

Modelling stomatal conductance (g_s), CO₂ assimilation (A), and transpiration ($E_{L,a}$) of an individual leaf, using the response to the leaf to its local or "aerial" environment and to ABA as a root-sourced signal of water stress.

1. Introduction

There is a long history of models to estimate g_s and thus A and $E_{L,a}$ from the environment of the plant and its physiology. The aim here is to present one full model recently developed by V. P. Gutschick (New Mexico State University, Las Cruces, NM, USA) and Thierry Simonneau (INRA / Ecole Nationale Supérieure Agronomique - Montpellier, France) with the cooperation of François Tardieu (INRA / ENSA - M). This model combines, in one of two choices of mathematical form, the water-stress or ABA response of stomata with the stomatal response to the aerial environment. The latter response is modelled as a combination of the Ball-Berry stomatal-control model (Ball *et al.*, 1987) with standard equations of energy balance (to set leaf temperature, T_L) and of CO₂ assimilation. (Our manuscript, under review, details how we chose the Ball-Berry model in particular.)

The ABA response is modelled as an negative-exponential response to ABA, which we may denote as a factor g_{fac} . It is combined with the Ball-Berry response in two forms. Let the Ball-Berry response be represented as a linear relation, $g_s = m I_{BB} + b$. The parameters m and b are fitting parameters, and the index I_{BB} will be detailed later; it depends on CO₂ assimilation and other variables. The first form, which we found a better fit in our manuscript in review, is what we term the multiplicative model; the ABA factor simply multiplies the Ball-Berry slope, m :

$$g_s \approx g_{fac} m_0 I_{BB} + b \quad (1)$$

The second form sets g_s as the minimum of a Ball-Berry form and a form responsive to ABA and a maximal conductance, $g_{s,max}$:

$$g_s \approx \min [m I_{BB} + b, g_{fac} g_{s,max}] \quad (2)$$

This we term the model of the minimum.

Our model begins with the purely abiotic variables (meteorological, soil hydraulic), fixed structural descriptors of the plant (leaf dimensions, canopy geometry if one wishes, root geometry), and plant physiology (carboxylation capacity, ABA-response parameters). The full model is presented here in narrative form, to enable one to use the Fortran-77 version of the model. While the Fortran code is extensively commented, it does not serve as a useful introduction of the model. In order for one to know what descriptors are needed and in what units, to know the complete description of the model (all its equations), and to understand the mathematical method of solution, we provide this narrative.

The local environment of the leaf is described by the abiotic variables of PAR irradiance (PPFD), other shortwave energy flux density (in the near infrared, or NIR), thermal infrared flux density, windspeed (to set boundary-layer conductance), air temperature, and air humidity (as water-vapor partial pressure, e_a). These variables drive A , leaf energy balance (setting leaf temperature, T_L), and stomatal conductance, but these three relations involve each other and each relation is nonlinear, so that special techniques of mathematical solution are needed. The leaf also responds to ABA, which is generated in the roots in response to root water potential (ψ_r) and

the root transpirational stream through the root per unit area (J_r). The root water potential depends upon the soil water potential (ψ_s) and the drop in ψ in transport of water through the soil; thus, it depends on soil hydraulic conductivity and some basic elements of root geometry (diameter, spacing, clumping factor). Because ψ_r depends on the whole-plant transpiration rate, there is another linkage to the leaf transpiration rate (the three equations above) and to the canopy geometry (total leaf area and the distribution of light, often modelled simply). The leaf response to ABA is modelled (Gutschick *et al.*, in review) as an exponential decrease in responsiveness of stomatal conductance, specifically as this factor applied to the slope in the Ball-Berry model. The response parameter, β , in some plant species has a further dependence upon leaf water potential (ψ_L), again bringing in a feedback loop.

This guide is a practical one. Relatively few literature references are presented, since much of the formulation is standard. It is the composition of the model and its method of mathematical solution that is unique and which is the focus here. This narrative is intended to allow anyone to use the model by specifying the environment and the physiology of the leaf.

2. The response of the leaf to the local or "aerial" environment

2.A. Standard equations of leaf energy balance

Leaf temperature reacts in response to radiative exchanges, convective heat transfer, and transpirational cooling...which involves g_s . The key prediction is that of leaf temperature, T_L . The basic equation of energy balance is written for the steady state (we don't deal with transients, at present; most important for succulents and for understory plants sustained by sunflecks).

Radiant energy is intercepted as PAR, near infrared (NIR), and thermal infrared (TIR). The respective energy flux densities may be denoted as Q_i , $i = \text{PAR, NIR, or TIR}$; SI units are W m^{-2} . In the current version of the model, aimed at some simplicity and primarily for leaves near the top of the canopy, the PAR and NIR energy-flux densities are taken as equal. The common PAR flux density that one measures is the quantum flux density, PPF. The average mole of PAR photons (at a wavelength of 550 nm) has an energy content of 220 kJ. Thus, if we specify the PPF in $\mu\text{mol m}^{-2}\text{s}^{-1}$, the conversion to total shortwave energy flux *absorbed* is

$$Q_{\text{SW}}^+ @ = 0.22 (a_{\text{PAR}} + a_{\text{NIR}}) \text{ PPF} \quad (3)$$

The factors a_{PAR} and a_{NIR} are clearly the absorptivities.

TIR flux density can be complicated to model, but some simple approximations capture the essentials. Nearby terrestrial surroundings, often mostly other vegetation, has a reasonably well-defined average temperature, which we may call T_{veg} . It produces an isotropic flux density

$$Q_{\text{TIR}}^{\text{veg}} \approx \sigma (T_{\text{veg}} + 273.2)^4 \quad (4)$$

Here, σ is the Stefan-Boltzmann constant and the addend 273.2 converts to absolute T in Kelvin. We omit the emissivity, ϵ , because the vegetation also reflects other TIR at roughly the same T (this can cause an error at the top of the canopy; better approximations exist). Continuing, we also ascribe an effective radiative temperature to the sky, T_{sky} . In dry areas in cloudless conditions, this can be more than 35 K below air temperature. Various approximations exist to estimate either T_{sky} or its TIR flux density (*e.g.*, Brutsaert, 1975, 1982). In any event, given T_{sky} , one

computes the corresponding TIR flux density, $Q_{\text{TIR}}^{\text{sky}}$, by an exact analog of Eq. (4). To get the total TIR flux density intercepted, one sums the two. One can also account for a leaf below the top of the canopy not being fully exposed to the sky. If the sky is seen in a fraction f_{sky} of solid angle at the leaf location, the appropriate sum is

$$Q_{\text{TIR}}^+ \approx f_{\text{sky}} Q_{\text{TIR}}^{\text{sky}} + (2 - f_{\text{sky}}) Q_{\text{TIR}}^{\text{veg}} \quad (5)$$

Radiant energy is emitted by the leaf at the blackbody rate, approximated simply as $\sigma (T_L + 273.2)^4$. The unknown to be solved for is T_L , as in the remaining terms of the energy-balance equation.

Convective cooling of the leaf follows Newton's law of cooling. The leaf has a boundary layer of nearly-laminar air. It has a corresponding conductance for water vapor, in molar units, that is closely approximated as dependent on windspeed u (m s^{-1}) and a characteristic leaf linear dimension d_{leaf} as

$$g_b \approx 0.264 (\text{mol m}^{-2} \text{s}^{-1/2}) \sqrt{u/d_{\text{leaf}}} \quad (6)$$

The characteristic dimension is readily estimated for entire leaves. It is trickier for dissected leaves and compound leaves; see Gurevitch and Scheupp (1990).

Given g_b along with air temperature (T_a) and leaf temperature, the rate of heat loss from leaf to air is written as

$$Q_c = C_{p,m} g_b (T_L - T_a) \quad (7)$$

The molar heat capacity of air at constant pressure, $C_{p,m}$, is very closely $29 \text{ J mol}^{-1} \text{ K}^{-1}$.

Latent heat loss or transpirational cooling equals the leaf transpiration rate per area ($E_{L,a}$, in units of $\text{mol m}^{-2} \text{s}^{-1}$) multiplied by the molar heat of vaporization of water, λ . There is a slight variation of λ with temperature in the biological range, which we ignore in setting $\lambda = 45000 \text{ J mol}^{-1}$. The transpiration rate equals the total conductance (stomata plus boundary layer) multiplied by the vapor-pressure deficit from leaf interior to ambient air as a mole fraction,

$$E_{L,a} = g_{\text{tot}} \frac{(e_L - e_a)}{P_{\text{air}}} \quad (8)$$

Here, P_{air} is the total air pressure (in Pa). The total conductance of the series resistors is

$$g_{\text{tot}} = \frac{1}{1/g_s + g_b} \quad (9)$$

(Note that conductances presented without qualifiers are for water vapor. Terms such as CO_2 will be added to subscripts for other cases.) In Eq. (9), the water-vapor pressure inside the leaf at temperature T_L is taken as the saturated vapor pressure of pure water. A very accurate formula to approximate the latter is

$$e_L = 610.8 \text{ Pa } e^{17.269 * T_L / (237.2 + T_L)} \quad (10)$$

The only unknown is again T_L . (A correction can be applied for the lower vapor pressure when the leaf is at a known ψ_L , by applying the multiplier $\exp(\psi_L V_w / RT)$, with V_w as the molar volume of liquid water ; we do not do this presently in the model.)

Summary

One needs to know standard physical constants such as λ , plus the following "fixed" quantities describing the environment and the leaf structure:

PPFD ($\mu\text{mol m}^{-2}\text{s}^{-1}$); this ranges up to about 2300 in the noted units

$a_{\text{PAR}}, a_{\text{NIR}}$ (-, meaning unitless); typically about 0.85

$T_{\text{veg}}, T_{\text{sky}}$ (both in $^{\circ}\text{C}$)

T_{a} ($^{\circ}\text{C}$)

d_{leaf} (m)

u (m s^{-1})

e_{a} (Pa)

P_{air} (Pa)

The one unknown is g_{s} . Any guess for g_{s} allows one to solve a transcendental equation for T_{L} :

$$0 = Q_{\text{SW}}^+ + Q_{\text{TIR}}^+ - \sigma (T_{\text{L}} + 273.2)^4 - C_{\text{P,m}}g_{\text{b}}(T_{\text{L}} - T_{\text{a}}) - \lambda g_{\text{tot}}(e_{\text{L}}(T_{\text{L}}) - e_{\text{a}})/P_{\text{air}} \quad (11)$$

2.B. The Ball-Berry equation of stomatal control (Ball et al., 1987)

This is written as

$$g_{\text{s}} \approx m A h_{\text{s}}/C_{\text{s}} + b \quad (12)$$

Here, m and b are fitting parameters (fairly robust = nearly constant among species and conditions other than water relations), and $h_{\text{s}}, C_{\text{s}}$ are the relative humidity and the CO_2 mixing ratio at the leaf surface, beneath the leaf boundary layer. This involves T_{L} (in computing h_{s}), so that at least two nonlinear equations, (11) and (12), must be solved simultaneously. The calculation also involves A (directly, and in computing s), so that an equation (C, below) must also be solved simultaneously.

The relative humidity at the leaf's surface, h_{s} , is simply the ratio of waer-vapor partial pressure at the leaf surface, e_{s} , divided by the saturated vapor pressure at leaf temperature, e_{L} . We can derive an expression for e_{s} by equating two expressions for the leaf transpiration rate,

$$E_{\text{L,a}} = g_{\text{s}}(e_{\text{L}} - e_{\text{s}}) = g_{\text{b}}(e_{\text{s}} - e_{\text{a}}) \quad (13)$$

The result is that

$$h_{\text{s}} = \frac{e_{\text{s}}}{e_{\text{i}}} = \frac{e_{\text{a}}/e_{\text{L}} + g_{\text{s}}/g_{\text{b}}}{1 + g_{\text{s}}/g_{\text{b}}} \quad (14)$$

Again, once g_{s} is specified (and Eq. (11) for L is solved), all the other quantities are known.

The CO_2 partial pressure at the leaf's surface, C_{s} , is computed simply from the transport equation for CO_2 ,

$$C_{\text{s}} = C_{\text{a}} - 1.37 A P_{\text{air}}/g_{\text{b}} \quad (15)$$

The factor 1.37 converts from conductance for water vapor to conductance for the heavier CO_2 molecule. The factor P_{air} is needed because A is expressed as a molar conductance multiplied by a CO_2 "gradient" expressed as a mole fraction, $[\text{CO}_2]/P_{\text{air}}$.

The terms A and C_{s} bring in the assimilation equation, which must also be solved simultaneously with Eqs. (11) and (12).

Summary. One needs to know standard physical constants, plus the following "fixed" quantities describing the environment and the leaf structure:

m , or, really, m_0 (-); common value is 10
 b ($\text{mol m}^{-2}\text{s}^{-1}$); commonly near 0, rarely as high as 0.5
 e_a (Pa) - already needed in energy balance
 u and d_{leaf} to compute g_b - already needed in energy balance
 C_a (Pa)

The unknown is A , which involves the next equation:

2.C. The leaf's CO_2 assimilation rate, A

This is modelled using the well-tested model of Farquhar, von Caemmerer, and Berry (1980). It describes:

(i) A *light-saturated rate*, A_{sat} that depends upon leaf-internal CO_2 partial pressure (C_i) and on temperature (as well as O_2 partial pressure, O)

$$A_{\text{sat}} = V_{\text{c,max}} \frac{(C_i - \Gamma)}{(C_i + K_{\text{CO}})} \quad (16)$$

Here, $V_{\text{c,max}}$ is the maximal carboxylation rate (light- and CO_2 -saturated) of the leaf, per area; Γ is the CO_2 compensation partial pressure, a function purely of T_L ; and K_{CO} is the effective Michaelis constant for CO_2 binding by Rubisco enzyme, a function of temperature and of O . See de Pury and Farquhar (1997) for numerical constants and the forms of temperature dependence, which are built into our model.

(ii) A *light-limited rate*, A_{LL} , dependent on the PAR photon-flux density (I_L), C_i , L , and a CO_2 -saturated initial quantum yield (Q_{00}):

$$A_{\text{LL}} = Q_0 I_L = Q_{00} \frac{(C_i + \Gamma)}{(C_i + 2\Gamma)} \quad (17)$$

(iii) A *transition between the two limiting cases*, involving a convexity parameter (θ).

$$\theta A^2 - A (A_{\text{sat}} + A_{\text{LL}}) + A_{\text{sat}} A_{\text{LL}} = 0 \quad (18)$$

When θ is 1, this factors into two equations with solutions $A = A_{\text{sat}}$ or $A = A_{\text{LL}}$. When θ is 0, Eq. (18) describes the older approximation, the rectangular hyperbola, $A = A_{\text{sat}} I_L / (I_L + I_{\text{sat}})$, with $I_{\text{sat}} = A_{\text{sat}} / Q_0$.

In order to solve Eqs. (16)-(18), one needs to express C_i in terms of the environmental variables such as C_a and A itself,

$$A = g_{\text{tot,CO}_2} (C_a - C_i) / P_{\text{air}} \quad (19)$$

One can substitute the form Eq. (19) into Eq. (18) and obtain a quartic equation in C_i . This can be solved numerically, and then C_i can be substituted into Eqs. (16) and (17) to obtain A . Again, one must have an estimate of g_s (in order to compute $g_{\text{tot,CO}_2} = 1 / (1.6/g_s + 1.37/g_b)$), plus the environmental variables.

Summary. One needs to know some universal physiological constants for carboxylation, plus the following "fixed" quantities describing the environment and the leaf structure:

$V_{\text{c,max}}$ ($\mu\text{mol m}^{-2}\text{s}^{-1}$)
 O (Pa)
 $\text{PPFD} = I_L$ ($\mu\text{mol m}^{-2}\text{s}^{-1}$) (already needed for energy balance)
 θ (-); commonly, it is near 0.8 or 0.9

Again, one must know T_L from solving Eq. (11) and g_s from solving Eq. (12).

2.D How the "aerial" response equations are solved

This is a self-contained exercise; the effect of water stress and the ABA signal is to alter the Ball-Berry slope, m , as a parameter of Eq. (12) above.

An effective way to proceed is as follows:

(i) *Guess a value for g_s .* This allows one to solve Eq. (11) for leaf temperature. The model incorporates exhaustively-tested methods for generating guesses for g_s , actually as upper and lower limits that will be progressively halved in a binary search. Our model, as a Fortran program, includes comment cards that explain the way these initial estimates are derived. The energy-balance Eq. (11) is nonlinear, but is readily solved by either Newton-Raphson iteration from an initial guess, say, $T_L = T_a$ (as done in our model), or a binary search from an initial upper and lower limit.

(ii) *Use this value of T_L to solve the assimilation Eqs. (16)-(18).* The quartic equation for C_i noted earlier is solved by a Newton-Raphson search.

(iii) *Evaluate if A and T_L solve the Ball-Berry equation.* Simply, one composes the measure

$$F = g_s - (m A h_s / C_s + b) \quad (20)$$

When F is positive, the estimate for g_s is too large; it is negative when the estimate is too low. This allows effective binary searching: given upper and lower estimates $g_{s,hi}$ and $g_{s,lo}$, one then computes the midpoint $g_{s,mid}$ and the corresponding value of F . If $F < 0$, then the root of Eq. (20) must lie between $g_{s,mid}$ and $g_{s,hi}$; one simply takes $g_{s,mid}$ as the new $g_{s,lo}$ and proceeds to the next iteration. The case $F > 0$ is similar, with $g_{s,mid}$ becoming the new $g_{s,hi}$.

3. The response of the leaf to water stress, mediated by ABA

3.A Response of g_s to ABA in xylem sap

The formulation of g_s as responding to the concentration (not flux) of ABA in xylem sap is discussed in a number of articles by Tardieu and co-workers (*e.g.*, Tardieu *et al.*, 1993). With a sign change to make the parameter β a positive number, we write the modifier of conductance, g_{fac} , as

$$g_{fac} = e^{\beta[ABA] \exp(-\delta\psi_L)} \quad (21)$$

In some species such as sunflower, δ is zero, such that leaf water potential deficit does not amplify the effect of ABA.

Clearly, there are two parameters needed:

β (nM^{-1} is convenient, since $[ABA]$ is commonly quoted in nM); in sunflower, the magnitude we used is 0.003 if we use the multiplicative model, or 0.009 in the model of the minimum.

δ (MPa^{-1}); typically 0 for sunflower, or near -1 for isohydric species.

In the event we are using the alternative model of the minimum, we also need:

$$g_{s,max} \text{ (mol m}^{-2}\text{s}^{-1}\text{)}$$

3. B Generation of ABA

ABA is generated more strongly by roots at low water potential. From Tardieu and Davies

(1993; see also Simonneau *et al.*, 1998), we write the concentration, [ABA], as responding to root water potential, ψ_r , and the total flux density of water in the root, J_r :

$$[\text{ABA}] = - \frac{a_{\text{ABA}} \psi_r}{(J_r + b_{\text{ABA}})} \quad (22)$$

Note that we can write the synthesis of ABA, $J_r [\text{ABA}]$, as a Michaelis-Menten form, $-a \psi_r J_r / (J_r + b_{\text{ABA}})$, as if low water flow allows internal accumulation of ABA that suppresses ABA generation.

The flow of water in the root is expressed per unit surface area, as $\text{mol m}^{-2}\text{s}^{-1}$. The parameters needed for this portion of the model are:

a_{ABA} ($\text{nM mol m}^{-2}\text{s}^{-1} \text{ MPa sup}^{-1}$); in sunflower, we used 2.05

b_{ABA} ($\text{mol m}^{-2}\text{s}^{-1}$); in sunflower, we used 0.0072

3.C Completing the circuit: describing water potentials

Soil to root. The flow of water is driven by the difference in water potential from bulk soil (ψ_s) to root surface (ψ_r). The flow is approximately in cylindrical geometry, traversing the radial distance from d = mean inter-root spacing to r_r = the mean radius of a root. Because flows are conserved, the radial flow, J , at any radial distance, x , equals the root radius multiplied by the flow at the root surface, J_r (a quantity of central interest to us). We can write J at any distance also in terms of D'Arcy's law to get

$$J = J_r r_r / x = -k_{h,s} \partial \psi / \partial x \quad (23)$$

Here, $k_{h,s}$ is the soil hydraulic conductivity. We assume it to be constant between bulk soil and root surface, though this condition is increasingly violated as soil gets drier (Caldwell, 1976); a more accurate formulation describes $k_{h,s}$ as a power law in ψ , also yielding an integrable form.

We can readily integrate Eq. (23) to obtain

$$\psi = \psi_s - \frac{J_r r_r}{k_{h,s}} \ln(x/d) \quad (24)$$

In particular, we can solve for ψ at the root surface. We obtain an expression for the drop in water potential from bulk soil to root surface,

$$\psi_s - \psi_r = (r_r / k_{h,s}) \ln(d/r_r) \quad (25)$$

Bruckler *et al.* (1991) showed empirically that root clumping is common and makes the drop in ψ larger than this. We apply his factor F as a function of soil type. In loamy soil, $F = 5$! We use a lookup table for F (with only one value currently).

We need to express the conductivity in terms of soil water potential. Some ready expressions exist (van Genuchten, 1980) for $k_{h,s}$ in terms of volumetric water content, θ (not to be confused with the convexity parameter in photosynthesis):

$$k_{h,s} \approx 10^{(c_0 + c_1 \theta_m + c_2 \theta_m^2 + c_3 \theta_m^3)} \quad (26)$$

Here, the c_i are empirical constants, specific to a soil type. Also, θ_m is the soil water content as a mass fraction; if we have θ as a volumetric fraction, we need to convert it by using the dry soil bulk density, as a specific gravity, ρ_b : $\theta_m = \theta / \rho_b$. We then need to express water content in terms of ψ . We use van Genuchten's (1980) form for ψ_s ,

$$\psi_s = \frac{1}{\alpha} \left[\left(\frac{\theta - \theta_r}{\theta_s - \theta_r} \right)^{1/m_s} - 1 \right]^{1/n_s} \quad (27)$$

Here, θ_s is the familiar saturated soil water content, θ_r is a residual content, and m_s and n_s are empirical constants. This can be inverted to give θ for any value of ψ_s :

$$\theta = \theta_r + (\theta_s - \theta_r) [1 + (\alpha \psi_s)^{n_s}]^{-m_s} \quad (28)$$

Now that we have θ , we can use Eq. (26) to estimate the conductivity, $k_{h,s}$.

There are a number of parameters here, which, fortunately, are commonly tabulated by soil type:

c_0, c_1, c_2, c_3 (-); tabulated in a data statement in the program; for loam, we use -15.1, 60.4, -409, 1250, respectively

ρ_b (-); we use 1.4 for loam

θ_s, θ_r (-); also tabulated. For loam, we use 0.338, 0.001, respectively

n_s, m_s (-); for loam, we use 1.132 and 0.1166

α (MPa⁻¹); for loam, we use -172

Flux at the root surface in terms of whole-plant water flux and root geometry. The flux E is simply the mean flux density at the root surface, J_r , multiplied by the total root surface area of the plant, A_{root} . This area is simply the volume of the entire root system multiplied by the area per volume of cylinders, which is just $2/r_r$ for roots of radius r_r . We typically know the root mass, m_r and the density of the roots in dry mass per m³, ρ_r , so we compute the root volume as m_r/ρ_r . We can now compute J_r as

$$J_r = E/A_{\text{root}} = E \rho_r r_r / (2 m_r) \quad (29)$$

This allows us to compose the water potential drop as

$$\psi_s - \psi_r = \frac{J_r r_r \ln(d/r_r)}{k_h} = E \frac{\rho_r r_r^2 \ln(d/r_r) F}{2 m_r k_h} \quad (30)$$

The one quantity we have yet to calculate is the mean distance between roots as if they were arranged in a regular array. This is a function of the total root length per ground area and the depth of soil into which the roots are dispersed, d_{soil} . One can readily derive

$$d = \frac{1}{2} r_r \sqrt{\rho_r \pi D_{\text{soil}} / m_r} \quad (30)$$

The parameters we have introduced here are:

r_r (m); this varies, but for sunflower we use 0.0008 m = 0.8 mm

D_{soil} (m); for a typical field, we used a rooting depth of 0.4 m

ρ_r (kgm⁻³); roots are about 25% dry matter, so we use 250

m_r (kg m⁻²); this varies with stage of stand development; in our example, we used 0.1608 for a specific field experiment

F (-); we used 5. This factor can also incorporate an accounting for the fraction (<1) of root system that is active (thin roots, nonsuberized), by multiplying the clumping factor by 1/(fraction of root mass active)

3.D Final stage: converting from leaf transpiration rate, $E_{L,a}$, to whole-plant rate, E

The leaf responses are formulated in terms of the ABA concentration, which is generated in response to whole-plant water flux and ψ_r . There is a real issue of scaling; a model of the whole plant must be used. In practice, the model we present might be split into two pieces, one of which computes $E_{L,a}$ for a sampling of leaves throughout the plant (or stand), and the other of which computes water potentials, soil-to-root conductivity, and E . For a quicker view, we might consider a closed canopy and the simple approximation that sunlit leaf area index is 2.0. Thus, we would take $E = 2 E_{L,a}$.

4. Discussion

The immediate state of a plant is described by

- A. Its structure (root and shoot: masses, leaf area, leaf and root dimensions, etc.),
- B. its physiological and biophysical parameters (carboxylation capacity, photosynthetic convexity parameter, Ball-Berry slope and intercept or equivalent descriptors of stomatal control, absorptivities for radiation, etc.),
- C. Leaf and root environments (air temperature, humidity, and windspeed; soil texture class, depth, and water potential...)

It is a demanding task to specify all of these parameters and state variables but a necessary one. Fortunately, many of the parameters that are not commonly measured in a field experiment are "robust," or predictable from broad categorizations. For example, the soil hydraulic conductivity and the parameters relating ψ_s to volumetric or mass water content are readily estimated from soil texture classes such as loam or sandy loam. The same holds for many physiological parameters. The Ball-Berry slope is commonly near 10 and the intercept is near zero (but m and b do respond to growth conditions and are correlated with each other. This leads to some interesting features in stand water use; Gutschick *et al.*, in review for *Global Change Biology* as of Nov. 2001). In brief, the task is not as onerous as it seems. Other parameters are less constrained and represent real, physical or physiological conditioners of plant performance, including soil depth, root radius, and sunlit leaf area index. It is well worth thinking about these carefully and deriving accurate estimates.

The Fortran 77 program is available in a separate file on this Web site. It was written in 1999. We recently (Nov. 2001) translated the comments and the terminal prompts into English. We also modified it to incorporate our recent improvements in the solution of the Ball-Berry + assimilation + energy-balance equations. The program compiles and runs on our Sun workstations; with a very few cosmetic changes, it should run on any other platform. We have found that Visual Fortran handles our Fortran style well.

An annotated data-input file is also included in the listing of the Fortran program.

4. Selected references

Other references are cited in our manuscript in review at *Plant, Cell and Environment*.

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