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Carbon-water balance and patchy stomatal conductance

Received: 15 May 1998 / Accepted: 14 October 1998

Abstract Stomata govern carbon-water balance by simultaneously controlling photosynthesis (A) and transpiration (E). It is unclear how patchy stomatal conductance influences this control. Cowan and Farquhar showed that for a given water supply available during a fixed time interval, carbon gain is maximized by a pattern of stomatal behavior that keeps the partial derivative of A with respect to E constant. This result implies that spatially uniform stomatal conductance is optimal (provided photosynthetic performance and environmental conditions are spatially uniform), so patchy stomatal conductance should be detrimental to carbon-water balance. However, these results required that the curvature of A versus E be uniformly negative. Using mathematical arguments and computer modeling, we show that (1) this caveat is violated under some environmental conditions, (2) water-use efficiency (A/E) is nearly unaffected, and can actually be improved, by patchiness under these conditions, and (3) patchiness has most often been observed under conditions similar to these. These results imply that under many conditions, patchiness may not significantly influence carbon-water balance, consistent with recent work suggesting patchiness may be common but unobserved. Additionally, we discuss implications of these results that muddle the definition of ‘optimal’ in the context of plant gas exchange in some situations, and extend the work of Cowan and Farquhar under conditions causing positive curvature in A versus E .

Key words Patchy · Stomata · Optimal · Boundary layer · Water-use efficiency

Introduction

Groups of stomata in adjacent areas of a leaf often respond differently from one another to certain environmental stimuli. These patches vary in size from dozens to thousands of stomata and are usually delimited by veins. The conductance of each patch may oscillate independently of other patches or may be temporally stable. This phenomenon, which we term ‘patchy stomatal conductance’ has been documented in response to low humidity (Beyschlag et al. 1992; Mott et al. 1993; Cardon et al. 1994), water stress (Downton et al. 1988), changing photon flux density (PFD; Eckstein et al. 1996), and exogenous abscisic acid (ABA; Terashima et al. 1988; Daley et al. 1989; Mott 1995), and has several important implications (for reviews, see Terashima 1992; Pospisilova and Santrucek 1994, 1997; Weyers and Lawson 1997; Beyschlag and Eckstein 1998; Mott and Buckley 1998). Much of the recent work on this phenomenon has focused on artifactual changes in the apparent photosynthetic demand curve (A vs c_i) calculated by gas exchange (Terashima et al. 1988; Farquhar 1989; Cheeseman 1991; Mott 1995; Buckley et al. 1997). Also under study are the mechanisms, not yet identified with certainty, that produce patchiness (Haefner et al. 1997; Mott et al. 1997; Mott and Buckley 1998).

Yet another question, which has received little attention thus far, is whether patchy stomatal conductance affects carbon-water balance of a plant. Patchiness appears to be linked with plant responses to factors associated with detrimental shifts in water balance (e.g., soil water stress, increased evaporative demand, changing PFD, and applied ABA), so a reasonable a priori hypothesis is that patchy stomatal conductance helps to conserve water. However, as will be discussed below, this is not believed to be the case under most conditions. Patchy stomatal conductance may also be an unavoid-

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able consequence of the hydraulic architecture of stems and leaves – merely a manifestation of spatial and temporal variation in the kinetics of responses to changes in water supply to different regions of a leaf. Even if this is the case, one would expect patchiness to occur less readily in conditions that increase its detrimental impact, if any mechanisms exist that can even marginally control its occurrence. To explore the adaptive (or maladaptive) significance of patchy stomatal conductance under conditions where it is known empirically to occur, it is necessary first to determine the magnitude and nature of its effects on carbon-water balance under various environmental conditions.

Stomata influence carbon-water balance through the trade-off between CO_2 uptake (assimilation, A) and water loss by evaporation (transpiration, E). An optimal pattern of stomatal behavior in this context should tend to maximize A while minimizing E . There are several ways to formalize this problem; perhaps the simplest would be to define as ‘optimal’ a pattern of stomatal behavior that maximizes the instantaneous water-use efficiency (W , defined as A/E). This does not yield a meaningful answer under most conditions, however, because W is usually greatest for conductances approaching zero. Cowan (1977) and Cowan and Farquhar (1977) approached the problem differently, by defining optimal stomatal behavior as a pattern that procures the most carbon for a given total water supply and a given period of time to use that water.

These authors used the calculus of variations to identify the optimal pattern of stomatal conductance under changing environmental conditions, and concluded that this pattern should keep the quantity ‘ $\partial A/\partial E$ ’ (the partial derivative of A with respect to E) constant. The conclusions of Cowan (1977) and Cowan and Farquhar (1977) thus predict that in plants behaving ‘optimally’ with respect to the trade-off between CO_2 uptake and water loss, stomatal responses to changing environmental conditions will yield a gas exchange pattern in which $\partial A/\partial E$ is constant. However, if environmental conditions and biochemical parameters do not vary, then $\partial A/\partial E$ and g_s are uniquely related, implying a single optimal value of g_s . Therefore, in a temporal context, Cowan and Farquhar’s results suggest that stomatal conductance should remain constant.

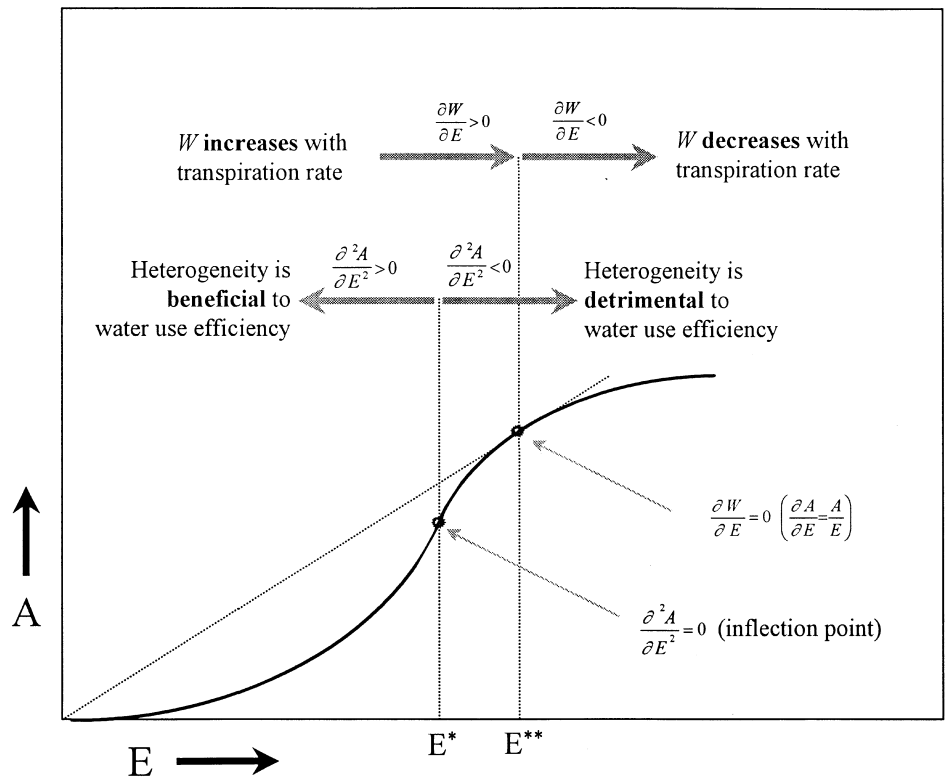
In a *spatial* context – if conditions and parameters are spatially uniform – these results imply that stomatal conductance should be spatially uniform across a leaf (Cowan and Farquhar 1977; Cowan 1982), and thus heterogeneous (patchy) stomatal conductance is necessarily detrimental to carbon-water balance. This can be extended to include the systematic, gradual variations in environmental and biochemical parameters that are often observed in leaves (Weyers and Lawson 1997) by allowing heterogeneity in g_s that follows the same predictable patterns, and simply excluding such *systematic* heterogeneity from the category of patchy stomatal conductance (after Mott and Buckley 1998). (Note that the shift from a temporal context to a spatial context

implicitly redefines the word ‘optimal’: in a spatial context, optimality is an *instantaneous* property of spatial patterns of g_s rather than a dynamic property of temporal responses. Throughout this paper, carbon-water balance will be discussed from a purely spatial, instantaneous perspective. Additionally, the phrase ‘carbon-water balance’ is sometimes used in place of ‘water-use efficiency’ because it refers collectively to all measures of the trade-off between carbon gain and water loss, and it will become apparent that gas exchange patterns maximizing water-use efficiency per se are not always unambiguously ‘optimal’.)

Two questions then remain: (1) how significant are the predicted detrimental effects of stomatal patchiness on instantaneous carbon-water balance, and (2) are there any exceptions to this result – that is, can stomatal patchiness ever benefit the plant? The first question can be addressed directly by comparing performance for patchy and nonpatchy leaves with a quantitative model of photosynthesis and transpiration (such a model and its predictions are developed and described below). To address the second question, we must examine the conditions identified by Cowan (1977) and Cowan and Farquhar (1977) under which their results imply that heterogeneity is inefficient. In particular, that conclusion requires a mathematical caveat: the curvature of the relationship between A and E must be negative. This caveat is satisfied under most environmental conditions because successive increments in A tend to become smaller as stomatal conductance increases, whereas successive increments in E tend to remain more nearly constant as g_s increases (E vs g_s is more nearly linear). This leads to negative curvature in the A versus E relationship. Cowan (1977) and Cowan and Farquhar (1977) noted that in cases where this caveat is not satisfied (i.e., when the curvature becomes positive), the above conclusions do not apply. “It is evident ... that $\partial A/\partial E$ constant within such a region defines not the minimum, but the maximum possible loss of water corresponding to a given amount of assimilation. ... Leaf conductance ... must either be zero or be sufficiently great for A and E to exceed the magnitudes corresponding to the point of inflexion [E^* in Fig. 1] at which the curvature of the surface becomes [negative]” (Cowan and Farquhar 1977). Therefore, if some environmental conditions lead to positive curvature, then patchy stomatal conductance might not always be detrimental to instantaneous carbon-water balance.

The goal of this study was to identify the effects of patchy stomatal conductance on carbon-water balance at a fixed point in time, for a spatially uniform environment. To accomplish this, it is necessary first to identify environmental conditions in which the curvature of A versus E can become positive, and then to determine the influence of various heterogeneous (patchy) stomatal conductance distributions on carbon-water balance under those conditions. To this end, a model of transpiration and assimilation was used to calculate the curvature of A versus E under various environmental

Fig. 1 Diagram showing an A vs E curve that has positive curvature at low conductances (low A and E), and subsequently changes to negative curvature. The point at which the curvature changes signs (the inflection point) is marked with a circle, and a dotted vertical line passes through this point to the value E^* on the horizontal axis. Below this point, heterogeneity in E (about a fixed total transpiration rate) will increase A and therefore also increase W ($= A/E$), and above this point heterogeneity will decrease W . A second point, at a higher transpiration rate (E^{**}), is also marked with a circle. This is the point where W stops increasing with E . A convenient graphical interpretation of this point is that the tangent line passing through it also passes through the origin; this tangent line is also represented by a dotted line. Below E^{**} , W increases with transpiration rate for a homogeneous leaf (or more generally for any homogeneous patch of stomatal conductance), and above this point W decreases with E .



conditions. The model was then used to calculate whole-leaf A and E for normal and bimodal stomatal conductance distributions. For simplicity, and also for analogy to the work of Cowan (1977) and Cowan and Farquhar (1977), homogeneous and patchy leaves were compared at the same whole-leaf transpiration rate. These simulations showed that for most environmental conditions, patchiness had large detrimental effects on water-use efficiency, but under some conditions, patchiness had negligible or slightly positive effects.

Theory

CO₂ assimilation (A) usually exhibits a saturating (negatively curved) response to stomatal conductance (g_s) because CO₂ diffusion occurs into a closed compartment (the leaf intercellular spaces). An increase in conductance raises the intercellular CO₂ partial pressure (c_i), and since this additional CO₂ can never be entirely absorbed by increased rates of biochemical CO₂ fixation, the diffusional gradient will always decrease to some degree with increasing g_s (unless increases in evaporative cooling with g_s significantly affect leaf temperature and thus photosynthetic parameters). As a result, A versus g_s is negatively curved. If a leaf is relatively small, and/or the wind speed is relatively large, the boundary layer for heat transfer that surrounds the leaf will be fairly small. Such a leaf is said to be 'highly coupled' to the air. In this case, leaf temperature is close to air temperature and

evaporative cooling has little effect on the gradient for water vapor diffusion (Δw). Therefore transpiration (E) is approximately linearly related to conductance, and a fixed change in g_s results in a fixed change in E . Given that A versus g_s is negatively curved, this implies that A versus E tends to be negatively curved as well.

However, in leaves that are not highly coupled to the air, transpirational water loss can lower leaf temperature through evaporative cooling. This decreases the saturated vapor pressure within the leaf, which in turn decreases the gradient for water vapor diffusion (Δw), introducing negative curvature in the E versus g_s relationship. If this effect is sufficiently large, the curvature of A versus E may approach zero or even become positive. Leaf cooling may also influence the assimilation rate directly by changing temperature-dependent kinetic parameters related to photosynthesis, and this may also result in positive curvature of A versus E for some range of conductance values.

To understand the effects of stomatal heterogeneity on W , imagine a simple bimodal patchy distribution as a pair of balanced increments in E (one positive and one negative) from some initial homogeneous value of E . These increments will yield different-sized increments in assimilation if A versus E has any curvature. If the curvature is negative, then the negative increment in A will be larger than the positive increment, and if curvature is positive the reverse will be true. Therefore, heterogeneity in g_s and E within a region of negative curvature will decrease whole-leaf A and W relative to a homogeneous leaf with the same total E . Conversely,

Table 1 Parameters and variables used in the model, with nominal values or values at 25°C. Temperature dependencies for photosynthetic parameters (not shown) are those used by de Pury and Farquhar (1997)

Description	Symbol	Value: (a) nominal, (b) fixed, or (c) at 25°C	Source
Ambient humidity (mmol H ₂ O mol ⁻¹ air)	w_a	15 (a)	
Air temperature (°C)	T_a	25 (a)	
Absorbed radiation (kW m ⁻²)	Φ	1.2 (a)	
Ambient CO ₂ partial pressure (Pa)	c_a	35 (b)	
Ambient O ₂ partial pressure (Pa)	O	21×10^3 (b)	
Rubisco-limited rate of RuBP carboxylation (mol CO ₂ m ⁻² s ⁻¹)	V_m	115.6×10^{-6} (c)	T. June, unpublished results from <i>Glycine max</i>
Electron-transport-limited rate of RuBP carboxylation (mol CO ₂ m ⁻² s ⁻¹)	J	203.9×10^{-6} (c)	T. June, unpublished results from <i>Glycine max</i>
Michaelis-Menten constant for carboxylation (Pa)	K_C	40.4 (c)	von Caemmerer et al. (1994)
Michaelis-Menten constant for oxygenation (Pa)	K_O	24.8×10^3 (c)	von Caemmerer et al. (1994)
CO ₂ compensation point without mitochondrial respiration (Pa)	Γ_*	36.9 (c)	von Caemmerer et al. (1994)
Respiration that continues in the light (mol CO ₂ m ⁻² s ⁻¹)	R_l	$0.0089 V_m$ (c)	Watanabe et al. (1994)
Specific heat of air (J mol ⁻¹ air K ⁻¹)	c_{pa}	29.25	Jones (1992)
Latent heat of vaporization of water (J mol ⁻¹ H ₂ O)	L	18.01	Jones (1992)
Stephan-Boltzmann constant (J m ⁻² K ⁻⁴ s ⁻¹)	σ	5.67×10^{-8}	Jones (1992)

heterogeneity within a region of positive curvature will increase W relative to a homogeneous leaf with the same total E .

Our simulations showed that regions of positive curvature are generally confined to low transpiration and assimilation rates, and therefore to low values of stomatal conductance. Figure 1 shows a typical scenario, in which the curvature is positive at low assimilation and transpiration rates, but negative at higher rates. The effects of patchy conductance on W are made complex by the fact that heterogeneity in g_s can occur (1) entirely within a range of g_s , A and E where the curvature is negative, (2) entirely within a range of positive curvature, or (3) in a range spanning an inflection point (where the curvature changes signs) in the A versus E curve. The effect on W of variation in g_s and E within a region spanning an inflection point in the A versus E curve will depend on the actual distribution of conductance (and E) and on the magnitude of the curvature in the neighborhood on either side of the inflection point.

For a given whole-leaf transpiration rate, within-leaf heterogeneity in E always decreases W if the curvature in A versus E is negative. This study is complicated by the fact that W does not decrease monotonically with transpiration rate if A versus E is positively curved. If curvature is positive, W increases with transpiration up to the point at which $\partial W/\partial E = 0$ and declines after that. This occurs when the tangent line through the operating point on the A versus E curve goes through the origin (when $\partial A/\partial E = A/E$); the transpiration rate at this point is defined in this paper by the symbol E^{**} . Figure 1 shows this diagrammatically (the diagonal dotted line is the tangent, and the point in the A vs E curve that this line passes through is where $\partial W/\partial E$ equals zero). It can be seen that if the curvature is initially positive, as in Figure 1, the point where $\partial W/\partial E$ equals zero occurs at a higher transpiration rate than the

inflection point. In this case water-use efficiency continues to increase for an interval extending into a region of negative curvature. Of course, a heterogeneous distribution of E within a region of negative curvature will still yield less photosynthesis than a homogeneous distribution; Figure 1 only shows that although A increases more slowly than E above the inflection point (so that heterogeneity is inefficient), W for a homogeneous region (e.g., a single patch of stomata) still increases with E for a finite interval.

Several factors may complicate the translation of this analysis to real leaves. First, if cuticular transpiration (E_c) is taken into account, then W is zero when $E = E_c$, maximal when E_c is equal in magnitude to noncuticular transpiration ($E = 2E_c$), and declines monotonically for $E > 2E_c$. Simulations were performed for zero and positive E_c (described below) to examine the qualitative influence of this factor. Second, in a leaf with patchy stomatal conductance, patches with higher transpiration rates must cool relative to other patches to produce the changes in curvature discussed above. This in turn requires the assumption, supported by experimental evidence (e.g., Hashimoto et al. 1984; Pospisilova and Santrucek 1997), that leaf temperature can vary across the leaf. Our model extends this assumption to the limiting case in which leaf temperature can vary arbitrarily in space – in other words, thermal equilibration by conduction through the leaf is ignored. Finally, the model also assumes that intercellular CO₂ partial pressure and water vapor mole fraction (c_i and w_i , respectively) can vary arbitrarily between adjacent patches, though this is only true for heterobaric leaves. Either lateral diffusion in a homobaric leaf or heat conduction would tend to mitigate the local changes in leaf temperature, c_i and w_i associated with variable transpiration rate, blunting any topological changes in the A versus E relationship and reducing the magnitude of the effects shown in this study.

The model

A model of transpiration and CO₂ assimilation in a C₃ plant was constructed, combining a biochemical model of photosynthesis (Farquhar et al. 1980) with physical models for leaf energy balance and for diffusion of CO₂ and water vapor through the stomatal pores and the leaf boundary layer. The model is described in greater detail in the Appendix, and parameters are given in Table 1. An explanation of how the model was implemented to answer the questions posed in the Introduction is provided below.

General modeling procedure

The model consisted of three independent equations, each describing a different physical relationship. The first equation (energy balance, Eq. A1) defined leaf temperature as a function of transpiration rate and other fixed environmental parameters; the second equation (a relationship between saturation vapor pressure and temperature) defined Δw as a function of ambient humidity and leaf temperature (assuming the intercellular spaces were saturated with vapor); and the third equation (the combination of Eqs. A2 and A3, for water vapor diffusion and total conductance) defined g_s as a function of transpiration rate, boundary layer conductance to water vapor (g_{bw}) and Δw . Because these three independent functions included four variables (leaf temperature, T_l ; water vapor mole fraction gradient, Δw ; transpiration rate, E ; and stomatal conductance, g_s), the model contained one free variable, allowing the transpiration rate to be varied independently.

The physical and biological parameters for the model are described in Table 1; the nominal values were used in all model runs unless otherwise noted. The boundary layer conductances to water vapor, CO₂ and heat were calculated in one of two ways: assuming flow across the leaf was laminar, or assuming it was turbulent. In the former case, the different diffusivities of water vapor, CO₂, and heat had to be accounted for, but in the latter case, bulk flow/forced convection was assumed to dominate gas transfer and the three conductances were assumed equal. These considerations are discussed further in the Appendix.

A versus E relationship

To generate relationships between A and E for homogeneous leaves, the stomatal conductance and total assimilation rate for a homogeneous leaf were determined by applying the model to the parameters described above with transpiration rate and one other chosen parameter (ambient humidity, air temperature, or absorbed radiation) as free variables. Because the model could not be solved analytically, an iterative procedure was used in which the leaf temperature was repeatedly

adjusted until the sum of heat loss terms (the right side of Eq. A1) equaled the specified value for absorbed radiation (ϕ).

E was incremented by a constant value (0.3 mmol H₂O m⁻² s⁻¹) between each of 51 subsequent model runs, so that it ranged between zero and 15 mmol H₂O m⁻² s⁻¹. The curvature ($\partial^2 A / \partial E^2$) at each value of E (corresponding to the subscript i in the following) was estimated numerically from these discrete A versus E curves (using the algorithm given by Eq. A9 in the Appendix). Inflection points (where the curvature equals zero, E^* in Fig. 1) were located by comparing the sign of the curvature between each two adjacent points; the stomatal conductance at the inflection point (g_s^*) was estimated as the average value of g_s for the two points between which the curvature changed sign. W was calculated from the A versus E relationship as the ratio A/E . Values of g_s where W stopped increasing with E (E^{**} in Fig. 1) were identified in the same way that inflection points were located, by finding sign changes in the derivative $\partial W / \partial E$ (estimated by $\Delta W / \Delta E$) and calculating the mean g_s between the two points.

The chosen environmental parameter was then incremented by a fixed value and another A versus E curve was generated. Curvature, $\partial W / \partial E$, and their roots (values of g_s where these variables equaled zero) were calculated as described above. This sequence was repeated for a total of 51 values of the chosen parameter, yielding three-dimensional relationships between E , the chosen parameter, and each of A , curvature, and W .

To examine the effects of cuticular transpiration (E_c) on the modeling results, all figures were generated using two values for cuticular conductance (g_c): 0 and 5 mmol m⁻² s⁻¹ (the latter was a mean calculated by Boyer et al. 1997 for five leaves of *Vitis vinifera* L.). However, the results presented and discussed below are from model runs where cuticular conductance was set equal to zero, because the results for cuticular conductances of 0 and 5 mmol m⁻² s⁻¹ were qualitatively indistinguishable and showed only slight and insignificant quantitative differences.

Effects of stomatal heterogeneity

Model runs were performed comparing W for leaves with uniform g_s to leaves with heterogeneous g_s . W was calculated for a homogeneous leaf by the procedure described above, as the ratio of total leaf assimilation rate (A_h , where the subscript means 'homogeneous') to the total leaf transpiration rate (E_h). Three stomatal conductance distributions were generated: two normal distributions with 50 distinct conductance values and with coefficients of variation (standard deviation divided by mean) equal to 0.1 and 1.0, respectively, and one bimodal distribution with two values of g_s (one value at zero, and one positive value). For each distinct conductance value, the model was used to calculate the transpiration rate by the procedure described in the

preceding paragraph. These transpiration rates were each weighted by the frequency for the associated conductance value, and summed to yield the total transpiration rate for the leaf (E_p , where the subscript means 'patchy').

This procedure was iterated, scaling the entire conductance distribution linearly (multiplying the conductance of every patch by the same number), until the total transpiration rate for the patchy leaf (E_p) was equal to that generated by the homogeneous model for the same set of parameters (E_h). For the bimodal distribution, this amounted to scaling the conductance of a single patch, because the other patch had a conductance of zero. The resulting values for total leaf assimilation and transpiration rates (A_p and E_p , respectively) were used to calculate W for the patchy distribution.

Results

As discussed in the *Theory* section, the effect of patchy stomatal conductance on water-use efficiency is a function of the distribution of conductance values among patches, and of the curvature in the A versus E relationship over the range of conductance values. To identify factors that influence the curvature of A versus E , the model was used to predict relationships between the curvature and environmental variables over a range of conductance values. Subsequently, the model was used to predict whole-leaf assimilation rates over a range of transpiration rates for patchy and homogeneous conductance distributions.

Topology of A versus E

Surfaces of curvature in A versus E

Figure 2, described below, presents three-dimensional surfaces relating the curvature of A versus E (on the vertical axes) to environmental variables and transpiration rate (on the horizontal axes). The surfaces on the left-hand side of Fig. 2 show results for large boundary layers ($g_{bh} = 0.25 \text{ mol m}^{-2} \text{ s}^{-1}$), and surfaces on the right-hand side are for small boundary layers ($g_{bh} = 10.0 \text{ mol m}^{-2} \text{ s}^{-1}$). (These two values for g_{bh} were chosen as limiting but feasible values on the basis of models relating g_{bh} to wind speed and leaf size. For example, the lower value ($g_{bh} = 0.25 \text{ mol m}^{-2} \text{ s}^{-1}$) corresponds to a 30-cm leaf at a wind speed of roughly 1 m s^{-1} (3.6 km h^{-1}), and the higher value ($g_{bh} = 10.0 \text{ mol m}^{-2} \text{ s}^{-1}$) represents a 2-mm leaf at about 10 m s^{-1} ; see Appendix.) Regions of the surfaces in Fig. 2 for which the curvature of A versus E was negative are plotted without shading, and regions of positive curvature are shaded grey. For leaves with small boundary layers, curvature was always negative (surfaces on the right side of Fig. 2). However, for leaves with large boundary layers, curvature was positive in

some conditions (surfaces on the left side of Fig. 2). Positive curvature generally occurred at low transpiration rates, for high air temperatures and high levels of absorbed radiation. Ambient humidity had little effect on curvature.

Two odd characteristics of these surface plots are evident and require explanation. In the high- g_{bh} plot for air temperature and the low- g_{bh} plots for both air temperature and absorbed radiation, a jagged ripple transects the surface. These are numerical artifacts corresponding to the sharp edge in A versus E caused by the biochemical photosynthesis model shifting from limitation by RuBP-saturated Rubisco kinetics to limitation by electron transport. Additionally, there are regions of apparently missing data in Fig. 2. These regions correspond to situations in which the imposed transpiration rate requires a negative stomatal resistance. These regions were generally much greater in extent for the low- g_{bh} surfaces.

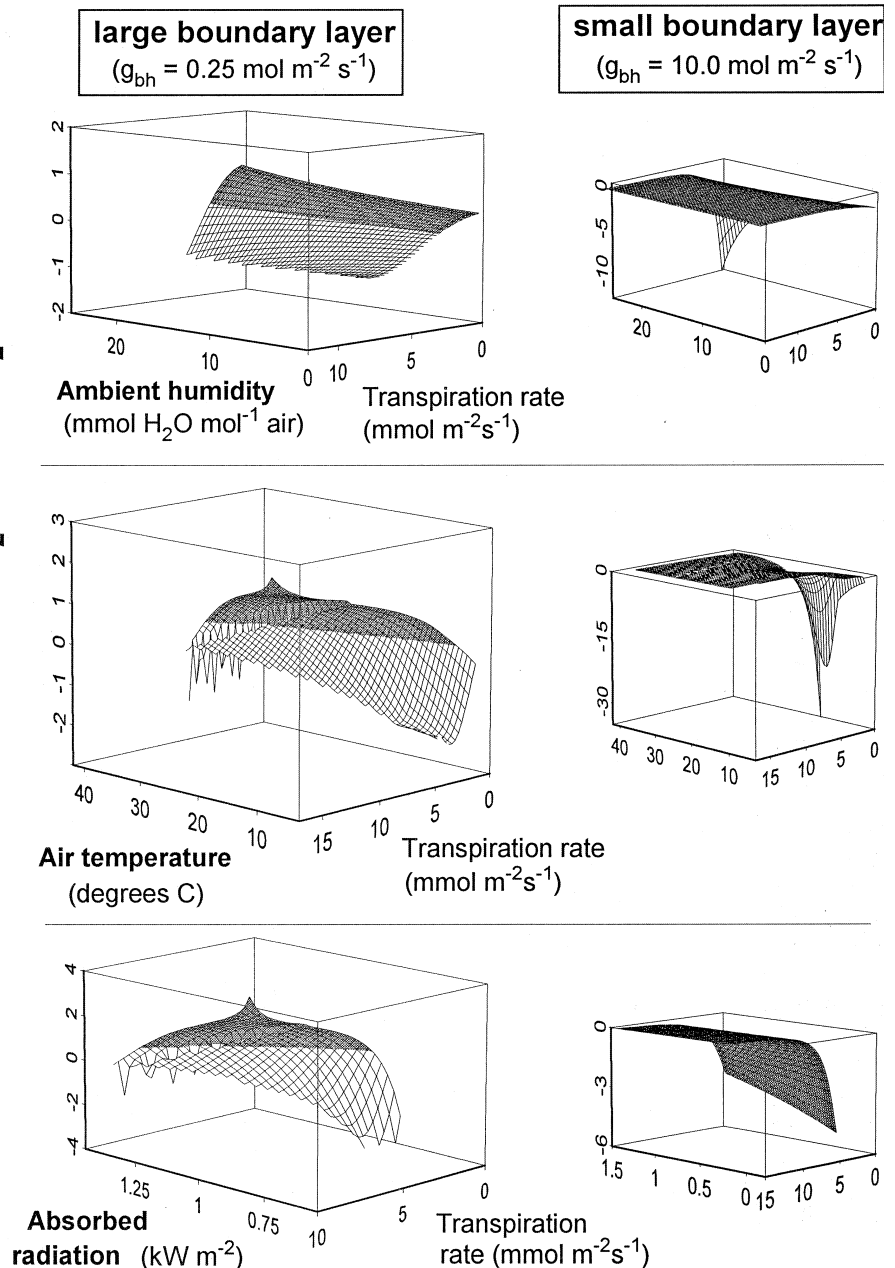
The stomatal conductance at which curvature is zero

To more clearly delineate conditions that produce positive curvature, the stomatal conductance at which the curvature of A versus E is zero (the inflection point, corresponding to the left-hand vertical dotted line through E^* in Fig. 1, and the transition from white to grey surface shading in Fig. 2) was plotted against environmental variables (solid lines in Fig. 3). To visualize the sensitivity of positive curvature to boundary layer conductance, these plots were generated for two low values of g_{bh} (0.25 and $0.50 \text{ mol m}^{-2} \text{ s}^{-1}$). Figure 3 also plots the stomatal conductance at which W stops increasing with transpiration rate (the point where $\partial W/\partial E = 0$ and $E = E^{**}$, corresponding to the right-hand vertical dotted line in Fig. 1) against environmental variables (dotted lines in Fig. 3).

The stomatal conductance at the inflection point is a measure of the size of the region of positive curvature that occurs under a particular set of environmental conditions. The conductance at which $\partial W/\partial E = 0$ is a measure of the range of conductance values over which water-use efficiency increases with g_s and E (in fact, this conductance value is numerically equal to that range). Both of these critical values of stomatal conductance generally increased with absorbed radiation and air temperature. The conductance at the inflection point in A versus E changed very little with ambient humidity, but the conductance at which $\partial W/\partial E = 0$ increased with humidity. The conductance at which $\partial W/\partial E = 0$ tended to show a sharp rate of increase at higher values of these environmental variables, and this value of g_s was in nearly all cases significantly higher (often two to five times greater in magnitude) than the conductance at the inflection point in A versus E . Further simulations suggested that as the boundary layer conductance was increased beyond $0.50 \text{ mol m}^{-2} \text{ s}^{-1}$, the size of the region of positive curvature rapidly diminished to zero, along

Fig. 2 Three-dimensional surfaces of the curvature of A vs E ($\partial^2 A / \partial E^2$, $\text{mol CO}_2 \text{ mol}^{-2} \text{ s}^{-1} \text{ H}_2\text{O m}^{-2} \text{ s}^{-1}$) as a function of transpiration rate (E , $\text{mmol m}^{-2} \text{ s}^{-1}$) and various environmental parameters [ambient humidity (w_a , $\text{mmol H}_2\text{O mol}^{-1} \text{ air}$), air temperature (T_a , $^\circ\text{C}$), and absorbed radiation (ϕ , kW m^{-2})] for two different values of boundary layer conductance (g_{bh} , $\text{mol m}^{-2} \text{ s}^{-1}$): low (0.25) and high (10.0). Regions of each surface where the curvature is positive are unshaded, and regions of negative curvature are colored grey (surfaces for high g_{bh} had uniformly negative curvature). Regions of missing data in the low- g_{bh} surfaces correspond to regions where the stomatal conductance was predicted to be negative for the imposed parameter regime, and sharp discontinuities in the low- g_{bh} surfaces are a numerical artifact of the shift from CO_2 fixation to RuBP regeneration (see text)

Curvature in A vs. E ($\mu\text{mol CO}_2 \text{ mmol}^{-2} \text{ H}_2\text{O m}^2 \text{ s}$)



with both critical values of stomatal conductance. These results show that W can increase with transpiration rate for physiologically significant stomatal conductances.

The effects of stomatal heterogeneity on W

To determine the influence of patchy stomatal conductance on water-use efficiency, the model was used to compare W between a homogeneous leaf and three leaves with different patchy stomatal conductance distributions all yielding the same total transpiration rate. Water-use efficiency was indistinguishable between homogeneous leaves and those with normal distributions of stomatal conductance with a 10% coefficient of

variation CV for the nominal parameter set and any boundary layer conductance (Fig. 4, solid lines). For leaves that were weakly coupled to the air ($g_{bh} = 0.25 \text{ mol m}^{-2} \text{ s}^{-1}$) and for which photosynthetic parameters were allowed to vary with leaf temperature [Fig. 4a; the inset (Fig. 4c) shows results for low- g_{bh} simulations where parameters were fixed at 25°C , and is discussed below], W increased with transpiration rate up to a point and subsequently declined. The highest possible transpiration rate for all distributions was limited by the large boundary layer resistance. Normal distributions with $CV = 100\%$ increased W by roughly 1–2% over homogeneous distributions up to a transpiration rate of $3 \text{ mmol m}^{-2} \text{ s}^{-1}$, beyond which homogeneous distributions were more efficient (dashed line,

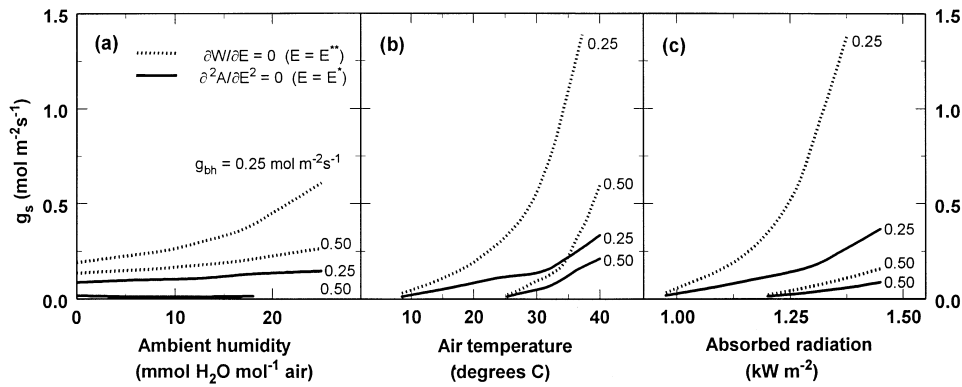


Fig. 3a–c The value of stomatal conductance (g_s) at the point where the curvature in A vs E changes signs (the ‘inflection point’ in A vs E , where $\partial^2 A / \partial E^2 = 0$, corresponding to the value ‘ E^* ’ in Fig. 1) is represented by *solid lines*, and the value of g_s at which W stops increasing with E (where $\partial W / \partial E = 0$, corresponding to the right-hand vertical dotted line in Fig. 1) is plotted with *dotted lines*. These critical values of g_s are plotted against the following environmental variables: ambient humidity (w_a , $\text{mmol H}_2\text{O mol}^{-1}$ air) (a), air temperature (T_a , $^{\circ}\text{C}$) (b), and absorbed radiation (ϕ , kW m^{-2}) (c). Curves are presented for two values of the boundary layer conductance to heat transfer (g_{bh}): 0.25 and $0.50 \text{ mol m}^{-2} \text{ s}^{-1}$

Fig. 4a; note that the y -axis is truncated in panel Fig. 4a). Bimodal distributions, which should represent the extreme case of stomatal heterogeneity, increased W by 1–5% relative to homogeneous distributions up to a transpiration rate of $2.4 \text{ mmol m}^{-2} \text{ s}^{-1}$ (Fig. 4a); higher total leaf transpiration rates were not possible for this type of distribution, because only half of the stomata were open.

In leaves that were well coupled to the air ($g_{bh} = 10.0 \text{ mol m}^{-2} \text{ s}^{-1}$; Fig. 4b), normal distributions with $\text{CV} = 100\%$ decreased W by roughly 5–10% relative to homogeneous leaves with the same total transpiration rate (dashed line, Fig. 4b). Bimodal distributions decreased W by 10–30% (dotted line, Fig. 4b) for high g_{bh} . W declined monotonically with transpiration rate for all distributions at high g_{bh} , and most steeply at low transpiration rates.

These results show that although patchy stomatal conductance improved W slightly under some conditions for leaves with low boundary layer conductances, these effects were generally small. In contrast, the detrimental effects of patchiness on W in leaves with high boundary layer conductances were quite large under most conditions (note scales of y -axes in Fig. 4). This suggests that patchy stomatal conductance is either detrimental (at high g_{bh}) or neutral (at low g_{bh}) with respect to direct effects on carbon-water balance.

Temperature-dependent photosynthetic parameters and W

There are two important effects of leaf cooling on W . One involves the gradient for transpiration (Δw) and the other involves direct effects of leaf temperature on the kinetic parameters of photosynthesis. To separate these

effects, model runs were performed in which these kinetic parameters were held equal to their values at 25°C , independently of leaf temperature. In these simulations for $g_{bh} = 10.0 \text{ mol m}^{-2} \text{ s}^{-1}$, the g_s distributions had identical effects on W whether or not kinetic parameters were fixed. These results are consistent with the prediction that leaf temperature should be close to air temperature (a constant in these simulations) for high g_{bh} , so any T_l -dependent effects should be irrelevant.

However, at low g_{bh} ($0.25 \text{ mol m}^{-2} \text{ s}^{-1}$) W was generally lower for temperature-independent photosynthesis (parameters were fixed at their values for 25°C ; Fig. 4c) than for temperature-dependent photosynthesis (Fig. 4a). This implies that for low g_{bh} , leaf temperature was *above* the optimum temperature for photosynthesis for a substantial range of transpiration rates (so evaporative cooling was able to bring the leaf closer to the optimum temperature) but the difference between actual and optimum leaf temperatures was smaller than the difference between 25°C and optimal temperature. In other words, the photosynthetic parameters were always farther from their optima in Fig. 4c, because 25°C was farther from the optimum than was the actual leaf temperature. This inference was verified by more detailed analysis of the simulation output (not shown).

Discussion

This work was undertaken to determine the effects of patchy stomatal conductance on whole leaf carbon-water balance. Stomatal heterogeneity is usually detrimental to carbon-water balance because of negative curvature in the A versus E relationship (verified by the simulations presented above). However, under some conditions, evaporative cooling can create positive curvature in this relationship by decreasing the evaporative gradient; under these conditions, stomatal patchiness may increase W . The simulations presented here show that if the boundary layer conductance is small (e.g., large leaves and/or low windspeeds), the effects of patchiness on W can be slightly beneficial. When boundary layer conductances are large (small leaves and/or high windspeeds), the effects of patchiness on W are larger, and are always detrimental.

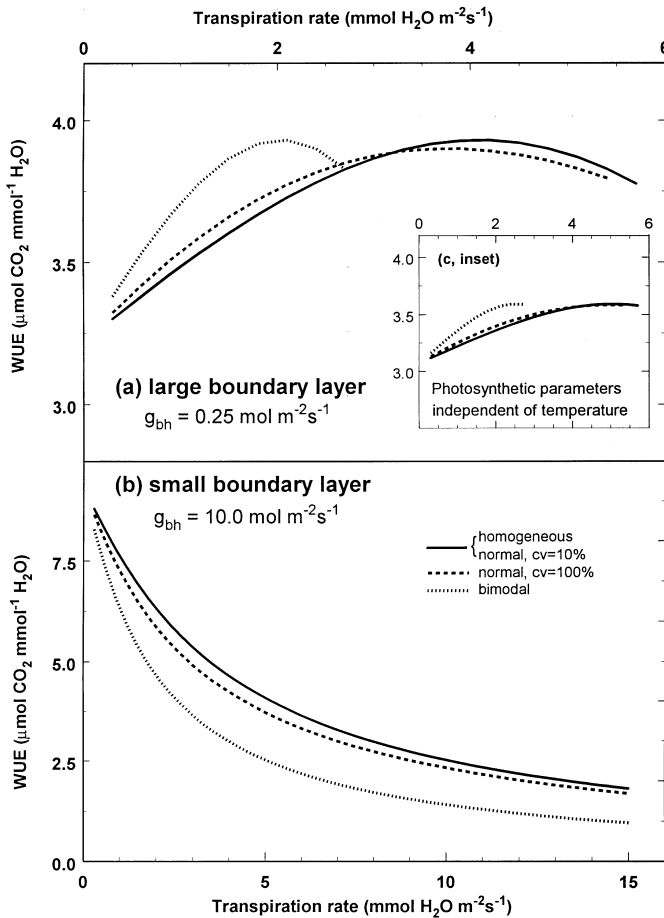


Fig. 4a–c Water-use efficiency (WUE ; $W = A/E$) as a function of total transpiration rate (E , $\text{mmol m}^{-2} \text{ s}^{-1}$) for four types of stomatal conductance distributions. In each case, the *solid lines* are for homogeneous distributions and normal distributions with $CV = 10\%$ (these two types of distributions produced indistinguishable results), *dashed lines* are for normal distributions with $CV = 100\%$, and *dotted lines* are for bimodal distributions: **a** W vs E for low g_{bh} ($0.25 \text{ mol m}^{-2} \text{ s}^{-1}$), when the kinetic parameters of photosynthesis were allowed to vary with temperature; **b** W vs E for high g_{bh} ($10.0 \text{ mol m}^{-2} \text{ s}^{-1}$); **inset c** as **a**, but with photosynthetic parameters fixed to their values at 25°C , regardless of actual leaf temperature. Results for **b** were indistinguishable whether or not photosynthetic parameters were allowed to vary with temperature. Note that **a** and **c** are plotted on truncated vertical axes with a smaller range than in **b**, and on smaller horizontal ranges than in **b**.

One use of these results is to identify conditions under which patchiness may be expected to occur more often. From the perspective of ecological fitness, one would expect patchiness to occur less often under environmental conditions where it has a negative effect on W and, conversely, to occur more often under conditions where it increases W or has little influence on carbon-water balance. The results of this study predict that patchiness has little effect on carbon-water balance in leaves with low boundary layer conductance (clearly the most important parameter controlling these effects); patchiness may thus be more likely to occur in such leaves. However, there are few data available to test this

prediction. Most gas exchange studies assume a fixed and known boundary layer conductance, usually determined by the flow and mixing characteristics of the gas exchange chamber, so g_{bh} has not been manipulated as an experimental variable to test its influence on the incidence of patchiness. Boundary layer conductance probably varies significantly over time and among leaves in natural settings, but very few data exist documenting the nature and occurrence of patchy stomatal behavior in the field, and most field observations from which patchiness could be inferred have been made with portable gas exchange systems or porometers, which fix g_{bh} .

Independent of boundary layer conductance, patchy stomatal closure tends to be less detrimental or slightly beneficial for W under conditions of high air temperature, high radiation loads, and low transpiration rates. These conditions are similar to those that have been shown experimentally to promote patchiness. For example, patchiness has been shown to occur under water stress (e.g., Downton et al. 1988; Düring 1992), which is often accompanied by high air temperatures, high radiation loads, and low transpiration rates. Additionally, patchiness has often been induced experimentally by decreases in humidity (e.g., Mott et al. 1993; Cardon et al. 1994). Although the results of this study showed that humidity has little influence on the effects of patchiness on W at low g_{bh} , lower humidities decreased the detrimental effects of patchiness on W at high g_{bh} . Thus, the available data suggest that patchiness tends to occur under conditions for which it has a positive effect, or little effect (either beneficial or detrimental) on W .

Another implication of the results described above is that under some circumstances, stomatal patchiness represents a confirmation of the conclusions of Cowan (1977) and Cowan and Farquhar (1977), which predict stomatal behavior should act to avoid conditions where $\partial^2 A / \partial E^2$ is positive, and that these conditions are more prevalent at large boundary layer thicknesses. The simulations presented above show that the curvature of A versus E may be positive for a substantial set of environmental conditions. Thus, for a fairly broad range of reasonable parameter values, including values of g_{bh} that are not extreme, W increases with transpiration rate for a homogeneous leaf. As discussed in the Theory section, this characteristic emerges whenever the curvature of A versus E is positive for some finite region beginning at zero, and it extends beyond the inflection point into a region of negative curvature. Recall that if W always decreases with transpiration rate, W is maximized only at zero conductance, so one must instead maximize the long-term (integrated) carbon gain for a given water supply (following Cowan 1977; Cowan and Farquhar 1977). This method assumes that the plant has access to 'information' about the size of this water supply and its frequency of replenishment. If the curvature becomes positive, however, it is possible to identify a nonzero value for stomatal conductance that maximizes instantaneous W .

The existence of a nonzero optimum g_s under a broad range of conditions may therefore alter the mathematics

of long-term optimization. Four general scenarios can be identified. First, if curvature is always negative, $\partial A/\partial E$ should remain constant in space and time. The other three scenarios arise if curvature is positive at low transpiration rates (as in Fig. 1). If the water supply is large enough to allow an average transpiration rate greater than E^{**} (the value of E where W is maximized; Fig. 1), the plant can either (1) use all of the available water, optimizing its use by holding $\partial A/\partial E$ constant (the 'competitive optimum'), or (2) maximize W per se, by holding E equal to E^{**} (the 'conservative optimum'). Finally, (3) if the available water supply is small enough that the sustainable average transpiration rate is below E^{**} , then E^{**} is a global optimum, and it can only be achieved by ceasing transpiration entirely in some regions so that other regions can achieve the higher optimum E ($= E^{**}$). This represents a situation where patchy stomatal conductance is optimal, and is therefore the scenario most relevant to the results described in this paper.

Acknowledgements T.N.B thanks Jon Lloyd and Ian Cowan for insightful discussions on the subject, and the Research School of Biological Sciences at the Australian National University, Canberra, for providing a stimulating research environment and warm hospitality during the development of this work. This work was supported by a grant from the National Science Foundation (IBN-9420862).

Appendix: description of model

Energy balance model

The following energy balance model was applied independently to each area of the leaf with uniform conductance. It was assumed that any given region of the leaf quickly achieved and subsequently maintained a constant temperature following any imposed environmental or biochemical changes. For simplicity, heat conduction through the leaf was ignored. The model included four energy transfer pathways between the leaf and its environment: infrared emission from the leaf, convective heat transfer with the air, latent heat loss through evaporation, and absorption of radiation from the sun, sky, and ground. Chemical storage and metabolism were ignored. Conservation of energy then implies:

absorbed radiation = emission + convective heat loss + latent heat loss, or

$$\Phi = 2\sigma T_l^4 + 2c_{pa}g_{bh}(T_l - T_a) + LE \quad (A1)$$

The longwave emissivity of the leaf is assumed to be unity. c_{pa} is the specific heat of air ($J mol^{-1} air K^{-1}$), g_{bh} is the boundary layer conductance to sensible heat transfer ($mol air m^{-2} s^{-1}$; see Boundary layer conductances, below), T_a and T_l are the air and leaf temperatures, respectively (K), L is the latent heat of vaporization ($J mol^{-1} H_2O$; Table 1), σ is the Stephan-Boltzmann constant ($J m^{-2} K^{-4} s^{-1}$; Table 1). Φ is the total absorbed radiation ($J m^{-2} s^{-1}$; Table 1). The radiation and sensible heat terms include a multiplier of two

to account for both leaf surfaces (the models relating g_{bh} to wind speed and leaf dimensions (see Boundary layer conductances, below) apply to single leaf surfaces, so their numerical predictions would apply in the equation above).

Diffusion models

Movements of water vapor and CO_2 through the stomata and boundary layer were described by serial-resistance diffusion models, as follows. The flux of water vapor out of the leaf (E , transpiration, $mmol H_2O m^{-2} s^{-1}$) for any given area of the leaf was given as

$$E = \frac{g_{tw}(w_a - w_l)}{1 - 0.5(w_a + w_l)} \quad (A2)$$

where w_a is the mole fraction of water vapor in the ambient air ($mmol H_2O mol^{-1} air$), w_l is the mole fraction of water vapor in the leaf intercellular spaces (assumed to be saturated with water vapor; $mmol H_2O mol^{-1} air$), and g_{tw} is the total leaf conductance to water vapor diffusion ($mol air m^{-2} s^{-1}$, Eq. A3):

$$g_{tw} = \left((g_{sw} + g_c)^{-1} + g_{bw}^{-1} \right)^{-1} \quad (A3)$$

g_{sw} is the stomatal conductance to water vapor ($mol air m^{-2} s^{-1}$), g_c is the cuticular conductance to water vapor ($mol air m^{-2} s^{-1}$), and g_{bw} is the boundary layer conductance to water vapor ($mol air m^{-2} s^{-1}$; Table 1).

The flux of CO_2 through stomata (A_s , $\mu mol CO_2 m^{-2} s^{-1}$) is described by Eq. A4:

$$A_s = (g_{tc} \cdot 10^6) \left(\frac{c_a - c_i}{p} \right) - \frac{1}{2} (E \cdot 10^3) \left(\frac{c_a + c_i}{p} \right) \quad (A4)$$

where c_a and c_i are the partial pressures of CO_2 in the ambient air and the leaf intercellular spaces, respectively (Pa), p is the total atmospheric pressure (Pa) and E ($mmol H_2O m^{-2} s^{-1}$) is from Eq. A2. The second term is an approximate correction for the ternary interactions between air, water vapor, and CO_2 (von Caemmerer and Farquhar 1981). The numerical factors of 10^6 and 10^3 convert A and E , respectively, to $\mu mol m^{-2} s^{-1}$. g_{tc} ($mol air m^{-2} s^{-1}$) is the total conductance to CO_2 diffusion through the stomata and the leaf boundary layer (Eq. A5):

$$g_{tc} = (1.65g_{sw}^{-1} + g_{bc}^{-1})^{-1} \quad (A5)$$

g_{sw} is stomatal conductance to water vapor diffusion (see above), and g_{bc} is boundary layer conductance to CO_2 diffusion (Table 1) (Eq. A5 assumes the cuticle is impervious to CO_2).

Photosynthetic CO_2 assimilation was modeled after Farquhar et al. (1980) as the minimum of two equations for CO_2 flux (Eq. A6). These equations were each determined as the intersection of the function describing CO_2 diffusion through stomata (A_s ; Eq. A4) with an equation for CO_2 demand by biochemical fixation. One

demand function described the biochemistry of CO₂ fixation limited by RuBP carboxylation (A_v , Eq. A7), and the other function described CO₂ uptake as limited by RuBP regeneration (A_j ; Eq. A8):

$$A = \min\{A_v \cap A_s, A_j \cap A_s\} \quad (\text{A6})$$

where

$$A_v = \frac{V_m(c_i - \Gamma_*)}{c_i + K_c(1 + O/K_o)} - R_l \quad (\text{A7})$$

$$A_j = \frac{J(c_i - \Gamma_*)}{c_i + 2\Gamma_*} - R_l. \quad (\text{A8})$$

In Eqs. A7 and A8, c_i is the intercellular CO₂ partial pressure, V_m is the potential rate of RuBP carboxylation due to Rubisco (mol CO₂ m⁻² s⁻¹), J is the potential rate of RuBP carboxylation limited by electron transport (mol CO₂ m⁻² s⁻¹), Γ_* is the CO₂ compensation point in the absence of mitochondrial respiration (Pa), K_c and K_o are the Michaelis-Menten constants for RuBP carboxylation and oxygenation, respectively (both Pa), and R_l is the rate of respiration that continues in the light (mol CO₂ m⁻² s⁻¹). The parameters were allowed to vary from their values at 25°C (given in Table 1) according to the temperature dependencies used by de Pury and Farquhar (1997).

The curvature of A versus E was estimated numerically (Eq. A9) from relationships obtained by varying E while all parameters were held constant (see General modeling procedure in the main text). The following algorithm is based on the fact that the increment in E was fixed (ΔE).

$$\begin{aligned} \frac{\partial^2 A}{\partial E^2} &\approx \frac{\Delta(\frac{\partial A}{\partial E})}{\Delta E} \approx \frac{\Delta(\frac{\Delta A}{\Delta E})}{\Delta E} = \frac{(A_{i+1} - A_i)}{(\Delta E)^2} - \frac{(A_i - A_{i-1})}{(\Delta E)^2} \\ &= \frac{A_{i+1} - 2A_i + A_{i-1}}{(\Delta E)^2} \end{aligned} \quad (\text{A9})$$

Boundary layer conductances

Modeling boundary layer conductances to heat transfer and gas diffusion is problematic. Most available mathematical models for these conductances apply to simple physical models such as flat, rigid metal plates. Real leaves are topologically complex, and factors such as leaf pubescence and flexibility make the application of these simple physical models to real leaves questionable. These problems were circumvented by simply specifying numerical values for boundary layer conductance to heat transfer. We used existing mathematical models for diffusive transport and free convection (described in Monteith and Unsworth 1990, and Ball et al. 1988, respectively) to give the reader a rough idea of the leaf sizes and windspeeds to which these values may correspond (example values are presented at the beginning of

the Results section), but for the sake of brevity we do not present the models here: details are available in the sources.

The boundary layer conductances to water vapor (g_{bw}) and CO₂ diffusion (g_{bc}) are not necessarily equal to the conductance to heat transfer (g_{bh}). During laminar flow, transport occurs through the boundary layer by diffusion, so these conductances will vary in relation to their diffusion coefficients (Jones 1992). During turbulent conditions, transport occurs primarily by bulk flow in eddies, so differences in diffusion coefficients become unimportant (Jones 1992). The result (Jones 1992) is that in laminar conditions, $g_{bw} = 1.08g_{bh}$ and $g_{bc} = 0.76g_{bh}$, whereas in turbulent conditions, all three conductances are nearly equal. All model runs were repeated assuming turbulent flow and qualitatively similar results were obtained. The model runs presented in the Results section assumed flow was laminar.

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