

# An overview of models of stomatal conductance at the leaf level

GAËLLE DAMOUR<sup>1\*</sup>, THIERRY SIMONNEAU<sup>2</sup>, HERVÉ COCHARD<sup>3</sup> & LAURENT URBAN<sup>4</sup>

<sup>1</sup>CIRAD Persyst – UR HortSys, Station de Bassin Plat, 97455 Saint Pierre Cedex, La Réunion, France,

<sup>2</sup>INRA – UMR LEPSE, SupAgro, 34060 Montpellier Cedex 1, France,

<sup>3</sup>INRA – UMR PIAF, Site de Crouël, 63039 Clermond-Ferrand Cedex 02, France and

<sup>4</sup>University of Avignon – LPFL, Agrosiences, 84916 Avignon Cedex, France

## ABSTRACT

**Stomata play a key role in plant adaptation to changing environmental conditions as they control both water losses and CO<sub>2</sub> uptake. Particularly, in the context of global change, simulations of the consequences of drought on crop plants are needed to design more efficient and water-saving cropping systems. However, most of the models of stomatal conductance ( $g_s$ ) developed at the leaf level link  $g_s$  to environmental factors or net photosynthesis ( $A_{net}$ ), but do not include satisfactorily the effects of drought, impairing our capacity to simulate plant functioning in conditions of limited water supply. The objective of this review was to draw an up-to-date picture of the  $g_s$  models, from the empirical to the process-based ones, along with their mechanistic or deterministic bases. It focuses on models capable to account for multiple environmental influences with emphasis on drought conditions. We examine how models that have been proposed for well-watered conditions can be combined with those specifically designed to deal with drought conditions. Ideas for future improvements of  $g_s$  models are discussed: the issue of co-regulation of  $g_s$  and  $A_{net}$ ; the roles of CO<sub>2</sub>, abscisic acid and H<sub>2</sub>O<sub>2</sub>; and finally, how to better address the new challenges arising from the issue of global change.**

*Key-words:* abscisic acid; hydraulic conductance; hydrogen peroxide; photosynthesis; transpiration; water stress.

## INTRODUCTION

Stomata consist in pores scattered over the relatively waterproof and CO<sub>2</sub>-tight cuticle covering the leaf surface. They play an essential role in controlling both water losses by transpiration and CO<sub>2</sub> uptake for photosynthesis and plant growth. Stomatal aperture is controlled by the turgor pressure difference between the guard cells surrounding the pores and the bulk leaf epidermis. Changes in the turgor of

*Correspondence:* G. Damour. Fax: +(590) 590 86 29 79; e-mail: gaelle.damour@cirad.fr

\*Present address: UR 26 – Systèmes de culture bananes, plantains et ananas, Station de Neufchâteau, Sainte Marie, 97130 Capesterre-Belle-Eau, Guadeloupe, France.

the guard cells can be very quick, thus allowing for fast adaptation to rapidly changing conditions. This capacity to respond quickly is essential for plants which have to optimize CO<sub>2</sub> uptake and water losses in continually fluctuating environmental conditions. Stomata also play a key role in modulating the transpiration-driven water flow through the soil–plant–atmosphere continuum, and consequently determine the rate of soil water depletion. Eventually, stomata play a very important role in preventing leaf surfaces from reaching excessive temperatures through the control of plant transpiration they provide and its associated cooling effect. Because stomatal regulation plays a key role in plant adaptation to changing environmental conditions and to stress, it appears of paramount importance to try to improve our understanding of the way stomata respond to environmental parameters and optimize their responses in the presence of often conflicting priorities.

Stomatal aperture is sensitive to multiple environmental influences. Among them, drought appears of particular concern to plant ecophysicologists. Water stress has indeed detrimental effects on community development of natural plants, and growth and productivity of crops. In the coming years and decades, as a consequence of global change, drought events are expected to strengthen in terms of intensity, frequency and geographic expanse (IPCC 2007). This issue will become all the more important that world water supply is limiting, while demand for food and water for irrigation will raise along with the human population (Somerville & Briscoe 2001). There is thus an increasing need to anticipate the consequences of drought on crop plants, with the objective to design more efficient and water-saving cropping systems.

Modelling appears as the most effective and well-adapted tool for integration, simulation and prediction purposes. Carbon assimilation, water losses and stomatal aperture – estimated by the stomatal conductance to CO<sub>2</sub> and H<sub>2</sub>O,  $g_s$  – are among the functions that have been the most extensively modelled during the last 40 years. Some approaches, particularly in ecology, have described the global response of vegetation (Reichstein *et al.* 2002). Global models are very useful, but they are generally incapable to provide an insight into the mechanisms through which stomata respond to environmental conditions. Among the numerous

modelling approaches at the leaf level, many are essentially empirical, based on statistical correlations between environmental or internal factors and  $g_s$ , and very few are really mechanistic. The majority of stomatal conductance models are 'semi-empirical' (i.e. built on physiological hypotheses, but still combined with empirical functions). Most of these models focus on one or two factors that affect stomatal aperture. For many years,  $g_s$  models did not include the effects of drought, impairing our capacity to model plant functioning in conditions of limiting water supply. Following the increasing awareness of the importance of drought, more and more empirical or semi-empirical functions of water stress have been implemented into models previously constructed for non-stress conditions. These models are based on the different approaches reviewed below.

Responses of stomata to the local environment of the plant (soil water status, light, air humidity, temperature and atmospheric  $\text{CO}_2$  concentration) have been studied for decades and were the subject of an abundant literature. The pattern of each individual response has been extensively described (Jarvis 1976; Jones 1992; Monteith 1995). Underlying mechanisms have been partially elucidated, but there are still missing pieces and links to bridge the gap between environmental conditions, how they are sensed and transduced into whole plants and how they end in stomatal responses. This hampers the development of integrative approaches of stomatal responses to multiple environmental influences where possible couplings and interactions could be taken into account. Gathering the missing pieces and links appears of particular importance in the context of global change because combinations of environmental shifts are expected. How stomata will integrate changes in  $\text{CO}_2$  concentration, temperature, air and soil humidity directly questions the way the signalling cascades interact from the plant to the cell level. The rate of stomatal response to fluctuating environmental conditions should also deserve attention. Slow response of stomata to rapid changes in conditions like sunflecks introduces distortion from steady state and requires proper parameterization of  $g_s$  models (Stegemann, Timm & Koppers 1999). However, this last aspect will not be covered in this review considering, like the vast majority of models, that stomata follow a succession of steady states.

Plant responses to environmental stimuli are mediated from short to long distances by many internal signals such as hormones, reactive oxygen species (ROS),  $\text{CO}_2$  concentration in the leaf intercellular space and hydraulic signals (Hetherington & Woodward 2003). Within the leaf epidermis, solute accumulation and redistribution between the different cell types and compartments also play a major role in the regulation of cell turgor and the turgor-driven stomatal movements (Schroeder *et al.* 2001). In guard cells, numerous molecular actors are involved in solute transport, ranging from membrane ion channels and transporters to ATPases, regulating proteins, cytoplasmic  $\text{Ca}^{2+}$  or pH (see the reviews of Schroeder *et al.* 2001; Roelfsema & Hedrich 2005; Pandey, Zhang & Assman 2007). The way guard cells integrate signalling cascades remains still incompletely

understood. In the absence of a true understanding of the underlying mechanisms, modelling approaches remain fragmental. There have well been a few attempts to propose integrated views of molecular cascades triggering stomatal response to drought. Such approaches are mainly based on the key role of abscisic acid (ABA) on ion trafficking and osmotic regulation in guard cells (Pei *et al.* 2000; Schroeder *et al.* 2001; Roelfsema & Hedrich 2005; Li, Assmann & Albert 2006). Although they provide a very stimulating view of the determinism of stomatal movements, they remain purely qualitative because information remains fragmental.

The existence of long-distance signalling in stomatal responses makes the picture even more complex because it hints at the possibility that interactions with other environmental factors within the plants also play a role. For example, it has been shown that the response to soil water deficit is mediated by ABA production by roots and its transport to the guard cell membranes via the xylem stream (Davies & Zhang 1991; Tardieu & Davies 1993; Tardieu, Lafarge & Simonneau 1996; Zhang & Outlaw 2001). Some authors have also demonstrated the co-existence of hydraulic signals that trigger stomatal closure in response to a shift in the balance between evaporative demand and soil water availability (Saliendra, Sperry & Comstock 1995; Cochard, Breda & Granier 1996a; Comstock & Menuccini 1998; Nardini & Salleo 2000; Salleo *et al.* 2000; Christmann *et al.* 2007). Indeed, as water depletion progresses in the soil, strong tensions develop in the xylem that can lead to vessel cavitation (i.e. the formation of air bubbles that stop water circulation) (Tyree & Zimmermann 2002). Tight correlations have been evidenced between water potential thresholds for stomatal conductance and xylem embolism across species from contrasted agroecological environments (Sperry 1986; Cochard *et al.* 1996a; Cochard, Ridolfi & Dreyer 1996b; Salleo *et al.* 2000; Cochard 2002; Lemoine, Cochard & Granier 2002; Singsing *et al.* 2004). The so-called hydraulic theory says that stomatal closure prevents xylem vessels from embolism (Tyree & Sperry 1989; Oren *et al.* 1999; Sperry *et al.* 2002). From a mechanistic point of view, stomatal closure in response to low air humidity is suspected to be mediated by changes in water potential of the cells surrounding the stomatal pore caused by evaporation in the substomatal cavity (Mott & Parkhurst 1991; Comstock & Menuccini 1998) or through the cuticle (Eamus *et al.* 2008). However, mechanistic or physiological knowledge is often difficult to translate into equations, and it is generally easier to build models using empirical observations, like the ones collected as part of the hydraulic theory.

Optimization theories can be effectively exploited to combine multiple individual responses to each environmental influence into simplest models. In most conditions, plants tend to maximize  $\text{CO}_2$  assimilation for a fixed amount of water loss, or tend to minimize water loss for a fixed amount of  $\text{CO}_2$  assimilation, which is equivalent (the so-called stomatal optimization theory) (Cowan 1977; Cowan & Farquhar 1977). Using Lagrange transformation, this translates mathematically into the assumption that stomata behave in

such a manner that the ratio of the sensitivities of the rates of transpiration ( $E$ ) and net carbon assimilation ( $A_{\text{net}}$ ) to changes in  $g_s$  (the marginal water cost per unit carbon gain  $\partial E/\partial A_{\text{net}}$ ) remains constant and equal to the Lagrange multiplier  $\lambda$  over a given time-frame. However,  $\lambda$  was shown to vary with environmental conditions, mainly with soil moisture (Cowan 1982; Makela, Berninger & Hari 1996; Thomas, Eamus & Bell 1999; Buckley 2008). The optimization theory thus states that  $\partial E/\partial A_{\text{net}}$  does not vary taking water supply as an *a priori* constraint, captured by  $\lambda$ . On a daily time-scale, soil and air moisture can be considered as constant, and so can be  $\lambda$ . Under these conditions, it is mathematically demonstrated that  $E/A_{\text{net}}$  [or  $A_{\text{net}}/E$ , the photosynthetic water-use efficiency (WUE)] remains constant. It has also been hypothesized that stomatal aperture is controlled so as to maintain  $\text{CO}_2$  concentration in the intercellular space ( $C_i$ ) almost constant whatever the changes in light (but under conditions of steady soil and air water status), which actually translates into a stable  $g_s$ -to- $A_{\text{net}}$  ratio or WUE (Wong, Cowan & Farquhar 1978; Norman 1982; Ball, Woodrow & Berry 1987; Mott 1988; Aphalo & Jarvis 1993). This assumption is consistent with the optimization theory developed above in that sense that stomatal response and photosynthetic acclimation tend to preserve the relative contributions of biochemical and diffusion limitations to  $\text{CO}_2$  uptake. The  $C_i$  conservative assumption has been supported by experimental results (e.g. Leuning 1995), and was incorporated into models of whole-plant transpiration where stomatal conductance is a function of assimilation rate (Tuzet, Perrier & Leuning 2003). Because the assimilation rate is in turn sensitive to light,  $\text{CO}_2$  partial pressure and temperature, such models are supposed to indirectly encapsulate the responses to these climatic factors. However, most models based on the  $C_i$  conservative hypothesis do not take into account the impact of soil water stress (Vico & Porporato 2008). In conditions of water deficit (captured by  $\lambda$ ), the hydraulic theory states that stomatal closure occurs to prevent the formation of embolism in xylem vessels. The hydraulic theory implies that stomata are also regulated so as to maintain the xylem water potential above a critical cavitation threshold ( $\Psi_{\text{cav}}$ ). The optimization theory of stomatal functioning and the hydraulic theory of stomata regulation were proven successful when applied for modelling purposes.

The objective of this review was to draw an up-to-date picture of the  $g_s$  models that have been proposed so far, along with their mechanistic or deterministic bases. It mainly focuses on models capable to account for multiple environmental influences with special attention to drought conditions. We examine how models that have been developed for conditions characterized by the absence of water deficit can be combined with those specifically designed to deal with drought conditions. A critical review is provided of the various models that have been proposed so far, from the empirical ones designed for field studies, to the more complex, process-based ones. Table 1 summarizes the major characteristics of these models: major hypothesis, response to water stress, coupling with a photosynthesis model and

number of parameters. We also provide an evaluation of ease-of-use. Finally, we discuss some ideas for future improvements of models of  $g_s$ , among others to better address the new challenges arising from the issue of global change.

It is important to note that, because of the differences in diffusion coefficients existing between water vapour and  $\text{CO}_2$ , stomatal conductance to  $\text{H}_2\text{O}$  ( $g_{s,w}$ ) is 1.6 times higher than stomatal conductance to  $\text{CO}_2$  ( $g_{s,c}$ ). For the sake of clarity, this paper will only deal with  $g_{s,w}$ , noted  $g_s$ .

A list of all variables and parameters used in this review is provided in Table 2.

## STOMATAL CONDUCTANCE MODELS IN THE ABSENCE OF WATER STRESS

### Empirical models of responses to climate

Light intensity ( $Q$ ) is certainly the most fluctuating factor that modulates stomatal aperture;  $g_s$  is correlated with  $Q$  through a non-linear asymptotic relationship. In accordance with their role in water loss regulation, stomata also close with decreasing air humidity (Lange *et al.* 1971) or alternative-related variables such as water vapour pressure deficit ( $VPD$ ) (Aphalo & Jarvis 1991; Monteith 1995). Concentration of  $\text{CO}_2$  in the ambient air ( $C_a$ ) is also negatively correlated to stomatal aperture. Lastly, air temperature influences stomatal aperture. The response to temperature can be represented either by a more or less linear function or by an optimum response curve (Jarvis 1976; Jones 1992). We present in this section the most current empirical models based on the observed responses of  $g_s$  to environmental factors. Influences of air pollutants will not be detailed, although their contribution to stomatal closure could be substantial in some conditions (see the influence of ozone, Uddling *et al.* 2009).

### Multiplicative models of environmental influences

Some authors have integrated all or parts of the effects of environmental factors in empirical 'multiplicative' models. In these models,  $g_s$  is the product of the response functions to individual factors, each function being generally determined by boundary line analysis (Webb 1972; Chambers *et al.* 1985). The hypothesis behind this approach is that the response to each environmental factor is independent of the others. Jarvis (1976) was the first to propose such a model that integrates responses to  $Q$ , leaf temperature ( $T_l$ ),  $VPD$ ,  $C_a$  and leaf water potential ( $\Psi_l$ ) (Table 2; Eqn 1). A first laboratory validation concluded that this model explains 95% of the observed variation of  $g_s$ .

Following Jarvis, White *et al.* (1999) modelled the instantaneous stomatal conductance in well-watered conditions as the product of maximal stomatal aperture ( $g_{s,\text{max}}$ ) and empirical responses to  $Q$ ,  $T_l$  and  $VPD$  (Table 2; Eqn 2).

The main criticism formulated against these models was that interactive effects between environmental factors are

**Table 1.** Major characteristics of the models of  $g_s$

Author	Eqn	Main hypothesis	Water stress response	Photosynthesis coupling	Number of parameters	Use
Models based on climatic control only						
Jarvis 1976	1	Factors are independent (multiplicative model)	No	No	10	Prediction of $g_s$ under variable environment – heavy parameterization
White <i>et al.</i> 1999	2	Factors are independent (multiplicative model)	No	No	7	Prediction of $g_s$ under variable environment – heavy parameterization
Noe & Giersch 2004	3	Factors are independent (multiplicative model)	No	No	5	Prediction of $g_s$ under variable environment – heavy parameterization
Lohammer <i>et al.</i> 1980	4	–	No	No	1	Rough estimation of $g_s$ from air humidity
Monteith 1995	5–6	–	No	No	2	Rough estimation of $g_s$ from air humidity
Stewart 1988	15	Factors are independent (multiplicative model)	Yes	No	10	Prediction of $g_s$ under variable environment – heavy parameterization
Misson <i>et al.</i> 2004	16	Factors are independent (multiplicative model)	Yes	No	10	Prediction of $g_s$ under variable environment – heavy parameterization
MacFarlane <i>et al.</i> 2004	17	Factors are independent (multiplicative model)	Yes	No	10	Prediction of $g_s$ during the course of a drought – heavy parameterization
Ogle & Reynolds 2002	18	–	Yes	No	7	Prediction of $g_s$ under variable environment – heavy parameterization
Models mainly based on the $g_s$ –photosynthesis relationship						
Ball <i>et al.</i> 1987	9	Linear relationship between $g_s$ and $A_{net}$	No	Yes	2	Very practical and accurate prediction of $g_s$ under variable environment
Aphalo & Jarvis 1993	10	Linear relationship between $g_s$ and $A_{net}$	No	Yes	4	Prediction of $g_s$ under variable environment – heavy parameterization
Leuning 1990	11	Linear relationship between $g_s$ and $A_{net}$	No	Yes	3	Very practical and accurate prediction of $g_s$ under variable environment
Leuning 1995	12	Linear relationship between $g_s$ and $A_{net}$	No	Yes	+ $\Gamma$	Very practical and accurate prediction of $g_s$ under variable environment
Farquhar & Wong 1984	13	$g_s$ Responds to the photosynthetic capacity via ATP concentration in the mesophyll cells	No	No	>10	Theoretical use – very heavy parameterization – variables difficult to measure ([RuBP])
Jarvis & Davies 1998	14	$g_s$ Responds to the residual photosynthetic capacity ( $A_{max} - A_{net}$ )	No	No	2	Practical prediction of $g_s - A_{max}$ required
Tenhunen <i>et al.</i> 1990	19	$g_s - A_{net}$ Relationship is function of plant and soil water status (via empirical coefficient)	Yes	Yes	2	Practical prediction of $g_s$ under variable environment
Baldocchi 1997	20	$g_s - A_{net}$ Relationship is function of plant and soil water status (via $P_s$ , $E/TP$ )	Yes	Yes	2	Practical and accurate prediction of $g_s$ under water stress
Sala & Tenhunen 1996	21	$g_s - A_{net}$ Relationship is function plant and soil water status (via $\Psi_{pd}$ )	Yes	Yes	3	Practical and accurate prediction of $g_s$ under water stress
Misson <i>et al.</i> 2004	22	$g_s - A_{net}$ Relationship is function plant and soil water status (via $\Psi_{pd}$ )	Yes	Yes	4	Practical and accurate prediction of $g_s$ under water stress
Wang & Leuning 1998	23	$g_s - A_{net}$ Relationship is function of plant and soil water status (via $\theta_t$ )	Yes	Yes	3	Practical prediction of $g_s$ under water stress – soil characteristics required ( $\theta_t$ and $\theta_{c,t}$ )
Van Wijk <i>et al.</i> 2000	24	$g_s - A_{net}$ Relationship is function of plant and soil water status (via $\theta_t$ )	Yes	Yes	5	Practical prediction of $g_s$ under water stress – soil characteristics required ( $\theta_t$ and $\theta_{c,t}$ )
Uddling <i>et al.</i> 2005	25	$g_s - A_{net}$ Relationship is function of the day of the year (effect on plant and soil water status)	Yes	Yes	6	Practical prediction of $g_s$ under variable environment during the year

Models mainly based on an ABA control									
Tardieu & Davies 1993	26	Stomata respond to ABA synthesized by roots as a response to soil water deficit	Yes	No	5	Prediction of $g_s$ under water stress integrating whole plant water transport – [ABA], plant and interface resistances required			
Gutschick & Simonneau 2002	27	Sensitivity to ABA depends on $\Psi$ $g_s - A_{het}$ Relationship is function of xylem ABA concentration	Yes	Yes	3	Practical prediction of $g_s$ under water stress – [ABA] required			
Models mainly based on a hydraulic control									
Oren <i>et al.</i> 1999	28	Flux laws govern water flux	Yes	No	0	Very practical prediction of transpiration and $g_s$ – total conductivity on the root–leaf pathway required			
Tyree & Sperry 1988	29	Flux are conservative	Yes	No	0	Prediction of transpiration and $g_s$ – hydraulic architecture required			
Sperry <i>et al.</i> 1998		Flux laws govern water flux	Yes	No					
Tuzet <i>et al.</i> 2003	30	Flux are conservative	Yes	Yes	4	Prediction of plant transpiration and $g_s$ – integration of hydraulic and photosynthetic aspects			
		$g_s - A_{het}$ Relationship depends on plant water status ( $\Psi$ )	Yes		$+I$				
		Flux laws govern water flux							
		Flux are conservative							
Jones & Sutherland 1991	31	Control of the formation of embolism in xylem vessels by stomatal closure (xylem water potential maintained above a critical threshold)	Yes	No	1	Practical prediction of transpiration and $g_s$			
					$+\Psi_{cav}, \Psi_{f0b}, K_{max}$				
					$\Psi_{cav}$				
Cochard <i>et al.</i> 1996b	32	Stomatal closure controls the formation of embolism in xylem vessels (maintenance of the xylem water potential above a critical threshold)	Yes	No		Practical prediction of maximal transpiration during the course of a drought			
Lu <i>et al.</i> 1996		Existence of a transpiration threshold							
Models mainly based on the turgor regulation of guard cell									
Cowan 1972	–	Electrical analogous model/stomatal movements are governed by water and osmotic potential of mesophyll, and subsidiary and guard cells	No	No	>10	Theoretical use – complicated mathematical formulation and numerical procedures			
Cooke <i>et al.</i> 1976	–	Shell model/stomatal pore width is related to turgor pressure of guard cells and subsidiary cells with	No	No	>10	Theoretical use – complicated mathematical formulation and numerical procedures			
Delwiche & Cooke 1977	7	Stomatal movements are governed by turgor pressure of guard cells and subsidiary cells	No	No	>10	Theoretical use – complicated mathematical formulation and numerical procedures			
Dewar 1995	8	Stomatal movements are governed by turgor pressure difference between guard cells and bulk leaf epidermis	No	Yes	2	Theoretical use – parameterization at cell level			
					$+I$				
Dewar 2002	33	Stomatal movements are governed by turgor pressure difference between guard cells and bulk leaf epidermis	Yes	No	4	Theoretical use – parameterization at cell level			
Gao <i>et al.</i> 2002	34	Stomatal movements are governed by guard cell turgor pressure difference	Yes	No	3	Theoretical use – parameterization at cell level			
Buckley <i>et al.</i> 2003	35	Stomatal movements are governed by turgor pressure of guard cells and bulk leaf epidermis	Yes	Yes	>10	Theoretical use – parameterization at cell level			
		Mechanical advantage of epidermal cells							

For each model, the equation number (Eqn) reports to Table 2. In the column ‘number of parameters’, parameters that can be estimated independently are mentioned preceded by +.

**Table 2.** Equations relative to the models of  $g_s$

1.	Jarvis 1976	$g_s = f_1(Q) \cdot f_2(T_i) \cdot f_3(VPD) \cdot f_4(C_a) \cdot f_5(\Psi_i)$
2.	White <i>et al.</i> 1999	$g_s = g_{smax} \cdot f(Q) \cdot f(T_i) \cdot f(VPD)$
3.	Noe & Giersch 2004	$g_{s,w} = g_{smax} \cdot \min[f(Q), f(VPD)]$
4.	Lohammer <i>et al.</i> 1980	$g_s = \frac{1}{\left(1 + \frac{VPD}{D_0}\right)}$
5.	Monteith 1995	$g_s = g_{smax} - a \cdot VPD$
6.	Monteith 1995	$g_s = a(1 - b \cdot E)$
7.	Delwiche & Cooke 1977	$A_{st} = \pi \cdot L_a \cdot L_b \quad L_b = f(P_g, P_{sub})$ +a set of differential equations integrated $P_g$ et $P_{sub}$ , water potentials, osmotic potentials, water vapour resistances and water fluxes
8.	Dewar 1995	$g_s = \chi(P_g - P_c) \quad g_s = \chi(\Delta\pi - \Delta\Psi)$ $\Delta\Psi = \frac{E}{k} \quad \Delta\pi = f(A_{net}, C_i, g_s)$
9.	Ball <i>et al.</i> 1987	$g_s = g_0 + a \cdot A_{net} \frac{H_r}{C_s} \quad g_s = g_0 + g_{bwb} \frac{A_{net} \cdot H_r}{C_s}$
10.	Aphalo & Jarvis 1993	$g_s = \frac{A_{net}}{C_s} [k_0 + k_1 \cdot VPD + k_2 \cdot T_1 + k_3 \cdot T_1 \cdot VPD]$
11.	Leuning 1990	$g_s = g_0 + a \cdot A_{net} \frac{H_r}{C_s - \Gamma}$
12a	Leuning 1995	$g_s = g_0 + a \frac{A_{net}}{\left(1 + \frac{VPD}{D_0}\right) \cdot (C_s - \Gamma)} \quad g_s = g_0 + g_L \frac{A_{net}}{\left(1 + \frac{VPD}{D_0}\right) (C_s - \Gamma)}$
12b	Supply function and biochemical model of $A_{net}$	$g_s = 1.6 \frac{A_{net}}{C_s \left(1 - \frac{C_i}{C_s}\right)} \quad A_{net} = f(J_{max}, V_{cmax}, R_d, Q, C_a, H_r, T_i)$
12c		
13.	Farquhar & Wong 1984	$g_s = 10^5 \rho \cdot T \quad T = f(A_{net}, E, J_{max}, V_{cmax}, Q, T_i, R_d, RuBP_{pots}, \dots)$
14.	Jarvis & Davies 1998	$g_s = G^* (A_{max} - A_{net}) \quad G^* = G - s \cdot E$
15.	Stewart 1988	$g_s = g_{smax} \cdot f(Q) \cdot f(T_i) \cdot f(VPD) \cdot f(\delta\theta) \quad f(\delta\theta) = 1 - \exp[k_6(\delta\theta - \delta\theta_m)]$
16.	Misson <i>et al.</i> 2004	$g_s = f(Q) \cdot f(T_i) \cdot f(VPD) \cdot f(\Psi_{pd}) \quad f(\Psi_{pd}) = g_{smax} - a(\Psi_{min} - \Psi_{pd})$
17.	MacFarlane <i>et al.</i> 2004	$g_s = g_{smax} \cdot f(Q) \cdot f(T_i) \cdot f(VPD) \cdot f(\Psi_{pd})$ $f(\Psi_{pd}) = 1.09 \exp^{-1.27S(\Psi)} \quad S(\Psi) = \frac{1}{n} \sum (-\Psi_{pd} - 0.2)$
18.	Ogle & Reynolds 2002	$g_s = \begin{cases} 0 & \text{if } VPD > \exp(-b_0/m) \\ g_{smax} & \text{if } VPD > \exp(-(b_0 - \tau)/m) \\ g_{smax} \frac{m \cdot \ln(VPD) + b_0}{\eta} & \text{else} \end{cases}$ $g_{smax} = \tau \cdot \exp\left(\frac{\rho \cdot \Psi_{pd}}{T_{gro}}\right) \cdot \frac{4(T_{max} - T_{gro})(T_{gro} - T_{min})}{(T_{max} - T_{min})^2}$
19.	Tenhunen <i>et al.</i> 1990	$g_{bwb} = GFAC$
20.	Baldocchi 1997	$g_{bwb} = a \frac{\sum P}{\sum ETP}$
21.	Sala & Tenhunen 1996	$g_{bwb} = b + a \cdot \Psi_{pd} \quad \text{if } \Psi_{pd} < -1 \text{ MPa}$
22.	Misson <i>et al.</i> 2004	$g_{bwb} = \frac{m}{1 + \left(\frac{\Psi_{pd}}{\Psi_0}\right)^n}$
23.	Wang & Leuning 1998	$g_L = a \cdot \min\left(1; 10 \frac{\theta_s - \theta_t}{3(\theta_{cc} - \theta_t)}\right)$
24.	Van Wijk <i>et al.</i> 2000	$g_{bwb}, g_L = a \left[1 - k_4 \exp\left(k_5 \frac{\theta_{cc} - \theta_s}{\theta_{cc} - \theta_t}\right)\right]$
25.	Uddling <i>et al.</i> 2005	$g_L = a \cdot f_{season} \quad f_{season} = \min(1; k_7 + k_8 \cdot DOY)$
26.	Tardieu & Davies 1993	$g_s = g_0 + \alpha \cdot \exp\{[ABA] \cdot \beta \cdot \exp(\delta\Psi_1)\} \quad [ABA] = \frac{J_{ABA}}{J_w + b} = \frac{a \cdot \Psi_r}{J_w + b}$ $J_w = \frac{\Psi_1 - \Psi_r}{R_p} \text{ et } J_w = \frac{\Psi_r - \Psi_s}{R_{sp}}$
27.	Gutschick & Simonneau 2002	$g_s = \exp(-\beta[ABA]) \cdot m \frac{A_{net} \cdot H_r}{C_s} + b$

Table 2. *Continued*

28.	Oren <i>et al.</i> 1999	$g_s = \frac{K_{\text{tot}}}{A_L} \cdot \frac{\Psi_s - \Psi_l}{VPD}$
29.	Tyree & Sperry 1988 Sperry <i>et al.</i> 1998	$F = K_{\text{AB}} (\Psi_A - \Psi_B)$ architecture description
30.	Tuzet <i>et al.</i> 2003	$g_s = 1.6 \left[ g_0 + f(\Psi_l) \cdot a \frac{A_{\text{net}}}{C_i - \Gamma} \right]$ $f(\Psi_l) = \frac{1 + \exp(s \cdot \Psi_l)}{1 + \exp[s(\Psi_l - \Psi_1)]}$ $E = \frac{\Psi_s - \Psi_l}{\chi_v}$
31.	Jones & Sutherland 1991	$\Psi_1 - \Psi_s = -\frac{c \cdot VPD \cdot g_s}{K_{\text{tot}}(\Psi)}$ $K_{\text{tot}}(\Psi) = \begin{cases} K_{\text{max}} & \text{if } \Psi_{\text{cav}} < \Psi_1 \\ K_{\text{max}} \frac{\Psi_1 - \Psi_{100}}{\Psi_{\text{cav}} - \Psi_{100}} & \text{if } \Psi_{\text{cav}} > \Psi_1 > \Psi_{100} \\ 0 & \text{if } \Psi_{100} > \Psi_1 \end{cases}$
32.	Cochard <i>et al.</i> 1996a Lu <i>et al.</i> 1996	$E_{\text{crit}} = K_{\text{tot}}(\Psi_s - \Psi_{\text{cav}})$
33.	Dewar 2002	$g_s = \chi(P_g - P_c)$ $g_s = \chi(\Delta\pi - \Delta\Psi)$ $\Delta\Psi = \frac{E}{k}$ $\Delta\pi = \frac{(A_{\text{net}} + R_d)/C_i}{d_{\text{min}} \exp\{[ABA] \cdot \beta \cdot \exp(\delta\Psi_c)\}}$
34.	Gao <i>et al.</i> 2002	$g_s = \frac{1}{\beta} P_g$ $g_s = \frac{1}{\beta} (\Psi_g - \pi_g)$ $g_s \cdot VPD = K_{\text{tot}}(\Psi_s - \Psi_g)$ $\pi_g = \pi_0 - \alpha \cdot Q$
35.	Buckley <i>et al.</i> 2003	$g_s = \chi(P_g - mP_c)$ $g_s = \chi[(\Psi_g - \pi_g) - mP_c]$ $g_s \cdot VPD = K_{\text{tot}}(\Psi_s - \Psi_g)$ $\pi_g = f(T, P_c)$

Complex functions are not detailed and are written as  $f$ (main variables). Abbreviations not listed in Table 3 are empirical constants.

not taken into account, although such interactions were reported, for example between  $VPD$  and  $\Psi_l$  (Tardieu *et al.* 1996).

Other authors based their approach on the principle of the existence of a limiting factor. Noe & Giersch (2004), for instance, proposed a model where  $g_s$  is a function of  $g_{\text{smax}}$  and the minimum among two response functions to  $Q$  and  $VPD$ , respectively (Table 2; Eqn 3).

Although successfully tested in numerous circumstances, multiplicative or limiting factor-based models are essentially empirical and require new parameterization for each new environmental condition. This is their main drawback likely resulting from the assumption that environmental factors have independent effects.

### Response of stomata to air humidity, transpiration rate and leaf water potential

It has been often observed that air humidity ( $H_r$ ) influences stomatal aperture (Lange *et al.* 1971), but the way  $H_r$  is sensed by the plant remains still a matter of debate (Oren *et al.* 1999; Meinzer 2002; Buckley 2005). Do stomata respond to  $H_r$  *per se*, or to one of its correlated derivatives, that is, partial pressure of water vapour, air or leaf-to-air  $VPD$  (respectively,  $VPDA$  or  $VPDL$ ), leaf transpiration rate ( $E$ ) or  $\Psi_l$ ? This section focuses on the relationship between  $g_s$  and these variables. By definition,  $VPDA$  is calculated at air temperature, while  $VPDL$  is calculated at leaf temperature. From a physiological point of view, because

stomatal response is driven by the local environment,  $VPDL$  is more informative than  $VPDA$ . Most authors thus consider  $VPDL$  when modelling  $g_s$ . We will use the term  $VPD$  henceforth to stay faithful to the original formulation of the models presented.

Aphalo & Jarvis (1991) showed that  $VPD$  was more appropriate than  $H_r$  to describe the response of  $g_s$  to humidity of the air, which makes sense considering that these variables are related by an equation derived from the diffusion equation of water vapour in the air:

$$E = \alpha(g_s^{-1} + g_b^{-1})^{-1} \cdot VPD \quad (1)$$

where  $\alpha$  and  $g_b$  (the boundary layer conductance to water vapour) can be considered as physical parameters dependent on atmospheric pressure, temperature, wind speed and shoot architecture.

Mott & Parkhurst (1991) tried to determine whether  $g_s$  responds either to humidity (partial pressure of water vapour) or  $E$ . By substituting helox for air in the atmosphere, which drastically changes gas diffusion properties, they could break the strong correlation existing between  $E$ ,  $g_s$  and air humidity, and thus demonstrate that stomata sense  $E$  rather than air humidity.

Following the same line, it may be argued that leaf water potential may also be substituted for  $E$  in models of stomatal response to fluctuating air humidity, because  $\Psi_l$  and the transpiration rate are closely linked. It may further be argued that this substitution has a mechanistic basis

**Table 3.** List of abbreviations

$A_L$	Leaf area
$A_{max}$	Maximal CO <sub>2</sub> assimilation rate
$A_{net}$	Net CO <sub>2</sub> assimilation rate
$A_{st}$	Stomata pore area
$ABA$	Abcisic acid
$C_a$	CO <sub>2</sub> concentration in the ambient air
$C_i$	CO <sub>2</sub> concentration in the intercellular spaces
$C_s$	CO <sub>2</sub> concentration at the leaf surface
$d_{mi}$	Minimum ion diffusion rate
DOY	Day of the year
$E$	Transpiration rate
$E_{crit}$	Transpiration rate threshold beyond which embolism can appear
ETP	Daily potential evapotranspiration
$F_{AB}$	Water flow between points A and B
$G^*$	Sensitivity of $g_s$ to variations in residual photosynthetic capacity (Jarvis & Davies 1998)
$g_b$	Boundary layer conductance to water vapour
$g_{bwb}$	Slope of the $g_s$ - $A_{net}$ relationship relative to BWB model
$g_L$	Slope of the $g_s$ - $A_{net}$ relationship relative to Leuning model
$g_s$	Stomatal conductance
$g_{sc}$	Stomatal conductance to CO <sub>2</sub>
$g_{sw}$	Stomatal conductance to H <sub>2</sub> O
$g_{smax}$	Maximal stomatal conductance
$g_0$	Minimal stomatal conductance
$H_r$	Relative air humidity
$J_{ABA}$	$ABA$ flow = amount of $ABA$ synthesis in the root system
$J_{max}$	Light-saturated potential electron flux
$J_w$	Water flow
$k$	Hydraulic conductivity between the bulk leaf epidermis and the guard cells
$K_{AB}$	Conductivity between points A and B
$K_{max}$	Maximal total conductivity on the soil-to-leaf pathway
$K_{tot}$	Total conductivity on the soil-to-leaf pathway
$L_a$	Length of the stomata pore major axis
$L_b$	Length of the stomata pore minor axis
$m$	Mechanical advantage of epidermal cells onto guard cells (Buckley <i>et al.</i> 2003)
$P$	Daily precipitation
$P_c$	Epidermal cell turgor pressure
$P_g$	Guard cell turgor pressure
$P_{sub}$	Subsidiary cell turgor pressure
$Q$	Light intensity
$R_d$	Day mitochondrial respiration
$R_p$	Resistance to water flow in the plant
$R_{sp}$	Resistance to water flow in the soil and at the interface soil-root
ROS	Reactive oxygen species
RuBP <sub>pot</sub>	Potential concentration of RuBP in the chloroplast (Farquhar & Wong 1984)
$s$	Sensitivity of $g_s$ to variations in $E$ (Jarvis & Davies 1998)
$T$	Semi-empirical parameter related to concentration of ATP in the chloroplast (Farquhar & Wong 1984; Buckley <i>et al.</i> 2003)
$T_{gro}$	Growth temperature: mean daily temperature averaged on the last 7 d (Ogle & Reynolds 2002)
$T_{max}$	Maximum $T_{gro}$ at which stomata operate (Ogle & Reynolds 2002)
$T_{min}$	Minimum $T_{gro}$ at which stomata operate (Ogle & Reynolds 2002)
$T_l$	Leaf temperature
$V_{cmax}$	Maximal carboxylation rate
VPD	Water pressure deficit
VPDA	Air water pressure deficit
VPDL	Leaf-to-air water pressure deficit
$\Delta\pi$	Osmotic potential gradient between epidermal and guard cells
$\Psi$	Water potential gradient between epidermal and guard cells
$\delta\theta$	Soil water deficit
$\chi_v$	Leaf-specific hydraulic resistance to water flow through the plant (roots-stomata)/constant
$\pi_g$	Guard cell osmotic potential
$\Psi_A$ ( $\Psi_B$ )	Water potential at point A (B)
$\Psi_{cav}$	Cavitation threshold
$\Psi_c$	Epidermal cell water potential
$\Psi_g$	Guard cell water potential
$\Psi_l$	Leaf water potential
$\Psi_{pd}$	Pre-dawn leaf water potential
$\Psi_r$	Root water potential
$\Psi_s$	Soil water potential
$\Psi_{100}$	Water potential at which the xylem conductivity equal 0 (100% embolism)
$\Gamma$	CO <sub>2</sub> compensation point
$\theta_{cc}$	Volumetric soil water content at wilting point
$\theta_f$	Volumetric soil water content at field capacity
$\theta_s$	Volumetric soil water content

because it is well demonstrated that stomatal movements result from variations in leaf (or guard cell) water status, which result themselves from variations of evaporation in the substomatal cavity, and thus of the transpiration flux (see Comstock & Menuccini 1998).

Numerous relationships between  $g_s$  and one of the three variables related to air humidity:  $VPD$ ,  $E$  or  $\Psi_i$ , have been proposed in the literature. For instance, Lohammer *et al.* (1980) proposed a widely used hyperbolic relationship between  $g_s$  and  $VPD$  (Table 2; Eqn 4). Monteith (1995) suggested to use a linear approximation of this relationship for the range of  $VPD$  commonly encountered in the field (Table 2; Eqn 5). Using Eqn 1, the linear relationship between  $g_s$  and  $VPD$  can also be transformed into a linear relationship between  $g_s$  and  $E$  (Monteith 1995) (Table 2; Eqn 6), provided that the boundary layer resistance  $g_b^{-1}$  is negligible. Conditions of low wind over dense vegetation may considerably increase  $g_b^{-1}$  compared to  $g_s^{-1}$ , and thereby distort the correlation coefficients between  $E$ ,  $g_s$  and  $VPD$  as given by Eqn 1. But the major problem associated with these approaches is that they rely on purely empirical parameters established in well-controlled conditions and considered as constants. Albeit very simplifying, these approaches have been widely used and proven useful in not-too-extreme conditions, generally characterized by non-limiting water supply.

Considering that stomata respond to short-term variations of guard cell water potential, some authors developed hydromechanical models, based on a precise description of water balance and turgor regulation of guard cells. Cowan (1972) first developed an electrical analogous model based on water transfer functions that explained several aspects of stomatal movements. Changes in water content with water potential of mesophyll, and subsidiary and guard cells were represented as 'capacitors' connected by 'resistances' that governed water flows. Cooke *et al.* (1976) then showed, using finite element shell analysis, that  $g_s$  can be related to turgor pressure of guard cells and subsidiary cells ( $P_g$  and  $P_{sub}$ , respectively) with a multilinear relationship, and not solely to the pressure difference between the two, as previously believed. The authors also theoretically demonstrated that the aperture width is more sensitive to variations in  $P_{sub}$  than to variations of  $P_g$ , which has been proved later using the pressure probe, and was called the 'mechanical advantage' of epidermal cells. They also showed that it is the elliptical shape of the stomata torus that allows to properly respond to turgor pressure changes: the major axis of the torus remains almost constant, while the minor axis varies. Based on these conclusions, Delwiche & Cooke (1977) developed an analytical hydraulic model based on the dynamic behaviour of stomata. Pore area ( $A_{st}$ ) is modelled geometrically as a function of the length of the major and the minor axes ( $L_a$  and  $L_b$ , respectively) (Table 2; Eqn 7). The length of the minor axis is dependent on  $P_g$  and  $P_{sub}$ , the two variables being integrated in a system of non-linear differential equations including water potentials, turgor pressures, osmotic potentials, water vapour resistances and water fluxes of guard cells and subsidiary cells. The

model suggests that hydropassive stomatal movements are insufficient to regulate water loss at low leaf water potentials. More recently, Dewar (1995) proposed a more comprehensible model of  $g_s$  in which stomatal movements are governed by difference in turgor pressure between the guard cells and the bulk leaf epidermis ( $P_e$ , closely related to  $P_{sub}$ ). Turgor pressure is deduced from water potential and osmotic pressure. Stomatal response to any stimuli is then separated into: (1) a hydropassive hydraulic response based on the water potential difference between guard cells and bulk leaf epidermis ( $\Delta\Psi$ ); and (2) a hydroactive response that involves energy-dependent osmotic regulation in guard cells (related to the osmotic potential difference between guard cells and epidermal cells,  $\Delta\pi$ ).

In Dewar's model,  $\Delta\Psi$  appears proportional to  $E$  by considering the hydraulic conductivity between the bulk leaf epidermis and the guard cells as a constant (Table 2; Eqn 8). As cell osmotic pressure is difficult to measure experimentally,  $\Delta\pi$  is interpreted, by analogy to Leuning's model (Leuning 1995, see 'Models based on a  $CO_2$  assimilation submodel' subsection), as a function of  $A_{net}$ ,  $C_i$ ,  $g_s$  and an empirical constant which is the equivalent of the  $a$  constant of Leuning's model (Table 2; Eqns 11–12). Roughly, guard cell turgor is considered to depend on the solute influx into the guard cells, and hence on  $CO_2$  assimilation rate. The analogy is not detailed here, but is discussed in section 'Some ideas for future development' as a possible bridge between empirical and semi-empirical models. Dewar's model introduces mechanistic bases of stomatal movements in a form easier to solve than previous proposals. However, some experimental observations are not well simulated, in particular, Dewar's model does not take into account the mechanical advantage of epidermal cells on guard cells. From a practical point of view, this model remains tricky to use, mainly because of the difficulty to estimate some parameters (e.g.  $k$ ).

### Models relating $g_s$ to photosynthesis

Numerous models have been built on the relationship existing between  $g_s$  and photosynthesis rate. Some authors have exploited the strong linear relationship commonly observed between  $g_s$  and  $A_{net}$  when  $Q$  varies, but under constant air and soil water status (Wong, Cowan & Farquhar 1979; Mott 1988; Aphalo & Jarvis 1991; Buckley, Mott & Farquhar 2003). In these conditions,  $g_s/A_{net}$  remains constant, in line with the idea that stomatal movements are optimized to minimize water loss for a given amount of carbon gain (Cowan 1977; Cowan & Farquhar 1977). Others have exploited the relationships observed between  $g_s$  and estimations of the photosynthetic capacity (i.e. the maximal photosynthesis observed when light and  $CO_2$  are not limiting) (Mitchell & Hinckley 1993; Le Roux *et al.* 1999; Buckley *et al.* 2003).

### Models based on a $CO_2$ assimilation submodel

Ball *et al.* (1987) developed one of the most commonly used models of  $g_s$  (abbreviated BWB model). In this model,  $g_s$

responds to  $A_{\text{net}}$ ,  $H_r$  and  $\text{CO}_2$  concentration at the leaf surface ( $C_s$ ). In its original form, the model predicts that  $g_s$  is equal to zero when  $A_{\text{net}}$  equals zero. However, a residual stomatal aperture ( $g_0$ ) was rapidly introduced (Table 2; Eqn 9). In the BWB model,  $g_s$  dependency to temperature is indirect, via  $H_r$  (and incidentally  $A_{\text{net}}$ ). Aphalo & Jarvis (1993) proposed an improved version of the BWB model by separating the effects of temperature and  $VPD$  (Table 2; Eqn 10).

Three main criticisms were formulated against the BWB model. Firstly, it does not simulate correctly  $A_{\text{net}}$  and  $g_s$  when  $C_s$  equals the  $\text{CO}_2$  compensatory point ( $\Gamma$ ). When  $C_s = \Gamma$ ,  $A_{\text{net}}$  and  $g_s$  should, respectively, equal zero and  $g_0$ . Leuning (1990) proposed a first modified version of the BWB model by including  $\Gamma$  (Table 2; Eqn 11). Secondly, stomata respond to  $VPD$  rather than to  $H_r$  (Aphalo & Jarvis 1991). A second modification was proposed by Leuning (1995) which consisted in replacing  $H_r$  by the more general Lohammer's function of  $VPD$  (Lohammer *et al.* 1980) (Table 2; Eqn 12a). Finally, stomata do not respond directly to  $C_s$  *per se*, but rather to  $C_i$  (Mott 1988).  $A_{\text{net}}$ ,  $g_s$ ,  $C_s$  and  $C_i$  are related by the so-called supply function expressing diffusion rate of  $\text{CO}_2$  (assumed equal to  $A_{\text{net}}$ ) across stomata (Table 2; Eqn 12b). Because  $C_i$  is unknown, the supply function must be coupled to models of photosynthetic assimilation (biochemical model of photosynthesis, e.g. Farquhar, von Caemmerer & Berry 1980) (Table 2; Eqn 12c). Either BWB or Leuning's model, coupled with the supply function, and the model of  $A_{\text{net}}$  form a system of three equations and three unknowns ( $g_s$ ,  $A_{\text{net}}$  and  $C_i$ ), which can be solved either numerically or analytically (Baldocchi 1994).

BWB and Leuning's models (Ball *et al.* 1987; Leuning 1995) are still extensively used at the leaf level and may also be extrapolated at field or forest stand level (Misson *et al.* 2002; Alton, North & Los 2007). They are relatively easy to use and to parameterize, but they do not capture responses to soil water status. We will see in section 'Models based on a  $\text{CO}_2$  assimilation sub-model' that they can be modified to include those responses. These two models represent a good compromise between ease-to-use, explicative power and predictive accuracy in various experimental conditions.

### Models based on a leaf photosynthetic capacity submodel

The existence of a causal link between  $g_s$  and the photosynthetic capacity is not demonstrated. However, experimental observations show a positive relationship between these two variables (Mitchell & Hinckley 1993; Le Roux *et al.* 1999; Buckley *et al.* 2003), which is tempting to exploit for modelling purposes.

Farquhar & Wong (1984) proposed an empirical relationship relating  $g_s$  to  $T$ , a parameter dependent on the concentration of ATP in the chloroplasts of the mesophyll, as a first estimate of the photosynthetic capacity.  $T$  is in turn estimated by extension of the biochemical model of photosynthesis of Farquhar *et al.* (1980) using ribulose bis-phosphate

(RuBP) concentration and other parameters related to the photosynthetic capacity (Table 2; Eqn 13). In spite of its mechanistic basis, the model of Farquhar & Wong (1984) remains largely empirical. Moreover, it is very complex to use, particularly because of the difficulty to estimate key variables in the field (mainly RuBP concentration).

More usefully, Jarvis & Davies (1998) related  $g_s$  to a 'residual photosynthetic capacity', the difference between actual  $A_{\text{net}}$  and maximal  $A_{\text{net}}$  when  $\text{CO}_2$  is not limiting ( $A_{\text{max}}$ ). The authors proposed that stomatal aperture is limited by the evaporative demand (estimated by  $E$ ) and the residual photosynthetic capacity (Table 2; Eqn 14). This model is easier to apply than Farquhar and Wong's (1984), but some experimental observations are not simulated correctly. In particular, positive response of  $g_s$  to oxygen concentration is predicted in all conditions, while the observed response is negative in some conditions and positive in others (Buckley *et al.* 2003). Besides, Buckley *et al.* (2003) suggested that if  $g_s$  actually responds to residual photosynthetic capacity, this response is mediated by a less direct variable than  $A_{\text{net}} - A_{\text{max}}$ , maybe ATP concentration in the mesophyll cells.

## STOMATAL CONDUCTANCE MODELS IN THE PRESENCE OF WATER STRESS

### Empirical models based on environmental factors

#### Multiplicative models

A simple approach to integrate the effects of water stress in  $g_s$  models consists in introducing a response function to soil water deficit into the multiplicative models presented in 'Empirical models of response to climate'. Numerous models were developed on the basis of Jarvis's model (Jarvis 1976) with a response function to soil water status replacing the response function to  $\Psi_1$ .

In Stewart's model (Stewart 1988),  $g_s$  responds to  $Q$ ,  $T$ ,  $VPD$  and soil water deficit ( $\delta\theta$ ) (Table 2; Eqn 15). Others, like Misson, Panek & Goldstein (2004), rather used pre-dawn water potential ( $\Psi_{\text{pd}}$ ) as an estimate of soil water availability near the roots (Table 2; Eqn 16).

White *et al.* (1999) proposed a similar model using a response function to  $\Psi_{\text{pd}}$ . But, they considered that the sum of stress accumulated during a given period of time is more relevant than the current daily stress. Response functions to environmental factors are thus integrated over the considered period, and a global  $g_s$  for this period can be simulated. However, the coupling with other sources of variations of  $g_s$  (like  $A_{\text{net}}$  or  $E$ ) requires instantaneous values of  $g_s$ . MacFarlane, White & Adams (2004) therefore used a simplified version of White's model, where  $g_s$  responds to instantaneous variations of  $Q$ ,  $T$  and  $VPD$  on the short term, and to integrated value of  $\Psi_{\text{pd}}$  over a period of  $n$  days of stress on the long term [sum of stress,  $S(\Psi)$ ] (Table 2; Eqn 17). The model well simulates field observations. As water stress effects are a

combination of its strength and duration, the concept of cumulative sum of stress seems very relevant.

As said previously in 'Multiplicative models of environmental influence', multiplicative models present two important drawbacks: (1) they suppose that the response to each factor is independent; and (2) they require to construct response curves for each experimental condition. However, in their range of parameterization, these models can provide rather satisfactory simulations.

### Specific approaches

Specific approaches have been adopted for isohydric species (see 'Leaf water potential and ABA') which regulate transpiration so as to maintain  $\Psi_l$  constant when soil and air water status vary. For such species, Ogle & Reynolds (2002) proposed: (1) that  $g_s$  regulation depends on climatic demand (estimated by  $VPD$ ); and (2) that the maximal stomatal conductance ( $g_{smax}$ ) depends on  $\Psi_{pd}$  and growth temperature ( $T_{gro}$ , the mean daily temperature averaged over the last 7 d). More precisely, the authors determined two empirical thresholds of  $VPD$  beyond which  $g_s$  is maximal or null (Table 2; Eqn 18). The authors showed that stomatal sensibility to  $VPD$  decreases with increasing water stress. This model successfully captured the large diurnal and seasonal fluctuations of  $g_s$  for a North American desert shrub *Larrea tridentata*. It provides accurate simulations of  $g_s$  in a wide range of environmental conditions.

### Models based on a CO<sub>2</sub> assimilation submodel: modifications of BWB and Leuning's models

Water stress modifies the relationship between  $g_s$  and  $A_{net}$ , and consequently the  $g_s/A_{net}$  ratio (Brodribb 1996; Katul, Leuning & Oren 2003; Tuzet *et al.* 2003; MacFarlane *et al.* 2004; Misson *et al.* 2004; Rouhi *et al.* 2007). As a consequence, the models of BWB and Leuning, which are based on a linear relationship between  $g_s$  and  $A_{net}$ , cannot properly simulate  $g_s$  in water stress conditions. Numerous authors adapted these two models to water stress conditions by expressing the slope of the  $g_s$ - $A_{net}$  relationship relative to these models (henceforth called  $g_{bwb}$ ,  $g_L$ )

(Table 2; Eqns 9 and 12a) as empirical functions of plant or soil water status.

Among the first proposals, Tenhunen *et al.* (1990) substituted  $g_{bwb}$  by a parameter called *GFAC* which has to be recalculated whenever the conditions change (Table 2; Eqn 19). More explicitly, Baldocchi (1997) introduced a cumulative drought index into  $g_{bwb}$ . This index is a function of the sum of rainfalls divided by cumulated evapotranspiration over the considered period (Table 2; Eqn 20). Other authors proposed to modify BWB and Leuning's models by introducing a function of  $\Psi_{pd}$ . Sala & Tenhunen (1996) observed a curvilinear relationship between  $g_{bwb}$  and  $\Psi_{pd}$  for water potentials ranging from -1 to 0 MPa, and a linear one for more negative potentials (Table 2; Eqn 21). Misson *et al.* (2004) introduced a power function of  $\Psi_{pd}$  into the BWB model (Table 2; Eqn 22). Wang & Leuning (1998) modified Leuning's model using a function of soil water content ( $\theta_s$ ) (Table 2; Eqn 23). Similarly, Van Wijk *et al.* (2000) introduced a function of  $\theta_s$ , although of a different form, in the models of BWB and Leuning (Table 2; Eqn 24). These last authors showed that the BWB model should also be modified to include a function of  $T_l$ . For simplicity, they preferred to use the model of Leuning. More recently, Uddling *et al.* (2005) introduced a function of the day of the year ( $f_{season}$ ) in Leuning's model (Table 2; Eqn 25), which integrates all seasonal effects including seasonal drought.

When available, the adjustment quality of these models, on the base of predictions versus observations regression, was reported in Table 4.  $R^2$  (the proportion of variation explained by the fitted regression) and slope deviation from unity are common measures of accuracy and bias. Equally important is the domain of validity of the model in terms of ranges of environmental conditions, level of fluctuations, species, time-scale, etc. In their original conditions of parameterization, all of the models presented in Table 4 very well simulate  $g_s$  or  $E$ , even for shade leaves (Sala & Tenhunen 1996). These models do not simulate the daily variations of stomatal conductance, nor transient responses, if any, to rapid, time-varying conditions, like sunflecks. However, they may be considered as suitable for long-term water stress studies.

**Table 4.** Prediction quality of four modified versions of BWB or Leuning model

Author	Species	Variable	Predict versus observed		Range of stress	
			$R^2$	Slope		
Uddling <i>et al.</i> (2005)	<i>Betula pendula</i>	$g_s$	0.80	1.00	$\Psi_{pd} = [-0.55; 0]$ MPa	
Van Wijk <i>et al.</i> (2000)	<i>Pseudotsuga menziesii</i>	$E$	0.88	0.94	$\theta_s = [4; 19]\%$	
Misson <i>et al.</i> (2004)	<i>Pinus ponderosa</i>	$g_s$	0.71	1.01	$\Psi_{pd} = [-1.7; 0]$ MPa	
Sala & Tenhunen (1996)	<i>Quercus ilex</i> (two sites)	Sun leaves	$g_s$	0.862	0.97	$\Psi_{pd} = [-2.7; -0.2]$ MPa
			$g_s$	0.813	1.00	
	Shade leaves	$g_s$	0.756	1.02		
		$g_s$	0.826	1.00		

## Towards more mechanistic approaches

The approaches presented in the previous sections are based on observed relationships. With a better understanding of plant physiology, particularly of the response to water stress, models with a more mechanistic basis have been proposed.

### Leaf water potential and ABA

Species differ by their degree of control of  $\Psi_l$  during water stress. Some species maintain  $\Psi_l$  almost constant during water stress (isohydric species), while others do not (anisohydric species). The  $g_s$  response to ABA depends on whether the species is rather isohydric or anisohydric. For isohydric species, stomata sensibility to ABA is negatively related to  $\Psi_l$ . Tardieu & Davies (1993) expressed  $g_s$  as a function of xylem ABA concentration and  $\Psi_l$ . ABA concentration is calculated from water and ABA fluxes equations within the plant (Table 2; Eqn 26). For anisohydric species, stomatal regulation in water stress conditions depends only on xylem ABA concentration (Tardieu *et al.* 1996). For such plants, Tardieu & Simonneau (1998) proposed to use the model of Tardieu & Davies (1993) with a  $\delta$  coefficient equal to zero (see Table 2; Eqn 26). In a more straightforward manner, Gutschick & Simonneau (2002) introduced a function of ABA concentration in the xylem in the BWB model (modification of the slope of the BWB model) (Table 2; Eqn 27).

Because they depend on ABA, all these models simulate well  $g_s$  in a wide range of environmental conditions, particularly for different levels of water deficit. A limitation was, however, formulated because xylem ABA concentration is commonly assessed in the sap extracted by pressurization from a shoot. This concentration is supposed to represent the average of the different concentrations inside the leaf (Tardieu & Simonneau 1998). However, from a mechanical point of view, it is the ABA concentration near the guard cells that determines stomatal closure and is expected to be correlated to  $g_s$ . Because of redistribution and neosynthesis within leaves, ABA concentration measured in sap collected by pressurization can differ from ABA concentration near the guard cells. However, the simplicity of measurement of concentration in the xylem sap and the strong correlation with  $g_s$  generally observed justify its use in models.

### Hydraulic models

Hydraulic models are based on water transfer in the xylem, governed by thermodynamics that allows analogy to Fick's law. For a segment AB within a plant, the flux between points A and B ( $F_{AB}$ ) depends on the xylem hydraulic conductivity between these two points ( $K_{AB}$ ) and the water potential ( $\Psi$ ) difference (or gradient if  $K_{AB}$  is expressed as a conductivity and not as a conductance):

$$F_{AB} = K_{AB}(\Psi_A - \Psi_B) \quad (2)$$

As water transfer in the xylem is conservative, in a first approximation, the water flux through the whole tree

equals transpiration. Hydraulic models are then primarily transpiration models, but they can easily be converted into  $g_s$  models using Eqn 1.

A first method to model  $g_s$  consists in using the flux equation for the soil-to-leaf pathway.  $E$  and  $g_s$  appear then as the product of the hydraulic conductivity of the soil-to-leaf pathway ( $K_{tot}$ ) divided by leaf surface, and of the water potential gradient between the soil and the leaf. This simplified approach assumes that the plant acts as a unique pipe. It was occasionally used, for example by Oren *et al.* (1999), at the tree level (Table 2; Eqn 28).

However, the pipe model may arguably represent an oversimplification where heterogeneity within branches is neglected, and a more precise description of tree hydraulic architecture is then required, especially for trees. Tyree & Sperry (1988) simulated transpiration of whole trees using flux equations (Eqn 2). In their approach, the water pathway from the soil to the leaves is separated in segments that represent the tree architecture (Table 2; Eqn 29). For each segment, a specific hydraulic conductivity, estimated from its diameter, is given. The system works as an electric circuit where resistances in series and conductances in parallel may be added. Similarly, Sperry *et al.* (1998) decomposed the tree into different organs, from the roots to the leaves, and simulated water fluxes for each organ. They also added a precise description of water transfer from the soil to the roots. With a somewhat different approach, Tuzet *et al.* (2003) proposed a model of  $g_s$  based on the relationship between  $g_s$  and  $A_{net}$ ,  $C_i$ ,  $\Psi_l$  and plant hydraulic architecture (Table 2; Eqn 30).  $\Psi_l$  is estimated by a flux equation from the soil to the leaves that takes into account the resistances of the different segments. Actually, this model is close to a modified version of Leuning's model where the slope of the  $g_s$ - $A_{net}$  relationship is a function of  $\Psi_l$ .

In conditions of water deficit, there is a large consensus that stomatal closure controls the formation of embolism in xylem vessels through the maintenance of the xylem water potential above a critical threshold called the cavitation threshold,  $\Psi_{cav}$ . Indeed, embolism can appear when xylem water potential becomes lower than  $\Psi_{cav}$ . A last group of models are based on the hypothesis that stomatal closure controls the decrease in xylem water potential and the formation of embolism (Tyree & Sperry 1989). Jones & Sutherland (1991) simulated  $g_s$  with a flux equation using the total hydraulic conductance of the plant in the soil-to-leaf pathway ( $K_{tot}$ ).  $K_{tot}$  is a function of the maximal hydraulic conductivity ( $K_{max}$ ), and a parameter which is an estimate of the xylem embolism rate based on  $\Psi_l$  and  $\Psi_{cav}$  (Table 2; Eqn 31). For the authors, this formulation is adequate for cereals, while hydraulic architecture should be introduced for trees. Cochard *et al.* (1996a) and Lu *et al.* (1996) calculated a transpiration threshold ( $E_{crit}$ ) beyond which embolism can appear. This threshold is estimated by a flux equation at the whole-plant level, considering that xylem water potential is maintained equal to  $\Psi_{cav}$  (Table 2; Eqn 32). With the hypothesis that stomata are regulated in order to prevent embolism formation, the observed

transpiration is expected to remain lower than the calculated threshold transpiration. This is observed on most species. Cochard *et al.* (2002) completed this approach by using a precise description of the architecture of the soil–plant–leaves continuum to estimate  $K_{\text{tot}}$ .

An important feature of hydraulic models is their facility of use and parameterization, which represents a serious practical advantage. They are also easy to understand as they proceed from the simple idea of the hydraulic determinism of stomatal closure. However, all these models (except Tuzet *et al.* 2003) focus on hydraulic mechanisms only. It is well established that various stimuli, some of which do not relate to any hydraulic control, influence  $g_s$ . Thus, hydraulic models cannot be considered as universal integrative models of  $g_s$  as a function of water relations.

### Hydromechanical models

We presented in ‘Response of stomata to air humidity, transpiration rate and leaf water potential’ a ‘hydromechanical’ model of  $g_s$ , based on a precise description of water balance and turgor regulation of guard cells (Dewar 1995). This approach, primarily developed for well-watered plant, was extended to water stress conditions.

Dewar improved his model by introducing a stomatal response to leaf xylem *ABA* concentration (Dewar 2002). In the most recent version of this model, stomatal movements are still governed by the difference in turgor pressure between guard cells and bulk leaf epidermis ( $P_g - P_e$ ), and the stomatal response is still separated into hydropassive and hydroactive responses, but the osmotic pressure difference between guard cells and epidermal cells ( $\Delta\pi$ ) is an explicit function of the quantity of ions entering the guard cells, and of the diffusion rate between guard cells and epidermal cells. This diffusion rate is estimated by the product of a minimal rate ( $d_{\text{min}}$ ) and an exponential function of *ABA* concentration in the leaf xylem and of water potential of epidermal cells, formulated by Tardieu & Davies (1993) (Table 2; Eqn 33). The quantity of ions entering the guard cells not being measurable is estimated by a function of  $A_{\text{net}}$ ,  $C_i$  and day respiration ( $R_d$ ).

Using the same concepts, but by modifying one of the fundamental hypotheses, Gao *et al.* (2002) more precisely simulated the effects of water stress. For them, stomata do not respond to the difference in turgor pressure between the guard cells and the bulk leaf epidermis, but rather to the turgor of guard cells ( $P_g$ ) (Table 2; Eqn 34);  $g_s$  is then solely dependent on water potential and osmotic pressure of the guard cells ( $\Psi_g$  and  $\pi_g$ , respectively).  $\Psi_g$  is expressed by a flux equation between the soil and the guard cells, considering the total conductivity from the soil to the guard cells ( $K_{\text{tot}}$ ). The relationship between  $E$ ,  $VPD$  and  $g_s$  (Eqn 1) is then used to express  $g_s$ ;  $\pi_g$  depends on the amount of assimilates in the guard cells, which is a function, in a first approximation, of photosynthesis.  $\pi_g$  can thus be estimated from  $Q$ .

An advantage of this model compared to Dewar’s model is that hydraulic components can be more easily

approximated: the total conductivity from the soil to the guard cell is easier to estimate than the hydraulic conductance between bulk leaf epidermis and the guard cells. However, osmotic regulation, modelled by the diffusion of ions between the guard cells and the apoplast, is not included.

Both of these models have their advantages and drawbacks, but none of them predicts one important behaviour observed experimentally: the mechanical advantage of epidermal cells over guard cells. Buckley *et al.* (2003) dealt with this issue in a model similar to Gao’s (Gao *et al.* 2002), but with the following main differences (Table 2; Eqn 35). Firstly, the epidermal mechanical advantage over the guard cells is taken into account by introducing a factor  $m$  ( $m > 1$ ), which allows to weigh the effects of  $P_g$  and  $P_e$  on  $g_s$ . Secondly, guard cell osmotic pressure ( $\pi_g$ ) depends on the flux of solutes resulting from the electrochemical gradient imposed by ATP synthases.  $\pi_g$  is then expressed as a function of ATP concentration of the guard cells (semi-empirical parameter  $T$ ). With the hypothesis that the same biochemical process controls ATP concentration in mesophyll and in guard cells, the guard cell ATP concentration can be simulated using the model of Farquhar & Wong (1984) (see ‘Models based on a leaf photosynthetic capacity sub-model’). Finally, the authors suggested that variations in local turgor pressure close to the guard cells are part of the signal leading to stomatal closure in conditions of water stress.  $\pi_g$  can thus be expressed as a function of ATP concentration and  $P_e$ . Experimental evidence of the existence of a water stress sensor localized close to stomata was reviewed later by Buckley (2005).

Important features of this model have to be highlighted. Firstly, the model relates osmotic pressure to photosynthetic activity expressed by ATP content. ATP content determines RuBP regeneration activity. Thereby,  $g_s$  is linked to photosynthetic activity (see ‘Models based on a leaf photosynthetic capacity sub-model’). Secondly, introducing the epidermal mechanical advantage enables to better simulate variations of  $g_s$  with  $VPD$  than in the previous models, namely the transient opening with increasing  $VPD$  which results from rapid, hydropassive responses, and the subsequent closure associated with the slower, hydroactive, energy-dependent osmotic response. Moreover, *ABA* effects can be introduced in the model, considering that the flux of ions entering the guard cells is *ABA* dependent. The main drawback of this model lies in its complexity and in the important number of parameters that have to be determined.

## SOME IDEAS FOR FUTURE DEVELOPMENTS

### Bridges between mechanistic and empirical models

We have presented numerous models of stomatal conductance suitable for water stress conditions that can be essentially qualified from empirical to mechanistic. At this stage, all these models well simulate variations of  $g_s$  in conditions of water stress.

In some cases, explicit bridges between models were proposed. Dewar presented his first model (Dewar 1995) as an improvement of Leuning's model (Leuning 1995), where the role played by turgor in the regulation of guard cell volume is clearly accounted for. As already seen in 'Response of stomata to air humidity, transpiration rate and leaf water potential', the osmotic gradient between guard and epidermal cells, one of the main variables of this model, was expressed as a function of  $A_{\text{net}}$ ,  $C_i$ ,  $g_s$  using the empirical constant  $a$  of Leuning's model (see Dewar 1995 for the mathematical analogy). Similarly, in the second version of his model, Dewar (2002) proposed to combine the essential features of Leuning's model with those of Tardieu and Davies's (Tardieu & Davies 1993; Leuning 1995) within a common mechanistic framework. The empirical constants  $a$  and  $D_0$  of Leuning's model were expressed in terms of guard cell parameters related to hydraulic or ion transport characteristics (see Dewar 2002 for the exact expressions). The dependency of  $g_s$  on  $ABA$  expressed in Tardieu and Davies's model (Tardieu & Davies 1993) was directly included into the expression of the osmotic gradient between the guard and epidermal cells (Leuning 1995; Table 2; Eqn 32).

These two models represent certainly the most advanced attempts to introduce mechanistic models into empirical ones. Such integrative approaches certainly deserve to be encouraged in the future for the potential benefits that may be derived from them. Our capacity to develop a universal, integrated and quantitative view of the effects of environmental factors with a large domain of validity probably depends on our capacity to design models built onto strong foundations, both physiological and empirical.

### The issue of seasonal variations

This review presents models that cover long-term phenomena especially water stress. An important issue not discussed yet is the seasonal variations of the factors introduced in  $g_s$  models. It is difficult to propose *a priori* laws of variation for empirical parameters. By contrast, predictive quality can be improved by incorporating pre-existing knowledge on seasonal changes in physiological factors (photosynthetic capacity and  $K_{\text{tot}}$  as examples). To date, seasonal variability in leaf photosynthetic capacity has been documented for only a few tree species. In tropical conditions, characterized by mild seasonal changes and non-limiting water supply, photosynthetic capacity of mango leaves appears rather stable (Urban, Montpied & Normand 2006). In contrast, photosynthetic capacity fluctuates substantially in leaves of temperate trees, as a function of either drought (Wilson, Baldocchi & Hanson 2000; Xu & Baldocchi 2003), leaf age (Wilson *et al.* 2000) or source-sink relationships (Walcroft *et al.* 2002). Observations made by Damour, Vandame & Urban (2009) suggest that the reversible decline in photosynthetic capacity of leaves from mango trees subjected to long-term drought may be attributable to the associated decrease in sink activity. The perspectives of modelling seasonal variations of

photosynthetic capacity were evaluated rather positively by Damour & Urban (2007). Similarly,  $K_{\text{tot}}$  was shown to vary seasonally, with age (Hubbard, Bond & Ryan 1999) and environmental conditions (Cochard *et al.* 1996a; Lu *et al.* 1996). We still need to increase our understanding and develop models of the variations of  $K_{\text{tot}}$  as a function of these factors.

### The issue of co-regulation of $g_s$ and $A_{\text{net}}$

As mentioned previously (section 'Models relating  $g_s$  to photosynthesis'), the most used models of  $g_s$ , namely the models of BWB and Leuning, are based on the concept of  $C_i$  homeostasis which implicitly assumes a stable ratio between water consumption and carbon gain (WUE). They consequently exploit the idea that the  $g_s$ -to- $A_{\text{net}}$  ratio is a constant in conditions characterized by non-limiting water availability and in the absence of limitations imposed by either carbohydrate accumulation or reduced sink activity. While easy to comprehend in a deterministic perspective, a constant  $g_s$ -to- $A_{\text{net}}$  ratio appears more difficult to explain mechanistically. Stable  $C_i$  may result from the source-to-sink balance for  $\text{CO}_2$  fluxes. A decrease in  $g_s$  lowers  $C_i$  and hence  $A_{\text{net}}$  because less  $\text{CO}_2$  enters the leaves. The decrease in  $A_{\text{net}}$  tends in turn to increase  $C_i$  because less  $\text{CO}_2$  is consumed, which eventually results in a more or less stable  $C_i$ . Alternatively, it has been suggested that a direct feedback control of  $g_s$  by  $C_i$  is at the origin of the relative maintenance of  $C_i$ . However, the  $g_s$  response to  $C_i$  appears too weak to permit such a feedback (Sharkey & Raschke 1981). More recent works suggest that part of the response of  $g_s$  to  $C_i$  (or red light) is linked to photosynthetic electron transport (Messinger, Buckley & Mott 2006), which provides a mechanistic basis for the  $g_s$ - $A_{\text{net}}$  relationship. The nature of the mediator remains unknown, but some evidence locates it in the mesophyll (Mott 2009). Moreover, considering that  $ABA$  inhibits several enzymes of the Calvin cycle (Rook *et al.* 2006), it is tempting to hypothesize that  $ABA$  co-regulates both  $g_s$  and  $A_{\text{net}}$ , and to use  $[ABA]$  for modelling both  $g_s$  (Tardieu & Davies 1993) and  $A_{\text{net}}$ .

However, there are conditions where either a constant  $C_i$  or  $g_s$ -to- $A_{\text{net}}$  ratio is not observed. In particular, it has been repeatedly observed that the  $g_s$ -to- $A_{\text{net}}$  ratio shifts in drought conditions (Brodribb 1996; Lawlor & Cornic 2002; Medrano *et al.* 2002; Katul *et al.* 2003; MacFarlane *et al.* 2004; Urban *et al.* 2006; Damour, Vandame & Urban 2008), which seriously limits the generalization of the use of several models of  $g_s$  and  $A_{\text{net}}$ . Similarly, it has been observed that carbohydrate accumulation or reduced sink activity not only reduces  $A_{\text{net}}$ , but also  $g_s$ , that may result in shifts in the  $g_s$ -to- $A_{\text{net}}$  ratio (Urban & Alphonsout 2007; Duan *et al.* 2008; Wu *et al.* 2008). Moreover, both issues are possibly linked: it has been suggested that the long-term negative effect of drought on  $A_{\text{net}}$  may be interpreted as the consequence not only of reduced  $g_s$  and  $C_i$ , but also of reduced sink activity relative to sources and subsequently of altered photosynthetic capacity (Damour *et al.* 2009). All these observations suggest that the relationship between  $g_s$  and

$A_{\text{net}}$  is a complex one, and that simple conceptions based on a reciprocal influence through  $C_i$  or co-regulation by *ABA* are not totally satisfying. However, these observations reinforce the idea that  $g_s$  responds to the balance between photosynthetic electron transport and carbon reduction (Messinger *et al.* 2006; Mott 2009).

The coupling of  $g_s$  models with  $\text{CO}_2$  assimilation submodels raises questions on which factors control  $A_{\text{net}}$  and how they can be influenced by water stress. As discussed above (section 'Models based on a  $\text{CO}_2$  assimilation sub-model'),  $A_{\text{net}}$  submodels incorporate effects of air humidity and temperature, light intensity and biochemical characteristics on the one hand, and of  $C_i$  on the other hand, which depends itself on  $g_s$ . It has been much debated whether  $A_{\text{net}}$  limitation by drought is of diffusive (stomatal) or biochemical (non-stomatal) origin. The answer clearly depends on drought intensity and duration (see e.g. Grassi & Magnani 2005). Most studies have been biased by the underestimation of the diffusive resistance to  $\text{CO}_2$  beyond stomata, within the mesophyll, that uncouples  $C_i$  from  $\text{CO}_2$  concentration in chloroplast, where assimilation operates (Flexas *et al.* 2008). It is now established that diffusive limitations are much more important than biochemical limitation in conditions of mild water deficit (Keenan, Sabate & Gracia 2010). Better understanding of the way water stress reduces mesophyll conductance to  $\text{CO}_2$  should help in quantifying its role and precisising the conditions when models should incorporate effects of water stress on either mesophyll and/or biochemical parameters.

### Including hydrogen peroxide in models of $g_s$

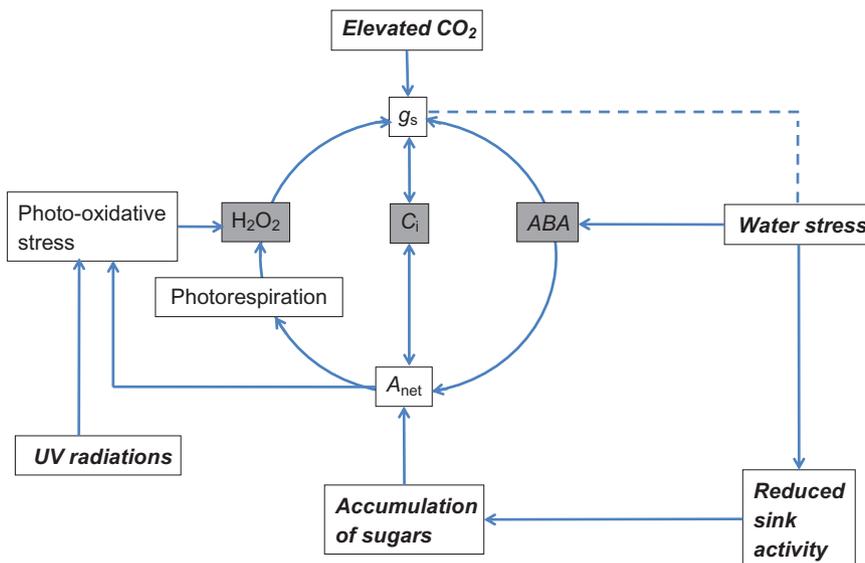
Current molecular models of guard cells functioning have not been exploited so far in the perspective of mathematical modelling of  $g_s$ , although they may provide some useful ideas. In the recent past, it has been established that ROS are essential signalling molecules that mediate *ABA*-induced stomatal closure and *ABA*-induced inhibition of stomatal opening (Yan *et al.* 2007). This is consistent with the current view of the crosstalk existing between the signalling pathways involving ROS and phytohormones in the control they exert on plant stress responses (Fujita *et al.* 2006). Among all ROS, hydrogen peroxide ( $\text{H}_2\text{O}_2$ ) emerges as the most important one considering its role in guard cell functioning and more specifically in the guard cell *ABA*-signalling network (Pei *et al.* 2000; Schroeder *et al.* 2001; Wang & Song 2008). The emerging view is one of great complexity, and there is certainly a challenging task ahead for elucidating the signalling networks in guard cells for *ABA* and  $\text{H}_2\text{O}_2$ . Meanwhile, it may appear tempting to try to design models of  $g_s$  using  $\text{H}_2\text{O}_2$  as one major entry parameter besides  $A_{\text{net}}$  and [*ABA*]. In addition to its leading role in the control of guard cell movements besides and in conjunction with *ABA*, there are several arguments in favour of using  $\text{H}_2\text{O}_2$  in future physiologically based models of  $g_s$ .

Firstly,  $\text{H}_2\text{O}_2$  concentration may provide an essential and complementary link between  $g_s$  and  $A_{\text{net}}$ , in addition to  $C_i$  and [*ABA*], which has been largely ignored so far in

$g_s$  models. The production of ROS in plants is ascribed to several potential sources, but photosynthesis represents the major one in plants (Asada 1999). A decrease in photosynthesis, or, more precisely, an increase in the imbalance between the energy entering under the form of photons and the energy used by photochemistry, like the one resulting from a decrease in  $g_s$  and  $\text{CO}_2$  supply, increases the probability of production of ROS, and especially  $\text{H}_2\text{O}_2$  (Grassmann, Hippeli & Elstner 2002). Interestingly, not only  $g_s$  and  $A_{\text{net}}$  are influencing each other through [ $\text{H}_2\text{O}_2$ ], but also [ $\text{H}_2\text{O}_2$ ] may co-regulate  $g_s$  and  $A_{\text{net}}$ , because it has been observed that  $\text{H}_2\text{O}_2$  inhibits several enzymes of the Calvin cycle (e.g. the FBPase; Charles & Halliwell 1981).

Secondly,  $\text{H}_2\text{O}_2$  production represents the converging point of several environmental factors known to influence  $g_s$  in addition to drought, such as UV radiation and sugar accumulation in leaves, the latter resulting from either reduced sink activity or elevated  $\text{CO}_2$ , because these factors are known to favour oxidative stress in leaves.  $\text{H}_2\text{O}_2$  arguably provides an opportunity to integrate into models of  $g_s$ , the influence of environmental factors that were discarded until now and that we absolutely need to consider as part of the issue of global change. For instance, UV-B radiations are expected to increase in the coming years and have been observed to reduce  $g_s$  (Paoletti 2005; Poulson, Boeger & Donahue 2006). UV-B radiations are known to favour ROS generation through their stimulating effects on peroxidases and NADPH oxidase. More specifically, it was observed that UV-B modifies  $\text{H}_2\text{O}_2$  and nitric oxide generation in guard cells (He *et al.* 2005). It may thus be hypothesized that UV-B stimulates stomatal closure via the guard cell response to  $\text{H}_2\text{O}_2$ . Atmospheric  $\text{CO}_2$  concentration is predicted to increase up to threefold since 2050 (IPCC 2007). Stomata of most species close in response to elevated  $\text{CO}_2$  concentration (Moore *et al.* 1999; Rogers *et al.* 2004; Ainsworth & Rogers 2007). But, elevated  $\text{CO}_2$  increases photosynthetic rate in the short term, while photosynthetic capacity is down-regulated in the medium/long term (Moore *et al.* 1999; Rogers *et al.* 2004; Aranjuelo *et al.* 2005; Ainsworth & Rogers 2007; Erice *et al.* 2007). Because of its potential impact on photo-oxidative stress, the short-term effects of elevated  $\text{CO}_2$  could be included in  $\text{H}_2\text{O}_2$ -based models of  $g_s$ . More generally, these observations are strong incentives in favour of more mechanistic approaches for  $g_s$  modelling, more specifically when there is a need to operate outside their empirical domain of construction, as imposed in the context of global changes.

Thirdly,  $\text{H}_2\text{O}_2$  production may lend itself to modelling. Noctor *et al.* (2002) has suggested that  $\text{H}_2\text{O}_2$  production can be modelled as a function of irradiance. Of course, such a model would have to be refined by including the exacerbating effect of sugar accumulation in leaves or sink limitation (Urban & Alphonsout 2007). Coupling models of  $g_s$  with models of carbon assimilation and carbohydrate repartition certainly represents an important objective as part of such an approach. Ideally, one should also include the effects of the scavenging enzymes or enzymatic systems. The rates of



**Figure 1.** Model of interactions between  $g_s$  and  $A_{net}$  under environmental stresses. A co-regulation of  $g_s$  and  $A_{net}$  based on abscisic acid (ABA),  $C_i$  and  $H_2O_2$  is proposed.

production of NADPH and of regeneration of ascorbate probably play an important role here. At this stage, there is no model of either ROS concentration or cell redox status that could be exploited. So, it will certainly be necessary to start by designing models of  $H_2O_2$  concentration based on simplifying hypotheses before integrating them in  $g_s$  models.

A model of co-regulation of  $g_s$  and  $A_{net}$ , including the pathways presented in this section, is proposed in Fig. 1.

### Other issues associated with the global change

In the context of global change, factors that appeared previously as minor become very important and require to be fully integrated into models (Xu & Baldocchi 2003). This is clearly the case of temperature. As air temperature is predicted to increase by a few degrees, stomatal conductance will be strongly affected (Jarvis 1976; Jones 1992). It is generally expected that  $g_s$  will globally decrease as the consequence of the increase in air temperature. Leaf temperature will increase more than expected as the consequence of the increased air temperature because of reduced cooling by transpiration when stomata close. This increase in leaf temperature will be even more marked in conditions of drought because of the negative effect of drought on  $g_s$ . Eventually, photosynthesis will be strongly reduced. That is not all: a synergetic effect between high temperature and elevated  $CO_2$  elevation has been reported, which results in down-regulation of photosynthetic capacity (Erice *et al.* 2007). So far, models of  $g_s$  are not capable to integrate the combined effect of the simultaneous increase in air temperature,  $CO_2$  concentration of the air and drought.

Models of  $g_s$  have eluded so far the question of the morphology-mediated effect of drought on  $g_s$ . In response to environmental stresses, modifications of the morphology of the plant were reported. It was observed that drought results in: (1) a decrease in the specific leaf area that leads in turn to a decrease of the evaporative surface (Assuero *et al.*

2002; Gomez-Del-Campo *et al.* 2003; Al-Khalifah *et al.* 2006); (2) a decrease of the number of leaves on new shoots (Gomez-Del-Campo *et al.* 2003) and abscission of existing leaves (Gu *et al.* 2007); (3) an increase in the root-to-shoot ratio (Assuero *et al.* 2002); and (4) modifications in vessel anatomy that favour small diameter vessels (Al-Khalifah *et al.* 2006). These adaptive strategies buffer the effects of water stress on  $g_s$  and, for that reason, should be integrated into models. An attractive way to achieve that should be to introduce whole-plant changes into a model of  $g_s$ . Here are some avenue of research: (1) intercepted light as affected by leaf area; (2) photosynthetic capacity as affected by root-to-shoot ratio; and (3) hydraulic resistance as affected by vessel anatomy (Buckley 2008).

### CONCLUSION

Modelling  $g_s$  represents a major objective and challenge for the scientific community. What is at stake in the long term is the capacity to develop an integrated view of the way interactive environmental factors influence, either directly or indirectly, carbon fixation by photosynthesis and water losses through transpiration. The capacity to develop such an integrated view conditions in turn our capacity to design models of  $g_s$  which can be used, among other objectives, for simulating the consequences of the climatic change. Roughly, two major types of models have been developed so far: models expressing  $g_s$  as a function of atmospheric factors, and models expressing  $g_s$  as a function of water availability. Considerable efforts have been made to design models of  $g_s$  of more universal value, capable to deal simultaneously with all the environmental factors. Arguably, the most advanced of them are based on the well-established role of ABA in the control of the movements of guard cells. Considering the recent advances in our understanding of the molecular bases of stomatal regulation, we advocate for the use of  $H_2O_2$  production in addition and in conjunction with ABA

concentration in future models of  $g_s$ . This should facilitate the integration of such factors as UV radiations and long-term drought, which have been more or less ignored by current models of  $g_s$ . With the same objective in mind (i.e. integrating better the complex influences of environmental factors, especially the ones associated with the global change), it would be stimulating to explore other ideas originating from the emerging molecular view of stomatal regulation. For instance, it is now well established that aquaporins play a key role in water relations and stomatal regulation (Tyerman *et al.* 1999; Johansson *et al.* 2000). Their regulation in response to environmental stresses opens promising perspectives, particularly in modelling.

While the progressive construction of a more and more complete view of stomatal regulation at the molecular level represents a source of novel ideas for the modeller, conversely the need to design more performing models of  $g_s$  represents a clear incentive for more fundamental research to be performed about the physiological determinism of guard cell functioning. Clearly, both approaches should greatly benefit from each other.

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