Stomatal control of transpiration: Examination of Monteith's formulation of canopy resistance

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Abstract. The stomatal response to air humidity has been recently reinterpreted in the sense that stomata seem to respond to the rate of transpiration rather to air humidity per se. Monteith suggested that the relation between canopy stomatal resistance r_s and canopy transpiration E can be written as $r_s/r_{sn} = 1/(1 - E/E_x)$, where r_{sn} is a notional minimum canopy resistance, obtained by extrapolation to zero transpiration, and E_x is a notional maximum transpiration rate, obtained by extrapolation to infinite resistance. The exact significance and possible values of these parameters have not been specified yet. In this study we show that this apparently new relation can be inferred from the common Jarvis-type models, in which canopy stomatal resistance is expressed in the form of a minimal resistance multiplied by a product of independent stress functions (each one representing the influence of one factor). This is made possible by replacing leaf water potential in the corresponding stress function by its dependence on transpiration and soil water potential. The matching of the two formulations (Monteith and Jarvis) allows one to express the two parameters r_{sn} and E_x in terms of the functions and parameters making up the Jarvis-type models; r_{sn} appears to depend upon solar radiation and soil water potential: it represents the canopy stomatal resistance when the leaf water potential is equal to the soil water potential, all other conditions being equal. E_x depends upon soil water potential and represents the maximum flux of water which can be extracted from the soil by the canopy.

1. Introduction

Any natural surface partitions the net supply of radiative energy into sensible and latent heat flux. In the case of vegetation the key factor in this partitioning is the stomatal behavior. Among numerous approaches allowing the calculation of this partitioning over vegetation, the "big leaf" model, as formulated by the Penman-Monteith equation [*Monteith*, 1981], has acquired a wide acceptance by its simplicity and its performance. In this approach the bulk behavior of stomata is represented by a canopy stomatal resistance assumed to be comparable with that of a single leaf and influenced by the same factors.

The stomatal resistance, at leaf scale as well as at canopy scale, has been correlated with many environmental conditions and plant factors such as solar radiation, air humidity, air temperature, ambient carbon dioxide, leaf water potential, or soil water potential. So far, however, no mechanistic model has been developed to describe the stomatal aperture, and only empirical approaches are available. For more than 20 years the most common approach to parameterize the effect of environmental factors on stomatal behaviour has been the so-called Jarvis-type models [*Jarvis*, 1976; *Stewart*, 1988], in which stomatal resistance is expressed as a minimum resistance multi-

plied by a series of independent stress functions combined in a multiplicative way (each function representing the influence of one factor). The response of stomata to solar radiation, temperature, and carbon dioxide concentration can be easily interpreted in terms of the process of photosynthesis. On the other hand, it has never been possible to understand the physiological basis for a direct effect of atmospheric humidity on stomatal resistance. No consensus has ever emerged as to the mechanism involved in this effect.

Recently, the response of stomata to humidity has been reinterpreted in a different way: it seems that the correlation between stomatal resistance and atmospheric humidity is purely empirical and that the mechanism underneath is based on the water-loss rate of the leaf [*Mott and Parkhurst*, 1991]. Stomata appear to respond to the rate of transpiration rather to air humidity per se. Reanalyzing 52 sets of measurements on 16 species, *Monteith* [1995a] showed that the leaf stomatal conductance can be interpreted as a linear decreasing function of transpiration with two empirical coefficients: a maximum conductance (obtained by extrapolation to zero transpiration) and a maximum rate of transpiration (obtained by extrapolation to zero conductance). *Monteith* [1995b] suggested also that this relationship between stomatal conductance and transpiration rate could be up-scaled from leaf to canopy, in the same way as the Jarvis model. However, little has been said about the significance and calculation of these parameters (maximum conductance and maximum transpiration) at canopy scale.

The aim of this paper is to assess and discuss this new formulation of stomatal behavior proposed by *Monteith*

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[1995b] and to interpret the parameters at canopy scale. The plan is as follows. Sections 2 and 3 examine respectively *Monteith*'s [1995b] and *Jarvis*' [1976] formulations. Section 4 shows how Monteith's formulation can be inferred from Jarvis' one and what is the expression of the two scaling parameters (in terms of the functions making up the Jarvis-type models). Section 5 is dedicated to numerical results obtained by simulation. Incorporating the stomatal resistance model of Monteith within a one-dimensional boundary layer model allows one to visualize and analyze the diurnal behavior of canopy resistance.

2. Monteith's Formulation of Canopy Resistance

The Penman-Monteith single-source model [*Monteith*, 1981] gives the flux of evaporation from a fully covering canopy in the form of

$$\lambda E = \frac{\varepsilon A + \rho \lambda D/r_a}{\varepsilon + 1 + r_s/r_a} \qquad (1)$$

where $A = R_n - G$ is the available energy (with R_n the net radiation and G the soil heat flux), $D = q^*(\theta) - q$ is the potential saturation deficit of the air (with θ the air temperature and q the specific humidity of the air), ε is the dimensionless slope of the saturation specific humidity q^* and varies with air temperature, r_a is the bulk aerodynamic resistance to heat and water vapor transfer through the surface layer, r_s is the bulk surface resistance to water vapour transfer, ρ is the air density, and λ is the latent heat of vaporisation. Defining potential evaporation from a given vegetation canopy (denoted by E_p) as the evaporation from this canopy when all the exchange surfaces are saturated, i.e., when $r_s = 0$ [*Lhomme*, 1997a], one can write

$$\lambda E_p = \frac{\varepsilon A + \rho \lambda \dot{D}/r_a}{\varepsilon + 1} \qquad (2)$$

and combining (1) and (2), evaporation can also be expressed as a function of E_p as

$$E = kE_p \qquad k = 1\Big/\Big(1 + \frac{1}{1+\varepsilon}\frac{r_s}{r_a}\Big) \qquad (3)$$

According to *Monteith* [1995a, b] the canopy conductance g_s ($=1/r_s$) is a linear function of transpiration E with the general form

$$g_s/g_{sx} = 1 - E/E_x \qquad (4)$$

where g_{sx} and E_x are two parameters empirically determined. The maximum conductance g_{sx} is obtained by extrapolation to zero transpiration, and the maximum rate of transpiration E_x is obtained by extrapolation to zero conductance. In terms of surface resistance, (4) is equivalent to

$$r_s/r_{sn} = E_x/(E_x - E) \qquad (5)$$

where $r_{sn} = 1/g_{sx}$. In this analysis, soil evaporation is assumed to be negligible, which means that transpiration rate in (4) or (5) is strictly the same as canopy evaporation in (1) or (3). Consequently, combining (3), expressing the thermodynamic dependence of E on r_s, with (5), expressing the physiological dependence of E on r_s, leads to a quadratic expression for r_s, which can be put in the following form:

$$X^2 + [(1 + \varepsilon)r_a(1 - E_p/E_x) - r_{sn}]X - (1 + \varepsilon)r_a r_{sn} = 0 \qquad (6)$$

$$X = r_s$$

The appropriate root of (6) is

$$r_s = [-\Lambda + \sqrt{\Lambda^2 + 4(1 + \varepsilon)r_a r_{sn}}]/2 \qquad (7)$$

$$\Lambda = (1 + \varepsilon)r_a(1 - E_p/E_x) - r_{sn}$$

When the quadratic equation obtained by combining (3) with (5) is solved in E instead of r_s, the appropriate root gives [*Monteith*, 1995b]

$$E = [E_p + \alpha_n E_x - \sqrt{(E_p + \alpha_n E_x)^2 - 4E_x E_p}]/2 \qquad (8)$$

$$\alpha_n = 1 + \frac{1}{\varepsilon + 1}\frac{r_{sn}}{r_a}$$

The limit rate of transpiration E_x is a notional maximum rate of water supply, the precise significance of which is not known. However, a simple physical interpretation can be inferred from (8). When atmospheric demand becomes very large, i.e., when E_p tends to infinity (all other parameters being kept constant), it can be shown from (8) that evaporation tends to E_x (this result is obtained by noticing that the square root in (8) is equivalent to $E_p + \alpha_n E_x - 2E_x$, when E_p tends to $+\infty$). So, E_x can be interpreted as the limit value of actual evaporation when the atmospheric demand tends to infinity. In other words, it is a notional maximum amount of water available in the soil for extraction by the canopy per unit time. It is worthwhile stressing that E_x cannot be parameterized as a function of E_p in the form of (3), i.e., $E_x = k_x E_p$ with k_x a constant depending on soil water availability ($0 \leq k_x \leq 1$). If it were the case, (7) shows that canopy resistance would no longer depend upon transpiration rate.

Little is known also on the significance and possible values of r_{sn}. *Monteith* [1995b], without clear justifications, parameterized r_{sn} as a function of solar radiation S in the following way: r_{sn} decreases from $+\infty$ down to a threshold of 50 s m^{-1}, when S increases from 0 to $S_0 = 400$ W m^{-2}, and then remains constant at 50 s m^{-1}, when $S > S_0$.

3. The Jarvis-Type Representation of Canopy Resistance

So far, the Jarvis-type models [*Jarvis*, 1976; *Stewart*, 1988] have represented the most common way of parameterizing the response of stomata to environmental factors, at leaf scale as well as at canopy scale. They describe this response in the form of a minimal resistance multiplied by the product of independent stress functions interacting without synergy [*Jacobs*, 1994]

$$r_s = r_{s\,min}F_1(S)F_2(T)F_3(D)F_4(\Psi_l) \qquad (9)$$

Here, $r_{s\,min}$ is the minimum stomatal resistance observed in optimal conditions, i.e., if none of the controlling variables is limiting. S is the incoming solar radiation, T is the air temperature, D is the water vapor saturation deficit, and Ψ_l is the leaf water potential, which at the scale of a stand of vegetation is often replaced by the bulk soil water potential or the soil water content averaged over the root zone. The influence of CO_2 is generally omitted because its concentration is almost constant during the diurnal part of the day. Each function (F_i) varies from unity to infinity. Their form is established in controlled environments, and the parameters of the functions are deter-

mined from statistical analysis of measurements covering a wide range of the relevant variables. *Kelliher et al.* [1995] showed that $r_{s \ min}$ takes average values of 30 and 50 s m^{-1}, respectively, for agricultural crops and natural vegetation.

The influence of solar radiation is crucial and cannot be skipped. It can be expressed in terms of an exponential function [*Fisher et al.*, 1981] or a hyperbolic function of the form [*Stewart*, 1988]

$$F_1(S) = (c + S)/(dS) \qquad (10)$$

where d is obtained from $d = 1 + c/1000$. When S is expressed in W m^{-2}, *Stewart* [1988] derived a mean value of about 100 for c in the case of a pine forest in England, and *Stewart and Gay* [1989] derived a mean value of about 400 in the case of the Konsa Prairie in Kansas (First International Satellite Land Surface Climatology Project Field Experiment (FIFE) data). The response of stomata to temperature may be represented by an exponential function [*Jarvis*, 1976] or a power function [*Stewart*, 1988]. A simpler representation [*Dickinson*, 1984; *Noilhan and Planton*, 1989] is written as

$$F_2(T) = [1 - k_T(T_x - T)^2]^{-1} \qquad (11)$$

with $k_T = 0.0016$ and $T_x = 298$ K. However, in many parameterizations of stomatal resistance the effect of temperature is neglected [*Deardorff*, 1978; *Stewart and Gay*, 1989; *Lynn and Carlson*, 1990; *Mascart et al.*, 1991; *de Ridder and Schayes*, 1997]. In our analysis, for the sake of convenience, we also assume that ambient temperature has no effect on stomatal resistance, and thus $k_T = 0$ and $F_2(T) = 1$. As to the dependence on saturation deficit $F_3(D)$, the common form generally adopted is a linear decrease of stomatal conductance with D [*Jarvis*, 1976; *Stewart*, 1988; *Noilhan and Planton*, 1989] leading to

$$F_3(D) = (1 - \alpha D)^{-1} \qquad 0 < D < 1/\alpha \qquad (12)$$

For the Konza Prairie in Kansas (FIFE data), *Stewart and Gay* [1989] give a mean value of about 24 to the empirical coefficient α, with D expressed in kg kg^{-1}. *Noilhan and Planton* [1989], give the value of α (derived for a coniferous forest from the Hydrologic Atmospheric Pilot Experiment/Modelisation du Bilan Hydrique (HAPEX-MOBILHY) data set) as 41. Several stomatal models do not take into account the effect of saturation deficit [*Deardorff*, 1978; *Mascart et al.*, 1991; *de Ridder and Schayes*, 1997]. Moreover, *Lynn and Carlson* [1990, p. 17] question the real effect of air humidity on stomatal resistance:

After reviewing the many stomatal resistance formulations summarised in Table 1 [13 references], we were unable to understand the basis for a direct effect of vapour pressure deficit on stomatal resistance. It may be possible to explain the response of the stomata to [D] as a response of the guard cells to epidermal leaf water potential.

They think the role played by the saturation deficit is indirect. An increase of D will damp the leaf water potential which, in turn, will be responsible for an increase of stomatal resistance, as specified hereafter.

The dependence of stomatal resistance on leaf water potential can be expressed in different ways. *Jarvis* [1976] suggested a negative exponential relationship between stomatal conductance and leaf water potential. *Choudhury and Idso* [1985] derived the following empirical function from data obtained on field-grown wheat
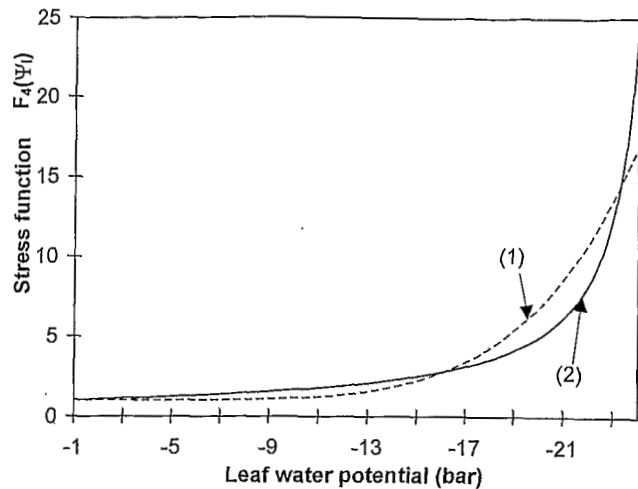

Figure 1. Comparison of the two curves $F_4(\Psi_l)$ representing the stress function for leaf water potential in Jarvis' parameterization of canopy resistance: (1) equation (13a) and (2) equation (13b), with $\Psi_{cr} = -14.5$ bars and $\Psi_{cc} = -25$ bars. $\Psi_{cr} = 14.5$ bars corresponds to the best fit between the two curves over the range $[-1, -24]$ for a fixed value of Ψ_{cc} of -25 bars.

$$F_4(\Psi_l) = 1 + (\Psi_l/\Psi_{cr})^n \qquad n = 5.5 \qquad (13a)$$

where Ψ_l is the bulk leaf water potential and Ψ_{cr} is a critical leaf water potential giving the limit beyond which the transpiration rate is strongly limited by water stress (about -20 bars for a cereal crop). When leaf water potential is not available, it is often replaced by soil moisture deficit [*Stewart*, 1988; *Noilhan and Planton*, 1989] or simply disregarded [*Stewart and Gay*, 1989]. *Lynn and Carlson* [1990] proposed a "discontinuous linear model" similar to that discussed by *Fisher et al.* [1981], where the exponential behavior of $F_4(\Psi_l)$ is represented by a pair of straight lines whose intersection defines a critical value Ψ_{cr}. *Mascart et al.* [1991] used the same formulation as *Choudhury and Idso* [1985]. In their Institut d'Astronomie et de Géophysique Georges Lemaître (IAGL) land surface model, *de Ridder and Schayes* [1997] employ an hyperbolic dependence of the form

$$F_4(\Psi_l) = (1 - \Psi_l/\Psi_{cc})^{-1} \qquad (13b)$$

where Ψ_{cc} represents the value of leaf water potential at which a complete stomatal closure occurs ($\Psi_{cc} \approx -25$ bars). Figure 1 compares the shape of the two curves proposed for F_4 (equations (13a) and (13b)) for fixed values of Ψ_{cr} and Ψ_{cc}. On the operational range of leaf water potential the two curves appear to be very close.

4. Matching the Two Formulations

A precise insight into the significance of the two parameters (E_x and r_{sn}) of Monteith's model can be obtained by matching the two formulations of canopy resistance (Monteith's one and Jarvis' one). In this section we show how the Jarvis model can be transformed and put in the same form as the Monteith model.

The bulk leaf water potential Ψ_l is related to the bulk soil water potential Ψ_s by means of the Ohm's law type equation originally proposed by *van den Honert* [1948]

Table 1. Base Values of the Variables and Coefficients Used in the Numerical Simulations

Variable	Significance	Value and Unit
r_{rs}	root-stem resistance	0.05 bar $(W\ m^{-2})^{-1}$
Z_{ef}	effective rooting depth	1 m
K_{sat}	soil hydraulic conductivity at saturation	$6.3 \times 10^{-v}\ m\ s^{-1}$
Ψ_{sat}	soil water potential at saturation	-0.03 bar
b	coefficient in the relation $K_s = f(\Psi_s)$	7.1
$r_{s\ min}$	minimal stomatal resistance in Jarvis' formulation	40 s m^{-1}
c	coefficient in the stress function $F_1(S)$	400
k_T	coefficient in the stress function $F_2(T)$	0
α	coefficient in the stress function $F_3(D)$	24
Ψ_{cc}	leaf water potential for a complete closure of stomata (in $F_4(\Psi_l)$)	-25 bars
r_a	canopy aerodynamic resistance	50 s m^{-1}
ε	dimensionless slope of the saturation specific humidity	2.8 at $\theta = 25°C$
δ	day length	12 hours
t_0	initial time for the CBL development simulation	6 hours
h_0	CBL height at $t = t_0$	10 m
A_x	maximum value of available energy	500 W m^{-2}
η	ratio between available energy and solar radiation	0.7

$$\Psi_l = \Psi_s - r_{sp}\lambda E \qquad (14)$$

where r_{sp} is the total soil-plant resistance and E is the water flux through the soil-plant system, assumed here to be equal to the total evaporation rate. The significance and value of r_{sp} have been extensively discussed by Lynn and Carlson [1990]. The parameter r_{sp} is the sum of a soil-root interface resistance (r_{sr}) and of a root-stem resistance (r_{rs}): $r_{sp} = r_{sr} + r_{rs}$. The plant component of $r_{sp}(r_{rs})$ remains relatively constant over a large range of leaf water potential: a typical value is 0.047 (Ψ being expressed in bar and λE in W m^{-2}). The soil component of $r_{sp}(r_{sr})$ expresses the resistance of the flow of liquid water from the soil to the roots. Its formulation was adapted by Choudhury and Idso [1985] from a model originally proposed by Feddes and Rijtema [1972]:

$$r_{sr} = 0.0013 k_1/(Z_{ef}K_s) \qquad (15)$$

where 0.0013 (m^2) is the ratio of a parameter relating root distance and geometry to the reciprocal of the effective rooting depth; k_1 is a conversion factor equal to 0.4×10^{-10} when r_{sr} is expressed in bar (W $m^{-2})^{-1}$; Z_{ef} is the effective rooting depth (m), assumed to be 1 m in our analysis; K_s is the soil hydraulic conductivity (m s^{-1}), which is linked to the soil water potential by [Campbell, 1974]

$$K_s = K_{sat}(\Psi_{sat}/\Psi_s)^{3/b+2} \qquad (16)$$

where K_{sat} and Ψ_{sat} are the conductivity and the water potential, respectively, at field saturation. The soil hydraulic parameters K_{sat}, Ψ_{sat}, and b have been determined by Clapp and Hornberger [1978] for the 11 soil types of the U.S. Department of Agriculture (USDA) textural classification: b varies from 4.05 for sand to 11.4 for clay. The values retained in our simulations and shown in Table 1 are those corresponding to a sandy clay loam.

Taking into account (13b) and (14), (9) can be rewritten as

$$r_s = \frac{r_{123}}{1 - (\Psi_s - r_{sp}\lambda E)/\Psi_{cc}} \qquad (17)$$

$$r_{123} = r_{s\ min}F_1(S)F_2(T)F_3(D)$$

Rearranging (17) leads to

$$r_s = \frac{r_{123}/(1 - \Psi_s/\Psi_{cc})}{1 - (r_{sp}\lambda E)/(\Psi_s - \Psi_{cc})} \qquad (18)$$

which is an expression similar and functionally equivalent to (5), when rewritten as $r_s = r_{sn}/(1 - E/E_x)$. Matching term by term these two equations leads to

$$r_{sn} = r_{123}/(1 - \Psi_s/\Psi_{cc}) = r_{123}F_4(\Psi_s) \qquad (19)$$

and

$$\lambda E_x = (\Psi_s - \Psi_{cc})/r_{sp} \qquad (20)$$

Consequently, it appears that Monteith's parameterization of canopy stomatal resistance is not different from the Jarvis approach since the former can be inferred from the latter. However, the perfect match between the two models (equations (19) and (20)) can be achieved only if $F_4(\Psi_l)$ is given by (13b) (from a strict mathematical standpoint it is worthwhile stressing that the specific match selected is logical, but not necessarily the only possible one). If instead of (13b), (13a) is chosen for expressing the dependence upon leaf water potential, the perfect matching shown above is not attainable. Nevertheless, in this case also, it is possible to infer similar expressions for r_{sn} and E_x, as detailed in Appendix A. Therefore we can state that the two parameters (r_{sn} and E_x) of Monteith's relationship are always interpretable in terms of the parameters and functions making up the Jarvis model: r_{sn} is expressed as $r_{123}F_4(\Psi_s)$ and λE_x as $(\Psi_s - \Psi_{cc})/r_{sp}$, whatever the mathematical expression given to $F_4(\Psi_l)$. Their physical significance appears now clearly. The parameter r_{sn} represents the canopy stomatal resistance when the leaf water potential is equal to the soil water potential ($\Psi_l = \Psi_s$), i.e., at zero transpiration (conditions experimentally encountered at predawn). E_x represents the flux of water extracted from the soil when the leaf water potential is equal to the limit value Ψ_{cc} (i.e., its lowest possible value according to the parameterization used for F_4). It is the maximum flux of water the canopy can potentially extract from the soil. As the Jarvis models are functionally equivalent to Monteith's model, (7) linking canopy resistance to potential evaporation is also valid for the Jarvis models, with r_{sn} and E_x given by (19) and (20).

The issue that arises now is the dependence of the canopy minimal stomatal resistance r_{sn} upon water vapor saturation deficit. To Monteith's mind, r_{sn} cannot depend upon saturation deficit, since in (5) the dependence of canopy resistance upon transpiration theoretically replaces the dependence upon saturation deficit. However, the matching of the two models leads to this apparent double dependence (r_{sn} is a function of r_{123} and then of $F_3(D)$, as shown by (17)). It is possible to keep only one dependence (that upon transpiration), either by assuming with *Lynn and Carlson* [1990] that stomata do not respond directly to D (but indirectly through Ψ_l) and by putting then $F_3(D) = 1$ or by replacing the dependence of r_{sn} upon D by a dependence upon E in the way described in Appendix B. In this last case the equation obtained for r_s is very different and far more complex than the one proposed by Monteith. Nevertheless, the numerical simulations performed further (Figure 4) show that assuming $F_3(D) = 1$ does not lead to significant differences with the case $F_3(D) \neq 1$. From a pragmatic viewpoint it seems recommendable to share the idea of *Lynn and Carlson* [1990] by opting for $F_3(D) = 1$. In effect, this alternative leads to a sound and simple interpretion of the action of saturation deficit on stomatal aperture: When D increases, transpiration increases and consequently leaf water potential decreases according to (14) (assuming Ψ_s and r_{sp} to remain constant), which provokes a stronger stomatal closure.

5. Numerical Results

The maximum canopy transpiration E_x is expressed by (20). For a particular type of soil, characterized by fixed values of K_{sat}, Ψ_{sat}, and b, and a given vegetation, characterized by fixed values of Ψ_{cc}, r_{rs}, and Z_{ef} (see Table 1), the soil-plant resistance r_{sp} and then the maximum canopy transpiration λE_x depend only upon the soil water potential Ψ_s. Figure 2a shows the variation of λE_x as a function of Ψ_s for different values of the limit leaf water potential Ψ_{cc}. λE_x is an increasing function of Ψ_s: When Ψ_s passes from 0 to -20 bars, λE_x is divided by 10, passing from 500 to 50 W m^{-2} (for $\Psi_{cc} = -25$ bars); and for a given value of Ψ_s, λE_x increases when the limit leaf

Figure 2b. Maximum canopy evaporation λE_x versus soil water potential Ψ_s for different values of the root-stem resistance r_{rs}.

water potential Ψ_{cc} decreases. The parameter λE_x is also a function of the root-stem resistance as illustrated in Figure 2b. Figure 3 gives the variation of the minimum stomatal resistance r_{sn} as a function of solar radiation S for different values of soil water potential. In the expression of r_{sn} given by (19) it is assumed that $F_2(T) = F_3(D) = 1$, which means that $r_{123} = r_1 = r_{s\,min}F_1(S)$. In this way, the minimum canopy resistance r_{sn} depends only upon solar radiation through $F_1(S)$ and soil water potential Ψ_s. The parameter r_{sn} appears to be a decreasing function of both solar radiation and soil water potential.

There is a permanent interaction and feedback between the transpiring vegetation and the characteristics of the convective boundary layer (specific humidity and temperature). In the rest of the section we examine the diurnal behavior of the stomatal resistance and of the evaporation when Monteith's resistance formulation (with the coefficients derived above) is coupled with a convective boundary layer (CBL) model. The CBL model used is described in Appendix C. It represents an ad-
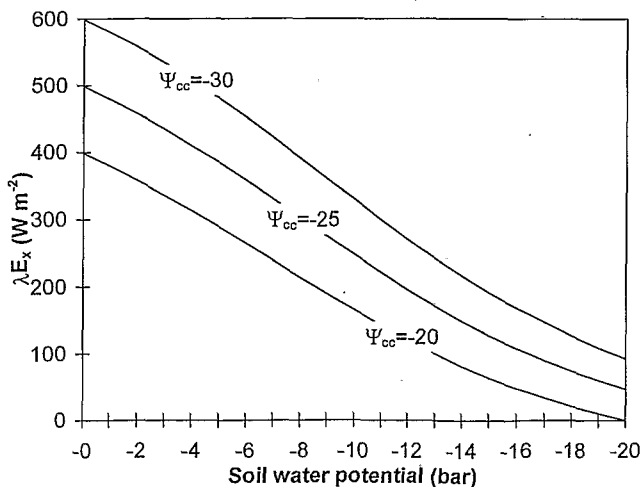

Figure 2a. Maximum canopy evaporation λE_x (given by equation (20)) versus soil water potential Ψ_s for different values of the leaf water potential Ψ_{cc} corresponding to a complete stomatal closure (defined by equation (13b)).
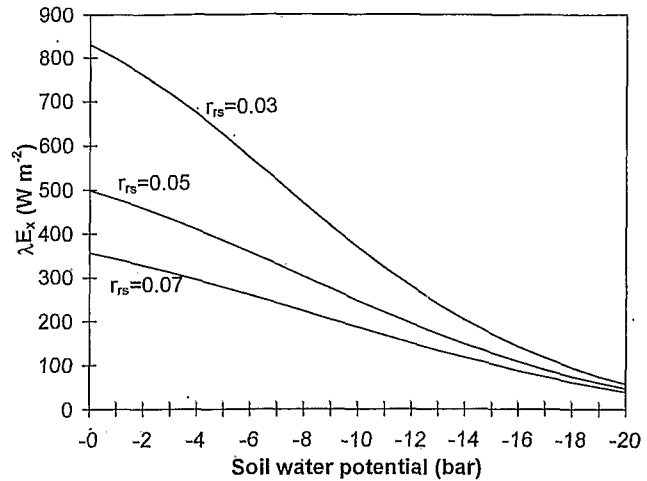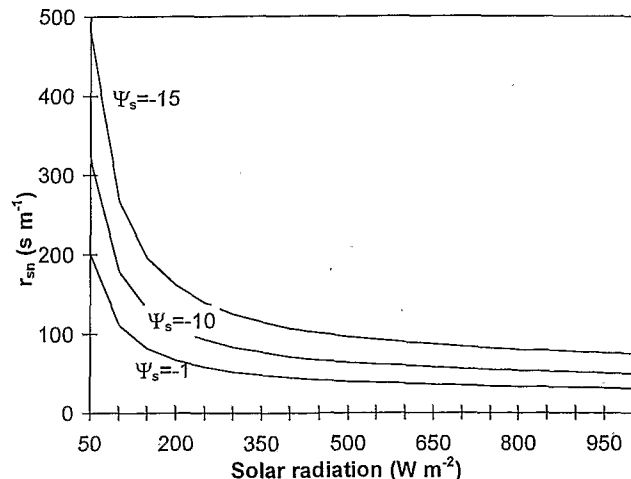

Figure 3. Minimum canopy resistance r_{sn} (given by equation (19)) versus solar radiation S for different values of the soil water potential Ψ_s.
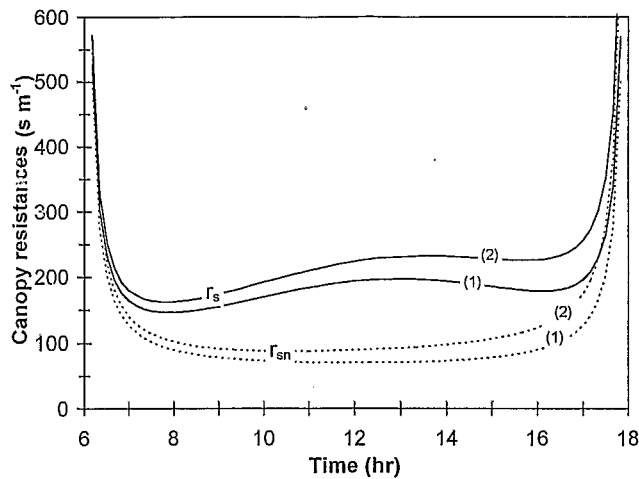
Figure 4a. Diurnal course of canopy resistance r_s (solid line) and of minimal canopy resistance r_{sn} (dashed line) with the values of the base parameters given in Table 1 and $\Psi_s = -5$ bars. Curves (1): with $F_3(D) = 1$; curves (2): with $F_3(D) \neq 1$ given by equation (12).

Figure 5. Diurnal course of canopy resistance for three different values $(-1, -10, -15$ bars) of soil water potential Ψ_s, with the values of the base parameters given in Table 1.

aptation of the slab model originally devised by *McNaughton and Spriggs* [1986], where the CBL is seen as a well-mixed layer with a potential temperature θ and a specific humidity q constant with height, topped by the undisturbed atmosphere, whose properties are determined by synoptic scale processes [*McNaughton*, 1989]. Between the ground surface and the well-mixed layer, there is a relatively thin surface layer, where the gradients of temperature and humidity may be significant. Figure 4a exemplifies the diurnal course of the canopy resistance r_s as expressed by the Monteith relationship. The minimal canopy resistance r_{sn} (given by (19)) is also shown. Curve (1) is plotted with $F_3(D) = 1$, which means that r_{sn}, and consequently r_s, do not depend directly upon saturation deficit. Curve (2) is plotted with the dependence of r_{sn} on saturation deficit ($F_3(D)$ is given by (12)). The two curves are not too different. The maximum difference between r_s (1) and r_s (2) is about 50 s m^{-1}, at the end of the diurnal period, when the saturation deficit is maximum. Figure 4b shows the impact of this difference on the diurnal course of canopy evaporation.
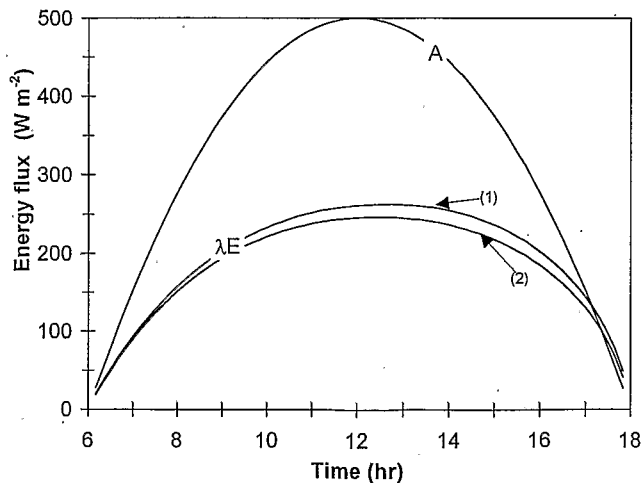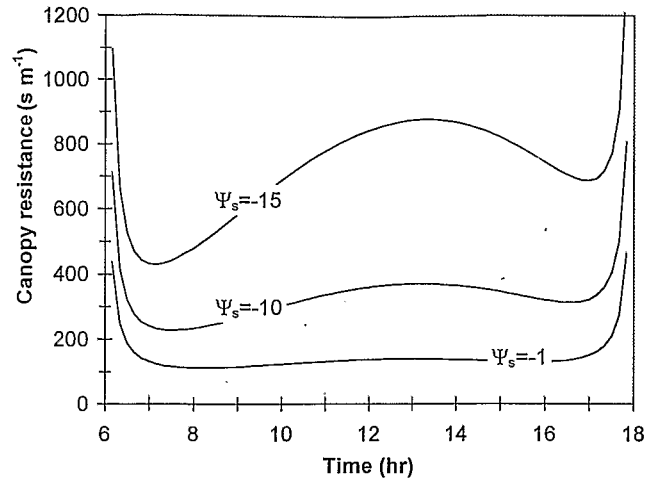
The maximum difference between the two curves represents about 20 W m^{-2}, which is rather weak. The fact that the effect of $F_3(D)$ is fairly slight provides an additional reason to think with *Lynn and Carlson* [1990] that stomata respond indirectly to saturation deficit through leaf water potential, which would legitimize the assumption that $F_3(D) = 1$. In Figure 5 the diurnal course of canopy resistance is plotted for three different values of soil water potential. For $\Psi_s = -1$ bar the canopy resistance is nearly constant during the central hours of the day (around 120 s m^{-1}). In this case the evaporation follows the available energy. For $\Psi_s = -15$ bars, r_s experiences a big increase in the middle of the day (up to around 900 s m^{-1}), which leads to a transpiration plateau (the increase in r_s offsets the increase in A). $\Psi_s = -10$ bars corresponds to an intermediate case with a relatively small increase of canopy resistance in the middle of the day. In Figure 6 the diurnal course of canopy resistance is plotted for two different values of the maximum available energy A_x, which occurs at midday (300
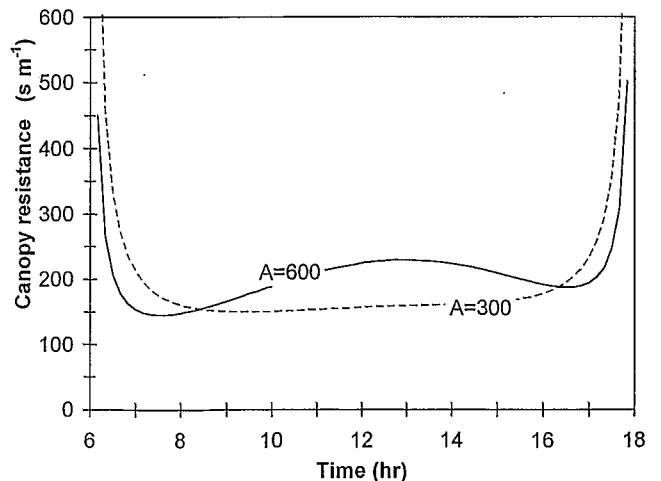

Figure 4b. Diurnal course of canopy evaporation and available energy A in the same conditions.

Figure 6. Diurnal course of canopy resistance for two different values of the maximum available energy A_x (300 and 600 W m^{-2}) with the values of the base parameters given in Table 1 and $\Psi_s = -5$ bars.

and 600 W m^{-2}). When the available energy is weak, the canopy resistance is relatively constant in the central hours (around 150 s m^{-1}), whereas for a strong available energy (which means a strong evaporative demand), r_s increases up to about 230 s m^{-1}.

6. Conclusion

The formulation of canopy resistance recently proposed by *Monteith* [1995b] expresses the idea (supported by many experimental evidences) that stomata respond to the rate of transpiration rather than to air humidity per se. In terms of resistance it reads as $r_s/r_{sn} = (1 - E/E_x)^{-1}$, where r_{sn} and E_x are two coefficients assumed to be functions of environmental or plant variables. This formulation has been examined and compared to the more common Jarvis-type parameterizations, where stomatal resistance is expressed as a minimal canopy resistance multiplied by various stress functions, each one representing the influence of one environmental or plant factor. It appears that Monteith's formulation of canopy resistance is not fundamentally new and can be inferred from Jarvis' one when the stress function $F_4(\Psi_l)$, involving leaf water potential, is expressed in the form of a hyperbolic function (equation (13b)). The perfect matching requires also that stomata do not respond directly to air humidity but indirectly through transpiration and leaf water potential. This means that the stress function for air humidity $F_3(D)$ (in the Jarvis formulation) equals unity. In the light of our analysis this last assumption, shared by other authors [*Lynn and Carlson*, 1990], seems sound and convincing.

It has been shown also that physical expressions can be derived for the two coefficients of Monteith's relationship, whatever the mathematical form given to the stress function $F_4(\Psi_l)$. In all circumstances the minimum stomatal resistance r_{sn} represents the canopy stomatal resistance when the leaf water potential is equal to the soil water potential ($\Psi_l = \Psi_s$ and $E = 0$), all other conditions being equal; and the maximum rate of transpiration E_x represents the flux of water extracted from the soil when the leaf water potential reaches its lowest possible value (according to the parameterization used for F_4): It is the maximum flux of water which can be extracted from the soil by the canopy.

Appendix A: Expressing r_{sn} and E_x When $F_4(\Psi_l)$ Is Given by Equation (13a)

When (13a) is used to express the dependence of stomatal resistance on leaf water potential, r_s is written as

$$r_s = r_{123}[1 + (\Psi_l/\Psi_{cr})^n] \quad r_{123} = r_{s\,min}F_1(S)F_2(T)F_3(D) \quad \text{(A1)}$$

Replacing Ψ_l by its expression as a function of evaporation (equation (14)) and rearranging leads to

$$r_s = r_{123}[1 + (\Psi_s/\Psi_{cr})^n(1 - r_{sp}\lambda E/\Psi_s)^n] \quad \text{(A2)}$$

which shows that canopy stomatal resistance is an increasing function of transpiration, as already attested by (5) or (18). Defining Ψ_{cc} strictly in the same way as in (13b), i.e., as the limit value of leaf water potential at which a complete stomatal closure occurs, the maximum canopy transpiration can be written as

$$\lambda E_x = (\Psi_s - \Psi_{cc})/r_{sp} \quad \text{(A3)}$$

Replacing in (A2) r_{sp} by its expression as a function of E_x leads to

$$r_s = r_{123}\{1 + (\Psi_s/\Psi_{cr})^n[1 - (1 - \Psi_{cc}/\Psi_s)E/E_x]^n\} \quad \text{(A4)}$$

which can be considered as the equation equivalent to (18). Because of the mathematical form of $F_4(\Psi_l)$, it is not conceivable to put (A4) in the exact form of Monteith's expression (equation (5)), as we did with $F_4(\Psi_l)$ expressed by (13b). However, the minimum canopy resistance r_{sn} can be inferred in the following way. When evaporation is nil, $r_s = r_{sn}$ according to (5), which means by matching (5) and (A4) that

$$r_{sn} = r_{123}[1 + (\Psi_s/\Psi_{cr})^n] = r_{123}F_4(\Psi_s) \quad \text{(A5)}$$

When evaporation is equal to E_x, the surface resistance r_s becomes very high, and its value is given by $r_{123}[1 + (\Psi_{cc}/\Psi_{cr})^n]$.

It is easy to anticipate that the same type of expression, with the same physical meaning, can be inferred for r_{sn} and E_x, whatever the mathematical form of the stress function $F_4(\Psi_l)$.

Appendix B: Expression of r_s as a Function of Canopy Transpiration

The saturation deficit of the air D can be expressed as a function of canopy evaporation E by inverting (1). This leads to the following expression of F_3:

$$F_3(D) = \left\{1 - \alpha(\varepsilon + 1)r_a\left[E\left(1 + \frac{1}{\varepsilon + 1}\frac{r_s}{r_a}\right) - E_{eq}\right]/\rho\right\}^{-1} \quad \text{(B1)}$$

where E_{eq} is the equilibrium evaporation ($= \varepsilon A/[\lambda(1 + \varepsilon)]$). Combining (B1) with (17) and (20) leads to a quadratic equation for r_s, which can be put in the form

$$\alpha E r_s^2 - [\rho - \alpha(\varepsilon + 1)r_a(E - E_{eq})]r_s$$
$$+ \rho r_{12}(1 - \Psi_s/\Psi_{cc})^{-1}(1 - E/E_x)^{-1} = 0 \quad \text{(B2)}$$

where $r_{12} = r_{s\,min}F_1(S)F_2(T)$. The appropriate root of (B2) is

$$r_s = [\Gamma - \sqrt{\Gamma^2 - 4\alpha\rho r_{12}E(1 - \Psi_s/\Psi_{cc})^{-1}(1 - E/E_x)^{-1}}]/(2\alpha E) \quad \text{(B3)}$$

with

$$\Gamma = \rho - \alpha(\varepsilon + 1)r_a(E - E_{eq}) \quad \text{(B4)}$$

Equation (B3) (which is strictly equivalent to (18) with $F_3(D) \neq 1$ given by (12)) represents the exact dependence of r_s on canopy evaporation in the Jarvis-type models without interference with the saturation deficit.

Appendix C: Convective Boundary Layer Modeling

The inversion cap of the CBL, whose height h grows during the daytime, is not impermeable. The incorporation of a thin layer of air of thickness dh, potential temperature $\theta_+(h)$, and humidity $q_+(h)$ into the mixed layer with potential temperature θ and specific humidity q leads to the following differential equations for sensible heat and water vapor, respectively [*McNaughton and Spriggs*, 1986]:

$$\rho c_p h \frac{d\theta}{dt} = H + \rho c_p(\theta_+ - \theta)\frac{dh}{dt} \quad \text{(C1)}$$

$$\rho h \frac{dq}{dt} = E + \rho(q_+ - q) \frac{dh}{dt} \qquad (C2)$$

where H is the sensible heat flux (obtained from the energy balance equation $H = A - \lambda E$) and E is the evaporation flux at the surface given by (1) (in which D is the potential saturation deficit within the mixed layer). Generally, $\theta_+(h) > \theta$ and $q_+(h) < q$, which means that entrainment tends to raise the temperature and to decrease the humidity within the CBL, both factors contributing to increase the evaporation rate. The rate of growth of the CBL is parameterized according to the "encroachment model" proposed by McNaughton and Spriggs [1986]:

$$\frac{dh}{dt} = \frac{H}{\rho c_p h \gamma_\theta} \qquad (C3)$$

where γ_θ is the gradient of potential temperature just above the inversion base. The vertical profiles of potential temperature and specific humidity in the undisturbed atmosphere are assumed to be linear $\theta_+(z) = \gamma_\theta z + \theta_{+0}$ and $q_+(z) = \gamma_q z + q_{+0}$, where γ_q is the gradient of specific humidity just above the CBL, θ_{+0} and q_{+0} are the potential temperature and the specific humidity above the CBL extrapolated at $z = 0$. Equations (C1), (C2), and (C3) have three dependent variables $(\theta(t), q(t), h(t))$ forming a set of three coupled first-order differential equations, which are solved using the Runge-Kutta numerical method. The calculation is initiated with a fixed value of the CBL height h_0, and the initial values of potential temperature θ_0 and specific humidity q_0 are taken to be equal respectively to $\theta_+(h_0)$ and $q_+(h_0)$. ρ, λ, c_p, γ_θ, γ_q, θ_{+0} and q_{+0} are taken as constant, and ε varies with the potential temperature θ of the mixed layer.

Available energy $A(t) = R_n(t) - G(t)$ is assumed to vary as a parabolic curve, which intends to simulate its diurnal behaviour over the day length δ [Lhomme, 1997b]: $A(t) = 0$ at the initial time $t = t_0$ and at the time $t = t_0 + \delta$, and $A(t) = A_x$ (a maximum value) at the time $t = t_0 + \delta/2$. Under these conditions, $A(t)$ can be written as

$$A(t) = A_x F(t) \qquad F(t) = -4[t^2 - (\delta + 2t_0)t + t_0(t_0 + \delta)]/\delta^2$$
$$(C4)$$

In the simulations performed, $\delta = 12$ hours and $t_0 = 6$ hours (local time), and a simple relationship of the type $A = \eta S$ (with $\eta = 0.7$) is assumed between available energy and solar radiation. The evaporation rate at the surface is computed by (8) with r_{sn} and E_x given by (19) and (20), respectively. The aerodynamic resistance r_a is assumed to keep a constant value of 50 s m^{-1}. The standard profiles of potential temperature and specific humidity above the CBL used in the simulations are the so-called McClatchey profiles as cited by Jacobs [1994]. They represent average atmospheric conditions in terms of latitude and season. Only one case has been considered here, the midlatitude summer case (MLS), and linear equations have been fitted to the curves given by Jacobs [1994, p. 156]:

$$\theta_+ = 4.78z + 293.6 \qquad q_+ = -0.00285z + 0.01166 \qquad (C5)$$

with z expressed in km, θ in K, and q in kg kg^{-1}.

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