Modelling stomatal conductance in response to environmental factors

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ABSTRACT

Stomata are an attractive system for modellers for many reasons, and the literature contains a large number of papers describing models that predict stomatal conductance as a function of environmental factors. The approaches and goals of these models vary considerably. This review summarizes these different approaches and discusses their strengths and weaknesses with a focus on mechanistically based models. The critical unresolved questions are highlighted and placed in the context of current research on stomatal physiology. Finally, directions for future research are considered.

Key-words: ABA; CO_2; humidity; light; temperature.

OVERVIEW AND HISTORICAL PERSPECTIVE

Stomata exert control over the fluxes of H_2O vapour and CO_2 between the leaf and the atmosphere, and they adjust their aperture in response to a number of environmental factors. Their behaviour is important for individual plant performance, agricultural productivity, and global CO_2 and water cycles. The response of stomatal conductance to environmental factors is an attractive system for modellers for many reasons. The system has enough inputs to be interesting and non-trivial, but not so many inputs as to be intractable. There are multiple signal transduction mechanisms involved, with both biochemical and biophysical aspects, and there is substantial interaction among the signaling pathways. Finally, there is a clearly defined output – stomatal conductance or aperture – that is easily measureable for model parameterization and validation, and this output has substantial biological relevance.

Because of this, models that predict stomatal conductance for a given set of environmental conditions are of interest to those working in several disciplines. The approaches used by these different groups vary according to the goal of the modelling effort. For example, models for predicting stomatal conductance are useful for understanding the factors that determine productivity and water use in either natural or agricultural systems, and for informing efforts to manipulate those factors for applied management goals. Conductance models are also interesting to those involved in making general circulation models (GCMs) and numerical weather

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prediction (NMW) models that are used in predicting weather over long and short periods of time, respectively, because stomata control the rate of water loss over vegetated areas and therefore affect atmospheric moisture levels and surface temperatures. Physiologists also use stomatal models in conjunction with experiments to understand the processes and sensing mechanisms by which stomata respond to environmental factors. Finally, because stomata regulate a critical resource trade-off faced by land plants – carbon gain versus water loss – stomatal functioning also has an economic dimension that is interesting to those who wish to understand *why* stomata behave as they do, and how that behaviour impacts other aspects of plant form and function.

This review attempts to discuss in broad terms the general aims and techniques that have been used in modelling of stomatal responses to environmental factors, with emphasis on the most recent developments and future challenges. In particular, we have tried to point out the strengths and weaknesses of the different approaches to this problem with reference to the ultimate goal of the model construction. We have also tried to emphasize that the widely divergent uses of stomatal models – whether to predict gas exchange, infer processes and their interactions at different scales, or analyse economics of water and carbon flows – each requires a very different perspective on how models should be interpreted and evaluated with respect to observations.

OVERVIEW AND HISTORICAL PERSPECTIVE

There have been three basic approaches to modelling stomatal conductance: empirical (data-based), mechanistic (process-based), and economic (optimization-based). In practice, the first two of these approaches can never be separated completely because even the most empirical models make assumptions about the factors to which stomata respond and are therefore at least partially mechanistic, and even the most detailed mechanistic models must resort to empiricism at some scale. Published models of stomatal responses to environmental factors cover the entire spectrum between these two hypothetical extremes, and the best trade-off between these two approaches depends on the intended use. Empirical models are often simpler and more numerically tractable than mechanistic models, and for those users who require a stomatal sub-model to plug into a larger model of global or canopy level processes, these models are often best. More mechanistic models are often more mathematically complex and are better suited for investigating the cellular and subcellular processes involved in environmental

sensing, signal transduction, and ion movements. While many mechanistic models are expressed as steady-state relationships, some are spatially and/or temporally explicit, which is helpful for studying interactions among regions or compartments within a leaf, or interactions between leaf and whole plant function.

The third approach, optimality, is philosophically related to empirical modelling in the sense that both approaches assume that certain emergent properties of stomatal functioning are conservative and are therefore useful for prediction. However, whereas empirical models are typically based on conserved relationships between two observables (e.g. stomatal conductance is often linearly correlated to net photosynthetic rate), optimality-based models attempt to *deduce* such emergent relationships from a more general proposition, namely, that plants tend to use limiting resources in a quantifiably optimal way. The underlying premise is that stomata are regulated by genomes that have been powerfully shaped by natural selection. This approach has potential to be more robust than empirical approaches, but it is fraught with definitional and philosophical challenges (Mäkelä *et al.* 2002). In particular, stomatal function has so many quantifiable and interacting effects (on CO_2 uptake, water loss, water potential, xylem cavitation, etc.) that a rigorous and thorough understanding of optimal stomatal control is difficult without a model that describes all of those effects with a high degree of accuracy.

We discuss each of these approaches below, with the goal of providing context for the role of mechanistic models and the main challenges to improving such models.

Empirical (phenomenological) models

Early models of stomatal conductance were largely empirical and were focused on prediction rather than on exploring the mechanisms by which stomata respond to the environment because knowledge of those mechanisms was quite limited. One of the first models to include interacting responses to multiple environmental factors was presented by Jarvis (1976). This model included five variables – light, temperature, CO_2, humidity and leaf water status – to which stomatal conductance (g_s) was known to vary. Recognizing that knowledge about guard cell processes was insufficient to model these responses mechanistically, Jarvis represented each response with a separate unit function, chosen to best fit the available data. These responses were then multiplied together to predict g_s. This approach is still widely used because it is simple and modular structure makes it easy to incorporate into larger models, such as GCMs (Egea, Verhoef & Vidale 2011), and because its separable responses can be visualized and parameterized using boundary-line analysis (Chambers *et al.* 1985). The main disadvantage of the Jarvis approach is that many data covering a wide range of environmental conditions are needed to estimate its parameter values, and those values often change over the life span of a leaf (Whitehead *et al.* 2011). It also offers little insight about the mechanisms of stomatal control, so its usefulness as a tool for basic research is limited.

One important empirical model that does not use the boundary-line method is the widely used 'Ball-Berry' model (Ball, Woodrow & Berry 1987) and variations thereof. The original version of this model (Eqn 1) described g_s as a function of net photosynthesis (A), CO_2 concentration at the surface of the leaf (c_s), the relative humidity at the surface of the leaf (h_s) and the residual stomatal conductance when A is zero (g_0). The parameter m is an empirical constant that varies among leaves.

$$g_s = g_0 + m \frac{A h_s}{c_s}. \tag{1}$$

This model had broad appeal because of its simplicity, with only two free parameters, and its ability to accurately predict g_s over wide ranges of environmental conditions. It has been widely used in canopy models and GCMs (Egea *et al.* 2011). Although it is easy to test the model against empirical measurements of A and g_s, using it to predict stomatal conductance from environmental variables also requires a separate model for A. This is typically done using a biochemical model of photosynthesis (Farquhar, Caemmerer & Berry 1980), which, combined with values for boundary layer and mesophyll conductances, yields a closed system that can be solved either iteratively or analytically (Baldocchi 1994). Several modifications of this model have been proposed. Leuning (1990) suggested replacing c_s with ($c_s - \Gamma$), where Γ is the CO_2 compensation point, to prevent A from becoming negative at low c_s, which could lead to negative g_s values. Leuning (1990) calculated A and Γ from a biochemical model of photosynthesis to test this model, but concluded the slight improvement in fit was not enough to justify the burden of calculating Γ. Later, the relative humidity term (h_s) was replaced with an inverse hyperbolic response to the leaf-to-surface vapour pressure difference (D_s): $1/(1 + D_s/D_o)$, where D_o is an empirical parameter (Leuning 1995).

The revised versions of the Ball-Berry model share some features with mechanistic models. For example, the hyperbolic relationship between g_s and D_s also arises in mechanistic models from the effect of transpiration on turgor pressures of cells in the stomatal complex (e.g. Dewar 1995; Gao *et al.* 2002; Buckley, Mott & Farquhar 2003). Similarly, the responses to A and $1/(c_s + \Gamma)$ can be interpreted as the effect of mesophyll ATP or NADPH on guard cell ion pumping (Dewar 1995).

Mechanistic (process-based) models

At the other end of the mechanistic/empirical spectrum are models whose main purpose is to generate testable predictions from hypotheses regarding the mechanisms of stomatal control. For example, several investigators in the 1970s constructed models of g_s based on principles of cell water relations, to investigate whether differences in the hydraulic properties of guard cells and epidermal cells could explain oscillations in stomatal conductance (Cowan 1972; Delwiche & Cooke 1977). Similarly, models of guard cell signaling pathways and their interactions have been constructed to test

specific hypotheses (Tardieu & Davies 1993; Li, Assmann & Albert 2006). Models of this nature have been crucial in developing our understanding of how stomata work. However, they are often not useful for predicting g_s as a function of environmental conditions, in part because their parameters represent biophysical properties that are quite difficult to measure by experiment.

The recent attempt to produce a very detailed mechanistic model of guard cell ion transport and osmolyte synthesis (Chen *et al*. 2012; Hills *et al*. 2012; Wang *et al*. 2012) showcases the strengths and weaknesses of detailed mechanistic modelling of stomatal conductance. The model contains a detailed treatment of guard cell ion channels and signaling, and it explicitly models the membrane potential, ion fluxes, and osmotic concentration of the guard cells. The model correctly predicts the effects of the *slac1* anion channel mutant of Arabidopsis on K^+ channels, cytosolic pH, $[Ca^{2+}]$, and the rate of stomatal opening in this mutant (Wang *et al*. 2012). Clearly, this model has promise to be profoundly useful for testing hypotheses about the subcellular processes underlying stomatal control. However, it does not use fully mechanistic descriptions for some other aspects of stomatal control, such as the effects of epidermal turgor pressure and the light response, and it ignores responses to humidity, temperature, and CO_2 altogether. This is not a criticism of the model but a reminder that all models must make trade-offs between completeness and tractability: the more comprehensively mechanistic a model is, the less likely that it will be useful for prediction at large scales, or even for analysis at intermediate scales of inquiry.

Spatial and kinetic models

Models that describe spatiotemporal variations in stomatal conductance are much less common than steady-state models. Many dynamical models are aimed at predicting photosynthesis under fluctuating conditions (e.g. Kirschbaum, Gross & Pearcy 1988; Gross, Kirschbaum & Pearcy 1991; Kirschbaum *et al*. 1998; Ooba & Takahashi 2003; Noe & Giersch 2004; Vialet-Chabrand, Dreyer & Brendel 2013). Similarly, some spatial models are concerned primarily with understanding how spatial variation in g_s, and particularly 'patchy' stomatal conductance, affects scaling of gas exchange (Cheeseman 1991; Terashima 1992; Buckley, Farquhar & Mott 1997) and water-use efficiency (Buckley, Farquhar & Mott 1999). Because these models are more concerned with the implications of stomatal function than with the underlying mechanisms, they describe spatial and temporal patterns of g_s phenomenologically rather than mechanistically.

Temporally and spatially explicit models of g_s typically simulate water and osmotic solute flow among cells in and around the stomatal complex (e.g. Cowan 1972; Delwiche & Cooke 1977; Rand *et al*. 1981; Haefner, Buckley & Mott 1997; Buckley & Mott 2002a; Buckley, Sack & Gilbert 2011; Hills *et al*. 2012). Because models of this nature include many parameters that describe reduced cellular properties, they are often not useful for prediction and instead are used to

examine the implications of hypotheses about water flow and stomatal control. For example, Haefner *et al*. (1997) used a spatially explicit model in which adjacent stomata interacted via the water potential of the intervening epidermal cells, and concluded that these interactions could cause the behaviour of stomata in a single areole to become entrained. More recently, Buckley *et al*. (2011) used a dynamical model that included mesophyll and xylem compartments to predict how bundle sheath extensions should affect transient 'wrong-way' responses of stomata to humidity and leaf excision. Peak & Mott (2011) recently proposed a steady-state model that was derived from a spatially explicit description of differences in water potential, vapour pressure and temperature within the leaf and among leaf compartments.

As we discuss below, analyses using spatially and temporally explicit models have fed a growing realization that changes in matter and energy transfer at quite small scales within leaves may be central to the mechanisms of some stomatal responses (Cochard *et al*. 2007; Mott 2007, 2009; Zwieniecki, Brodribb & Holbrook 2007; Scoffoni *et al*. 2008; Mott & Peak 2010, 2013; Buckley *et al*. 2011), so continued development and integration of such models is a high priority.

Optimality models

Although the emphasis of this review is mechanistic modelling of stomatal control, for completeness, we should say a few words about the use of optimization theory to predict and understand stomatal behaviour. The modern approach was pioneered by Cowan & Farquhar (1977), who sought to explain stomatal behaviour from a top-down basis; that is, by computing the theoretically optimal pattern of g_s and comparing this pattern to observations. They posed the problem as one of constrained optimization: if a leaf has a finite daily total (or average) supply of transpirable water, how should g_s vary over time and in relation to unpredictable variations in environmental conditions so that daily total (or average) carbon gain will be greatest? The abstract solution to this problem was that g_s should vary such that a particular property of the gas exchange equations – the marginal carbon product of water ($\partial A/\partial E$) – remains invariant over the day. This predicts qualitative trends in g_s quite well, including the short-term responses to irradiance and humidity, and the mid-day depression in photosynthesis under moderately water stressed conditions (e.g. Cowan & Farquhar 1977; Ball & Farquhar 1984). Buckley (2005) also showed that the 'apparent feedforward' response of stomata to humidity, in which transpiration rate declines at high evaporative demand, is consistent with, and indeed required for optimality in some conditions.

It has been difficult to implement optimality as a predictive tool in practice. This is partly because the 'target' value of $\partial A/\partial E$, often denoted $1/\lambda$, must be specified arbitrarily (or inferred from a model of optimal whole plant carbon allocation, for example, Givnish 1986; Buckley 2008), and partly because it can be mathematically and computationally difficult to compute the value of g_s that produces this target $\partial A/\partial E$ at each point during the day – the optimal solution

depends rather sensitively on fine details of the model of photosynthesis and gas exchange used to compute $\partial A/\partial E$ (Buckley, Farquhar & Miller 2002; Buckley, Cescatti & Farquhar 2013). Nevertheless, several recent studies have had some success in advancing this approach to predicting g_s (Schymanski *et al*. 2008; Katul, Palmroth & Oren 2009; Manzoni *et al*. 2011; Medlyn *et al*. 2011).

WHAT ARE THE REAL INPUTS FOR PROCESS-BASED MODELS OF STOMATAL FUNCTION?

With the exception of the detailed mechanistic model of ion channels discussed above (Hills *et al*. 2012), most models of stomatal behaviour at the leaf level are computationally simpler than many other models in physiology (Gavaghan *et al*. 2006; Nagele *et al*. 2010; Ruffel, Krouk & Coruzzi 2010), perhaps because of the high value placed by ecophysiologists on application at larger scales. The need for tractability places a premium on determining the best way to synthesize the ultimate mechanisms of stomatal control, some of which are subcellular, into process descriptions of more proximate mechanisms. These latter process descriptions should apply at the tissue or leaf scale, yet retain the potential to be directly informed by continuing research at more reduced scales. This synthesis is generally approached from the top down: changes in g_s are parsed into proximate effectors, such as cell turgor pressures, which are in turn parsed into changes in water potential and osmotic pressure. This approach has led to the emergence of two common themes in most recent mechanistic models of g_s. Firstly, stomatal conductance is assumed to be a linear function of guard cell turgor (P_g), which is in turn determined by the water potential and the osmotic potential of the guard cells. Secondly, stomatal aperture and conductance are negatively related to epidermal turgor pressure (P_e). These themes imply that

$$g_s = \chi(P_g - mP_e),\qquad(2)$$

where $\chi > 0$ is an empirical parameter and $m \geq 0$ is the epidermal mechanical advantage, a dimensionless parameter. Although P_e is a function of both epidermal water potential and osmotic pressure, the latter is generally assumed to be constant (but see Franks & Farquhar 2007). There are, therefore, only three things that can directly affect stomatal conductance *in vivo*: (1) the osmotic potential of the guard cells; (2) the water potential of the guard cells; and (3) the water potential of the epidermal cells. All environmental factors that influence stomatal conductance must do so through one or more of these three factors. Below, we categorize the major environmental factors that affect stomatal conductance, and the current controversies surrounding hypothesized tissue- or leaf-level mechanisms for those effects.

Evaporative demand: humidity and temperature

The stomatal response to humidity has long been considered to be a response to water loss, mediated by a feedback mechanism wherein reductions in guard cell turgor are caused by the water potential drawdown associated with the transpirational flux (Delwiche & Cooke 1977; Rand *et al*. 1981; Dewar 1995, 2002; Haefner *et al*. 1997; Buckley *et al*. 2003). Some models assume this feedback operates simply through the direct effect of low water potential on guard cell turgor (Gao *et al*. 2002). However, to make this assumption work, one has to ignore the effect of epidermal turgor on stomatal conductance, which offsets or even reverses the effect of P_g if guard and epidermal cells are in hydraulic equilibrium (i.e. $m > 1$ in Eqn 2). Several mechanisms have been proposed, and expressed in models, to explain how the initial, passively induced change in guard cell turgor might be amplified such that it exceeds the passively induced change in epidermal turgor pressure, thereby overcoming the epidermal mechanical advantage. Dewar (1995, 2002) postulated that $m = 1$, so that P_g and P_e have equal control over g_s, and that evaporation directly from guard cells creates a water potential gradient that causes P_g to be more sensitive than P_e to changes in transpiration rate. However, Buckley and Mott (2002a) found that this hypothesis required the resistance to the guard cells to vary in complex fashion in relation to transpiration rate, and most data show that $m \gg 1$ (Edwards, Meidner & Sheriff 1976; Delwiche & Cooke 1977; Franks, Cowan & Farquhar 1998).

An alternative hypothesis is that guard cell osmotic pressure (π_g) is actively regulated in proportion to the turgor pressure of the epidermis, so that π_g is proportional to P_e at steady state; that is, $\pi_g - \pi_e = BP_e$ with $B > 0$ a dimensionless parameter. Buckley *et al*. (2003) used this hypothesis to derive a model of the form

$$g_s = \chi\frac{\alpha(\psi_s + \pi_e)}{1 + \chi\alpha R\Delta w},\qquad(3)$$

where $\alpha = B - m + 1$, ψ_s is soil water potential, R is the hydraulic resistance from the soil to the epidermis, and Δw is the water vapour mole fraction gradient between the leaf's intercellular spaces and the leaf surface ($\Delta w = D_s/P$, where P is atmospheric pressure). This model correctly predicts the observed steady-state responses to changes in R, ψ_s and humidity. It does not directly predict the apparent feedforward response (Franks, Cowan & Farquhar 1997), in which transpiration rate declines at high Δw, although the feedforward pattern can emerge from this model if hydraulic resistance increases at high Δw (Oren *et al*. 1999; Buckley & Mott 2002b).

However, this model fails to predict the increase in g_s observed when Δw is increased by increasing leaf temperature (T_l) (Mott & Peak 2010). This response may be more important for field predictions than the response to humidity *per se* because temperature tends to vary more widely than humidity during a typical day. The effects of T_l on g_s are difficult to model because T_l affects both Δw and photosynthesis. Some published models simply ignore temperature (e.g. Gao *et al*. 2002; Hills *et al*. 2012); most others either include temperature as an independent, phenomenological driver of g_s (Jarvis 1976), or as an implicit factor that affects another driver of g_s such as photosynthesis.

A recently published model of stomatal responses to humidity and temperature may provide a mechanistic explanation for T_l-mediated Δw responses (Peak & Mott 2011). This model proposes that stomatal guard cells are hydraulically isolated from the rest of the leaf and are in water potential equilibrium with the air just inside the stomatal pore. The water potential of this air varies because of the concentration gradient for water vapour caused by the transpiration stream, and because of small temperature differences between the epidermis and an internal evaporating site. The Peak and Mott model is

$$g_s = \frac{g_s^0 - \Theta \Delta w/w_{es}}{1 + Z\Delta w}, \tag{4}$$

where $g_s^0 = \chi(\pi_g - mP_e - M\psi_s)$ is the stomatal conductance at saturating humidity, w_{es} is the saturated vapour pressure at the temperature of the epidermis, $\Theta = \chi\sigma R_d/v_l$ where σ is the fraction of the total gas diffusion resistance that resides between the evaporating site and the guard cells (R_d is the gas constant and v_l is the molar volume of liquid water), and $Z = \chi(R_g' - MR)$, where R_g' is the thermal resistance between the evaporating site and the epidermis. Because Z and Θ are based on anatomical, rather than physiological aspects of the leaf, they should be relatively conserved among all leaves of a given species grown under the same conditions. This 'vapour phase' model has several strengths, in addition to predicting responses to Δw caused by either humidity or temperature changes. For instance, it correctly predicts that the ratio Z/Θ should be higher for plants with sunken stomata (Mott & Peak 2013), and it directly predicts the feedforward response. However, it predicts negative responses to ψ_s and R; this is consistent with the initial 'wrong-way' portion of those responses but not with the subsequent steady-state response.

These two models may be more helpfully compared by expressing them as special cases of a general expression,

$$g_s = \frac{\chi(\pi_g - m\pi_e - M\psi_s) - Q}{1 + \chi(R_g' - MR)\Delta w}, \tag{5}$$

where $M = m-1$, the net epidermal mechanical advantage. It is easily shown that the liquid phase model (Eqn 3) is equivalent to $Q = R_g' = 0$, combined with the hydroactive feedback hypothesis, $\pi_g - \pi_e = BP_e$, whereas the vapour phase model (Eqn 4) is equivalent to $Q = \Theta\Delta w/w_{es}$ and $R_g' - MR$. In the vapour phase model, Q and R_g' represent the roles of diffusive and thermal resistance, respectively, between the evaporating site and the guard cells. Both of these resistances amplify changes in P_g to produce the 'right-way' steady-state reduction in g_s following an increase in Δw. This model requires $R_g' >> MR$ to give the correct steady-state response under most conditions, and it requires Q to be on the same order as $\chi\pi_g$ to produce a substantial feedforward response at high Δw. In the liquid phase model, B represents the osmotically mediated metabolic amplification of changes in P_g. This model requires $B >> M$ to give the right steady-state response, and it requires that R decline substantially at high Δw to produce a feedforward response. Thus, resolution of

the hypotheses underlying these two models will require not only verification of the mechanistic feasibility of each model's core hypothesis – namely, that guard cells are hydraulically sequestered (for the vapour phase model) or that π_g is actively regulated in proportion to P_e (for the liquid phase model) – but also better knowledge of the magnitude of the resistances captured by Q and R_g' and of the sensitivity of R to changes in Δw.

We note as well that the two models can be combined by applying the hydroactive feedback hypothesis to Eqn 4 and rearranging, which gives

$$g_s = \frac{\chi\alpha(\psi_s + \pi_e) - \Theta\Delta w/w_{es}}{1 + \chi((\alpha)R + R_g')\Delta w}. \tag{6}$$

This third, synthetic model captures the strengths of both the liquid and vapour phase approaches, while tying together the hypothesis structures of both models, so it may prove a useful platform for continuing study of these issues.

Light and CO₂

The response to light has generally been assumed to be a direct response of guard cell osmotic pressure to light, and most mechanistic models assume that it is caused by light activated ion pumping into the guard cells (Lloyd 1991; Dewar 1995; Dewar 2002; Buckley *et al.* 2003; Hills *et al.* 2012). There are at least two separate photoreceptors involved in the response of stomata to light. The first is the blue light response, which has an action spectrum that peaks around 470 nm, and the second is the so-called red light response, which has an action spectrum similar to chlorophyll. Most evidence suggests that the blue light response is activated by one or more receptors located in the guard cell, whereas the red light response is sensed by chlorophyll (Shimazaki *et al.* 2007). This raises the possibility that the red light response is actually tied to photosynthesis and is therefore linked to changes in intercellular CO_2 concentration (c_i); however, the red light response has been shown to occur even when c_i is held constant experimentally (Messinger, Buckley & Mott 2006). An alternative idea is that conductance responds to some measure of the balance between photosynthetic electron transport and carbon reduction, such as the adenylate concentration in photosynthesizing cells (Farquhar & Wong 1984; Busch 2013). Light and CO_2 would affect that balance in opposite ways, causing the observed responses to both red light and c_i. This idea has been incorporated into a more complete model of stomatal conductance in which guard cell osmotic pressure was assumed to be dependent on cellular ATP concentration, which in turn is affected by light- and CO_2-dependent changes in guard cell photosynthesis (Buckley *et al.* 2003). There are, however, no models that explicitly model the blue and red light responses independently.

Root signals

It is clear that in some species, stomata respond to water stress at least partially through the pH of the transpiration

stream (Wilkinson & Davies 1997; Wilkinson 1999) and abscisic acid (ABA) carried through the xylem from the roots. However, this response varies among species (Sharp & Davies 2009) and with leaf water potential (Schurr, Gollan & Schulze 1992). Although there is a great deal known about the mechanism of ABA action on guard cells (Lee & Luan 2012) and at least one mechanistic model of ABA action on guard cells (Li *et al.* 2006), no model to date has incorporated the effects of ABA in a manner consistent with all known mechanistic constraints. Most stomatal models that include an ABA effect are based on empirical relationships among root water potential, ABA concentration, leaf water potential and g_s. The most widely used model of the combined effects of ABA and leaf water potential (Ψ_l) was developed by Tardieu & Davies (1993). That model is: $g_s = g_{smin} + \alpha \cdot \exp\{[ABA]\beta \cdot \exp\{\gamma \psi_l\}\}$, where α, β and γ are empirical parameters. This model has been incorporated into a more complete, but essentially empirical model of stomatal conductance (Tardieu & Simonneau 1998), and there have been two attempts to combine it with the Ball-Berry model. In the first, Dewar (2002) derived a mechanistic model similar in form to Ball-Berry, in which ion leakage from guard cells was assumed to depend on ABA concentration and leaf water potential as described by the Tardieu-Davies model. The resulting model predicted homeostatic regulation of leaf water potential, but as discussed above, its central mechanism was inconsistent with observations of the epidermal mechanical advantage. In the second, Gutschick & Simonneau (2002) incorporated sensitivity to xylem ABA into the Ball-Berry model in two ways: either by multiplying the parameter *m* by an exponential function of xylem [ABA], or by computing g_s as the lesser of the unmodified Ball-Berry value and an exponential function of [ABA]. Although both approaches worked reasonably well in predicting conductance of field-grown sunflower, neither has a solid mechanistic basis.

QUESTIONS FOR FUTURE RESEARCH

One obvious future direction for stomatal modelling is to continue to make models more and more mechanistic as new information is acquired. More complex and detailed models are needed to translate hypothesized mechanisms into testable predictions, and the recent ion transport model (Hills *et al.* 2012) is a good first step in this direction. Further progress in producing a truly mechanistic model that captures the stomatal response to multiple factors will be dependent on deciphering the mechanisms by which stomata are actually sensing these factors. One immediate challenge in this quest is to identify the mechanism for the red light effect on conductance and its connection to the CO_2 response and to photosynthesis. Although the sensing mechanisms for red light and CO_2 have often been assumed to be separate and to be located in the guard cells, there is now evidence that both of these responses may originate in the mesophyll and may be tied to photosynthesis in the mesophyll cells (Mott, Sibbernsen & Shope 2008; Mott 2009). Another challenge is to incorporate a mechanistic description of the blue light response into stomatal models. This is important

because the photon efficiency and saturation points for the blue and red light responses are quite different, so a model that accurately predicts the response to white light must treat these responses separately.

Another problem area is the response to humidity. There is still no consensus on whether the decoupling of guard cell turgor from epidermal turgor that is needed to overcome the epidermal mechanical advantage is achieved passively, by hydraulic isolation of the guard cells, or if it requires active transport of solutes. It seems possible that both mechanisms could operate in a single plant depending on the conditions and size of the humidity or temperature perturbation. Any further progress in producing a mechanistic model to capture this response depends on the resolution of this question. The recent proposal that some responses to humidity and temperature might be caused by water potential equilibrium between the guard cells and the air in the stomatal pore may shed new light on this question, but the idea has yet to be explored in depth. Any hypothesis to explain these steady-state responses must also be consistent with the transient 'wrong-way' responses typically observed immediately after a change in humidity or source water potential. This places a premium on an integrated approach to developmental modelling, in which the implications of hypotheses about stomatal function for both steady-state and dynamical behaviour are assessed concurrently.

While it is clear that long-term stomatal responses to root water stress may be mediated by ABA transport in the xylem, the role of xylem ABA in other responses remains unclear. Relatively simple experiments comparing responses in attached and detached leaves might shed significant light on this question.

Towards a lingua stomata

As our knowledge of stomatal and whole plant function has improved in recent decades, we have come ever closer to the 'holy grail' of a tractable yet integrated process-based model of plant gas exchange. In continuing this effort towards a consensus model, or suite of models, it is important to recognize how powerfully the language embedded in our formal models can impact the progress and direction of research. For example, nearly all research on photosynthesis at the leaf scale or above is now carried out in the *lingua franca* of the biochemical model created by Farquhar *et al.* (1980). This has worked out well because the parameters in that model – for example, carboxylation capacity, $V_{c,max}$ – are transparently related to reduced biochemical properties, yet they are relatively straightforward to estimate empirically in the field. This benefits not only predictive modellers but also physiological ecologists, who, in order to meaningfully compare the character of photosynthetic adaptation among species and in relation to environment, need parameters that tie ecological features to reduced processes. It may be useful to aim for a similar outcome as we refine our process-based models of stomatal function.

What are the key parameters that may end up in a *lingua franca* for stomatal function? Field-based comparative

studies should, ideally, be measuring variations and dynamics in these parameters, if the results of such studies are to inform continuing model refinement. Plant and leaf hydraulic resistance seem to play an important role in both short-term stomatal responses and differences among species in stomatal behaviour (Brodribb & Jordan 2008; Sinclair, Zwieniecki & Holbrook 2008; Buckley *et al*. 2011). Stomatal size and density have recently emerged as important comparative variables that, because they are relatively easy to measure, are particularly useful for inferring aspects of gas exchange ecology in fossil leaf records and among extant species (Franks & Beerling 2009; Doheny-Adams *et al*. 2012). As discussed above, the thermal and gaseous resistance between the guard cells and the mesophyll may play an important role in species differences in humidity/temperature responses (Peak & Mott 2011). Leaf osmotic pressure is also easily measured from pressure-volume curves and is important in drought responses of many species (Bartlett *et al*. 2012; Bartlett, Scoffoni & Sack 2012), but more work is needed to determine how well this variable predicts the osmotic pressure of the epidermis, which plays an important yet overlooked role in the models discussed above.

Many important issues in plant ecophysiology involve the coordination of stomatal conductance with another property, such as photosynthetic capacity or hydraulic conductance. At present, stomatal–photosynthetic coordination is most often analysed using the parameter '*m*' in the phenomenological Ball-Berry model (e.g. Medlyn *et al*. 1999, 2001; Leakey *et al*. 2006), and stomatal–hydraulic coordination is commonly assessed in the context of the empirical stomatal model of Oren *et al*. (1999) (Ewers *et al*. 2001; Oren *et al*. 2001). The useful insights gained in analyses using those models could be enhanced and integrated if future investigators also had access to a consensus process-based model of stomatal function, so that stomatal coordination could be expressed more explicitly in terms of physiological or anatomical parameters. For example, Buckley, Turnbull & Adams (2012) used a simplified form of the liquid phase model (Eqn 2) to show that the often-reported conservation of the parameter $dg_{s,max}/d\ln D$ in the Oren model is equivalent to conservation of the quantity $\chi\alpha_m R$ from Eqn 2, where α_m is the value of α at saturating irradiance. A particularly powerful approach might be to parameterize plant and leaf models of hydraulic function, such as the SACC model of Sperry *et al*. (1998) or the *K_leaf* model of Cochard, Nardini & Coll (2004), concurrently with a stomatal model. This approach has already proven useful for evaluating the regulation of multiple constraints on photosynthetic productivity in the field (Diaz-Espejo *et al*. 2012). A more integrative approach to mechanistic modelling may also be needed to clarify the potential role of short-term changes in hydraulic conductivity in relation to light or water potential (Scoffoni *et al*. 2008, 2011, 2012) in stomatal responses.

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