for model constraint. Numerically we find solution to the equation set requires iteration, and in particular as the value of g_s affects c_i , which in turn affects a_n , upon which g_s depends. Such iteration may be avoidable in the event of direct soil moisture modulation of a_n (see above) due to equation term cancellation, and for similar reasons to those in Cox et al. (1998). More sophisticated canopy models (e.g. Mercado et al., 2007), determining meteorological profiles vertically through vegetation, would require any iteration to occur at multiple levels.

The role of ABA in regulation of specific crop responses to drought-induced soil moisture change is becoming significantly better understood (see for instance Zingaretti et al., 2013 and references therein). This suggests that despite any additional complexity and parameterisation, there is potential to make better predictions of the fate of particular crop types in a changing climate. This is potentially more achievable at present, rather than generating parameters appropriate for a more generic limited-number of Plant Function Types (PFTs) that are present in DGVMs (e.g. Sitch et al., 2008). Such crop models may be driven offline, forced by, for example, diagnostics from the Coupled Model Intercomparison Project phase 5 (CMIP5) ensemble (Taylor et al., 2012). ABA-based description of stomatal response to soil moisture status may aid in understanding the food security implications of any estimated

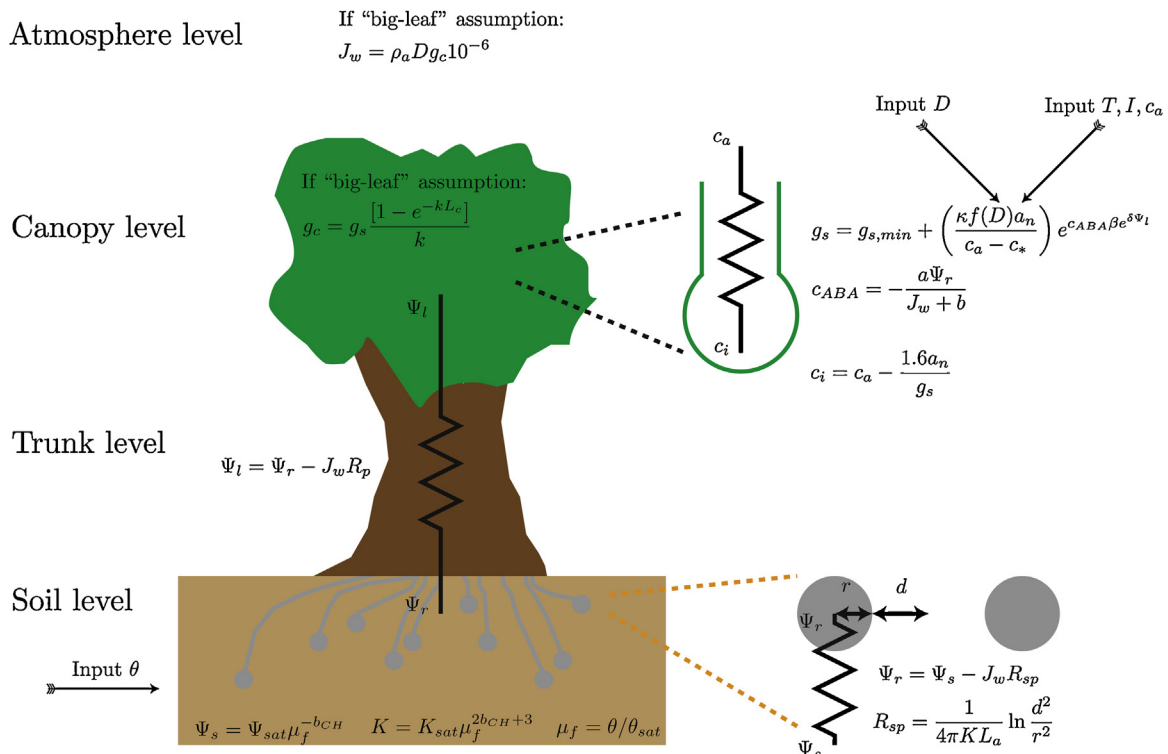


Fig. 2. A schematic of the governing equations used at the different soil, trunk, canopy and atmosphere levels.

changes to drought frequency by the CMIP5 ensemble. There is evidence that some stomatal-based changes expected in a changing climate might already be observable. For instance, increasing atmospheric CO₂ (c_a) causing reduced stomatal opening (Fig. 1e) may be detected in river runoff records (Gedney et al., 2006). Despite the caveat that many ABA measurements are crop-based, there are often similarities between how DGVMs model these and natural PFTs. Crops are frequently represented as a natural grass type, but with enhanced turnover to represent harvesting. Hence with appropriate measurements, an ABA signalling model framework could be readily extended to be part of DGVM descriptions of natural vegetation types.

An emerging environmental concern is the impact of raised tropospheric ozone on vegetation, which can have strong implications for global plant productivity (e.g. Huntingford et al., 2011) and which can therefore feedback via the carbon cycle (Sitch et al., 2007). Similar to the soil moisture control representation in GCMs, the ozone (O₃) response adjusting stomatal opening is currently given by a more empirical description. Here too the explicit modelling of ABA could ultimately bring a more mechanistic depiction of O₃ in to large-scale terrestrial models. Mills et al. (2009) provide one recent updated estimate of O₃ damage to stomatal functioning. Sun et al. (2012) argue that the mechanism behind the findings of, for instance, Mills et al. (2009) are that a reduced sensitivity to ABA occurs. This is a consequence of raised canopy-level ozone concentrations increasing ethylene production, also a plant growth regulator, which lowers ABA's effect on stomata (Wilkinson and Davies, 2010). McLaughlin et al. (2007a,b) and Sun et al. (2012) highlight the importance of ozone-vegetation interactions on the hydrological cycle, including streamflow. Hence this additional more mechanistic process knowledge – potentially via ABA modelling – could aid any search with detection and attribution algorithms for an ozone signal in runoff (thus extending the analysis of Gedney et al. (2006) for contemporary periods, and aiding future runoff projections (Betts et al., 2007)).

4. Conclusions

Medlyn et al. (2011) state: “very few studies have directly examined how the relationship between photosynthesis and stomatal conductance is affected by drought”. Such better understanding is required as part of preparation for any changing climatic conditions. Prudhomme et al. (2014), for example, demonstrate across climate models and global impact models, there is high potential for major changes to drought frequency in a greenhouse gas enriched world. They also observe the largest uncertainty is in the impacts responses, although noting that better future description of the dynamic responses of plants to CO₂ and climate change may show a capability to offset some effects of drought conditions. Yet despite its importance and continuously improving physiological knowledge of soil moisture controls on stomatal opening, as yet most large-scale climate models tend to rely on regression-based empirical fits to describe this linkage.

Understanding of hormonal regulation of stomatal opening in response to soil moisture status, transmitted from root to canopy by xylem [ABA] concentration, is an advanced science at the laboratory or field scale (e.g. Wilkinson and Davies, 2002). In the theoretical analysis presented here, we consider a consistent and complete set of ABA-based equations and discuss how these could be incorporated in to the terrestrial ecosystem component of climate models. Building on the study of Dewar (2002), we show how this might be achieved through combining two descriptions of stomatal conductance, i.e. (1) a dependence upon ABA signalling (e.g. Tardieu and Davies, 1993) and (2) a dependence upon photosynthetic flux (e.g. Ball et al., 1987). At the minimum, calculations could

be made for the responses of specific plant types, including crops, to changed hydrological regimes. Ultimately, for global applicability in climate simulations, then availability of ABA-related parameterisations needs to increase to the extent that it becomes possible to construct a table of values for the small number of generic plant functional types utilised in DGVMs. Such a table, with uncertainty bounds, would be for ABA-specific parameters β , a , b and related additional hydrological quantities R_p , L_a , d , r . If modelled ABA representation does improve DGVM process representation of soil-plant-atmosphere fluxes of water, then implementation in a fully coupled GCM framework may reveal new insights as to the likelihood of drought stress for different locations and levels of climate change. Similarly, it may aid better assessment of future evolution of terrestrial ecosystems as a component of the global carbon cycle.

That the dependencies of the combined model presented can be reduced to just the four of net assimilation, water flux, atmospheric CO₂ concentration and soil moisture content is remarkable. This may have implications for the photosynthetic strategies of terrestrial ecosystems and their response to and role in the carbon and water cycles. It can be conjectured that instantaneous water fluxes provide additional and refining high frequency information of imposed weather variability to plants, over and beyond a more slowly changing soil water status. This could alert to more immediate raised drought risk in the event that evaporative demand suddenly increases. Similarly, it may be that instantaneous net assimilation provide a similar mediating role for behaviour of vegetation in the global carbon cycle, beyond responding to any slowly changing atmospheric CO₂ concentrations. On-going plant physiological research will confirm whether the apparent dependences on fluxes are more a consequence of equation re-arrangement, or genuine drivers as “seen” by vegetation.

Acknowledgements

This work was supported by the NERC CEH Integrating Fund and the NERC CEH National Capability Fund. The authors thank Richard Harding, John Roberts and John Gash for their valuable suggestions on an early draft.

References

- Assmann, S.M., Snyder, J.A., Lee, Y.-R.J., 2000. ABA-deficit (*aba1*) and ABA-insensitive (*abi1-1*, *abi2-1*) mutants of *Arabidopsis* have a wild-type stomatal response to humidity. *Plant Cell Environ.* 23, 387–395.
- Ball, J.T., Woodrow, I.E., Berry, J.A., 1987. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: Biggins, I. (Ed.), *Progress in Photosynthesis Research*. Martinus Nijhoff, Springer, Dordrecht, pp. 221–224.
- Best, M.J., et al., 2011. The joint UK land environment simulator (JULES) model description – Part 1: Energy and water fluxes. *Geosci. Model Dev.* 4, 677–699.
- Betts, R.A., et al., 2007. Projected increase in continental runoff due to plant responses to increasing carbon dioxide. *Nature* 448, 1037–1041.
- Calvet, J.-C., 2000. Investigating soil and atmospheric plant water stress using physiological and micrometeorological data. *Agric. For. Meteorol.* 103, 229–247.
- Clapp, R.B., Hornberger, G.M., 1978. Empirical equations for some soil hydraulic properties. *Water Resour. Res.* 14, 601–604.
- Clark, D.B., et al., 2011. The Joint UK Land Environment Simulator (JULES) model description – Part 2: Carbon fluxes and vegetation dynamics. *Geosci. Model Dev.* 4, 701–722.
- Collatz, G.J., Ball, J.T., Grivet, C., Berry, J.A., 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary-layer. *Agric. For. Meteorol.* 54, 107–136.
- Collatz, G.J., Ribas-Carbo, M., Berry, J.A., 1992. Coupled photosynthesis-stomatal conductance model for leaves of C₄ plants. *Aust. J. Plant Physiol.* 19, 519–538.
- Collins, W.J., et al., 2011. Development and evaluation of an Earth-System model – HadGEM2. *Geosci. Model Dev.* 4, 1051–1075.
- Cosby, B.J., Hornberger, G.M., Clapp, R.B., Ginn, T.R., 1984. A statistical exploration of the relationships of soil moisture characteristics to the physical properties of soils. *Water Resour. Res.* 20, 682–690.
- Cowan, I.R., 1977. Stomatal behaviour and environment. In: Preston, R.D., Woolhouse, H.W. (Eds.), *In: Advances in Botanical Research*, vol. 4. Academic Press, London, pp. 117–228.

- Cowan, I.R., Farquhar, G.D., 1977. Stomatal function in relation to leaf metabolism and environment. In: Jennings, D.H. (Ed.), In: *Integration of Activity in the Higher Plant*, vol. 31. Society for Experimental Biology, Cambridge, pp. 471–505.
- Cox, P.M., Huntingford, C., Harding, R.J., 1998. A canopy conductance and photosynthesis model for use in a GCM land surface scheme. *J. Hydrol.* 212, 79–94.
- Cox, P.M., Betts, R.A., Bunton, C.B., Essery, R.L.H., Rowntree, P.R., Smith, J., 1999. The impact of new land surface physics on the GCM simulation of climate and climate sensitivity. *Clim. Dynam.* 15, 183–203.
- de Arellano, J.V.G., van Heerwaarden, C.C., Lelieveld, J., 2012. Modelled suppression of boundary-layer clouds by plants in a CO₂-rich atmosphere. *Nat. Geosci.* 5, 701–704.
- Dewar, R.C., 2002. The Ball–Berry–Leuning and Tardieu–Davies stomatal models: synthesis and extension within a spatially aggregated picture of guard cell function. *Plant Cell Environ.* 25, 1383–1398.
- Garratt, J.R., 1993. Sensitivity of climate simulations to land-surface and atmospheric boundary-layer treatments – a review. *J. Clim.* 6, 419–449.
- Gedney, N., et al., 2006. Detection of a direct carbon dioxide effect in continental river runoff records. *Nature* 439, 835–838.
- Huntingford, C., Cox, P.M., 1997. Use of statistical and neural network techniques to detect how stomatal conductance responds to changes in the local environment. *Ecol. Model.* 97, 217–246.
- Huntingford, C., Monteith, J.L., 1998. The behaviour of a mixed-layer model of the convective boundary layer coupled to a big leaf model of surface energy partitioning. *Bound. Layer Meteorol.* 88, 87–101.
- Huntingford, C., Cox, P.M., Lenton, T.M., 2000. Contrasting response of a simple terrestrial ecosystem model to global change. *Ecol. Model.* 134, 41–58.
- Huntingford, C., et al., 2011. Highly contrasting effects of different climate forcing agents on terrestrial ecosystem services. *Phil. Trans. R. Soc. A* 369, 2026–2037.
- IPCC, 2007. In: Solomon, S., et al. (Eds.), *Climate Change 2007: The Physical Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom/New York, NY, USA, 996 pp.
- Jacobs, C.M.J., DeBruin, H.A.R., 1992. The sensitivity of regional transpiration to land-surface characteristics: significance of feedback. *J. Clim.* 5, 683–698.
- Jarvis, P.G., 1976. The interpretation of the variations of leaf water potential and stomatal conductance found in canopies in the field. *Phil. Trans. R. Soc. B* 273, 593–610.
- Jarvis, A.J., Davies, W.J., 1998. The coupled response of stomatal conductance to photosynthesis and transpiration. *J. Exp. Bot.* 49, 399–406.
- Jia, W., Davies, W.J., 2007. Modification of leaf apoplastic pH in relation to stomatal sensitivity to root sourced ABA signals. *Plant Physiol.* 143, 68–77.
- Jung, M., Reichstein, M., Bondeau, A., 2009. Towards global empirical upscaling of FLUXNET eddy covariance observations: validation of a model tree ensemble approach using a biosphere model. *Biogeosciences* 6, 2001–2013.
- Khalil, A.A.M., Grace, J., 1993. Does xylem sap ABA control stomatal behaviour of water-stressed sycamore (*Acer pseudoplatanus* L.) seedlings? *J. Exp. Bot.* 44, 1127–1134.
- Lange, O.L., Lösch, R., Schulze, E.-D., Kappen, L.K., 1971. Responses of stomata to changes in humidity. *Planta* 100, 76–86.
- Leuning, R., 1995. A critical appraisal of a combined stomatal-photosynthesis model for C3 plants. *Plant Cell Environ.* 18, 339–355.
- Lhomme, J.-P., 1998. Formulation of root water uptake in a multi-layer soil-plant model: does van den Honert's equation hold? *Hydrol. Earth Syst. Sci.* 2, 31–40.
- Long, S.P., Ainsworth, E.A., Leakey, A.D.B., Nosberger, J., Ort, D.R., 2006. Food for thought: lower-than-expected crop yield stimulation with rising CO₂ concentrations. *Science* 312, 1918–1921.
- Martin, G.M., et al., 2011. The HadGEM2 family of Met Office Unified Model climate configurations. *Geosci. Model Dev.* 4, 723–757.
- McLaughlin, S.B., Nosal, M., Wullschleger, S.D., Sun, G., 2007a. Interactive effects of ozone and climate on tree growth and water use in a southern Appalachian forest in the USA. *New Phytol.* 174, 109–124.
- McLaughlin, S.B., Wullschleger, S.D., Sun, G., Nosal, M., 2007b. Interactive effects of ozone and climate on water use soil moisture content and streamflow in a southern Appalachian forest in the USA. *New Phytol.* 174, 125–136.
- Medlyn, B.E., et al., 2011. Reconciling the optimal and empirical approaches to modelling stomatal conductance. *Glob. Change Biol.* 17, 2134–2144.
- Medlyn, B.E., et al., 2012. Corrigendum: reconciling the optimal and empirical approaches to modelling stomatal conductance. *Glob. Change Biol.* 18, 3476.
- Meidner, H., Mansfield, T.A., 1968. *Physiology of Stomata*. McGraw Hill, Maidenhead, United Kingdom.
- Mercado, L.M., Huntingford, C., Gash, J.H.C., Cox, P.M., Jogireddy, V., 2007. Improving the representation of radiation interception and photosynthesis for climate model applications. *Tellus Ser. B* 59, 553–565.
- Mercado, L.M., et al., 2009. Impact of changes in diffuse radiation on the global land carbon sink. *Nature* 458, 1014–1017.
- Mills, G., Hayes, F., Wilkinson, S., Davies, W.J., 2009. Chronic exposure to increasing background ozone impairs functioning in grassland species. *Glob. Change Biol.* 15, 1522–1533.
- Monteith, J.L., 1981. Evaporation and surface temperature. *Quart. J. R. Meteorol. Soc.* 107, 1–27.
- Monteith, J.L., 1995. A reinterpretation of stomatal responses to humidity. *Plant Cell Environ.* 18, 357–364.
- Mott, K.A., Parkhurst, D.F., 1991. Stomatal response to humidity in air and helox. *Plant Cell Environ.* 14, 509–515.
- Neilson, R.E., Jarvis, P.G., 1975. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). VI. Response of stomata to temperature. *J. Appl. Ecol.* 12, 879–891.
- Newman, E.I., 1969. Resistance to water flow in soil and plant. I. Soil resistance in relation to amount of roots, theoretical estimates. *J. Appl. Ecol.* 6, 1–12.
- Prudhomme, C., et al., 2014. Hydrological droughts in the 21st century, hotspots and uncertainties from a global multimodel ensemble experiment. *Proc. Natl. Acad. Sci. U.S.A.* 111, 3262–3267.
- Raupach, M.R., 1998. Influences of local feedbacks on land-air exchanges of energy and carbon. *Glob. Change Biol.* 4, 477–494.
- Roberts, J., Cabral, O.M.R., Aguiar, L.F., 1990. Stomatal and boundary-layer conductances in an Amazonian terra firme rain forest. *J. Appl. Ecol.* 27, 336–353.
- Saugier, B., Katerji, N., 1991. Some plant factors controlling evapotranspiration. *Agric. For. Meteorol.* 54, 263–277.
- Sitch, S., Cox, P.M., Collins, W.J., Huntingford, C., 2007. Indirect radiative forcing of climate change through ozone effects on the land-carbon sink. *Nature* 448, 791–794.
- Sitch, S., et al., 2008. Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Glob. Change Biol.* 14, 2015–2039.
- Stålfelt, M.G., 1955. The stomata as a hydrophobic regulator of the water deficit of the plant. *Physiol. Plantarum* 8, 572–593.
- Stewart, J.B., 1988. Modelling surface conductance of a pine forest. *Agric. For. Meteorol.* 43, 19–35.
- Sun, G.E., et al., 2012. Interactive influences of ozone and climate on streamflow of forested watersheds. *Glob. Change Biol.* 18, 3395–3409.
- Tardieu, F., 1993. Will increases in our understanding of soil-root relations and root signalling substantially alter water flux models? *Phil. Trans. R. Soc. B* 341, 57–66.
- Tardieu, F., Davies, W.J., 1993. Integration of hydraulic and chemical signalling in the control of stomatal conductance and water status of droughted plants. *Plant Cell Environ.* 16, 341–349.
- Tardieu, F., Simonneau, T., 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. *J. Exp. Bot.* 49, 419–432.
- Tardieu, F., Zhang, J., Davies, W.J., 1992. What information is conveyed by an ABA signal from maize roots in drying field soil? *Plant Cell Environ.* 15, 185–191.
- Tardieu, F., Zhang, J., Gowing, D.J.G., 1993. Stomatal control by both [ABA] in the xylem sap and leaf water status: a test of a model for droughted or ABA-fed field-grown maize. *Plant Cell Environ.* 16, 413–420.
- Taylor, K.E., Stouffer, R.J., Meehl, G.A., 2012. An overview of CMIP5 and the experiment design. *Bull. Am. Meteorol. Soc.* 93, 485–498.
- Verma, S.B., Kim, J., Clement, R.J., 1992. momentum, water vapour, and carbon dioxide exchange at a centrally located prairie site during FIFE. *J. Geophys. Res.* 97, 18629–18639.
- Wilkinson, S., Davies, W.J., 2002. ABA-based chemical signalling: the co-ordination of responses to stress in plants. *Plant Cell Environ.* 25, 195–210.
- Wilkinson, S., Davies, W.J., 2010. Drought, ozone, ABA and ethylene: new insights from cell to plant to community. *Plant Cell Environ.* 33, 510–525.
- Wong, S.C., Cowan, I.R., Farquhar, G.D., 1979. Stomatal conductance correlates with photosynthetic capacity. *Nature* 282, 424–426.
- Xie, X., et al., 2006. The identification of genes involved in the stomatal response to reduced atmospheric relative humidity. *Curr. Biol.* 16, 882–887.
- Zhang, J., Davies, W.J., 1989. Abscisic acid produced in dehydrating roots may enable the plant to measure the water status of the soil. *Plant Cell Environ.* 12, 73–81.
- Zhang, J., Davies, W.J., 1990. Changes in the concentration of ABA in xylem sap as a function of changing soil water status can account for changes in leaf conductance and growth. *Plant Cell Environ.* 13, 277–285.
- Zhou, S.X., Duursma, R.A., Medlyn, B.E., Kelly, J.W.G., Prentice, I.C., 2013. How should we model plant responses to drought? An analysis of stomatal and non-stomatal responses to water stress. *Agric. For. Meteorol.* 182, 204–214.
- Zingaretti, S.M., Inácio, M.C., Pereira, L.D.M., Paz, T.A., França, S.D.C., 2013. Water stress and agriculture. In: Akinci, S. (Ed.), *Responses of Organisms to Water Stress*. InTech, <http://dx.doi.org/10.5772/53877>.