

Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit

R. OREN,¹ J. S. SPERRY,² G. G. KATUL,¹ D. E. PATAKI,¹ B. E. EWERS,¹ N. PHILLIPS¹ & K. V. R. SCHÄFER¹

¹School of the Environment, Duke University, Durham, North Carolina 27708, USA and ²Department of Biology, University of Utah, Salt Lake City, Utah 84112, USA

ABSTRACT

Responses of stomatal conductance (g_s) to increasing vapour pressure deficit (D) generally follow an exponential decrease described equally well by several empirical functions. However, the magnitude of the decrease – the stomatal sensitivity – varies considerably both within and between species. Here we analysed data from a variety of sources employing both porometric and sap flux estimates of g_s to evaluate the hypothesis that stomatal sensitivity is proportional to the magnitude of g_s at low D (≤ 1 kPa). To test this relationship we used the function $g_s = g_{sref} - m \cdot \ln D$ where m is the stomatal sensitivity and $g_{sref} = g_s$ at $D = 1$ kPa. Regardless of species or methodology, m was highly correlated with g_{sref} (average $r^2 = 0.75$) with a slope of approximately 0.6. We demonstrate that this empirical slope is consistent with the theoretical slope derived from a simple hydraulic model that assumes stomatal regulation of leaf water potential. The theoretical slope is robust to deviations from underlying assumptions and variation in model parameters. The relationships within and among species are close to theoretical predictions, regardless of whether the analysis is based on porometric measurements of g_s in relation to leaf-surface D (D_s), or on sap flux-based stomatal conductance of whole trees (G_{Si}), or stand-level stomatal conductance (G_S) in relation to D . Thus, individuals, species, and stands with high stomatal conductance at low D show a greater sensitivity to D , as required by the role of stomata in regulating leaf water potential.

Key-words: hydraulic model; stomatal conductance; stomatal sensitivity; vapour pressure deficit.

Abbreviations: $A_S : A_L$, sapwood-to-leaf area ratio; D , vapour pressure deficit outside of leaf boundary layer; D_s , vapour pressure deficit at the leaf surface; E , transpiration per unit of leaf area; g_{bl} , boundary layer conductance for water vapour; g_s , stomatal conductance for water vapour; G_{Si} , mean conductance for water vapour of individual trees, mostly based on single sensors; G_S , mean canopy stomatal conductance for water vapour; g_{sref} , $G_{Si ref}$, and $G_{S ref}$ are the maximum of the corresponding conductance at $D = 1$ kPa;

g_{sm} , maximum stomatal conductance for water vapour; J_S , sap flux density; k/A_L , leaf-specific hydraulic conductance; LAI, leaf area index; $\Delta\Psi_{S-L}$, water potential difference between soil and leaf.

INTRODUCTION

As the vapour pressure deficit between leaf and air (D) increases, stomata generally respond by partial closure (Lange *et al.* 1971). In most cases, stomatal conductance (g_s) decreases exponentially with increasing D (Massman & Kaufmann 1991; McCaughey & Iacobelli 1994; Monteith 1995). The stomatal closure response to increasing D generally results in a non-linear increase in transpiration rate (per unit leaf area, E) to a plateau and in some cases a decrease at high D (Jarvis 1980; Monteith 1995; Pataki, Oren & Smith 1999). By avoiding high E that would otherwise be caused by increasing D , stomatal closure avoids the corresponding decline in plant water potential (Saliendra, Sperry & Comstock 1995). It is a reasonable premise that the closure response evolved to prevent excessive dehydration and physiological damage.

It is established that the cue for the closure response is linked to E rather than D (Mott & Parkhurst 1991) and is therefore fundamentally a feedback response to water loss from the leaf tissue. The only known mechanism by which the plant can sense E is a change in the water potential (or its proxy, relative water content) of cells in the leaf. However, the identity of these cells, and the details of the signal transduction are unknown. Nevertheless, these results argue for an analysis of stomatal responses to D from the standpoint of the regulation of E (Monteith 1995) and water potential (Saliendra *et al.* 1995).

In this paper, we focus on the *sensitivity* of the stomatal response to D , where sensitivity refers to the magnitude of the reduction in g_s with increasing D . While most plants exhibit a decline in g_s with D , there is considerable variation at the intra- and interspecific levels in the sensitivity of the response (e.g. Whitehead, Okali & Fasehun 1981; Aphalo & Jarvis 1991; McNaughton & Jarvis 1991). It is commonly observed that greater sensitivity is associated with a higher g_s at low D (Kaufmann 1982; McNaughton & Jarvis 1991; Yong, Wong & Farquhar 1997). Here we test the generality of this relationship for data obtained by both porometric and sap flux methods across a variety of species

Correspondence: Ram Oren. Tel.: (919) 613 8032; fax: (919) 684 8741; e-mail: ramoren@duke.edu

and for D determined at the leaf surface (D_s) or beyond the leaf boundary layer (D). We compare this literature-based and empirical survey with theoretical predictions of stomatal sensitivity based on the role of stomata in regulating and responding to water potential.

EMPIRICAL ANALYSIS OF STOMATAL SENSITIVITY

Selection of the empirical function

To accomplish our analysis it was necessary to choose a function to describe the response of g_s to changes in D_s or D . Several have been used in the past including: e^{-bD} (Martin *et al.* 1997), b/D_s , and $bD_s^{-1/2}$ (Lloyd 1991), $1 - b_1D + b_2D^2$ (Shuttleworth 1989) $(1 + b_2D)^{-1}$ (Granier & Loustau 1994; Loustau *et al.* 1996), and Lohammar's hyperbolic function $(1 + D_s/D_o)^{-1}$ (Lohammar *et al.* 1980; Lindroth & Halldin 1986; Dang *et al.* 1997), where b , b_1 , and D_o are empirical parameters determined by least-square regression. Models use one of these functions to generate a multiplier, one of several used in multiple-constraint functions to reduce maximum g_s to estimates of actual conductance (see Schulze *et al.* 1994). The maximum conductance (g_{sm}) is determined for each species under very favourable conditions (e.g. non-limiting light and water availability, and optimum temperature, Dai, Edwards & Ku 1992). Often, instead of subjecting the entire data set to analysis using a non-linear, multivariate model, data sets are subjected first to conditional sampling, whereby data collected during adverse environmental conditions (e.g. soil drought, low temperatures) are excluded before the analysis (Bréda *et al.* 1993; Cienciala *et al.* 1994). Often, data of one variable is partitioned into intervals (i.e. made ordinal), and the model is simplified for analysis of conductance responses to continuous variation in another variable (Granier & Bréda 1996; Hogg & Hurdle 1997).

An important limitation of many of the above functions is that g_{sm} cannot be measured because it occurs near water vapour saturation where measurements of g_s and D suffer large relative errors (Arneith *et al.* 1996), and because in field measurements low D often occurs when irradiance is low (Martin *et al.* 1997). In lieu of direct measurement, g_{sm} must be extrapolated from the data. This is done by first using conditionally sampled data to generate a relationship between g_s and D , and then extrapolating to $D = 0$ (Sandford & Jarvis 1986; Monteith 1995; Martin *et al.* 1997). At low D , g_s rises sharply with decreasing D , and extrapolation beyond the data risks large errors in g_{sm} estimates. This is especially true under field conditions where the effects of D on g_s most often begin to be noticeable only as D increases to near 1 kPa (Körner 1993).

To solve the problem of extrapolating to g_{sm} , $f(D)$ in Lohammar's function is often modified to:

$$g_s = -m \cdot \ln D + b \quad (1)$$

or some variation of this function (Bréda *et al.* 1993; Granier & Loustau 1994; Lu *et al.* 1995; Arneith *et al.* 1996;

Granier *et al.* 1996a; Granier & Bréda 1996; Granier, Huc & Barigah 1996), where m and b are parameters generated in a least-square regression analysis. The relationship between conductance and $\ln D$ provides several convenient benchmarks for comparisons among conditions and species (Fig. 1a). The parameter b is a reference conductance ($b = g_{sref}$) at $D = 1$ kPa, which conveniently occurs within the range in D of most data sets. In the following, the parameter $-m$ quantifies the sensitivity of g_s to D ; it is equal to $-dg_s/d \ln D$, and is constant over the entire range of D , unlike $-dg_s/dD$. This definition of sensitivity permits comparisons independent of a specific D range.

Equation 1 is the function we selected to analyse the relationship between stomatal conductance at low D (i.e. $g_{sref} = b$) and stomatal sensitivity (i.e. $-dg_s/d \ln D = -m$). In terms of the parameters in Eqn 1, our hypothesis was that $-dg_s/d \ln D \propto g_{sref}$.

Although Eqn 1 is useful for quantifying the sensitivity of g_s to D , calculations of g_s use both E and D . Thus, modelling stomatal response to these variables will suffer from lack of independence in the explanatory variable. Monteith (1995) proposed calculations of g_s as a proportion of an extrapolated maximum conductance (g_{sm} , in this context not a physiological value) obtained from parameters of the linear portion of the relationship between $1/E$ and $1/D$, and direct measurements of either E or D . In this manner, g_s/g_{sm} may be calculated from one variable, and regressed on the other variable without incurring autocorrelation error:

$$\frac{g_s}{g_{sm}} = 1 - \frac{E}{E_m} \quad (2)$$

$$\frac{g_s}{g_{sm}} = \frac{1}{1 + [(g_{sm}D)/E_m]} \quad (3)$$

where E_m is the extrapolated maximum transpiration rate (again, not a physiological value in this context).

Although mathematically Eqn 1 does not result in a linear relationship between g_s and E as required by the Monteith analysis, it is evident that there are two approxi-

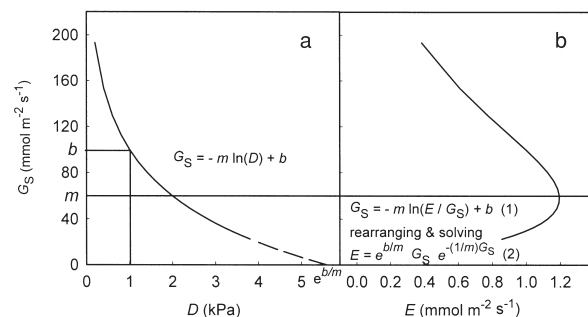


Figure 1. Schematic representation of the relationship between (a) G_s and D according to the function represented (Eqn 1), and (b) the relationship between G_s and E resulting from the function in (a). Parameter values used were: $b = 100$ mmol m⁻² s⁻¹, $-m = 58$ mmol m⁻² s⁻¹ ln(kPa)⁻¹.

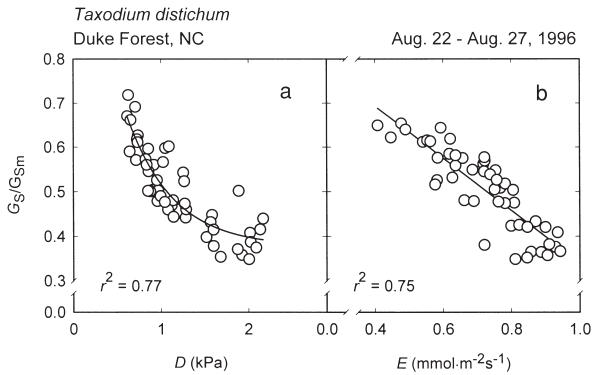


Figure 2. Average canopy stomatal conductance relative to the maximum value (G_s/G_{Sm}) based on Monteith (1995) in relation to (a) vapour pressure deficit (D) and (b) canopy transpiration per unit of leaf area (E). Data used are those presented as filled symbols in Fig. 1a.

mate linear portions in the relationship (Fig. 1b). The linear portion corresponding to high g_s range (when g_s decreases with E) is because the product $g_s \cdot e^{-g_s/m}$ is approximately linear for $g_s/m \in [1,3]$. The linear portion corresponding to low g_s range is derived by noting that, for small g_s/m , $e^{-g_s/m}$ approaches unity and $E \approx e^{b/m} \cdot g_s$. Thus, when evaluating data, a linear decrease of g_s with $\ln D$ would correspond to a statistically linear decrease of g_s with E as long as $g_s > m$, because the parameter m corresponds to g_s at which E is maximum (Fig. 1). However, if a greater range in g_s is used, g_s will curl back, showing a positive relationship with E at $g_s < m$, as has been demonstrated elsewhere (Monteith 1995; Meinzer, Hinckley & Ceulemans 1997). The term $e^{b/m}$ is the extrapolated value of D at which $g_s = 0$.

Employing the conditional sampling and analytical approach proposed by Monteith (1995; in our sap-flux-based analyses we replaced g_s with G_s to denote canopy level conductance) significantly improved the relationship between G_s/G_{Sm} and E ($r^2 = 0.75$; Fig. 2) relative to the relationship between G_s and E ($r^2 = 0.31$; Fig. 2, data from Oren *et al.* 1999). However, Monteith's approach did not improve the already tight relationship between G_s and D ($r^2 = 0.79$). Most importantly, the shapes of the responses of the relative expression of stomatal conductance (G_s/G_{Sm}) to E and D were the same as the responses of the absolute expression (G_s), reflecting that the relationship shown among the three variables in Fig. 1 is robust using either expression. This indicates that with either expression, the sensitivity of stomata to D can be quantified, and is reflective of the response to increasing E .

We proceeded with analysing stomatal responses to D in terms of Eqn 1 rather than Eqns 2 and 3 because (i) the response of stomata to D seem less influenced by the choice of G_s used in the analysis than the response to E ; (ii) it required less exclusion of data from the analysis, and (iii) data were more easily obtained from published relationships.

Stomatal sensitivity at the leaf level

To evaluate the relationship between $-dg_s/d \ln D$ and g_{sref} at the leaf level, we fit Eqn 1 to literature data from porometry-based leaf-level measurements (Table 1), and regressed with $-dg_s/d \ln D_s$ and g_{sref} . Inter-specific response of $-dg_s/d \ln D$ to g_{sref} was tight with a slope of 0.60 (Fig. 3). The log-log inset in Fig. 3 is provided in order to permit a better representation of the data at low values. Our results generalized the findings that the sensitivity of g_s to D increased with g_{sref} , regardless of whether the variation in g_{sref} were related to light (Black & Squire 1979), CO_2 (Morison & Gifford 1983), or to genetic differences among bean cultivars (Comstock & Ehleringer 1993). Similar to Morison & Gifford's (1983) findings for two C_3 and two C_4 grass species, Fig. 3 shows that a variety of species and measurement conditions produced a relatively tight, interspecific relationship between $-dg_s/d \ln D$ and g_{sref} .

Stomatal sensitivity at the whole-tree and canopy level

To test the generality and robustness of the findings, we analysed mean whole-tree and stand stomatal conductance (G_{Si} and G_s , respectively) obtained from sap flux studies. There are several challenges to scaling sap flux to conduc-

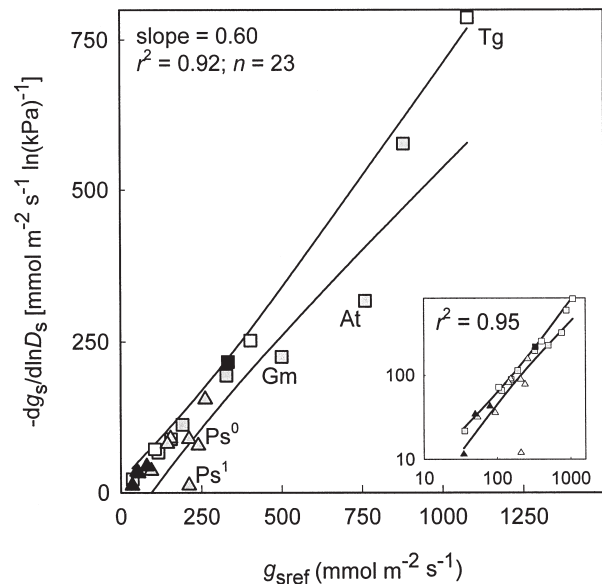


Figure 3. The sensitivity of leaf-level stomatal conductance (g_s) of individual species to increasing vapour pressure deficit at the leaf surface ($-dg_s/d \ln D_s$) as a function of the canopy stomatal conductance at $D_s = 1$ kPa (g_{sref}), with data presented in the inset on a log-log scale (r^2 was calculated after excluding the one outlier). The two axes represent the slope and intercept of the relationship $g_s = -m \cdot \ln(D_s) - b$. Lines – 99% confidence interval, dotted – $g_s = 0$ at 5.1 and 6.1 kPa (see text). Symbols: triangles – non-porous; squares, diffuse-porous; full, boreal species; shaded, temperate species; open, tropical species. Species codes are in Table 1.

Table 1. Values used for evaluating the dependency between the two parameters in the function: $g_s = -m \cdot \ln D_s + b$ at the leaf level [except *P. banksiana* (Pbb) at the branch level] as shown in Fig. 3 [where b is g_{sref} in $\text{mmol m}^{-2} \text{s}^{-1}$, m is in $\text{mmol m}^{-2} \text{s}^{-1} \ln(\text{kPa})^{-1}$, D_s is the vapour pressure deficit at the leaf surface in kPa, and $e^{b/m}$ is the extrapolated D_s where stomata are completely closed (designated as > 10 kPa for large values)]

Species	Code	b	m	$e^{b/m}$	Source
Diffuse-porous trees					
<i>Acacia</i> spp. (six species)	A6	191	113	5.4	Ullmann <i>et al.</i> (1985)
<i>Anacardium exelsum</i>	Ae	105	72	4.3	Meinzer <i>et al.</i> 1993
<i>Eucalyptus pauciflora</i>	Ep	328	194	5.4	Körner & Cochrane (1985)
<i>Gmelina arborea</i> ^b	Ga	403	252	5.0	Whitehead, Okali & Fasehun 1981
<i>Populus tremuloides</i>	Pt	333	216	4.7	Dang <i>et al.</i> 1997
<i>Tecton grandis</i> ^b	Tg	1080	787	3.9	Whitehead, Okali & Fasehun 1981
Non-porous trees					
<i>Larix x eurolepis</i>	Le	94	36	> 10	Sandford & Jarvis 1986
<i>Picea abies</i>	Pa	54	32	5.4	Falge <i>et al.</i> (1996) Lange <i>et al.</i> (1989) Zimmermann <i>et al.</i> (1988)
<i>Picea mariana</i>	Pm	35	12	> 10	Dang <i>et al.</i> 1997
<i>Picea sitchensis</i>	Ps	154	90	5.5	Sandford & Jarvis 1986
<i>Pinus banksiana</i>	Pb	50	35	4.2	Dang <i>et al.</i> 1997
<i>Pinus banksiana</i>	Pbb	80	43	6.4	Saugier <i>et al.</i> (1997)
<i>Pinus contorta</i>	Pc	211	89	> 10	Sandford & Jarvis 1986
<i>Pinus pinaster</i>	Pp	67	47	4.2	Loustau <i>et al.</i> 1996
<i>Pinus sylvestris</i> new leaf	Ps ⁰ K	144	81	5.9	Körner 1993
<i>Pinus sylvestris</i> old leaf	Ps ¹ K	262	155	5.4	
<i>P. sylvestris</i> new leaf	Ps ⁰	240	78	> 10	Sandford & Jarvis 1986
<i>P. sylvestris</i> old leaf	Ps ¹	211	12	>> 10	
Other plants					
<i>Abutilon theophrasti</i>	At	760	317	> 10	Bunce (1985)
<i>Brachypodium pinnatum</i> ¹	Bp	155	89	5.7	Wedler <i>et al.</i> (1996)
<i>Carex alba</i> ¹	Ca	116	66	5.8	Wedler <i>et al.</i> (1996)
<i>Carex flacca</i> ¹	Cf	36	22	5.1	Wedler <i>et al.</i> (1996)
<i>Datura stramonium</i>	Ds	880	577	4.6	Bunce (1985)
<i>Glycine max</i>	Gm	500	225	9.2	Bunce (1985)

^a Parameter estimates were obtained from modelled data, otherwise by interpolating data in figures from the corresponding citations.

^b Original values in mm s^{-1} , converted by a factor: 41 (for 25 °C), otherwise in $\text{mmol m}^{-2} \text{s}^{-1}$.

Code: superscript 0 indicates new foliage, and 1 indicates old foliage.

tance. These challenges originate from issues related to scaling sap flux to E and issues related to calculation of stomatal conductance from E .

Scaling

Problems in scaling sap flux to E arise from the fact that a relatively small area of sapwood is sensed in each tree, and that a particular xylem patch usually cannot be linked to a known foliage area. Commonly, estimates of weighted average flux per unit of sapwood area are related to average sapwood area per unit leaf area ($A_S : A_L$). Both averages can be taken at the individual tree level (with a sufficient quantity of sensors, as demonstrated by Olbrich 1991; and an accurate estimate of tree leaf area), or, more often, at the population level (Oren *et al.* 1998a). Although the effect of spatial variability in sap flux on whole-tree transpiration estimates have been addressed extensively (see Oren *et al.* 1998a), not accounting for the variability in $A_S : A_L$ may influence our ability to test the hypothesis

using sap-flux-scaled conductance, and must be explicitly addressed.

The $A_S : A_L$ changes systematically: increasing as the distance between the sensor height and base of crown increases (Waring, Schroeder & Oren 1982), as evaporative demand increases (Oren, Werk & Schulze 1986; Mencuccini & Grace 1995), and as hydraulic conductance decreases with growth rate (see Margolis *et al.* 1995). Thus, in the absence of detailed information on $A_S : A_L$ of individual trees, evaluation of the responses of stomata to the environment can be made based on estimating the population G_S , but not estimating G_{Si} of leaves supplied by each measured xylem patch. However, after the systematic radial and azimuthal variations in sap flux are removed, large differences in flux among xylem patches can be associated with intertree variation (Martin *et al.* 1997; Schäfer 1997). Because the variation in $A_S : A_L$ is small relative to the variation in flux – the relationship between leaf and sapwood area commonly has a zero intercept, and most data for large trees is within 20% of average leaf-to-sapwood area

ratio (see Jarvis 1976; and Margolis *et al.* 1995) – using a population-level $A_S : A_L$ to estimate individual tree E and G_{Si} would not introduce large artificial variation in G_{Si} . Most importantly for testing the hypothesis that $-dg_s/d \ln D$ is proportional to g_{sref} , an error in estimation of $A_S : A_L$ will affect both variables similarly, thus not affecting the conclusions.

Estimating G_{Si} and G_S

Sap flux in the xylem of trees is increasingly used to estimate G_S on the basis of equations in Monteith & Unsworth (1990). These equations use D only, or D in combination with a radiation term, as necessary (Köstner *et al.* 1992; Granier & Loustau 1994; Granier *et al.* 1996b). One assumption when using sap flux to estimate G_S is that (1) weighted average sap flux in the sapwood multiplied by $A_S : A_L$ is equal to E , i.e. the diffusion of the transpiration signal by depletion and replenishment of stem-stored water is relatively small. An additional assumption when the radiation term is ignored is that (2) conductance of the leaf boundary layer (g_{bl}) is large relative to g_s .

As a result of the water storage capacity in tissues above the sensor, sap flow can be decoupled from transpiration (Čermák, Huzulák & Penka 1980; Schulze *et al.* 1985; Tyree & Yang 1990; Loustau *et al.* 1996; Williams *et al.* 1996; Phillips & Oren 1998), confounding the quantitative link between G_S and environmental driving variables. Here, we used published and unpublished G_S data corrected when necessary for the effect of storage or selected for conditions in which storage has a small effect on E (Table 2).

The second assumption, that $g_{bl} \gg g_s$, is generally considered true for narrow leaves (Whitehead & Jarvis 1981; Landsberg 1986). In this case, D is considered approximately equal to leaf-to-air vapour pressure difference, and can be calculated from measurements within the canopy volume but outside of the leaf boundary layer. Often, g_{bl} is calculated using windspeed and a characteristic leaf dimension (e.g. Jones 1992) and the second assumption is tested by comparing the calculated g_{bl} to a 'typical' value of stomatal conductance of the same species.

The amount of variability in g_s explained by D approaches that explained by D_s as g_{bl} increases (Sandford & Jarvis 1986; McNaughton & Jarvis 1991). Thus, for example, in comparing the relationship between g_s and D_s with that between G_S and D , Meinzer *et al.* (1993) found that at 1 kPa, $g_s = 0.85 \cdot G_S$, but that $-dg_s/d \ln D_s = 0.67 \cdot -dG_S/d \ln D$. Although at low D the conductance obtained with a porometer was similar to that from sap flux, the sensitivity of conductance at both leaf and branch levels to increasing D was less than the sensitivity to increasing D_s at the leaf level, reflecting the effects of relatively low g_{bl} . As emphasized by McNaughton & Jarvis (1991), despite the unfortunate use of D rather than D_s , there is little difference between the two variables in well-coupled canopies of small-leaved forests. In other forests, as shown by Meinzer *et al.* (1993), stomatal sensitivity to D_s will be underestimated when it is related to D , but D appears to account for

a large proportion of the variation in the combined stomatal and leaf boundary-layer conductance, again providing a useful empirical relationship. In forests in which the air in the canopy volume is well mixed with the air above the canopy (Jarvis, Landsberg & James 1976; Parker 1995), one point for measurements of air temperature and relative humidity is sufficient to provide D for calculating G_S (e.g. Sullivan, Bolstad & Vose 1996). Thus, despite several sources of uncertainty in estimating conductance from sap flux measurements, variations in G_S and G_{Si} have been unambiguously linked to environmental variables, including D (Granier & Loustau 1994; Pataki *et al.* 1998; Pataki, Oren & Tissue 1998; Oren *et al.* 1998b), and can be used to compare G_S response to D among species (Granier *et al.* 1996b; Pataki *et al.* 1998).

Testing the hypothesis

From our own previous sap flow studies (see Table 2), we tested the hypothesis of stomatal sensitivity to D on 14 species: six from the Duke Forest, four from Medicine Bow Mountains in Wyoming (Pataki *et al.* 1999), two from Germany (Schäfer, Oren & Tenhunen, unpublished), and two from the Mojave desert (Pataki, unpublished). As expected, individuals within each species, including ring- and diffuse-porous deciduous broadleaf species, non-porous conifers, and desert shrubs (the latter shown only in Table 2) showed an increase in stomatal sensitivity ($-dG_{Si}/d \ln D$) in relation to $G_{Si ref}$ (Fig. 4a). Except for three cases, r^2 was > 0.6 ($P > 0.05$), and average r^2 for all analyses ($n = 16$) was 0.75.

To the data in Fig. 4a, we added data on species with too few replicates to permit intraspecific analysis, and data from other sap flux studies from the literature (Table 2). These data include tropical trees (Granier, Huc & Colin 1992; Granier *et al.* 1996). The combined data are shown as a species-level relationship between mean $-dG_S/d \ln D$ and mean $G_{S ref}$ (Fig. 4b). More sap-flux-based data points fell outside the 99% confidence interval than in the evaluation of the porometric data. Nevertheless, for the mesic species, the overall slope of $-dG_S/d \ln D$ versus $G_{S ref}$ was 0.59 and very close to the 0.60 obtained from porometric data (Fig. 3). The similarity in slope of $-dG_S/d \ln D$ versus $G_{S ref}$ at the species-level obtained with sap flux-scaled conductance (Fig. 4b) to that obtained with porometry (Fig. 3) suggests a minor influence of g_{bl} on the relationship. Values for the same species are always lower than leaf-level values, as would be expected given that, leaf-level measurements often represent sun foliage of higher maximum conductance.

As Figs 3 and 4 indicate, the hypothesis that there is a proportionality between stomatal conductance at low D and the sensitivity of the closure response is strongly supported. The relationship is robust, showing little sensitivity to methodology, site of the D measurement, and magnitude of the boundary layer conductance. The relationship was also insensitive to whether the response was measured at low versus high light (small symbols in Fig. 4b). There was

Table 2. Values (means) used for evaluating the dependency between the two parameters in the function: $G_s = -m \cdot \ln D + b$ using sap flux measurements as shown in Fig. 4 [where b is G_{sref} in $\text{mmol m}^{-2} \text{s}^{-1}$, m is in $\text{mmol m}^{-2} \text{s}^{-1} \ln(\text{kPa})^{-1}$, D is the vapour pressure deficit in the canopy volume in kPa, and $e^{b/m}$ is the extrapolated D where stomata are completely closed]

Species	Code	n	b	$-m$	$e^{b/m}$	LAI	Source
Diffuse-porous							
<i>Acer rubrum</i>	Ar	6	88	67	3.7	0.1/4.0	*Oren & Pataki
<i>Anacardium exelsum</i> ^a	Ae	1	89	45	7.2		Meinzer <i>et al.</i> 1993
<i>Fagus sylvatica</i>	Fs	9	88	92	2.6	5.0/6.2	*Schäfer, Oren & Tenhunen
<i>Goupia glabra</i> ^{a,c}	Gg	6	194	91	8.4	3.7	Granier, Huc & Colin 1992
<i>Liquidambar styraciflua</i>	Ls ¹	3	98	64	4.6	0.4/4.0	*Oren & Pataki
	Ls ²	7	63	47	3.8	0.5/5.0	Phillips, Oren & Zimmermann 1996
	Ls ³	5	94	64	4.3	0.6/3.3	*Pataki & Oren
<i>Liriodendron tulipifera</i>	Lt	5	97	61	4.9	0.4/3.3	*Pataki & Oren
<i>Populus termuloides</i>	Pt	5	51	23	9.2	2.6/3.3	Pataki, Oren & Smith 1999
<i>Simarouba amara</i> ^{a,c}	Sa	5	112	76	4.4	3.5	Granier, Huc & Colin 1992
Tropical forest ^{a,c}	T6		53	30	5.9	(8.6)	Granier, Huc & Barigah 1996
<i>Caryocar glabrum</i>		1					
<i>Cassipourea guianensis</i>		1					
<i>Eperua falcata</i>		2					
<i>Eperua grandifolia</i>		2					
<i>Hirtella glandulosa</i>		1					
<i>Lecythis idatimon</i>		1					
Ring-porous							
<i>Carya tomentosa</i>	Ct ¹	1	115	80	4.2	1.3/4.0	*Oren & Pataki
	Ct ³	6	44	37	3.2	1.4/3.3	*Pataki & Oren
<i>Fraxinus americana</i>	Fa	2	73	51	4.2	0.1/3.3	*Pataki & Oren
<i>Quercus alba</i>	Qa ¹	6	18	13	4.1	2.5/4.0	*Oren & Pataki
	Qa ²	9	18	10	6.0	3.1/5.0	Phillips, Oren & Zimmermann 1996
	Qa ³	3	29	26	3.1	0.3/3.3	*Pataki & Oren
<i>Quercus falcata</i>	Qf	1	130	84	4.7	0.1/4.0	*Oren & Pataki
<i>Quercus petraea</i> ^{b,c}	Qp ¹	9–14	71	43	5.2	6.0	Granier & Bréda 1996
	Qp ₁ ¹		50	29	5.6		
	Qp ¹	5	50	36	4.0	1.2/6.2	*Schäfer, Oren & Tenhunen
<i>Quercus rubra</i>	Qr	1	139	86	5.0	0.5/3.3	*Pataki & Oren
<i>Quercus velutina</i>	Qv	1	126	107	3.2	0.1/4.0	*Oren & Pataki
Non-porous							
<i>Abies amabilis</i> ^{b,c}	Aa	1	73	42	5.7	9.4	Martin <i>et al.</i> 1997
<i>Abies lasiocarpa</i>	Al	5	12	6	6.2	5.7/9.5	Pataki, Oren & Smith 1999
<i>Picea abies</i> ^{b,c}	Pa	8	17	11	4.7	(5.6)	Lu <i>et al.</i> 1995
<i>Pinus contorta</i>	Pc	5	38	21	6.1	2.9/9.5	Pataki, Oren & Smith 1999
<i>Pinus flexilis</i>	Pf	5	39	23	5.6		Pataki, Oren & Smith 1999
<i>Pinus pinaster</i> ^{b,c}	Pp ¹	10	138	99	4.0	2.3	Granier & Loustau 1994
	Pp ₁ ¹		76	52	4.3		
<i>Pinus pinaster</i> ^{a,c}	Pp ²	8	167	82	7.7	2.3	Granier <i>et al.</i> 1996a
<i>Pinus sylvestris</i> ^{b,c}	Ps	5	111	75	4.4	2.9	Granier <i>et al.</i> 1996b
	Ps ₁		60	40	4.5		
<i>Taxodium distichum</i>	Td	10	67	39	5.6	2.2	Oren <i>et al.</i> 1999
Desert shrubs							
<i>Ephedra nevadensis</i>	En	10	357	147	>11		*Pataki
<i>Larrea tridentata</i>	Lt'	9	161	63	>12		*Pataki

Parameters were: ^a interpolated from data in figures from the corresponding citations, or ^b provided by the authors, otherwise estimates were calculated from available data.

^c Original values in mm s^{-1} , converted by a factor: $41/\text{LAI}$ (for 25°C) to mmol m^{-2} leaf area s^{-1} (Percy, Schulze & Zimmermann 1989).

n , sample size; *, unpublished; LAI, leaf area index (or LAI_i/LAI for mixed stands); a code with the subscript '1' designates global radiation of 200 W m^{-2} , while all other measurements represent conditions of high global radiation or non-limiting light.

remarkable consistency across mesic species of diverse growth form and habitat in the slope of the relationship between sensitivity ($-dg_s/d \ln D$) and g_{sref} . This slope was approximately 0.6 for the mesic adapted species.

Although there was a remarkable convergence in stomatal response among species, there were some noteworthy exceptions. Individuals of the two desert species formed tight relationships between $-dg_s/d \ln D$ and g_{sref} ($r^2 > 0.95$;

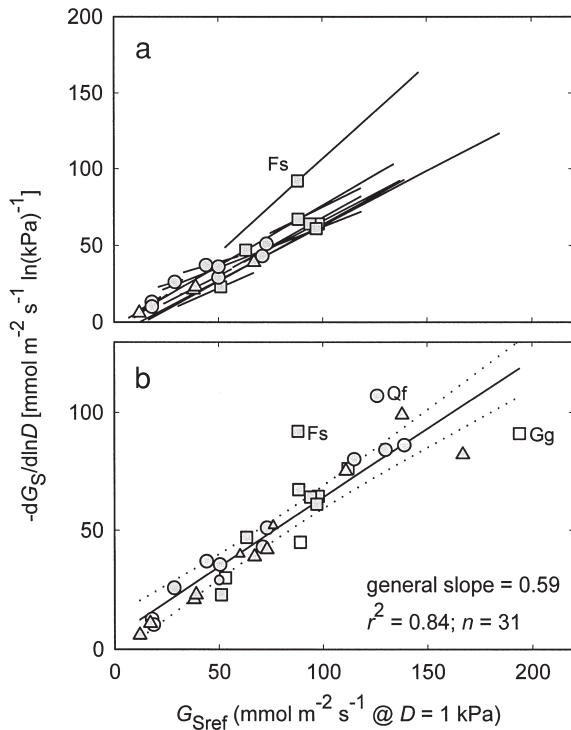


Figure 4. (a) The sensitivity of average stomatal conductance of individual crown patches to increasing vapour pressure deficit outside the leaf boundary layer ($-dG_s/d \ln D$) as a function of the canopy stomatal conductance at $D = 1$ kPa (G_{Sref}). The two axes represent the slope and intercept of the relationship $G_s = -m \cdot \ln(D) - b$. Each line represents a least-square fit to the data of one species, for which the symbol represents the means ($-dG_s/d \ln D$, and G_{Sref}). (b) As in (a), but showing means only. Lines: full, least-square fit through the entire data not forced through the origin; dotted, 99% confidence interval. Symbols: triangles, non-porous; circles, ring-porous; squares, diffuse-porous; small, low irradiance; shaded, temperate species; open, tropical species. Species codes in Table 2.

slope = 0.42 and 0.38 for *Ephedra nevadensis* and *Larrea tridentata*, respectively; see Table 2), but their slopes were significantly less ($P < 0.01$) than the 0.59 for the mesic species (Fig. 4b).

Among the mesic species, *Fagus sylvatica* (Fs in Fig. 4a) exhibited greater sensitivity than the other species. *Fagus sylvatica* was the only species represented by individuals deliberately selected to represent a wide range in tree height within a single stand. The results indicate that, even under conditions of light saturation, shorter trees developed in shade (those with higher G_{Sref}) have more sensitive stomata than can be expected based on the general response in Fig. 4a, but that stomatal sensitivity of tall trees is close to the general response as expected given their lower G_{Sref} . There was also a tendency ($P > 0.05$) for the stomata of ring-porous species to be more sensitive to D than would have been expected based on their G_{Sref} . For example, populations of two ring-porous species from a bottomland forest (*Carya tomentosa* and *Quercus alba*, Pataki & Oren, unpublished; see Table 2), showed a greater

stomatal sensitivity than co-occurring diffuse-porous species. Furthermore, a bottomland population of *Q. alba* (Qa³ in Table 2) showed a greater sensitivity than an upland population of this species (Qa¹; Oren & Pataki, unpublished; Phillips, Oren & Zimmermann 1996). In addition, the sensitivity of individuals in the bottomland populations of *C. tomentosa* and *Q. alba* (Ct³ and Qa³ in Table 2) increased less with G_{Sref} than all other species.

THEORETICAL ANALYSIS OF STOMATAL SENSITIVITY

We compared the empirical analysis of stomatal sensitivity with a theoretical analysis based on the role of stomata in regulating and responding to E and water potential. Stomatal conductance and D are coupled to leaf water potential (Ψ_L) under steady-state conditions by the following relationship:

$$g_l = (k/A_L) \cdot (1/D) \cdot (\psi_s - \psi_L) \quad (4)$$

where g_l is leaf conductance to water vapour (g_{bl} and g_s in series), Ψ_s is soil water potential, and k/A_L is the leaf-specific hydraulic conductance of the soil-to-leaf pathway (flow rate per $\Delta\Psi_{s-L}$ per leaf area).

We used Eqn 4 to predict the relationship between g_s and D . We assumed that g_l has an upper limit defined by a maximum physiological g_s (g_{sm}) as set by stomatal density and maximum aperture. We assigned g_{sm} , g_{bl} , k/A_L , Ψ_s , and Ψ_L . We assumed perfect regulation of a constant Ψ_L with respect to D . Unless noted, we chose water potentials so that $\Delta\Psi_{s-L} = (\Psi_s - \Psi_L) = 1$ MPa. It is important to note that our analysis is valid for any Ψ_s or Ψ_L ; the assumption is simply that Ψ_s and Ψ_L remain constant as D varies over the short-term. The g_{sm} and k/A_L were chosen to give values of E and g_s in the physiological range. When $g_s > g_{sm}$, we set g_s equal to g_{sm} and re-solved the equation for Ψ_L which in this case would be above (less negative than) the regulated value. For $g_s < g_{sm}$, all variables on the right side become constant except for D , and g_l is proportional to $1/D$. There is no assumption regarding light saturation of g_s , only that stomata are regulating leaf water status.

The solid circles in Fig. 5a show the predicted relationship between E and D for $g_{sm} = 500$ and $g_{bl} = 1000$ mmol s⁻¹ m⁻². E increases linearly with D while leaf water potential is above the regulated threshold and $g_s = g_{sm}$. E becomes constant when the regulated Ψ_L threshold is reached and maintained by reduction in g_s below g_{sm} . To test the relationship between $-dg_s/d \ln D$ and g_{Sref} we generated different g_{Sref} values by selecting different values for k/A_L . We applied the constraint that $g_{Sref} < g_{sm}$. This was acceptable because as noted previously it is rare to observe a constant g_s even at low D indicating that g_{sm} is seldom achieved *in vivo*. To calculate $-dg_s/d \ln D$, we had to reckon with the fact that this value is not constant over the entire range of D in the theoretical model. We will return to conflicts between theory and observation below. To allow comparison, we calculated $-dg_s/d \ln D$ as $-\Delta g_s/\Delta \ln D$ for a series of ΔD 's (1 to 3, 1 to 4 and 1 to 5 kPa).

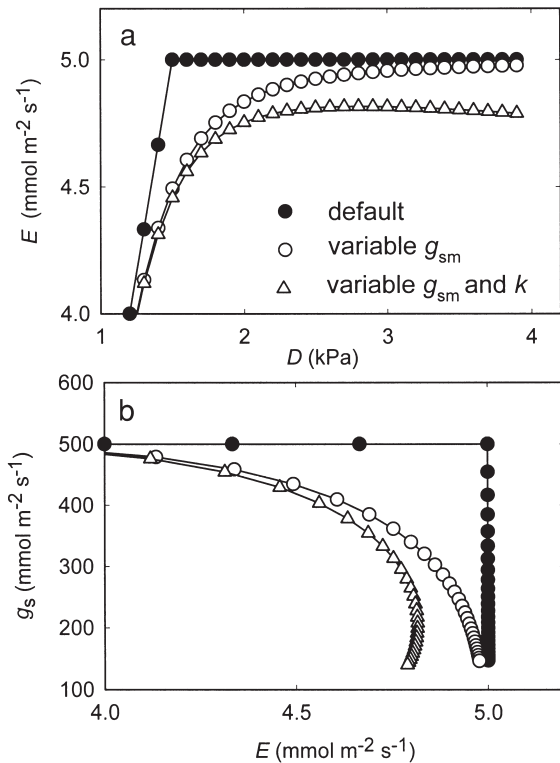


Figure 5. (a) Transpiration rate (E) versus vapour pressure deficit (D) predicted by the hydraulic model based on Eqn 4. The default relationship (solid circles) represents uniform g_{sm} . The variable g_{sm} relationship (open circles) represents patchy g_{sm} across the foliage surface where the mean g_{sm} is the same as the default, but with 33% coefficient of variation (a normal distribution of g_{sm} was assumed). The variable g_{sm} and k relationship (open triangles) represents the spatial variation in g_{sm} with a 3% decline in k/A_L as D increased from 1 to 4 kPa. (b) Transpiration rate (E) versus stomatal conductance (g_s) for the same conditions in (a).

The theoretical relationship between $-\Delta g_s/\Delta \ln D$ and g_{sref} for each ΔD range is shown in Fig. 6a for $g_{sm} = 500$ and $g_{bl} = 1000$ mmol s⁻¹ m⁻². The slope decreases from 0.68 to 0.53 as the D range broadens from 1–3 to 1–5. The D range of 1–4 encompasses the range over which $-\Delta g_s/\Delta \ln D$ was calculated for most of the field data. The theoretical slope for this ΔD range is 0.59, nearly identical with the empirical value of approximately 0.60, for mesic species in Figs 3 and 4. The 1–4 kPa ΔD range will be assumed for the following analyses except where noted.

It is informative to determine the sensitivity of the theoretical slope to the constants k/A_L , $\Delta \Psi_{S-L}$, and g_{bl} . Changing the value of k/A_L and $\Delta \Psi_{S-L}$ simply moves data points along a given line but does not alter the slope. This also means that the relationship is independent of tree height since changes in height would alter k/A_L and the portion of $\Delta \Psi_{S-L}$ that was available to drive water flow. Thus, the deviant trend observed for *Fagus sylvatica* (Fig. 4a) trees of different height may be due to other factors (see below).

The influence of g_{bl} on the slope is shown in Fig. 6b. As g_{bl}/g_{sm} increases from 0.5 to 10, the slopes decrease from 0.64 to 0.55 indicating a relatively minor influence of g_{bl} on the analysis. A lower g_{bl}/g_{sm} requires a greater stomatal response (greater sensitivity) to keep E and $\Delta \Psi_{S-L}$ constant as required by perfect regulation of leaf water potential.

The assumption that k/A_L and Ψ_L remain constant with respect to D can be relaxed to test their influence on the analysis. The k/A_L could decrease as D is increased because of xylem cavitation or changes in leaf mesophyll physiology. The result is to increase the stomatal sensitivity to D (at a given g_{sref}), because as k/A_L decreases, a greater stomatal response is required to keep E and $\Delta \Psi_{S-L}$ constant. However, allowing k/A_L to decrease by 20% between $D = 1$ and $D = 4$ caused only a slight increase in the slope from 0.59 to 0.61. The Ψ_L could increase as D is increased if the stomatal closure was not sufficient to perfectly offset a reduction Ψ_L . For example, a 20% increase in $\Delta \Psi_{S-L}$ from $D = 1$ to $D = 4$ (resulting from a drop in Ψ_L) caused the slope to decrease from 0.59 to 0.55.

The model is also consistent with the shallower slope of approximately 0.4 observed for the two desert species (Table 2) if two adjustments are made that reflect their desert habitat and greater drought tolerance. Broadening the ΔD range from 1–4 kPa to 1–5 kPa better represents the environmental range in D during the Mojave desert

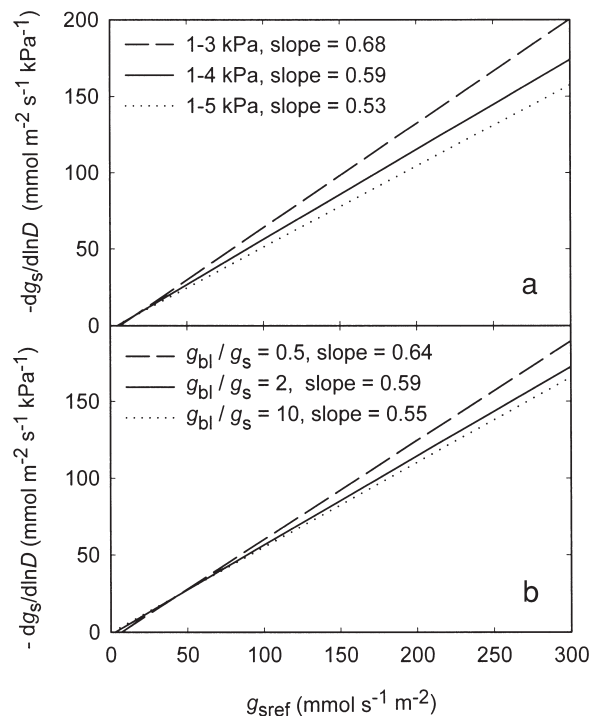


Figure 6. (a) The sensitivity of stomatal conductance ($-\Delta g_s/\Delta \ln D$) versus stomatal conductance at $D = 1$ kPa predicted by the hydraulic model based on Eqn 4. The sensitivity is shown for three ΔD ranges. (b). Same as (a), but sensitivity for $\Delta D = 1-4$ kPa shown for three values of g_{bl}/g_{sm} .

measurements. As shown in Fig. 6a, this decreases the theoretical slope from 0.59 to 0.53. A further flattening of the slope would result if these desert species exhibited less strict regulation of Ψ_L with increasing D compared to mesic species. Given the drought tolerance of desert plants this seems likely, especially under conditions of ample soil moisture such as was the case during the El Niño year of 1998 when the measurements were made. According to the model, a 94% increase in $\Delta\Psi_{S-L}$ would be necessary as D increased from 1 to 5 kPa to bring the theoretical slope to 0.41 and near the empirical value for the desert species.

The model can be used in a similar manner to generate hypotheses concerning the more subtle deviations seen among the mesic species in Fig. 4. For example the tendency towards greater sensitivity in *Fagus sylvatica* and the ring-porous trees may be a result of a greater loss of conductivity at high D in these species as compared to others. Differences in g_{bl} may also be involved since the leaf dimensions of several of the ring porous species were larger than some of the co-occurring diffuse-porous species, and a lower g_{bl} requires a more sensitive stomatal closure response (Fig. 6b). Differences in D range (Fig. 6a) were probably not responsible since the mesic species in Fig. 4b were measured over a similar range.

The theoretical analysis suggests that the empirical relationship seen in Figs 3 and 4 is a reflection of the essentially self-evident role of the stomatal response in regulating plant water status. According to the simplest version of the model, $g_l \cdot D = E$ is constant. To the extent that g_{bl} determines g_l , the higher g_s is at low D , the lower it must fall for a given step increase in D if it is to maintain E constant.

Theory versus observation

Despite the successful prediction of the model for the slope of the $-dg_s/d \ln D$ versus g_{sref} relationship, there are a number of points where it departs from reality. A relatively trivial one is that it does not predict a linear relationship between g_s and $\ln D$ as is often observed empirically and modelled in Eqn 1. However, over the moderate to high D (> 1.5 kPa) where much of the data exists, the scatter can hide the rather subtle distinction between the two models. Furthermore, Eqn 1 can be faulted for predicting g_s to reach zero at D near the usual environmental maximum (Fig. 1); a result that has never been observed to our knowledge, or predicted from Eqn 4.

A more important shortcoming of the theoretical relationship is its prediction of a constant E as g_s is declining (Fig. 5a, solid circles). In this case, when g_s is plotted versus E as suggested by Monteith (1995) there is no relationship (Fig. 5b, solid circles). As already mentioned, for most data sets E increases to a plateau as D is maximized, and can decrease at high D (Jarvis 1980; Pataki *et al.* 1999).

A reasonable modification to the model can account for this discrepancy. In this modification, we assumed spatial variation in g_{sm} across the surface area of the foliage. In the model this was represented by a mean $g_{sm} \pm$ a standard

deviation partitioned among n units of equal foliage area. This could represent variation between aeroles of a leaf, different leaves, or branches in the crown. As shown in Fig. 5 (open circles) this results in a more realistic relationship between g_s , E and D , although none of the g_s versus E relationship is linear as suggested by Monteith (1995). The change in the model results from the gradual triggering of stomatal regulation across the canopy as the threshold leaf water potential is reached. The same result is seen if k/A_L to different foliage units of the canopy is varied instead of g_{sm} (results not shown).

In a final refinement, the model with variable g_{sm} was combined with the effect of declining k/A_L with D . The result is to produce a reduction in E at high D as seen in some data sets. This causes the E versus g_s relationship to 'curl back' at high D as remarked by Monteith (1995; as also seen in Fig. 1). The effect of these more realistic versions of the model on the slope of $-dg_s/d \ln D$ versus g_{sref} is trivial as long as $g_{sref} < \text{mean } g_{sm}$.

DISCUSSION

Our empirical analysis of stomatal sensitivity to D revealed a consistent relationship between g_s at low D and the sensitivity of the closure response to increasing D . In terms of the empirical function used in the analysis (Eqn 1), the slope of $-dg_s/d \ln D$ versus g_{sref} was approximately 0.60 for a wide variety of relatively mesic species despite variation in growth form, habitat, methodology, potential variation in g_{bl} , and location of D measurement (leaf surface versus mixed air, Figs 3 & 4). The theoretical analysis suggested that this relationship is consistent with the role of stomata in regulating E and water potential. According to theory, as long as stomata are regulating leaf potential near a constant value, a slope near 0.60 is expected with variation around that value depending on ΔD range, g_{bl} , and changes in hydraulic conductance associated with D (Fig. 6). The shallower slope of the desert species (0.40) is consistent with a broader ΔD range for the desert habitat, and the hypothesis that these drought-tolerant species exhibited less strict regulation of leaf water potential as D increases.

Data would deviate from the model when stomata are not responding to changes in leaf water potential. These conditions would include sufficiently high k/A_L or sufficiently low D such that $g_s = g_{sm}$. Low light might also be expected to cause deviations from the predicted slope. However, the data indicated otherwise (Fig. 4b, Table 2), suggesting that stomata continued to regulate leaf water status even in non-saturating light.

Our analysis implies that the interpretation of stomatal responses to humidity will benefit from a better understanding of the feedback loop between g_s and water potential. However, the model we present is a gross simplification of this feedback. The plant 'solves' the relationships in Eqn 4 stoma by stoma and aerole by aerole across the leaf surface, and generally under non-steady-state conditions. A change in E must cause a change in water potential of the

sensing cells, the change in water potential must be converted into a chemical and/or hydraulic signal moving to the guard cells, and the arrival of the signal must trigger the adjustment of the aperture. Each step involves a time lag, a sensitivity, and a hysteresis that may differ for increasing versus decreasing E . Each step may operate independently in different parts of the leaf or canopy. The canopy or leaf-averaged value of E , g_s and water potential can mask the considerable spatial and temporal variation required by this feedback loop. We can state without paradox that g_s can respond to E and leaf water potential even though the steady-state values of both of these variables may be constant at the leaf or canopy level.

Monteith (1995) emphasized the linearity of the g_s versus E relationship seen in some data sets, and implied that this supported a mechanistic link between the two. His analysis is misleading on this point because Eqn 4 indicates that a non-linear relationship between g_s and E , or no relationship at all, is consistent with a mechanistic link involving leaf water status (Fig. 5). Although Monteith's approach may be useful for testing effects of autocorrelation and for some pragmatic modelling purposes, it is not predicted from any simple mechanistic relationship between g_s and E . It is doubtful that the extrapolated values of E_m and g_{sm} in Eqns 2 and 3 have a physiological significance that could not be captured more directly by Eqn 4 or some modification thereof.

The application of Eqn 4 to the g_s versus D relationship suggests that the most appropriate function relating the two (assuming perfect leaf water potential regulation and $g_s < g_{sm}$) would be $g_s = b/D^c$ where $c = 1$ for infinite g_{bl} . This function is similar to several used in the past (e.g. Lloyd 1991). Our selection of Eqn 1 for the empirical analysis was made for practical purposes as described, and we emphasize its lack of mechanistic underpinning relative to the predictions of Eqn 4. Nevertheless, it is useful because it allows the quantification of stomatal sensitivity to D on the basis of measured stomatal conductance at low D as opposed to extrapolated estimates.

The theoretical model explicitly accounts for the influence of hydraulic conductance on the g_s versus D response as has been shown experimentally (Saliendra *et al.* 1995). Although we show that a decline in hydraulic conductance with increasing D could explain the reduction in E at high D , we note that any 'over-expression' of the closure signal or instability in the signal transduction pathway at high D could also cause the same phenomenon, in which case the leaf water potential would increase at high D (Schulze *et al.* 1972; Cowan 1995). Instability in the feedback response could be associated with the heterogenous stomatal closure sometimes observed in response to high D (Mott & Parkhurst 1991). Previous speculation of a true feedforward response of g_s to D lacks strong experimental support (Meinzer 1993). Although the decrease in E with D may mimic a feedforward response (Franks, Cowan & Farquhar 1997) with respect to bulk leaf water potential and the spatial and temporal average E that is measured, the response is likely to be one of complex feedback to E and

water potential at smaller spatial and temporal scales (Cowan 1995).

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