

Some plant factors controlling evapotranspiration

Bernard Saugier^a and Nader Katerji^b

^a*Laboratoire d'Ecologie Végétale (URA CNRS n° 121), Bat. 362, Université Paris-Sud, 91405 Orsay, France*

^b*INRA Bioclimatologie, Plateau de Grignon, 78850 Thiverval-Grignon, France*

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ABSTRACT

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Stomatal conductance varies within a leaf, between leaves in a canopy and between layers. It depends primarily on light and it is possible to derive a canopy conductance, g_c , by summing the stomatal conductances of leaves of all layers. This may be done by measurements or by using a simple model. Such a calculated canopy conductance can be used successfully in the Penman–Monteith formula to predict the evapotranspiration of a closed canopy well supplied with water.

For incomplete canopies, soil and plant evaporation require different treatments. The ratio E_c/E_o of canopy transpiration to open water evaporation varies roughly in proportion with the fraction of soil covered by vegetation, while the ratio E_s/E_o of soil evaporation to E_o is controlled both by net radiation at the soil surface and surface soil moisture.

Soil water limitation may be modelled by making E_c/E_o a function of soil water reserve or through a variable stomatal conductance, g_s . In the latter case, g_s may be related to either soil water potential or leaf water potential, which depends on transpiration and resistance to liquid water flow through the plant. Such resistance is shown to be relatively conservative at the canopy level, but its usefulness for predicting evapotranspiration is debatable since a part of stomatal closure is now attributed to hormonal control.

INTRODUCTION

The evaporation of water requires a source of energy to separate molecules of liquid water and a diffusion mechanism to transfer water vapour away from the evaporating surface. Both mechanisms have been recognized by Bowen (1926) and by Penman (1948, 1953) who combined them into a simple formula for computing the evaporation of open water and of vegetated surfaces. The transfer of water vapour in the atmosphere was first treated as an empirical function of wind speed and later computed from the aerodynamic characteristics of the surface (Van Bavel, 1966; Thom, 1971). In plants, evaporation sites are located inside the leaves and water vapour has to diffuse

through the epidermis before entering the atmosphere. Penman's ideas on evapotranspiration have been popularized by Monteith (1965) who presented a clear picture of leaf transpiration using stomatal and boundary-layer conductances g_s and g_b , and a good approximation of canopy evapotranspiration using canopy and aerodynamic conductances g_c and g_a . (Conductance is the inverse of resistance and will be often used in this paper even when the original results were given in terms of resistance.)

A large number of papers dealing with the evaporation of natural surfaces use this last approach in the so-called Penman–Monteith (P–M) formula, although the problem of relating conductances at the canopy level to their counterparts at the leaf level is by no means trivial, as was shown and clarified by Thom (1972).

The present paper has several aims. The first is to suggest a simple relationship between g_c and g_s for a closed canopy, and to give representative figures of g_c for vegetations not short of water. The second aim is a practical approach to the evapotranspiration of incomplete canopies. The third aim is an attempt to take into account the effect of water stress on transpiration through the use of leaf water potential, a somewhat old-fashioned approach that has retained some advantages.

STOMATAL CONDUCTANCE: FROM LEAF TO CANOPY

The first problem when relating canopy to leaf parameters is of a theoretical nature: how are the conductances defined, mainly that of the canopy? Micro-meteorologists, following Monteith (1963), used to equate the boundary-layer resistance for heat or water vapour to that for momentum using a logarithmic wind profile. Monteith was criticized by Philip (1966) on the basis that heat, water and momentum had different source/sink distributions within the canopy. Thom (1972) clarified the discussion. He showed (Thom, 1968) that the exchange of heat or gases between a leaf and the air encountered more resistance to transfer than that of momentum, which is facilitated by bluff-body forces that have no counterpart in heat/gas diffusion. Thom (1972) extended this idea to the exchange of a canopy and showed that the boundary-layer resistance of a canopy should be written for heat or water vapour as

$$r_a = \ln^2 [(z_r - d)/z_0] / (k^2 u) + B^{-1} / u_* \quad (1)$$

In this expression, the first term is the classical term resulting from a logarithmic wind profile and the second term is the excess resistance due to the absence of bluff-body forces. When this second term is neglected, the canopy resistance is a function not only of stomatal resistance, but also partly of boundary-layer resistance, which results in errors that may be important (Thom, 1972). A good compilation of data concerning the parameter B^{-1}

has been presented by Garratt and Hicks (1973) for seven artificial surfaces and 14 natural ones ranging from a frozen lake to forests.

They found that kB^{-1} increased monotonically from 0 to 2 as the roughness Reynolds number Re_* ($u_* z_0/\nu$ with ν kinematic viscosity) increases from 2 to about 20. For higher roughness ($Re_* > 20$), the curve splits into two lines; for homogeneous vegetations with randomly distributed fibrous roughness elements kB^{-1} stays constant and decreases slightly for $Re_* > 1000$ (to < 1 for pine forests with $Re_* = 3 \times 10^4$); for heterogeneous vegetations such as vineyards kB^{-1} increases from 2 to 8 as Re_* increases from 20 to 1000, and seems to level off for $Re_* > 1000$.

The second problem encountered in deriving a canopy conductance from measurements of stomatal conductance is the great variability of these measurements. Stomatal conductance is measured with porometers that enclose only part of the leaf area. There is variability within a leaf, among leaves in a canopy layer and among various layers within a canopy. For instance, Katerji et al. (1983) and Katerji and Perrier (1985) took many measurements of stomatal resistance of both sides of alfalfa leaves (Table 1). The coefficient of variation of the measurements increased from 25% in the top layer to 35% in the two other layers. Stomatal resistance increases rapidly from the top downwards and as a result the bottom layer contributes very little to the canopy conductance g_c . g_c was computed as $L_i \times (1/r_{s,i}^u + 1/r_{s,i}^l)$ where L_i , $r_{s,i}^u$ and $r_{s,i}^l$ are the leaf area index, and the average stomatal resistances of the upper and lower side of the leaf, respectively, for each layer i .

The increase in stomatal resistance and in its coefficient of variation from the top to the bottom of the canopy follows the decrease in the average light received by the leaves and the increase in light variability. We may calculate g_c from g_s , knowing the light dependence of g_s and the light profile through the canopy.

TABLE 1

Variability of stomatal resistance on the two sides of the leaf in an alfalfa canopy (from Katerji and Perrier, 1985). The resulting canopy resistance is $1000/46 = 22 \text{ s m}^{-1}$

<i>i</i>	Canopy layer	Stomatal resistance and s.e. (s m^{-1})		LAI and s.e.	Canopy conductance (mm s^{-1})
		Upper side	Lower side		
1	Top	117 ± 29	115 ± 29	1.75 ± 0.35	30.2
2	Medium	199 ± 70	559 ± 196	2.1 ± 0.42	14.3
3	Bottom	1044 ± 365	1200 ± 420	0.85 ± 0.17	1.5
	Canopy			4.7	46.0

s.e. = standard error.

If S_o is the short-wave radiation above the canopy, the radiation S below a layer of leaf area index (LAI) equal to L may be written as

$$S = S_o \exp(-k_e L) \quad (2)$$

while the average radiation received by a leaf is $-dS/dL = k_e S$.

Let us assume the stomatal conductance, g_s , depends on available radiation in a hyperbolic way, given by

$$g_s = g_{smax} S / (S + S_1) \quad (3)$$

where S_1 is a parameter depending on species. The canopy conductance may be computed by summing the conductances of the leaves of various layers

$$g_c = g_{smax} \int_0^L \frac{k_e S_o \exp(-k_e L) dL}{k_e S_o \exp(-k_e L) + S_1}$$

$$\text{i.e. } g_c = \frac{g_{smax}}{k_e} \ln \frac{S_1 + k_e S_o}{S_1 + k_e S_o \exp(-k_e L)} \quad (4)$$

Thus g_c approaches $(g_{smax}/k_e) \ln[(S_1 + k_e S_o)/S_1]$ at high L , which is quite different from $g_{smax} L$ which is often used in the P-M formula. Equation (4) shows a strong dependence on S_1 that varies between 30 and 300 W m^{-2} depending on the species (Table 2). As a result, g_c/g_{smax} calculated from eqn. (4) varies between 3.57 and 1.50 for $S_o = 800 \text{ W m}^{-2}$ (full sun) and $k_e = 0.7$. Measured values (Table 3) range from 3.5 (oil palm, Dufrène, 1989) to 2.6 (alfalfa, Katerji and Perrier, 1985) and 1.33 (sunflower with $L = 1.8$, Saugier, 1976). Table 4 gives maximum and minimum values of g_c for a few vegetation types. g_c may decrease by an order of magnitude during water stress or senescence of the foliage.

Equation (2) was originally proposed by Monsi and Saeki (1953) and remains the simplest model of light penetration within a canopy. It does not take into account foliage clumping, although the extinction coefficient k_e may be modified according to clumping (Palmer, 1977). Equation (4) is thus

TABLE 2

Solar radiation level, S_1 , for which stomatal conductance is half its maximum value

Species	S_1 (W m^{-2})	Source
Alfalfa	180	Katerji et al. (1983)
Sunflower	200–350	Berger (1973)
Scots pine	150	Jarvis and Morison (1981)
Scots pine	125	Lohammar et al. (1980)
Apple tree	50	Warrit et al. (1980)
Oil palm	30	Dufrène (1989)

TABLE 3

Comparison between values of surface conductance calculated (g_c^{calc}) from L and maximum stomatal conductance, or estimated (g_c^{meas}) from direct measurements of evapotranspiration

Vegetation	$g_{s\text{max}}$ (mm s ⁻¹)	S_1 (W m ⁻²)	L	g_c^{calc} (mm s ⁻¹)	g_c^{meas} (mm s ⁻¹)	$g_c^{\text{meas}}/g_{s\text{max}}$	Source
Alfalfa	17	180	4.7	31.7	45.5	2.7	Katerji and Perrier (1985)
Sunflower	8.3	270	1.8	7.8	11.1	1.3	Saugier (1976)
Oak forest	5	160	4.2	9.5	10.0	2.0	Nizinski (1986)
							Halldin et al. (1985)
Chestnut	7.6	170	5.6	15.1	20	2.6	Bobay (1985)
Oil palm	8.3	30	4.5	28.4	29.4	3.5	Dufrène (1989)

TABLE 4

Canopy (maximum and minimum values) and aerodynamic conductances in mm s⁻¹ for various vegetation types. The height in metres is given when available

Vegetation	h (m)	L	g_c^{max}	g_c^{min}	g_a	Year (meas.)	Source
Wheat	—	9	50	12.5	40	1975	Perrier et al., 1980
Wheat	—	6.5	33	3.5	37	1976	Perrier et al., 1980
Alfalfa	—	High	50	0.5	20	1964	Van Bavel, 1967
Alfalfa	—	4.7	50	—	36	1978	Katerji and Perrier (1985)
Sorghum	—	4.2	25	—	37	1966	Van Bavel and Ehrlar, 1968
Grassland	0.2	1.0	9	1	20	1971	Ripley and Saugier, 1978
Chestnut coppice	8.0	5.6	20	—	75	1985	Bobay, 1985
Oil palm	12.0	4.5	29	4	50	1988	Dufrène, 1989
Rubber tree	22.5	6.0	50	—	70	1981	Barbier, 1983

clearly an approximation, but it is a definite improvement over the expression $g_{s\text{max}}L$ which is still often used as a substitute for g_c .

EVAPOTRANSPIRATION OF INCOMPLETE CANOPIES

Soil evaporation, E_s , which is neglected in the P–M formula for closed canopies, has to be treated separately from canopy transpiration, E_c , in vegetation with incomplete soil cover. In crop models, the problem is usually simplified in the following expression

$$E = E_c + E_s = fE_{cc} + (1-f)E_{so} \quad (5)$$

where f is the fraction of soil covered by vegetation, E_{cc} is the transpiration of a closed canopy (as given by the P-M formula) and E_{so} is the evaporation of bare soil

Equation (5) is clearly a simplification that assumes no feedback between transpiration and soil evaporation. In the real world, when the soil surface dries out, its temperature increases and this causes an increase in the evaporative demand for transpiration. This, however, is a second-order effect that may be neglected in a first approximation. Figure 1 illustrates the variation of E_c/E_o (transpiration/open water evaporation) with LAI in three types of well-watered vegetation, together with a solid line representing the variation of fractional soil cover with LAI for a value of 0.7 for the light extinction coefficient. The figure shows a relatively good agreement between the crop data and the line that seems to underestimate transpiration at low LAI and to slightly overestimate it at high LAI. The grassland data are always above the line, but they represent total evapotranspiration (soil + plant) and not only transpiration, as with the crops. The difference may thus be explained partly by soil evaporation. Another possible explanation is the large amount of dead leaves in this ungrazed grassland that were intercepting radiation and warming the air around green leaves, increasing the evaporative demand.

Katerji and Perrier (1985) have proposed an extension of the P-M for-

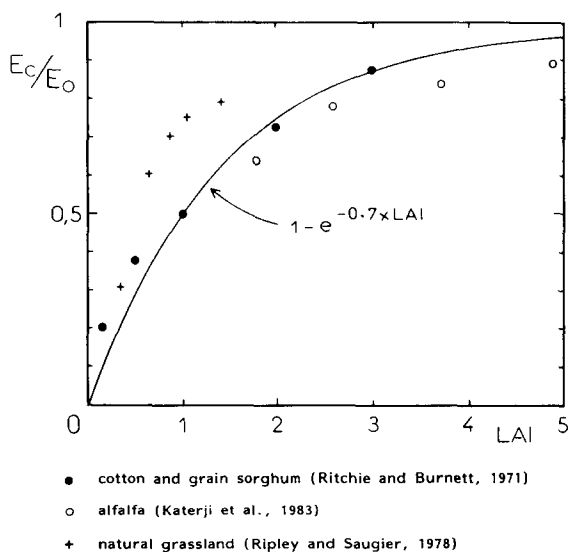


Fig. 1. Effect of LAI on the ratio of canopy transpiration, E_c , to open-water evaporation, E_o , for various vegetation types on well-watered soils.

mula for vegetations with incomplete cover, taking soil evaporation into account. Figure 2 summarizes their analysis. Transpiration, T , occurs through:

(1) a surface resistance of the canopy r_{sc} (calculated as $1/\sum [L_i(1/r_{s,i}^u + 1/r_{s,i}^l)]$);

(2) an aerodynamic resistance, r_p , between the leaves and the level h (top of vegetation);

(3) an aerodynamic resistance, r'_a , between h and a reference level z_r above the canopy.

Soil evaporation occurs through:

(1) a resistance, r_l , of a dry layer of soil of variable thickness;

(2) an aerodynamic resistance, r_{p*} , from the soil surface to h ;

(3) the resistance, r'_a , already mentioned. $r'_a (=r_a - r_p)$ is computed from a logarithmic wind profile, r_p and r_{p*} are computed using a multi-layered model (Perrier, 1976) of air flow within the canopy, and r_l is estimated from measurements of soil evaporation during a drying-out phase.

Perrier's model has been applied to an alfalfa crop using four measured profiles of leaf area density at four values of LAI (1.8, 2.6, 3.7 and 4.7). Figure 3, taken from Katerji and Perrier (1985), shows variations of r_{sc} , r_{p*} and r_p with LAI, as well as that of a global canopy resistance r_* (defined as $1/[1/(r_l + r_{p*}) + 1/(r_{sc} + r_p)]$). Two values of r_l have been used in these calculations: 0 (wet soil) and 350 s m^{-1} (dry soil).

This analysis shows that r_p is always small ($< 10 \text{ s m}^{-1}$), while r_{p*} increases linearly with LAI, reaching 1000 s m^{-1} for LAI=3 in the alfalfa crop. The effect of surface soil moisture (via r_l) on global canopy resistance, r_* , becomes negligible for LAI > 2 owing to the increase in r_{p*} , and stays small for $1 < \text{LAI} < 2$. This is clearly shown in Fig. 3 where the difference between r_* and r_{sc} is important only for values of LAI < 1 and when the soil surface is wet

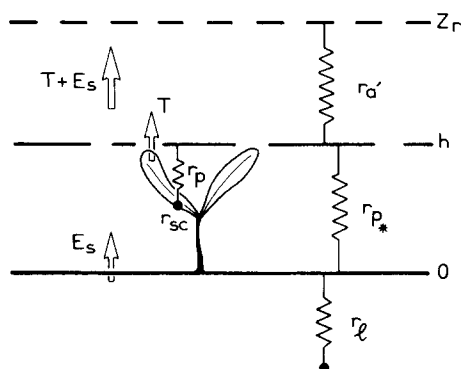


Fig. 2. Resistances to evaporation used in Katerji and Perrier (1985) in the case of incomplete canopies. r_l is a soil resistance, r_{p*} is the aerodynamic resistance between soil surface and the canopy top, r_p is the aerodynamic resistance between the leaves and canopy top, r'_a is the aerodynamic resistance between the canopy top and a reference height.

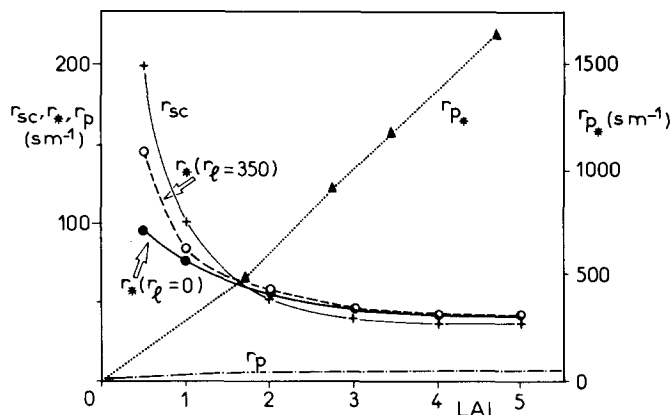


Fig. 3. Effect of LAI on the resistances defined in Fig. 2, after Katerji and Perrier (1985). r_{sc} is the canopy resistance and r_* is the surface resistance, for a wet soil ($r_l=0$) and for a dry soil surface ($r_l=350 \text{ s m}^{-1}$).

($r_l=0$). Katerji and Perrier (1985) found for $\text{LAI} > 1$ a good agreement between measured values of evapotranspiration over the alfalfa crop using the energy balance method, and values calculated from the P-M equation using r_{sc} as the canopy resistance.

Katerji and Perrier did not consider separately the energy balance of the soil, which may cause problems at lower values of LAI. Shuttleworth and Wallace (1985) have developed an interesting analytical expression for evaporation from sparse crops, applying the P-M equation separately to the soil and to the vegetation. They used a Beer's law for the extinction of net radiation through the canopy and assumed an exponential decrease with depth for the eddy diffusion coefficient. They found that the exact shape of this decrease had little effect on predicted evaporation. Their calculations show an important effect of surface soil moisture on total evaporation when $\text{LAI} < 2$. They assumed soil and vegetation aerodynamic resistances as being linearly related to LAI which could be improved in a more mechanistic model of air flow through the canopy, such as that of Perrier (1976). However, their formulation, explicitly considering the energy balance of both the soil and the vegetation, is probably the best analytical expression of evaporation from sparse crops.

Evaporation from sparse vegetation becomes more complex when the vegetation is partly senescent. The application of the P-M equation to three components (soil, dead leaves and green leaves) is very cumbersome. Saugier and Ripley (1975) have written explicitly the energy balance of these three components in a native grassland and solved it using an iterative technique for calculating the temperature and humidity of the air within the canopy. How-

ever, this approach is wasteful of computer time and should be replaced by a simpler one in global circulation models.

Effect of a water shortage

The simplest way to account for the effects of water shortage on evapotranspiration is to express the ratio E/E_o (of real to open water evaporation) as a function of soil water volume over the rooting zone, V . As V decreases from field capacity (V_{FC}) to wilting point (V_{WP}), E/E_o stays equal to 1 until V reaches a threshold or critical value, V_c . Then E/E_o decreases from 1 to 0 as V decreases from V_c to V_{WP} (Fig. 4). The difference $V_{FC} - V_c$ may be defined as easily available water (EAW), while the differences $V_{FC} - V_{WP}$ is the maximum available water (MAW) (Fig. 4).

The ratio EAW/MAW is often taken between 0.5 and 0.7, but may vary with rooting pattern, soil texture and evaporative demand. This last point can be understood if we think stomatal closure occurs at a critical leaf water potential. Since the difference between soil and leaf water potential usually increases with water flow through the plant, the critical leaf water potential will be reached sooner at high evaporative demand.

Slabbers (1980) has suggested a practical way of estimating EAW/MAW as a function of critical leaf water potential (taken as a crop characteristic) and of potential evaporation, E_p , in the following expression

$$f_w = 0.94 + 0.26 \psi_l^c / E_p \quad (6)$$

where $f_w = (V_c - V_{WP}) / (V_{FC} - V_{WP}) = 1 - \text{EAW/MAW}$ and ψ_l^c is in bars (1 bar = 0.1 MPa) and E_p is in mm day^{-1} . f_w usually varies between 0.3 and 0.6. The above expression assumes an empirical relationship between R_p , the plant resistance to water flow, and soil water potential. It neglects soil resistance before R_p and assumes that critical leaf water potential does not depend on potential evaporation. In spite of these restrictions, it gives a correct prediction of evapotranspiration in most cases (Slabbers, 1980) and might be considered as a way to vary the threshold at which soil water becomes limiting.

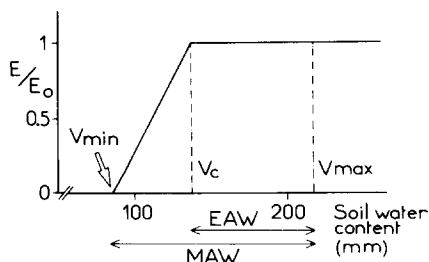


Fig. 4. Real to open-water evaporation ratio, E/E_o , as a function of soil water content.

TABLE 5

Values of plant resistance to liquid water flow (MPa h mm^{-1}), for various species. Maximum values are usually obtained under water stress

Species	R_p (MPa h mm^{-1})	Source
Kiwifruit	1.2	McAneney and Judd, 1983
<i>Vigna sinensis</i>	2.1–5.0	Hailey et al., 1973
<i>Capsicum annum</i>	3.0–6.0	Hailey et al., 1973
Sunflower	2.8	Van Bavel, 1974
Alfalfa	2.5	Katerji et al., 1983
Potato	1–3	Katerji et al., 1986
<i>Agropyron dasystachium</i>	2.5	Saugier, 1974
Sitka spruce	2.4	Jarvis, 1976
Scots pine	2.1	Jarvis, 1976

Another method that has been used with success is to write explicitly the dependence of transpiration and root water uptake on leaf water potential (via the stomatal conductance for transpiration), and to find leaf water potential as the value at which root water uptake equals transpiration (Ripley and Saugier, 1975). Several soil layers may be used (Saugier and Ripley, 1975) and variations in plant water storage may be taken into account (Katerji et al., 1986). The method is slightly more complex than that of Slabbers, but it is more mechanistic and relies directly on measured parameters such as R_p . Several authors have plotted leaf water potential against transpiration; Sometimes straight lines, but often curves with strange shapes and hysteresis, have been obtained. Katerji et al. (1986) have successfully explained the hysteresis loops encountered in alfalfa and potato crops by taking into account changes in water storage in the plants. It then becomes possible to calculate a constant plant resistance to water flow, R_p . Its value is relatively conservative between species and may vary between 1.2 and 6 MPa h mm^{-1} (Table 5), and increases with water stress.

Such an approach, using leaf water potential explicitly, remains a valuable tool for predicting hourly variations of evapotranspiration in spite of recent controversy about the role of leaf water potential in plant physiology (i.e. Boyer, 1989). It has been simplified and used with success for predicting daily evapotranspiration in dry areas (Rambal and Cornet, 1982), or in forests (Nizinski and Saugier, 1989).

CONCLUSIONS

The best approach to the evapotranspiration of vegetated surfaces probably remains the P–M formula, applied to a closed canopy not short of water. In this case, canopy conductance may be computed by assuming an exponential decrease in light through the canopy and a given relationship between leaf

stomatal conductance and incident light. Thus, values of maximum conductance, such as reviewed by Körner et al. (1979), may be transformed into canopy conductance values.

For partial canopies, the separation of the surface into a fraction of bare soil and a fraction of closed canopy yields relatively good values of evapotranspiration, except perhaps in arid environments with low LAI where the feedback between soil evaporation and transpiration becomes important. Then the approach of Shuttleworth and Wallace (1985) is preferred.

The effect of soil water limitation on transpiration may be tested simply using a threshold of soil water reserve below which transpiration is linearly related to the water reserve. The value of the threshold may be fixed arbitrarily or computed from an empirical expression of Slabbers (1980). If hourly transpiration is required, then a model predicting leaf water potential gives good results.

Once maximum canopy conductances are known for the major vegetation types, it will be necessary to have rooting depth and soil type (for computing available soil water), and variations in LAI for these biomes. LAI (or vegetation cover, f) may either be estimated from satellite observations of vegetation index, or calculated from simple phenological models (Nizinski and Saugier, 1988). In the future, it will be calculated in dynamic growth models. Such models exist for the major crops, but only for a few types of natural vegetation.

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APPENDIX: LIST OF SYMBOLS

<i>B</i>	empirical parameter
<i>d</i>	zero plane displacement height for wind profile
<i>E</i>	evapotranspiration
<i>E_c</i>	transpiration of a partial canopy
<i>E_{cc}</i>	transpiration of a closed canopy

E_o	open water evaporation
E_p	potential evaporation
E_s	soil evaporation (under a partial canopy)
E_{so}	evaporation of bare soil
EAW	easily available water ($V_{FC} - V_C$)
f	fraction of soil covered with vegetation
f_w	fraction of soil-available water that is not easily available to plants ($1 - \text{EAW/MAW}$)
g_a	canopy boundary-layer conductance
g_b	leaf boundary-layer conductance
g_c	canopy conductance
g_s	stomatal conductance
g_{smax}	maximum stomatal conductance at high solar radiation
h	height of vegetation
k	von Karman's constant (0.4)
k_c	extinction coefficient of solar radiation in the canopy
L	cumulated leaf area index from the canopy top
L_i	leaf area index of vegetation layer i
MAW	maximum available water ($V_{FC} - V_{WP}$)
r_*	global canopy resistance ($1/r_* = 1/(r_{sc} + r_p) + 1/(r_l + r_{p*})$)
r_a	boundary-layer resistance
r'_a	aerodynamic resistance between the canopy top (h) and a reference level z_r above the canopy
r_l	resistance of a dry layer of top soil of variable thickness mulch
r_p	aerodynamic resistance between leaves and the canopy top
r_{p*}	aerodynamic resistance between the soil surface and the canopy
r_{sc}	surface resistance of the canopy
$r_{s,i}^l$	average stomatal resistance of the lower side of leaf in layer i
$r_{s,i}^u$	average stomatal resistance of the upper side of leaf in layer i
Re_*	roughness Reynolds number ($u_* z_0 / \nu$)
R_p	plant resistance to liquid water flow (MPa h mm^{-1})
S	solar radiation within a canopy
S_l	solar radiation at which stomatal conductance is half of its maximum
S_o	solar radiation above the canopy
T	transpiration
u	wind velocity
u_*	friction velocity
V	soil water depth in the rooting zone
V_c	critical soil water depth below which E/E_o becomes < 1
V_{FC}	soil water depth at field capacity

V_{WP}	soil water depth at wilting point
z_0	roughness length
z_r	reference level
ν	kinematic viscosity of air
ψ_l^c	critical leaf water potential for stomatal closure