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Regulation of stomatal conductance and transpiration in forest canopies

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Summary Processes regulating stomatal conductance, g_s, and transpiration, E, from forest canopies are reviewed. The first section deals with the response of g_s to environmental variables. Phenomenological models have been used to interpret field data and predict diurnal and seasonal variability in g_s, but models that couple stomatal conductance to photosynthesis at the leaf scale are now being used more widely. The vertical distribution of foliar nitrogen concentration is helpful for scaling these processes from leaves to canopies, and the analysis of data from many studies has led to the emergence of simplified, general relationships for estimating evaporation and carbon uptake by forests at stand and regional scales.

Evidence for the regulation of stomatal conductance by hydraulic and chemical signals is presented in the second section. Rapid and reversible changes in g_s following a perturbation to the water potential gradient in the flow pathway suggest that stomata respond directly to hydrostatic signals. Other evidence supports the contention that signals are transmitted by abscisic acid (ABA), possibly originating in the roots. For large woody plants, the short-term responses of stomata are probably brought about by hydraulic signals that affect g_s by triggering the release of ABA in the leaves. Tardieu and Davies (1993) developed an interactive model that incorporates hydraulic and chemical effects to describe the response of stomata to soil drying and evaporative demand.

In the third section, evidence is presented that short-term changes in g_s are linked closely to the hydraulic properties of the conducting system to minimize loss of hydraulic coductivity through xylem by cavitation. Examples of homeostatic mechanisms that operate to ensure the long-term balance between evaporative demand and the potential hydraulic conductivity of trees growing in different environments are described. Two hypotheses are examined: (1) height growth in trees is limited by the capacity of the conducting system; and (2) the decline in productivity with stand age is attributable to a decrease in conductivity.

Keywords: hydraulic conductivity, modeling, scaling, stomatal conductance, transpiration.

Introduction

Water moves from the soil through roots, xylem and leaves along a gradient of decreasing water potential that drives the flow. Ignoring capacitance effects, water flow along the branched pathway can be described by the sum of the partial flow rates, q_i, and resistances (=1/G_i where G_i is conductance) linked in series:

$$\Psi_1 = \Psi_r - \sum(q_i/G_i) - h\rho_w g, \quad (1)$$

where Ψ_1 and Ψ_r are the leaf and root water potentials and $h\rho_w g$ is the gravitational pull on the column of water of tree height h and density ρ_w (van den Honert 1948, Richter 1973, Jarvis 1975). The individual resistances, and thus flow rates and water potential gradients, are not equally distributed, leading to the concept of segmentation along the pathway (Zimmermann 1978). However, because of technical difficulties in measuring the partial flows and water potential gradients along the pathway, it is frequently necessary to lump these together. The total flow through the pathway can then be expressed as the transpiration rate from the canopy, E, and the conductance for the entire pathway, G, becomes:

$$G = E/(\Psi_r - \Psi_1 - h\rho_w g). \quad (2)$$

Transpiration from the canopy can be described by the Penman-Monteith equation (Monteith 1965), which combines weather variables with bulk aerodynamic, g_a, and surface, g_c, conductances to give:

$$E = (\varepsilon R/\lambda + Dg_a)/(\varepsilon + 1 + g_a/g_c), \quad (3)$$

where R is available energy and D is air saturation deficit (expressed in terms of dimensionless mole fractions) at a reference height above the surface. The coefficient ε (= $\lambda s/c_p$) is dependent on temperature, T, and represents the rate of change of the latent heat content of saturated air with a change in sensible heat, where λ is latent heat of vaporization, c_p is specific heat of air at constant pressure and s is the slope of the relationship between the partial pressure of saturated air and temperature. If g_s is mean stomatal conductance for leaves in a canopy with leaf area index L, then $g_c = g_s L$, noting caution about simplification (Raupach and Finnigan 1988, McNaughton 1994) discussed later in this review.

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If D is expressed in terms of air saturation deficit at the notional evaporating surface, D_s, then Equation 3 can be reduced to (Jarvis and McNaughton 1986):

$$E = g_s L D_s. \quad (4)$$

Monteith (1990) noted the importance of using D_s, rather than D, when making comparisons of stomatal response to air saturation deficit between vegetation types differing in g_a. An analytical expression for calculating D_s from D and measured evaporation rates is given by Aphalo and Jarvis (1991) and Kelliher et al. (1993).

Equations 2–4 link the regulation of water flow through plants with evaporative demand and define the scope for this review. As pointed out by Monteith (1995*b*), vegetation accommodates the supply of water from the soil by the roots with the evaporative demand imposed by the atmosphere. At constant water supply, the response of stomata to increasing irradiance, Q, in the early morning, increasing D_s later in the day and decreasing Q late in the day leads to maximum values of g_s early in the morning with a gradual decline during the afternoon.

Accommodation can occur in response to short-term perturbations to the system over a time period of a few seconds, (e.g., when there is a sudden decrease in irradiance because of a transient cloud) or in response to long-term acclimation processes, (e.g., regrowth of a stand following thinning). Possible mechanisms for accommodating perturbations are identified explicitly in Equations 2–4 as: (i) canopy structural properties influencing g_a and the degree of coupling between the canopy and vegetation and the atmosphere; (ii) responses of stomata, and thus g_c, to environmental variables related principally to irradiance, D, and T; (iii) properties of the conducting pathway from roots to leaves that modify the water potential gradient and G; and (iv) direct response of stomata, and thus g_c, to changes in G. This review focuses on the last three topics because they are the most relevant to the regulation of stomatal and canopy conductance.

Stomatal response to environmental variables

Many field studies have shown that variability in diurnal and seasonal measurements of g_s can be accounted for by environmental variables (Jarvis 1980). Once stomata have opened in the morning as Q increases, there is often a close relationship between decreasing g_s and increasing D as the day progresses (Schulze and Hall 1982, Grantz 1990). However, the mechanism allowing stomata to sense changes in D has not been identified. For a range of C_3 and C_4 plants, Ball et al. (1987) found that the response of g_s to humidity with varying temperature and CO_2 concentration collapsed to a single relationship in an expression based on relative humidity at the leaf surface. Measurements of the response of g_s to changes in relative humidity and air saturation deficit at the leaf surface, D_s, led Aphalo and Jarvis (1991) to conclude that D_s was the appropriate variable for explaining changes in g_s. This conclusion is supported by the work of Bunce (1985) who manipulated the thickness of the boundary layer to vary the rate of transpiration from leaves. Leuning (1995) points out that relative humidity and D are equivalent when temperature is constant, but this is not usually the case for field measurements because diurnal variations in D are largely caused by changes in temperature, rather than absolute humidity. Mott and Parkhurst (1991) measured the response of stomata to humidity of several species in normal air and in a mixture of helium and oxygen (helox), which has a diffusion coefficient of more than twice the value for air, while maintaining temperature and CO_2 concentration at the leaf surface, c_s, constant. Thus, they were able to vary E and D_s independently. When air was replaced by helox, g_s increased but transpiration rate from the leaf remained the same, indicating that stomata were responding to water loss from the leaf, and not to D_s or the saturation deficit difference between the interior and the surface of the leaf.

Monteith (1995*a*) examined published data from 52 sets of measurements on 16 species and concluded that the majority of data showed a general linear dependence of g_s on transpiration rate, E (Regime A), supporting the conclusions reached by Mott and Parkhurst (1991). In some cases, E reaches a maximum beyond which any further increase in D_s results in decreases in g_s and E (Regime B). This could occur as a result of patchy closure of stomata in response to stress or decreased hydraulic conductivity. Monteith showed that a plot of $1/E$ against $1/D_s$ or a plot of g_s against E (if they are measured independently) allows estimation of g_m, a parameter that reaches an extrapolated maximum when E is zero (slope) and approaches zero when E reaches a maximum (intercept). Dewar's (1995) theoretical analysis suggests that stomata are able to sense the water potential gradient between the guard cells and epidermal cells. This provides a mechanism that would result in a linear decrease in g_s with increasing E. However, Bunce (1996) measured the response of g_s to D while manipulating either leaf water potential or CO_2 concentration and concluded that stomata respond to the rate of peristomatal transpiration, rather than to E or leaf water potential. Because almost all of the evidence for this reasoning is derived from plants growing in controlled conditions, Meinzer et al. (1997) recently measured g_s (with a porometer) and E (sap flux measurements) independently in 15-m tall, field-grown *Populus* trees. Their results provide evidence to support the view that stomata respond to epidermal or cuticular transpiration rate, rather than to bulk leaf or stomatal transpiration rate, without the need to postulate patchy closure of stomata.

The phenomenological model described by Jarvis (1976) provides a practical approach for interpreting field measurements of stomatal conductance in relation to environmental variables. The response of g_s to each environmental variable is described by a nonlinear function and it is assumed that each variable acts independently, such that:

$$g_s = g_{smax}\, f_1(Q), f_2(T), f_3(D), f_4(\theta) \ldots \text{ etc.}, \quad (5)$$

where, for example, Q is irradiance, T is temperature, D is air saturation deficit, and θ is the root zone water deficit. Maximum conductance, g_{smax}, is constrained by parameters in each

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function, where the value of f_x varies between 0 and 1. This creates a complex, multi-dimensional response surface. It is not possible to incorporate the mechanistic response to each variable because these are not known, but the functions are chosen to represent observed responses based on measurements from controlled cuvette work or boundary line analysis of field data. Using this approach, much of the variability in g_s in forest canopies has been accounted for successfully, e.g., Jarvis (1976) with *Pseudotsuga menziesii* (Mirb.) Franco and *Picea sitchensis* (Bong.) Carr., Whitehead et al. (1981) with *Gmelina arborea* Roxb. and *Tectona grandis* L.f., Livingston and Black (1987) with *Pseudotsuga menziesii*, *Tsuga heterophylla* (Raf.) Sarg. and *Abies amabilis* Dougl. *ex* J. Forbes. and Whitehead et al. (1994) with *Pinus radiata* D. Don. Stewart (1988) derived surface conductances from Bowen ratio measurements above a *Pinus sylvestris* L. forest and used the approach in Equation 5 to explain the variability in surface conductance. The model was less successful for estimating g_c on an hourly basis than on a daily basis.

In a complex tropical forest canopy, Dolman et al. (1991) used a multi-layer approach incorporating decreasing Q through the canopy. Maximum g_s declined with depth in the canopy, but at high irradiance more leaves deeper in the canopy were able to reach light saturation for stomatal conductance. So, the relationship between g_s and g_c was dependent on irradiance. More complex radiation transfer models requiring considerable detail about canopy architecture have been used to estimate g_c for tree stands (Baldocchi 1989, Wang and Jarvis 1990).

There has been some effort to identify the most appropriate form of the response of g_s to D. Jarvis (1976) and Collatz et al. (1991) used a linear response of g_s to D, but this implies that g_s will become negative at some high value of D. Lohammar et al. (1980) used a hyperbolic function, which is consistent with Monteith's (1995*a*) analysis.

The close link between g_s and the rate of photosynthesis, A, for leaves (Schulze and Hall 1982) has led to the development of coupled models. A proposed mechanism for this link is that stomata respond to a chemical signal transported between the mesophyll and guard cells and that the rate of transport is dependent on A, regulated by Q (Wong et al. 1985). Cowan and Farquhar (1977) proposed that stomata respond to environmental variables to optimize carbon uptake per unit rate of transpiration, and the inclusion of the term $g_s = f(D)$ by Lloyd (1991) for *Macadamia integrifolia* Maiden & Betche is consistent with the optimization hypothesis. However, evidence from laboratory and field measurements with *Pinus taeda* L., which shows that the sensitivity of E and A to changes in g_s is not constant, but changes throughout the day with increasing D, does not support this hypothesis (Fites and Teskey 1988).

In a coupled model, Leuning (1995) used an expression for stomatal conductance that is based on a modified version of the model described by Ball et al. (1987). For well-watered conditions, stomatal conductance to CO_2 transfer, g_{sc} (= g_s/1.6 where 1.6 is the ratio of the diffusivities of water and CO_2 in air) is given by:

$$g_{sc} = g_{sc0} + \frac{aA}{(c_s - \Gamma)(1 + D_s/D_{s0})}, \tag{6}$$

where g_{sc0} is the residual conductance at the light compensation point, Γ is the CO_2 compensation point, D_{s0} describes the sensitivity of g_{sc} to D_s, c_s is CO_2 concentration at the leaf surface and a is related to the intercellular CO_2 concentration, c_i, at saturating irradiance, where $1/a = (1 - c_i/c_s)$. The function, attributed to Lohammar (1980), to describe the response of g_{sc} to D_s is adopted and the term for Γ is included to ensure that g_{sc} does not decrease as A approaches zero when c_s is decreased. Combining this diffusion or supply function with the biochemical or demand function in the model of photosynthesis described by Farquhar et al. (1980) and von Caemmerer and Farquhar (1981) leads to the definition of a unique value for c_i where both functions describing limitation to photosynthesis are balanced. Leuning (1995) shows that the ratio of c_i/c_s varies with D_s such that c_i remains roughly constant with varying irradiance, which is consistent with field observations (e.g., Correia et al. 1995). Such coupled models are now used widely and have the advantage that the equations can be readily closed. However, coupled models cannot be fitted to all data sets, e.g., simulating stomatal conductance at low CO_2 concentrations (Wang and Polglase 1995), so caution is required.

Scaling issues

One advantage of Equation 3 is that it can be applied across individual leaf, canopy and patch scales, provided the appropriate values for R, D, T, g_a and g_c are used. For individual leaves, stomatal conductance, g_s, can be readily measured with portable gas exchange systems. At larger scales, transpiration from whole trees and stands is frequently estimated by sap flux and eddy covariance methods, respectively. If it is assumed that g_c is equal to the parallel sum of values of g_{si} for a number of cohorts of leaves in the canopy each with leaf area index L_i, such that $g_c = \Sigma\,(g_{si}\,L_i)$, then measurements made on leaves can be reasonably scaled to canopies. Known as the big-leaf model, such an approach, together with an analogous calculation for g_a and allowance for evaporation from the understory vegetation and soil, provides reasonable estimates of total stand evaporation (e.g., Kelliher et al. 1990, Roberts et al. 1990). However, Raupach and Finnigan (1988) and Monteith (1995*b*) call for caution when applying single-layer models to multi-layer stands based on bulk aerodynamic and canopy conductances. Their concerns include imperfect sampling and averaging of g_s within the canopy and the inclusion of evaporation from other components with different aerodynamic properties, e.g., soil surface. As emphasised by Leuning (1995) for leaves and Jarvis and McNaughton (1986) and Monteith (1990) for canopies, it is important that the air saturation deficit used is the value at the notional evaporating surface, D_s.

Because coniferous forests canopies are aerodynamically rough, values of g_a are generally much larger than values of g_c. Thus, the sensitivity of E to a change in g_c is much higher than

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for a similar change in g_a (Raupach and Finnigan 1988). A further consequence of rough canopies is that there is strong coupling between the canopy and the atmosphere, as indicated by low values of the decoupling coefficient Ω (Jarvis and McNaughton 1986). Analysis based on Ω shows the increasing dependence of transpiration on radiation and decreasing dependence on D as the scale increases from leaf to patch. Estimates of Ω are large in canopies of *Populus* (Hinckley et al. 1994) and for tropical species (Meinzer et al. 1993), indicating only weak coupling between the canopy and atmosphere. This can be explained by high g_a and low g_c for conifers, compared with low g_a and high g_c in broad-leaved canopies (Hinckley et al. 1994). Roberts et al. (1990) showed an increase in Ω with depth in a tropical forest canopy as the leaves become more isolated from the turbulent processes near the top of the trees.

Using control theory, McNaughton and Jarvis (1991) showed that increasing scale introduces more negative feedback responses that stabilize the system. If the ratio of g_s to g_a is small, such as for conifer forests, then E is sensitive to changes in g_s, and models that are capable of predicting g_s in relation to environmental variables are required. But as the ratio of g_s to g_a increases, less sophisticated models are adequate. With an increase in scale to the region, negative feedbacks become even stronger because they interact with the planetary boundary layer, and so the need for complex, multilayered models diminishes. However, transfer of parameters between scales across large heterogenous areas is more complex (McNaughton 1994).

Analysis of data from a wide range of forest conditions has led to the emergence of simplifying relationships for estimating conductances at the patch or regional scale. Generalizing from 15 studies for 10 species of conifers, Jarvis et al. (1976) showed that $g_a \approx 0.1u(h)$ where $u(h)$ is the hourly mean wind speed at canopy height h in m s^{-1}. Kelliher et al. (1993) reviewed evaporation rates from 13 coniferous forest and eight grassland sites on dry days in well-watered conditions and found that, although g_a for forest was an order of magnitude larger than that for grassland, E and g_c (including evaporation from the understory vegetation and soil) were remarkably similar on an hourly basis. However, on a daily basis, maximum E for forest was less than maximum E for grassland. Further, relationships between g_c and D_s were reasonably similar for forests but more variable for grassland. This supports the earlier work of Roberts (1983) who found that annual rates of transpiration from temperate coniferous and deciduous forests are similar. Körner (1994) surveyed values of maximum g_s for more than 20 vegetation classes incorporating nearly 200 species and found large differences in maximum g_s among broad vegetation classes, but within each class, the variation was remarkably small. Kelliher et al. (1995) chose seven vegetation classes from Körner's data set where independent measurements of g_c (including understory vegetation and soil components) were available for well-watered conditions and high irradiance, and showed that, for sites with high leaf area index, the ratio of maximum g_c to maximum g_s was consistently close to 3.

To estimate conductance and thus transpiration and carbon assimilation on a regional or global basis, foliar nitrogen concentration is used as an index for scaling. Positive correlations between leaf nitrogen concentration and photosynthetic capacity for leaves are well established (Field 1983, Hirose et al. 1988), because Rubisco makes up a significant fraction of total leaf protein (Björkman 1968) although evidence for causal relationships is lacking. Field's (1983) hypothesis that nitrogen is distributed optimally within canopies in relation to the distribution of irradiance has been used as the basis for modeling by Leuning et al. (1995); however, observations made in a *Nothofagus fusca* (Hook.f.) Ørst. canopy do not fully support this hypothesis (Hollinger 1996). Nevertheless, foliar nitrogen has proved to be a useful index in accounting for differences in maximum stomatal conductance and photosynthesis among vegetation types. For example, Schulze et al. (1994) used foliage nitrogen distribution to estimate potential carbon assimilation for 15 major biomes across the globe.

Responses of stomatal conductance to hydraulic and chemical signals

Substituting for E from Equation 4 in Equation 2 and expressing $(\Psi_r - \Psi_l - h\rho_w g)$ as $\Delta\Psi/h$ where h is tree height, gives an expression that anticipates that g_s is sensitive to changes in G:

$$g_s \propto \frac{G\Delta\Psi}{hD_sL}. \tag{7}$$

Hydraulic signals are transmitted rapidly, at the speed of sound in water, throughout the plant (Malone 1993), and a link between g_s and G may provide a mechanism to maintain leaf water potential within narrow limits and sustain water and carbon balances within the plant (Sperry et al. 1993). However, although this implies that stomata are able to detect changes in G, the mechanism for such a response is unknown and Equation 7 should be reserved for descriptive purposes only.

There is inconclusive evidence for a link between g_s and G. Teskey et al. (1983) showed that the response of g_s in branches and small seedlings of *Abies amabilis*, when the stem was partially severed and when the roots were partially removed or cooled, was independent of evaporative demand and bulk leaf water potential. Meinzer and Grantz (1990, 1991) demonstrated that stomatal and hydraulic conductances were coordinated in *Saccharum* spp. during development. Lloyd et al. (1991) also concluded that there was a coordinated decrease in g_s and G with soil drying in *Macadamia integrifolia*. A similar relationship was evident for species growing in natural communities. For five woody hedgerow species with different responses of g_s to D, Küppers (1984) found that there was a good seasonal relationship between stomatal conductance and hydraulic conductance. For two of the species, both g_s and G decreased during the summer, although this change was not attributable to decreasing soil water content. Sánchez-Díaz and Mooney (1979) investigated stomatal regulation of water loss in three native desert shrubs in California. Regula-

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tion of transpiration by stomatal conductance was marked in *Atriplex hymenelytra* (Torr.) Wats. but weak in *Tidestromia oblongifolia* (Wats.) Standl. and *Larrea divaricata* Cav.

When 78% of the lower canopy of a 7-year-old *Pinus radiata* tree was shaded, there was an immediate increase in g_s and photosynthetic rate in the top part of the crown that remained illuminated, and canopy conductance per unit illuminated foliage area increased by more than 50%. This effect was rapidly reversible and independent of bulk leaf water potential (Whitehead et al. 1996). The rapidity of the effects in both of these studies suggests that the response was caused by sudden changes in the hydraulic pathway.

There is considerable evidence to suggest that stomatal conductance may be regulated by chemical signals that are independent of hydraulic signals. These chemical signals may be generated in roots and transmitted to leaves in the transpiration stream. Results from split root experiments with *Acer pseudoplatanus* L. (Khalil and Grace 1993) and *Zea mays* L. (Zhang and Davies 1990, 1991) and observations showing that g_s in *Vigna unguiculata* (L.) Walp. is regulated by root water status and is independent of leaf water potential (Bates and Hall 1981) support the role of a chemical messenger acting between roots and leaves.

Passioura and Munns (1984) sealed plant roots in a chamber, then applied pressure and showed that the effects of decreasing g_s in response to soil drying, reduced plant hydraulic conductivity or increased evaporative demand could not be reversed. Similar responses were found for herbaceous species (Gollan et al. 1986). These observations could be accounted for by the action of a chemical messenger, probably abscisic acid (ABA), formed in the roots and transported in the xylem stream (Passioura and Munns 1984, Zhang and Davies 1990). However, using the same technique, Fuchs and Livingston (1996) found that the effect could be reversed with woody plants. The decrease in g_s resulting from soil drying or increased D in *Pseudotsuga menziesii* and *Alnus rubra* Bong. seedlings was rapidly, fully or partially reversed by pressurizing the root system. When the pressure was relieved, g_s decreased almost immediately. Saliendra et al. (1995) used the same technique with *Betula occidentalis* Hook. by making cuts at the base of the stem, and showed that g_s increased when roots were pressurized. Lloyd et al. (1991) proposed that the initiation of the root signal could occur in response to a decrease in root conductance as the surrounding soil becomes progressively drier.

There is strong evidence for a relationship between stomatal conductance and ABA concentration in the xylem of woody plants, e.g., Khalil and Grace (1993), Tardieu et al. (1993). Fuchs and Livingston (1996) report a fourfold increase in xylem ABA concentration when well-watered seedlings of *Pseudotsuga menziesii* were subjected to drought. However, the flux of ABA into the leaves did not increase because g_s and E decreased. Correia et al. (1995) showed that ABA concentration in the xylem sap accounted for differences in midsummer maximum values of g_s in *Vitis vinifera* L. growing in soil with contrasting water availabilities. However, diurnal changes in ABA concentration were not consistent with changes in g_s (Wartinger et al. 1990, Correia et al. 1995). Experiments with detached leaves show that g_s responds to ABA applied to the transpiration stream in a manner consistent with its response in the same plants growing in drying soils (Tardieu et al. 1993).

A close relationship between g_s and ABA concentration does not provide conclusive evidence that stomata are regulated by the concentration of a chemical signal originating in the roots, because the same effect could be achieved by dilution of the messenger with increasing g_s and E (Tardieu 1993). Further, the rapidity of the response of g_s to a perturbation in the hydraulic pathway in large trees suggests that the mechanism is more complex than the generation of ABA in the roots and its transport in the xylem to the leaves (Davies and Zhang 1991, Saliendra et al. 1995, Whitehead et al. 1996). Sperry et al. (1993) induced reductions in conductance by making transverse cuts in the xylem of the stems of woody plants. The resulting decrease in g_s was not instantaneous, but occurred over a period of 20 min. The rooting environment was held constant during the experiments, suggesting that the response did not result from a chemical messenger from the roots.

The mechanism of the response of stomata to ABA is not known because a receptor for detecting changes in ABA concentration has not been identified (Meinzer and Grantz 1990, Sperry et al. 1993). Gowing et al. (1993) determined that the half-life of ABA in xylem sap is 36 min and concluded that turnover is sufficiently fast to allow regulation of its concentration in the leaf apoplast and guard cells without an apparent change in bulk leaf ABA concentration. The concentration of ABA in the guard cells is likely to result from both the rate of entry into the leaf (Jackson et al. 1995*b*) and the concentration in the transpiration stream. This is consistent with a direct link between xylem sap ABA concentration and the concentration reaching the guard cells (Tardieu and Davies 1993). Another explanation is that the source of ABA in the leaf and its release from the symplast of mesophyll cells results in a change in apoplastic ABA concentration (Hartung and Slovik 1991). Perhaps hydraulic signals resulting from a change in either hydraulic conductance or water potential gradient trigger the release of ABA in the leaf. A decrease in epidermal water potential would sensitize stomata to ABA delivered to the apoplast in the transpiration stream (Tardieu et al. 1993).

The relative importance of the chemical and hydraulic signals is likely to depend on plant size and growing conditions. The short-term response of stomata to environmental variables could result from hydraulic signals related to evaporative demand and this could be moderated by changes in the sensitivity of g_s to ABA concentration in leaves throughout the day. The long-term response of decreasing g_s as the soil becomes progressively drier could be regulated by a gradual, more stable change in ABA concentration of the xylem sap. The concentration would remain reasonably constant and stomatal response to this messenger would depend on evaporative demand. In large trees, a rapid response of g_s to a change in the water potential gradient could be initiated by a hydraulic signal, but in small plants, stomata may be more sensitive to changes in ABA concentration, possibly originating in the roots.

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To explain the response of stomata to changes in soil water status or air saturation deficit, Tardieu (1993) and Tardieu and Davies (1992, 1993) developed an interactive model that incorporates both hydraulic and chemical signals. The model has three criteria: (i) if the production of the chemical messenger depends on root water status, it will also depend on the rate of transpiration and soil water potential; (ii) an increase in transpiration will dilute the concentration of the messenger in the xylem sap; and (iii) stomatal sensitivity to the messenger will be increased as leaf water potential falls. Transpiration from the plant is estimated from weather variables and aerodynamic properties by the Penman-Monteith equation and this determines the water potential gradients between the roots and leaves and between the soil and roots, for a given soil water status and set of hydraulic properties. The ABA concentration in the xylem sap is dependent on root water potential and transpiration rate. Stomatal conductance is simulated from a function combining the effects of xylem ABA concentration and leaf water potential.

Although the model employs only five equations with five unknowns (g_s, E, xylem ABA concentration, Ψ_l and Ψ_r), it is exceptionally good at reproducing the effects of two very different mechanisms that regulate stomatal response. For example, for *Zea mays* the model reproduces the reduction in g_s of drought-exposed plants in the afternoon, but not in the morning, with little apparent change in leaf ABA concentration.

The significance of hydraulic signals and the role of chemical signals in regulating stomatal conductance are still uncertain and the effects have not yet been incorporated into canopy scale models of transpiration. However, Tardieu's modeling approach provides a rigorous basis for developing concepts and elucidating mechanisms.

Adaptive significance of links between hydraulic and stomatal conductances

Zimmermann (1978) mapped the hydraulic properties of entire trees by measuring the flow along branch sections throughout the tree crown and dividing this by the weight of leaves supported by each branch. This quantity is known as leaf specific conductivity and high values correspond to a low water potential gradient required to supply water to the leaves supported by the branch (Tyree and Ewers 1991). This work showed that the values of leaf specific conductivity for small branches near the tips were lower than for major branches and that branch insertions in the stem provided significant resistance to flow. In broad-leaved trees, changes in conductance within the crown occur as a result of a decrease in the cross-sectional area of sapwood, and also because of decreasing vessel diameter with height in the crown and physical constrictions at the base of branches. Yang and Tyree (1994) used a pressure perfusion method to estimate stem and leaf resistances to water flow in *Acer* species. On a leaf area basis, the distribution of resistance for trees less than 0.2 m in diameter was 50% in the leaves and petioles, 35% in crown xylem and 15% in trunk xylem. In conifers, conductance per unit sapwood cross-sectional area is determined principally by tracheid length (Pothier et al. 1989) or the size of the bordered pits (Panek 1996).

Tyree and Sperry (1988) used a model based on the work by Zimmermann to show that flow rates in the xylem often reach the maximum values that can be achieved within the limits set by evaporative demand, conductivity and the water potential gradient. Flow rates greater than the theoretical maximum would result in cavitation of the conducting vessels and evidence suggests that the margin of safety before cavitation occurs is frequently small. During drought, the peripheral parts of the tree are more vulnerable to cavitation (Zimmermann 1978). Tyree and Sperry (1988) proposed that decreasing stomatal conductance in response to falling leaf water potential is a mechanism that avoids catastrophic xylem embolism.

Machado and Tyree (1994) found that the tropical evergreen *Ochroma pyramidale* (Cav.) Urb. and the tropical deciduous *Pseudobombax septenatum* (Jacq.) Dug. were more vulnerable to cavitation when water was not limiting than temperate species. Hydraulic architecture of the evergreen tree was only slightly more efficient than that of the deciduous tree, and the vulnerability to embolism induced by water deficit was independent of water availability and phenology, indicating that the ability to avoid cavitation did not account for the deciduous nature. Jackson et al. (1995*a*) did not find *Pinus sylvestris* trees growing at a dry site any less vulnerable to cavitation, measured as the water potential when cavitation occurred, than trees growing at a wet site. However, Tognetti et al. (1997) found that *Pinus halepensis* Mill. seedlings originating from dry sites were more drought-tolerant than seedlings originating from wet sites. During drought, the reduction in conductivity was less for seedlings from dry sites than for seedlings from wet sites. The process of refilling tracheids in conifers after they have cavitated is not known, although seasonal changes in sapwood water content and, presumably, cavitation have been measured. Partial recovery from tracheid cavitation can occur overnight (Sobrado et al. 1992), but full recovery usually takes much longer (Waring et al. 1979) and may be achieved only by the growth of new xylem elements.

The link between g_s and conductivity and its role as a mechanism for avoiding cavitation has been tested experimentally for several woody species. Sperry and Pockman (1993) reduced hydraulic conductance in *Betula occidentalis* by injecting air into the vascular system to induce cavitation. There was a reduction in g_s, but it was not sufficient to avoid long-term cavitation and leaf dieback. Using the same technique, Sperry and Ikeda (1997) injected air into roots of *Pseudotsuga menziesii*. Smaller roots were more vulnerable to cavitation than larger roots and roots growing on the up-slope side of the tree were more resistant than roots growing on the down-slope side. The differences were correlated with tracheid diameter. Overall, roots were more vulnerable to cavitation than stems or branches, possibly because of a greater area of pit membranes. Sperry and Ikeda (1997) proposed that, during periods of drought, cavitation in small roots would hydraulically isolate the conducting system from dry soils. After a period of rain, tracheids in the isolated root system could become refilled and continue conducting, or newly grown roots could

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replace those lost from the conducting network. This is consistent with the conclusion from a modeling approach by Landsberg and McMurtrie (1984) that, for efficient water uptake, root development should be commensurate with G.

Several models have been developed to identify the significance of decreasing g_s in the balance between preventing catastrophic xylem embolism and maximizing photosynthesis and productivity. For example, Jones and Sutherland (1991) provide an analytical solution showing that stomatal behavior resulting in some embolism and loss of xylem elements is necessary if productivity is to reach its maximum. More recently, Williams et al. (1996) have developed a more complex model that scales leaf-level processes of transpiration and photosynthesis to stands. The ten-layer canopy model incorporates vertical distributions of leaf area, nitrogen concentration, radiation and boundary layer properties, based on an iterative approach. Each layer has an independent hydraulic system, including capacitance effects. The model demonstrated that, in the upper canopy of a mixed deciduous *Quercus–Acer* forest at midday, hydraulic conductance is reduced such that a decrease in g_s is necessary to avoid water potential reaching a critical limit and causing xylem cavitation. This effect was less pronounced deeper in the canopy.

To investigate further the balance between water potential gradient and transpiration in plants, it is helpful to introduce explicitly the physical properties of the conducting system in Equation 7. This is achieved by including the cross-sectional area of the conducting path (sapwood), A_s and the relative conductivity term, k, from Darcy's law to give:

$$g_s = \frac{kA_s\Delta\Psi}{h\eta LD_s}, \tag{8}$$

where η is the viscosity of water at the appropriate temperature (Whitehead and Jarvis 1981). It is also useful to define the flow properties with respect to the ratio of foliage area to conducting (sapwood) cross-sectional area, S. For a stand of trees with leaf area and sapwood area expressed in the same terms, rearranging Equation 8 gives:

$$S = \frac{k\Delta\Psi}{h\eta g_s D_s}. \tag{9}$$

This equation implies the hypothesis that the growth of stands in conditions with different evaporative demand (represented by D_s) will lead to differences in g_s, k or S as a result of a homeostatic response to maintain the water potential gradient ($\Delta\Psi/h$) within narrow limits. This analysis can be applied to stands to interpret changes in the balance between stomatal and hydraulic properties as the stands develop. The equation also identifies the dependence of S on local or regional climate, represented by D_s. For *Pinus sylvestris* at one site, Whitehead et al. (1984*b*) showed that the water potential gradient was maintained 14 years after a stand was last thinned by a near proportional increase in the foliage area and cross-sectional area of sapwood for the individuals in the stand. Comparisons between *Picea sitchensis* and *Pinus contorta* Dougl. *ex* Loud. growing at sites with similar evaporative demand showed that differences in S were accounted for by differences in k between the two species (Whitehead et al. 1984*a*). A similar conclusion was reached by Coyea and Margolis (1992) based on a comparison of 24 stands of *Abies balsamea* (L.) Mill., but variations in k were also accompanied by differences in h.

The first full test of the hypothesis in Equation 9 at different sites with contrasting conditions of evaporative demand was undertaken for two stands of the same provenance of *Pinus sylvestris* by Mencuccini and Grace (1995). There were no differences in k, but the value for S was less at the warmer, drier site (i.e., less foliage area per unit conducting cross-sectional area) than at the cooler, wetter site, so similar water potential gradients existed at both sites. This implies that trees respond to increased transpiration demand (higher D_s) by structurally reducing the ratio of foliage area to sapwood cross-sectional area.

The development of the theory of carbon isotope discrimination during photosynthesis is providing useful insights into the adaptive processes linking stomatal responses to water use efficiency (Comstock and Ehleringer 1992) and the flow properties of the conducting pathway. For stands of *Pseudotsuga menziesii* aged between 20 and 39 years, Livingston and Spittlehouse (1996) used a simple water balance model to demonstrate that differences between spring and summer cumulative transpiration accounted for more that 60% of the variability in early and latewood $\delta^{13}C$ between stands. Walcroft et al. (1996) measured $\delta^{13}C$ variability across individual annual rings in *Pinus radiata* and showed that it was closely related to changes in c_i associated with the seasonal onset of drought.

Read and Farquhar (1991) grew seedlings of 22 *Nothofagus* species from throughout the southern hemisphere in a common garden and found a negative correlation between leaf $\delta^{13}C$ values and growing season precipitation at their native habitats. The interpretation was that the species growing in drier climates had evolved higher values of k so that g_s and c_i would remain high during periods of drought. High values of k were observed especially for species from high latitudes, where the driest periods occur during the warmest months, and appeared to be a genetic adaptation to drought tolerance. Further support for genetic adaptation of hydraulic properties in relation to evaporative demand was provided from a comparison of several species growing in different environments by Williams and Ehleringer (1996). In the tropical species *Quercus gambelii* Nutt. there was a negative correlation between $\delta^{13}C$ values and monsoon precipitation. Morphological changes to accommodate seasonal changes in evaporative demand were not possible because of the fixed pattern of growth in this species. In two other species with more flexible morphology, *Juniperus osteosperma* (Torr.) Little and *Pinus edulis* Engelm., there was evidence that seasonal adjustments to hydraulic conductivity could occur to allow transpiration to vary with evaporative demand, while maintaining a similar g_s and c_i at all sites. This is consistent with the findings of Mencuccini and Grace (1995) with *Pinus sylvestris* and suggests a strong relationship between $\delta^{13}C$ and k. A theoretical basis for such a relationship is derived in the Appendix to the paper by Panek (1996) in which she shows a strong relationship between $\delta^{13}C$ and con-

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ducting capacity in branches of *Pseudotsuga menziesii* across a climate gradient in Oregon.

A hypothesis that has recently emerged is that the decrease in productivity as forest stands age is attributable, at least in part, to decreases in k, resulting in decreases in g_s and photosynthesis. Decreases in productivity with stand age are not entirely attributable to an increase in respiration (Ryan et al. 1997). There is also evidence that transpiration decreases with stand age (Kline et al. 1976, Yoder et al. 1994).

Mencuccini and Grace (1996*a*) measured hydraulic conductances in 7- to 59-year-old *Pinus sylvestris* trees at one site. The aboveground conductance per unit leaf area in mature trees was one quarter that in young trees. The increase in cross-sectional sapwood area per unit leaf area was 3.5 times higher in the mature trees, but this was not sufficient to offset the increase in pathlength, which was 20 times longer in mature trees than in young trees. Increased branchiness with stand age was also interpreted as a compensation mechanism to create more parallel conducting pathways and increase xylem flow. Estimated net primary productivity increased until the trees were about 15 to 20 years old, then decreased in older stands. This pattern of age-related changes in productivity was the same as that for conductance, and there was a strong positive correlation between conductance and growth efficiency, i.e., biomass increase per unit foliage area (Mencuccini and Grace 1996*b*). Part of the contribution to decreased productivity with stand age was the increase in maintenance respiration associated with greater sapwood volume.

A decrease in k with age is probably related to xylem structural properties. In *Pinus banksiana* Lamb., Pothier et al. (1989) measured an increase in tracheid length with tree age up to 50 years, but no further increase occurred in older trees. Likewise, Mencuccini et al. (1997) measured increases in diameter and length of tracheids with tree age in *Pinus sylvestris*, but the maxima were reached at ages 15 and 35 years, respectively. For older trees, a decrease in sapwood conductance with increasing tree height would be expected if tracheid diameter and length were no longer increasing. Mencuccini et al. (1997) also measured a decrease in the number of tracheids per unit area of sapwood with age. Ryan and Yoder (1997) speculate that the decrease in conductivity with age would result in loss of xylem by cavitation in the peripheral parts of the tree, providing a feedback mechanism to limit tree height.

Conclusions

Stomatal regulation of transpiration and photosynthesis at the leaf scale is well described, although the mechanisms underlying the response of stomata to environmental variables are not understood. The theoretical analysis by Dewar (1995) provides a mechanism for the linear decrease in g_s with increasing E observed by Monteith (1995*a*). However, the debate concerning how stomata sense changes in either E or D_s, and the implications for stomatal regulation, remains unresolved. Phenomenological models describing short-term changes in g_s (Jarvis 1976) are used widely for estimating transpiration rates over long time periods. Although the responses of transpiration and photosynthesis to seasonal water deficits can be modeled effectively, the functions describing the decrease in g_s with declining soil water availability (e.g., Giles et al. 1985) are usually determined empirically and do not consider the underlying mechanisms. Although the coupling of stomatal conductance with photosynthesis in models (e.g., Leuning 1995) recognizes the close relationship between g_s and A, inclusion of sufficient detail to describe stomatal responses to all conditions, particularly extremes in CO_2 concentration, has yet to be achieved. Aphalo and Jarvis (1993) point out that coupled models need independent functions describing the response of stomata to each environmental variable, not just a multiplicative approach. However, coupled models are attractive because fewer parameters are required.

Models incorporating processes at the leaf level can be used to determine fluxes of energy, water vapor and CO_2 at the canopy scale, providing that the distribution of irradiance and the turbulent properties are considered (Raupach and Finnigan 1988). Baldocchi et al. (1991) have compared the top-down and the bottom-up approaches to determine g_c in forest canopies. The top-down approach is attractive because it integrates across detail and the functions are based on simple laws. Only a few, simply measured variables are required as inputs, but predictions are often restricted to the conditions from which the models are derived. The bottom-up approach incorporates detailed process information, but simplifications to this are required when scaling upward. The big-leaf approach is used widely, but caution is required when there are several sources and sinks for water vapor and CO_2 (Raupach and Finnigan 1988). Multi-layer models are more complex, but allow for the allocation of parameters appropriate to different classes of foliage within the canopy. The vertical distribution of foliage nitrogen concentration is helpful for scaling the parameters with depth (Leuning et al. 1995, Williams et al. 1996). With an increase to the patch scale, the significance of negative feedback responses becomes stronger and the need for complex, multi-layer models diminishes (McNaughton and Jarvis 1991).

There is considerable evidence to suggest that stomata respond to signals generated within a plant that are independent of environmental variables. The nature of these signals is known to be hydraulic, but may also involve a chemical messenger. The demonstration that applying root pressure to plants growing in drying soils did not result in the reopening of stomata in some herbaceous plants (Passioura and Munns 1984) but did in other woody plants (Fuchs and Livingston 1996) has provided new insight, and highlighted important differences in response to soil drying between woody plants and herbaceous species.

Although evidence suggests that ABA acts as a chemical messenger in both short- and long-term responses of stomata to soil water status and hydraulic properties of the flow pathway, the sensing mechanism has not been identified. It seems unlikely that the ABA is of root origin, at least in large trees, because the stomatal response is very rapid (Saliendra et al. 1995). A more plausible explanation is that the generation of a hydraulic signal results in the release of ABA in the leaves. These interactive mechanisms are recognized in the

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model developed by Tardieu and Davies (1993). The success of this approach is a major step forward in understanding the mechanisms involved, although the need to incorporate the production and transport of a chemical messenger into models designed to predict stomatal response in field systems is not yet widely accepted.

The finding that many plants operate close to the limits for cavitation in the xylem (Tyree and Sperry 1988) emphasizes the tight regulation between stomatal conductance and the hydraulic properties of the flow pathway. In forest stands, homeostatic mechanisms operate to maintain leaf water potential within narrow limits. This is achieved by a balance between evaporative demand and the flow properties of the pathway as shown in Equation 9 (Mencuccini and Grace 1995). Transpiration is dependent on foliage area and mean stomatal conductance, and the properties of the pathway are determined by the cross-sectional area of sapwood and its conductivity. Evidence from stands of different ages suggests that hydraulic constraints may account for the decline in growth efficiency as stands age (Mencuccini and Grace 1996*b*, Ryan et al. 1997) and this concept is now being incorporated into models that predict productivity (Landsberg and Waring 1997).

Techniques for measuring the variables illustrated in the equations in this review have improved considerably during the last decade. Partial flows within tree stems and branches can readily be measured by means of continuous sap flux system and large numbers of measurements of stomatal conductance and photosynthesis in field conditions can be made with commercially available portable gas analysis systems. Rates of exchange of water vapor from forest canopies are now made continuously for periods of up to several years by the eddy co-variance technique. Soil water status can be monitored continuously by time domain reflectometry. The more recent measurement of carbon isotope discrimination in plant tissues, and the development of techniques for the measurement of concentrations of isotopes in very small quantities of gas sampled from within and above forest canopies, are contributing new insights into processes and providing data for validating models.

In contrast to the relative ease with which fluxes of water can be measured, techniques to measure the gradients of water potential between cells within leaves, or within whole plants have advanced little since the need to measure them was identified two decades ago (Jarvis 1975). This limitation impedes progress in elucidating many of the mechanisms discussed in this review. Another limitation on further progress is a lack of knowledge about the functional role of roots, their distribution, the processes of water uptake in relation to soil water availability, and the implications of these for the regulation of stomatal conductance by plants.

The further development of models will continue to identify research requirements. An example of the state-of-the-art in modeling water transport through plants is provided by Williams et al. (1996). This model combines our current understanding of leaf-level processes of energy balance, stomatal conductance, photosynthesis and hydraulic properties, including capacitance, in the flow path between soil and leaves for ten layers throughout the canopy. Vertical distributions of leaf area density, nitrogen concentration, radiation and aerodynamic properties in relation to windspeed are incorporated. The model has been tested for a *Quercus–Acer* forest in summer by comparing the estimated flux of CO_2 with measurements made with an eddy covariance system.

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