Stomatal control of transpiration: 
Examination of the Jarvis-type representation of canopy resistance in relation to humidity

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Abstract. The Jarvis-type parameterization of canopy resistance is commonly used to model the canopy energy balance in large-scale applications. In its most complete form it is written as a minimal stomatal resistance multiplied by five stress functions involving solar radiation $F_1(S)$, air temperature $F_3(T)$, air saturation deficit $F_5(D)$, soil or plant water status $F_4(\Psi)$, and CO$_2$ concentration of the air $F_5(C)$, respectively. One or several functions, however, can be missing according to the experimental conditions or the assumptions made for the modeling process. This general scheme is examined in relation to environmental humidity to determine the exact correspondence between the mathematical representation and the physiological response in terms of canopy resistance and actual transpiration. The strict feedback response, i.e., the response to air or soil humidity through plant water status, is simulated by means of the sole function $F_4$ involving leaf water potential $\Psi_l$ (without the need for another stress function related to environmental humidity). In this case, canopy resistance increases with increased saturation deficit, and transpiration also increases. When soil water potential decreases, canopy resistance increases and transpiration falls. A feedforward response to air humidity, i.e., a direct response of stomata independent of plant water status, is modeled through the stress function $F_5(D)$, with or without the function $F_4(\Psi_l)$, depending on whether the feedforward response is combined with or without a feedback effect. In this latter case, canopy resistance increases with an increased saturation deficit, while the transpiration rate increases up to a threshold and then falls. A strict feedforward response to soil moisture is modeled through function $F_4$ in which soil water potential replaces leaf water potential. When the canopy resistance formulation includes a feedback response, i.e., when the function $F_4(\Psi)$ is used with leaf water potential $\Psi_l$, Jarvis’ scheme is equivalent to the parameterization developed by Monteith (as a function of the rate of transpiration), and the transpiration rate can be rewritten as a simple function of the climatic demand, the soil water availability, and the decoupling factor $\Omega$.

1. Introduction

The canopy resistance to evaporation $r_s$ is commonly defined on the basis of the Penman-Monteith single-source model that represents a fully covering vegetation as a “big leaf.” In this model, $r_s$ is calculated for an amphistomatous canopy as the mean leaf stomatal resistance divided by two times the leaf area index [Monteith, 1963, 1981]. In spite of some problems of upscaling [Lhomme, 1991] the canopy resistance is comparable to that of a single leaf and generally assumed to be influenced by the same factors. No theoretical approach has ever allowed one to derive a mechanistic model for stomatal control. Consequently, at leaf as well as at canopy scale, stomatal resistance is parameterized by empirical correlation with the factors of the environment experimentally related to the stomatal behavior. In the scientific literature, there exist two major categories of models for canopy resistance: (1) those generally termed “meteorological” that are adapted from the seminal model of Jarvis [1976] and (2) those more recent, termed “physiological,” that involve the assimilation rate of CO$_2$ [Collatz et al., 1991; Leuning, 1995]. In this paper, only the Jarvis-type models are investigated including those based on a root-shoot chemical signaling [Tardieu and Simonneau, 1998], which can be considered as an extension of the former.

The Jarvis-type approach describes the response of stomata to environmental factors in the form of a minimal stomatal resistance multiplied by the product of $n$ independent stress functions interacting without synergy

$$r_s = r_{s \, \text{min}} \prod_{i=1}^{n} F_i(X_i).$$

(1)

In this formulation, valid at leaf as well as at canopy scale, $r_{s \, \text{min}}$ represents the minimal surface resistance observed under optimal conditions, when none of the controlling variables is limiting [Kelliher et al., 1995]. Each stress function $F_i(X_i)$ varies from unity to infinity and represents the action of a given factor $X_i$ on the stomatal behavior. In the original paper by Jarvis [1976] and in most of the meteorological parameterizations found in the literature the factors involved are solar radiation $S$, air characteristics (temperature $T$, water vapor
saturation deficit $D$, and CO$_2$ concentration $C$, and plant or soil water status $\Psi$. In its most extensive formulation, canopy stomatal resistance is written as

$$r_s = r_{soil} F_4(S) F_2(T) F_3(D) F_4(\Psi) F_5(C),$$

where the forms and the mathematical representations of the individual functions are obtained from controlled environment studies [Jones, 1992]. Some examples of these mathematical representations are given in Appendix A. In his original paper, Jarvis characterizes water status by leaf water potential $\Psi_l$, specifying, however, that [Jarvis, 1976, p. 602] "it is by no means the most relevant water status variable." Many authors have followed this approach and have used $\Psi_l$ as a water status variable: Fedeler [1979], Norman [1979], Choudhury and Idso [1985], Baldocchi et al. [1987], Pinty et al. [1989], Lynn and Carlson [1990], Winkai and Rambal [1990], Mascart et al. [1991], Grant and Baldocchi [1992], Rambal [1993], Taconet et al. [1995], de Ridder and Schayes [1997], and Lhomme and Egliou [1999]. Other authors prefer to use predawn leaf potential $\Psi_p$ [Teixeira Filho et al., 1998; White et al., 1999] or soil water potential $\Psi_s$ [Avisar et al., 1985; Avisar and Pielke, 1991] or soil water content [Deardorff, 1978; Dolman et al., 1988; Stewart, 1988; Noilhan and Planton, 1989]. The function $F_s$ can also be simply disregarded when no substantial water shortage occurs, for example, in a sub-Arctic wet sedge meadow [Lafleur and Rouse, 1990] or a tropical rainforest [Dolman et al., 1991]. In fact, the general formulation (2) is rarely employed with all its stress functions, and in many experimental or modeling works, one or several functions can be missing. For instance, the influence of CO$_2$ is often omitted because its concentration is almost constant during the diurnal part of the day. Whereas most of the factors involved in the Jarvis formulation are purely environmental factors (in the sense that they are external to the plant itself), leaf water potential $\Psi_l$ is an internal factor and cannot be treated like the others as an independent cause of stomatal control. It is not always possible to say whether $\Psi_l$ is a cause or a consequence of stomatal control because of the multiple feedback loops and interactions between different factors [Jones, 1998]. In this respect, Lhomme et al. [1998] investigated the parameterization proposed by Monteith [1958b] relating canopy resistance to the rate of transpiration. They showed that Monteith's formulation can be inferred from a Jarvis-type representation provided it is written with the stress function involving leaf water potential and that $F_s(\Psi_f)$ is expressed in a hyperbolic form. This means that the two formulations are basically equivalent under the conditions specified.

The present paper has been written as an extension of the former [Lhomme et al., 1998] in the sense that the Jarvis-type scheme of canopy resistance is reexamined with respect to the role of environmental humidity (air and soil) and to its equivalence to Monteith's formulation. The extended analysis is based on the works of Cowan [1977] and Farquhar [1978], who distinguish between two types of stomatal response to humidity, feedback and feedforward. This distinction is used as the cornerstone of this study, which has two main objectives: first, to investigate the relationships existing between the different ways of writing the Jarvis formulation with respect to environmental humidity and the physiological mechanisms they imply in terms of canopy resistance and transpiration and, second, to specify the conditions for Jarvis' and Monteith's parameterizations to be equivalent and its consequences on the formulation of transpiration. Sections 2 and 3 analyze the correspondence existing between the mathematical formulation, the physiological response of stomata, and the behavior of transpiration in the feedback and feedforward cases, respectively. Section 4 reexamines Monteith's model of canopy resistance and develops a new formulation of the transpiration rate.

2. Stomatal Response Through Leaf Water Status (Feedback Response)

The feedback behavior means that canopy resistance and transpiration respond to a change in air humidity or soil water content via leaf water status [Farquhar, 1978]. When air saturation deficit increases, transpiration tends to increase, which lowers leaf water potential. This, in turn, leads to a stomatal closure with a negative feedback effect on transpiration. Similarly, when soil water potential decreases with a constant evaporative demand, leaf water potential also decreases to maintain the transpiration rate, which leads to a stomatal closure with a negative feedback on transpiration. In this section, we show how these two feedback behaviors are accounted for by a Jarvis-type formulation with the sole function involving leaf water potential $F_s(\Psi_f)$ without an explicit reference to air humidity or soil moisture.

The procedure used is based on a simple representation of the soil-plant-atmosphere continuum which combines the equation governing the water transfer in liquid phase (between the soil and the plant) with that governing the same transfer in vapor phase (between the leaves and the atmosphere). The schematic diagram of this one-dimensional representation is illustrated in Figure 1. It is made up of three compartments:
air, plant, and soil. In each compartment, water status is characterized by a bulk parameter, saturation deficit $D$, leaf water potential $\Psi$, and soil water potential $\Psi_s$, respectively. Leaf water potential is related to $\Psi$, through an Ohm's law type equation originally proposed by van den Honert [1948]

$$\Psi_l = \Psi_s - r_s \rho \Delta E,$$  

(3)

where $r_s$ is the total soil-plant resistance, which is a function of soil water potential and is detailed in Appendix B. $E$ is the water flux through the soil-plant system, assumed here to be equal to the total evaporation rate and multiplied by the latent heat of vaporization $\lambda$ for conversion into energy units. In vapor phase the evaporation rate is given by the Penman-Monteith equation

$$\Delta E = \frac{\rho \Delta T}{e + 1 + \frac{r_s}{r_w}} + \frac{\rho \Delta T}{e + 1 + \frac{r_s}{r_w}} - G,$$  

(4)

where $\rho A - G$ is the available energy (with $R_a$ the net radiation and $G$ the soil heat flux), $D = q^s(T) - q$ is the potential saturation deficit of the air (with $T$ the air temperature and $q$ the specific humidity of the air), $e = \frac{(\lambda c_p) dq^s/dT}{\rho}$ is the dimensionless slope of the saturation specific humidity $q^s$ and varies with air temperature, $\rho$ is the air density and $c_p$ is the specific heat of air at constant pressure, $r_s$ is the bulk aerodynamic resistance to heat and water vapor transfer through the surface layer, and $r_w$ is the bulk surface resistance to water vapor transfer. The evaporation rate given by (4) can also be formulated as a function of potential evaporation, defined as the evaporation from a given canopy when all the exchange surfaces are saturated [Lhomme, 1997]. In this case, potential evaporation $E_p$ is expressed by (4) with $r_s = 0$, and actual evaporation can be rewritten as

$$E = \Omega E_p = \Omega \left( 1 + \frac{1}{1 + \frac{r_w}{r_s}} \right)^{-1},$$  

(5)

where $\Omega (0 < \Omega < 1)$ is the decoupling factor introduced by McNaughton and Jarvis [1983]. The canopy resistance $r_s$ is parameterized according to a Jarvis-type formulation (2) with the stress function involving leaf water potential $F_s(\Psi)$. The function $F_s$ involving air humidity is disregarded to avoid any direct action of air humidity on stomata. The hyperbolic form given to $F_s(\Psi)$ (see Appendix A) allows one to rewrite (2) in the following way (with $F_s(D) = F_s(C) = 1$):

$$r_s = r_{s_{\infty}} / (1 - \Psi_p / \Psi_{cc}),$$  

(6)

where $\Psi_{cc}$ is the limit leaf water potential corresponding to a complete stomatal closure (when $\Psi_l \rightarrow \Psi_{cc}$, $r_s \rightarrow +\infty$). According to (3), the rate of transpiration is determined when the equilibrium value of leaf water potential is known. This value can be calculated for a given set of environmental conditions by combining (3), (5), and (6). Putting $\Psi_p = \Psi_p - r_s \rho \Delta E_p$ ($\Psi_p$ represents the leaf water potential theoretically obtained when the transpiration rate equals the potential rate) and $X_p = \Psi_p / \Psi_{cc}$ leads to the following quadratic equation for $\Psi_p$:

$$X^2 - (1 + \mu + X_{\infty}) X + (X_p + \mu \Psi_p / \Psi_{cc}) = 0 \quad X = \Psi_p / \Psi_{cc},$$  

(7)

with the dimensionless parameter $\mu = r_{12} / [(1 + e) r_s]$. The appropriate root of (7), which verifies $0 < X < 1$, yields

$$\Psi_p = \Psi_{cc} \left( \Gamma - \sqrt{\Gamma^2 - 4(\Psi_p + \mu \Psi_p / \Psi_{cc})} \right) / 2 \quad \Gamma = 1 + \mu + X_p,$$  

(8)

Knowing $\Psi_p$, canopy stomatal resistance $r_s$, and canopy transpiration $\Delta E$ are calculated by means of (6) and (4), respectively. The leaf water potential $\Psi_l$ is a strictly decreasing function of air saturation deficit. This can be proved by examining the sign of the first derivative of $\Psi_l$ given by (8) with respect to $D$ (see Appendix C). In Appendix C it is shown that the first derivative $(\partial \Psi_l / \partial D)$ is strictly negative whatever the saturation deficit. Consequently, when $D$ increases, $\Psi_l$ decreases, and canopy resistance logically increases: There is no need to use a stress function involving saturation deficit to obtain an increased canopy resistance with an increased $D$; the function $F_s(\Psi_l)$ is sufficient. All other conditions being equal, (3) shows that although $r_s$ increases with an increased $D$, the transpiration rate keeps increasing $(\Delta E / \Delta D > 0)$ since $\Psi_p$ and $r_s$ are kept constant in this equation. With respect to (4), this means that the numerator increases with $D$ faster than the denominator. In the same way as for air saturation deficit, it is possible to demonstrate that leaf water potential is an increasing function of $\Psi_l$, by examining the sign of $(\partial \Psi_l / \partial \Psi_p)$ (see Appendix C). According to (4) and (6), this means that canopy resistance increases and transpiration decreases when soil water potential $\Psi_s$ falls, without any explicit function involving soil water status in the canopy resistance formulation. It is important to stress that the generality of these results concerning the role of $D$ and $\Psi_s$ is not hindered by the fact that they are obtained with a particular form of function $F_s(\Psi_l)$. The hyperbolic form given to this function allows a relatively simple mathematical derivatization (a quadratic equation) while respecting the general behavior of the relationship, as shown by Lhomme et al. [1998]. A more complicated representation of $F_s(\Psi_l)$, such as the power function proposed by Choudhury and Idso [1985], would have led to similar results but through a more cumbersome procedure.

A series of numerical simulations based on the above-described equations have been carried out to illustrate the feedback behavior. Solar radiation $S$ and air temperature $T$ are inputs to the model. Available energy is calculated as a given proportion of $S$: $A = 0.7 S$. The prescribed values of the coefficients and other variables involved in the simulations are given in Table 1. The variations of $\Psi_l$, $r_s$, and $\Delta E$ as a function of saturation deficit $D$ for different values of $\Psi_p$ are plotted in Figure 2. When $D$ increases, leaf water potential decreases, canopy resistance increases, and transpiration also increases (although very slightly for low soil water potentials). Similarly, the variations of $\Psi_l$, $r_s$, and $\Delta E$ as a function of soil water potential for different values of saturation deficit are plotted in Figure 3. As could be anticipated, when $\Psi_s$ falls, leaf water potential falls, which leads to an increased canopy resistance and a decreased transpiration. Infinite resistance and zero transpiration are obtained for a theoretical infinite value of soil water potential because $\Psi_l$ tends to $\Psi_{cc}$ when $\Psi_s$ tends to $-\infty$. The three-compartment model and (8) are also useful to examine the impact of soil compaction. Root clumping following soil compaction is reported to increase the soil-root resistance to water flux, which affects the hydraulic equilibrium with a consequence on stomatal resistance and transpiration rate [Tardieu et al., 1992]. This effect is indirectly accounted for by the feedback response, i.e., the function $F_s(\Psi_l)$, as shown in Figure 4. For given conditions of climate ($S$, $T$, and $D$) and soil ($\Psi_s$) the soil-root resistance $r_s$ has been arbitrarily in-
increased as a consequence of an increased soil compaction. The results show that canopy stomatal resistance modeled by (6) increases, leading to a diminished transpiration.

Cowan [1977] and Farquhar [1978] had already pointed out that the feedback response of stomata at leaf scale does not allow the transpiration rate to decrease with an increased evaporative demand (i.e., an increased D). The development above confirms this behavior at canopy scale. They noted, however, that a behavior with $dE/dD < 0$ had been observed in at least 23 plant species. We are going to see that only the feedforward scheme detailed below can account for such a behavior.

### 3. Direct Response of Stomata (Feedforward Response)

#### 3.1. Direct Influence of Air Humidity

Schulze et al. [1972] are maybe the first to have challenged the feedback approach by suggesting that stomata could sense air saturation deficit directly, independently of leaf water status. Feedforward occurs when a change in saturation deficit causes a change in stomatal resistance independent of the resulting change in transpiration rate and leaf water potential [Farquhar, 1978]. In fact, Monteith [1995a] reported that the feedforward response of stomata seemed to be fairly rare, and even Franks et al. [1997] suggested that it could arise from artifacts of experimental procedure. This behavior can be modeled by using the Jarvis formulation (2) without the stress function involving leaf water status $F_s(\Psi_i)$ but retaining the one involving saturation deficit $F_z(D)$. In this section, the feedforward dependence of transpiration on saturation deficit is examined following the lines drawn by Choudhury and Monteith [1986]. In this case, the Penman-Monteith model (4) is combined with the Jarvis parameterization (2) and $F_z(D)$ is written in its common hyperbolic form specified in Appendix A:

$$r_s = r_{12}/(1 - D/D_s)$$
$$r_{12} = r_{s_{min}}F_z(S)F_z(T),$$

where $D_s$ is the saturation deficit corresponding to a complete stomatal closure. The combination leads to

$$\lambda E = \frac{eA + \rho \lambda D/r_s}{e + 1 + (r_{12}/r_s)(1 - D/D_s)},$$

When $D$ increases, both the numerator and the denominator of (10) increase, leading to an antagonistic effect on the transpiration rate. Therefore the sense of variation of $\lambda E$ with respect to $D$ should be determined by studying the sign of the first derivative: $\partial E/\partial D$. Calculating the roots of $\partial E/\partial D = 0$ leads to the following quadratic equation:

$$X^2 - 2(1 + \mu)X + 1 + \mu(1 - \nu) = 0 \quad X = D/D_s, \quad (11)$$

where $\mu$ and $\nu$ are two dimensionless parameters. Here $\mu$ is defined as in (7), $\mu = (r_{12}/r_s)/(e + 1)$, and $\nu = e r_s A/ (\rho D_s)$. The appropriate root of (11) (which verifies $0 < X < 1$) is

$$D_s = D_s[1 + \mu - \sqrt{\mu(\mu + \nu + 1)}].$$

(12)

The transpiration rate increases when $D$ varies from zero to the critical value $D_s$ and then falls down to zero when $D$ varies from $D_s$ to $D_s$. The saturation deficit value $D_s$ is critical in the sense that it defines the limit between two opposite behaviors of the transpiration rate with respect to $D$. The maximum value of $\lambda E$ is obtained by substituting $D_s$ for $D$ in (10), which gives, after rearrangement,

$$\lambda E_c = [(e A D_s)/(e + 1)] [\nu + 2 \mu + 1 - 2 \sqrt{\mu(\mu + \nu + 1)}].$$

(13)

The leaf water potential follows the transpiration rate according to (3). Figure 5 illustrates the behavior of canopy resistance and transpiration in the feedforward case described above using the values of the parameters given in Table 1. The typical fall of $E$ with increased evaporative demand had already been documented at leaf scale by Jones [1992, p. 161] in the form of a parabolic relation between $E$ and $D$.

#### 3.2. Direct Influence of Soil Humidity

In the past decade many studies have shown that stomata can respond to soil water status independently of leaf water status. This led to invoke a root-shoot chemical signaling based on the concentration of abscisic acid (ABA) in the xylem sap [Davies and Zhang, 1991]. ABA would be synthesized by roots in response to soil drying and then transported in the xylem to the leaves [Tardieu et al., 1993, 1996]. There is still some uncertainty, however, as to whether stomatal control is better

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

<table>
<thead>
<tr>
<th>Variable</th>
<th>Significance</th>
<th>Value and Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b$</td>
<td>coefficient in the relation $K_s = f(\Psi_i)$</td>
<td>7.1</td>
</tr>
<tr>
<td>$c$</td>
<td>coefficient in the stress function $F_z(S)$</td>
<td>400</td>
</tr>
<tr>
<td>$D_s$</td>
<td>saturation deficit corresponding to a complete</td>
<td>0.04 kg kg⁻¹</td>
</tr>
<tr>
<td>$k_T$</td>
<td>stomatal closure in $F_z(D)$</td>
<td></td>
</tr>
<tr>
<td>$K_{sat}$</td>
<td>coefficient in the stress function $F_z(T)$</td>
<td>0.0016</td>
</tr>
<tr>
<td>$r_s$</td>
<td>soil hydraulic conductivity at saturation</td>
<td>$6.3 \times 10^{-6}$ m s⁻¹</td>
</tr>
<tr>
<td>$r_{stem}$</td>
<td>canopy aerodynamic resistance</td>
<td>50 s m⁻¹</td>
</tr>
<tr>
<td>$r_{s_{min}}$</td>
<td>root-stem resistance</td>
<td>0.05 bars (W m⁻²)⁻¹</td>
</tr>
<tr>
<td>$f_s$</td>
<td>minimal stomatal resistance (Jarvis' formulation)</td>
<td>40 s m⁻¹</td>
</tr>
<tr>
<td>$T_s$</td>
<td>optimal temperature in $F_z(T)$</td>
<td>25°C</td>
</tr>
<tr>
<td>$Z_{ef}$</td>
<td>effective rooting depth</td>
<td>1 m</td>
</tr>
<tr>
<td>$s$</td>
<td>dimensionless slope of the saturation specific humidity</td>
<td>28 at 25°C</td>
</tr>
<tr>
<td>$\Psi_0$</td>
<td>soil water potential corresponding to a complete</td>
<td>$-20$ bar</td>
</tr>
<tr>
<td>$\Psi_{ec}$</td>
<td>stomatal closure in $F_z(\Psi_i)$</td>
<td>$-25$ bar</td>
</tr>
<tr>
<td>$\Psi_{sat}$</td>
<td>soil water potential at saturation</td>
<td>$-0.03$ bar</td>
</tr>
</tbody>
</table>
related to the concentration of ABA or to its rate of arrival [Jones, 1998]. Tardieu [1993] proposed an empirical model of stomatal conductance \( g_s = 1/r_s \) to account for this signaling. The model applies only when light is saturating (photosynthetic photon flux density (PPFD) higher than 800 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)) and considers that stomatal conductance depends on xylem ABA following

\[
g_s = g_{s, \text{min}} + \alpha \exp \left( \beta [\text{ABA}]_{\text{root}} \right),
\]

where \( \alpha > 0 \) and \( \beta < 0 \) are constants empirically determined. \( [\text{ABA}]_{\text{root}} \) is assumed to be proportional to root water potential \( \Psi_r \). As the water flux \( E \) conveying the message from the roots to the leaves also dilutes the concentration of ABA, the model writes

\[
[\text{ABA}]_{\text{root}} = -a \Psi_r/(E + b),
\]

with two fitting parameters \( a \) and \( b \). Tardieu [1993] improved this first approach by multiplying \( \beta \) in (14) by an exponential function of leaf water potential \( \Psi_l \) (exp \( \delta \Psi_l \) with \( \delta < 0 \) to account for the increased stomatal sensitivity to the chemical message when leaf water potential falls. In fact, this model does not reflect a pure feedforward response even in its simplest form (i.e., without the exponential function of \( \Psi_l \)).
deed, $\Psi_s$ is related to soil water potential by $\Psi_s = \Psi_s - r_s E$, where $r_s$ is the soil-root resistance (see Appendix B and Figure 1) and $E = (\Psi_s - \Psi_f)/r_{sp}$. This means that stomatal conductance $g_s$ given by (14) (and hence $r_s$) is a function of leaf water potential and soil water potential according to

$$g_s = g_{s,\text{min}} + \alpha \exp \left\{ -\beta \left( r_s \Psi_s + r_o \Psi_f \right) \right\},$$

where $r_o$ is the root-stem resistance. Evidently, one cannot say that Tardieu's model represents a direct influence of soil humidity on stomatal conductance since leaf water status is involved in its formulation through $\Psi_s$.

To model a direct influence of soil humidity without interaction with plant water status, it seems more judicious to follow Jones [1998], who suggests that stomatal conductance is related to the rate of ABA supply $J_{ABA}$ according to

$$g_s = g_{s,\text{max}} (1 - \kappa J_{ABA}),$$

where $\kappa$ is a fitting parameter strictly positive. Under steady state conditions the rate of ABA supply depends only on its rate of synthesis, considered as linearly related to root water potential: $J = -\omega \Psi_s$ (with $\omega > 0$). It is generally accepted that soil resistance is low under most field conditions [Newman, 1969], so that $\Psi_s$ is not too different from $\Psi_f$, except apparently, under conditions of root clumping [Tardieu et al., 1992]. This assumption leads to $g_s = g_{s,\text{max}} (1 + \omega \kappa \Psi_f)$. In this way, $g_s$ is uniquely related to $\Psi_f$, and the canopy resistance $r_s$ can be expressed in a more general manner following a Jarvis-type formulation (2) with $F_s$ written as

$$F_s(\Psi_f) = (1 - \Psi_f/\Psi_0)^{-1},$$

where $\Psi_0 = -1/\omega \kappa$ and $\Psi_f > \Psi_0$. This type of formulation allows the transpiration rate to decrease from a maximum value down to zero when soil water potential falls from zero to the threshold $\Psi_0$, all other conditions ($S$, $T$, and $D$) being equal. Figure 6 shows the behavior of stomatal resistance and transpiration rate in such a case. The sense of variation is the same as for the feedback case, but the curves have a different shape. The zero transpiration rate is obtained here for $\Psi_f = \Psi_0$, instead of a theoretical infinite value in the feedback case. As the relationship between soil water potential and soil water content is well documented [Clapp and Hornberger, 1978], $\Psi_f$ can be easily replaced by soil water content in such a formulation [see, e.g., Noilhan and Planton, 1989].

4. Extension of Monteith's Parameterization

This section aims at specifying the conditions and the consequences of the equivalence between Jarvis' and Monteith's schemes. This question has already been investigated by Lhomme et al. [1998], and we begin with a brief review of the main results obtained.

4.1. Monteith's Parameterization

Mott and Parkhurst [1991] were the first to reinterpret the stomatal response to air humidity, stating that stomata respond to the rate of transpiration rather than to air humidity per se. Monteith [1995a, 1995b] extended this result by suggesting that canopy resistance $r_c$ was related to canopy transpiration $E$ by

$$r_c/r_{cm} = 1/(1 - E/E_s),$$

where $r_{cm}$ is a notional minimum canopy resistance, obtained by extrapolation to zero transpiration, and $E_s$ is a notional maximum transpiration rate obtained by extrapolation to infinite resistance. Lhomme et al. [1998] showed that Jarvis' and Monteith's formulations are equivalent provided the stomatal
response to environmental humidity is strictly feedback, which means that Jarvis' formula (2) is written with the function \( F_a(\Psi_f) \) without the function \( F_s(D) \). The perfect mathematical matching between the two formulations is made possible essentially by giving a hyperbolic expression to the function \( F_s \).

In fact, this equivalence could be easily foreseen bearing in mind that a linear relationship (3) exists between leaf water potential and transpiration. In Jarvis' formulation, canopy resistance increases with a decreased leaf potential, whereas in Monteith's formulation canopy resistance increases with an increased transpiration. As there is a strict equivalence between a decreased leaf water potential and an increased transpiration according to (3), it is not surprising to find that the two formulations match together.

The parameters \( r_{sn} \) and \( E_s \) can be given precise physical meanings inferred from Jarvis' model. The derivation detailed by Lhomme et al. [1998] shows that the minimum canopy resistance \( r_{sn} \) is written as

\[
r_{sn} = r_{12} F_s(D) = r_{mn} F_a(\Psi_f) F_s(T)(1 - \Psi_f/\Psi_{at})^{-1}.
\]

According to (2) and (A4), (20) represents effectively the canopy resistance at zero transpiration, when leaf water potential is equal to soil water potential. The maximum rate of transpiration \( E_s \) is written as

\[
\lambda E_s = (\Psi_f - \Psi_{at})/r_{sn}.
\]

It is the flux of water extracted from the soil when leaf water potential reaches its lowest possible value (\( \Psi_{at} \)) according to the parameterization (A4) used for the stress function \( F_s \). This means that \( E_s \) represents the maximum flux of water that can be extracted by a given canopy (characterized by a fixed value of \( \Psi_{at} \)) from a given soil (characterized by a fixed value of \( \Psi_f \)).

In feedforward conditions, when the function \( F_a(\Psi_f) \) does not appear in the Jarvis-type formulation, the matching between Jarvis' and Monteith's parameterizations is impossible. Monteith's formulation reflects only a feedback behavior. When the feedback process of stomatal control is combined with a feedforward response to air humidity, i.e., when the two types of response exist simultaneously, the two functions \( F_s(D) \) and \( F_a(\Psi_f) \) should be logically maintained in the Jarvis-type formulation. Lhomme et al. [1998, p. 2305] discussed the implications of such a case. The equivalence between Jarvis' and Monteith's formulations still holds, but the function \( F_s(D) \) should be added in the expression of \( r_{sn} \) (20):

\[
r_{sn} = r_{12} F_s(D) F_a(\Psi_f).
\]

In this case, as shown in Figure 7, transpiration conserves a typical feedforward response to air saturation deficit: When \( D \) increases from zero to \( D_s \), transpiration begins to increase slightly and then falls down to zero (this simulation is based on (8), (6), and (4) with \( r_{12} \) in (6) written with the function \( F_s(D) \)).

4.2. Formulation of Transpiration

The strict feedback response of stomata to air humidity (i.e., \( F_a(\Psi_f) \) appearing without \( F_s(D) \) in (2)) or the joint feedback-feedforward response (i.e., \( F_s(D) \) and \( F_a(\Psi_f) \) appearing together in (2)) means that Jarvis' and Monteith's schemes are equivalent. When this type of response prevails, the Penman-Monteith equation (4), which expresses the thermodynamic dependence of \( E \) on \( r_s \), can be combined with Monteith's parameterization of canopy resistance (19), which expresses the physiological dependence of \( r_s \) on \( E \) [Monteith, 1995b]. This leads to a quadratic equation in \( r_s \) or in \( E \). The appropriate root of the equation in \( E \) has been written in a synthetic manner by Lhomme et al. [1998, equation (8)]. This expression can be reformulated as a function of the decoupling factor \( \Omega \) previously introduced and expressed here with the minimum canopy resistance \( r_{sn} \) defined by (20):

\[
\Omega_{n} = \left( 1 + \frac{1}{r_{sn}} \right)^{-1}.
\]

This leads to the general expression

\[
E = \left[ E_{n} + E_{s}/\Omega_{n} - \sqrt{(E_{n} + E_{s}/\Omega_{n})^2 - 4E_{n}E_{s}} \right]/2,
\]

where \( E_{n} \) is the potential evaporation, as defined in (5), and \( E_{s} \) is the maximum rate of water extractable from the soil by the canopy, as defined by (21). The factor \( \Omega_{n} \), which lies between 0 and 1, depends on temperature (through \( E_{s} \) and \( r_{sn} \)), on solar radiation and possibly saturation deficit (through \( r_{sn} \)), and on wind speed and surface roughness (through \( r_{sn} \)). Equation (23) expresses in a concise manner that the actual rate of transpiration \( E \) results from an equilibrium between the soil water availability \( E_{s} \) and the climatic demand \( E_{n} \), this equilibrium being modulated by the decoupling factor \( \Omega_{n} \). For a given situation (\( \Omega_{n} \) fixed) the actual rate of transpiration is entirely determined if the soil potential supply \( E_{s} \) and the climatic potential demand \( E_{n} \) are known. When \( E_{s} \) tends to infinity (all other parameters being kept constant), Lhomme et al. [1998] have shown that \( E \) tends to \( E_{s} \), which implies that \( E \) is physically bound by soil water availability. When \( E_{n} \) = 0 (i.e., no water extractable from the soil), (23) reduces to zero. The transpiration rate is nil whatever the potential evaporation. The case corresponding to \( E_{s} \) tending to infinity (i.e., no limitation on the water extractable from the soil) needs a small mathematical manipulation. Equation (23) should be rewritten as

\[
E = (E_{n}/2\Omega_{n})\{E_{n}/E_{s} + 1 + \sqrt{\Omega_{n}E_{n}/E_{s} + 1} - 2\Omega_{n}E_{n}/E_{s} \}. (24)
\]

When \( E_{s} \) tends to +\( \infty \), (\( \Omega_{n}E_{n}/E_{s} + 1 \) is equivalent to 1 + 2\( \Omega_{n}E_{n}/E_{s} \), and the square root in (24) is equivalent to 1 + \( \Omega_{n}(1 - 2\Omega_{n})E_{n}/E_{s} \). Substituting this expression for the square root reveals that \( E \) is equivalent to \( \Omega_{n}E_{n} \). According to
Figure 8. Variation of actual transpiration $\lambda E$ as a function of potential evaporation $\lambda E_p$ for different values of soil water availability $\Omega_p$ (W m$^{-2}$), $\Omega_p = 0.5$, and $E_m = \Omega_p E_p$.

(5). $\Omega_p$ represents the maximum rate of transpiration from the canopy in given environmental conditions, i.e., the rate of transpiration when the canopy resistance reaches its minimum value $r_m$:

$$E_m = \Omega_p E_p = \frac{\varepsilon A + \rho \lambda D r_s}{\lambda (e + 1 + r_s r_a)}.$$  

(25)

So, the limits of (23) appear to be sound and conform to the experimental evidence. Figure 8 shows the variation of actual transpiration given by (23) as a function of potential evaporation for different values of soil water availability. All the curves $E = f(E_p)$ increase with $E_p$ up to the asymptotic value $E_s$, and the bundle of curves corresponding to different $E_p$ lies between the x axis and the asymptotic line $E = E_m = \Omega_p E_p$. Equation (23) can also be written in this alternative form:

$$E = \frac{E_m}{2}[1 + E_s/E_m - \sqrt{(1 + E_s/E_m)^2 - 4E_s/E_p}].$$  

(26)

This formulation shows how the actual rate of transpiration $E$ is related to the climatic demand $E_p$, the maximum transpiration capacity of the canopy $E_m$, and the maximum water supply of the soil $E_s$, and entirely determined by these three magnitudes. The major interest of such a formulation (23) or (26), with respect to the common Penman-Monteith model, is that the poorly understood canopy resistance $r_s$ is replaced by the parameter $E_s$ which represents the flux of water potentially extractable from the soil by the plant canopy. This is a new and relatively simple relationship that could be potentially useful in future theoretical developments on evaporation. Nevertheless, one should not underestimate the fact that the soil-plant resistance $r_s$ (a component of $E_s$) is also poorly understood.

5. Conclusion

The Jarvis-type scheme of canopy resistance has been examined in relation with air humidity and soil moisture by means of a simple one-dimensional soil-plant-atmosphere model. Its impact on transpiration has been analyzed as a function of the type of stress function involved in its formulation. To allow the mathematical derivations to be relatively easy, the simulations have been performed using particular and simple mathematical forms for the stress functions $F_s$ and $F_p$. These mathematical forms, however, are well representative of the experimental evidence obtained with a variety of plants and should not hinder the significance and the generality of the results presented. The main point of this analysis is that the manner of formulating the Jarvis-type representation of canopy resistance is not neutral with respect to the physiological mechanisms implied in the process of transpiration. Concerning the correspondences between the two and their implications, the following conclusions can be drawn:

1. A strict feedback response of stomata to environmental humidity, i.e., a response through leaf water status only, is modeled using the Jarvis formulation with the sole stress function $F_s(\Psi)$ and without any other function involving air or soil humidity, such as $F_s(D)$ or $F_s(\Psi)$. With this type of formulation the canopy resistance increases with an increased saturation deficit, but the transpiration rate increases simultaneously; under no circumstances can the transpiration rate decrease with an increased saturation deficit. With a decreased soil water potential the strict feedback formulation allows $r_s$ to increase, but in this case, the transpiration falls.

2. To model a strict feedforward response of stomata to air humidity, i.e., a direct response independent of leaf water status, the stress function involving saturation deficit $F_s(D)$ should be maintained in the general formulation, whereas the stress function for leaf water potential $F_s(\Psi)$ should be eliminated. In this case, the canopy stomatal resistance increases with an increased saturation deficit, but contrary to the feedback case, the transpiration increases up to a threshold and then falls. A strict feedforward response to soil moisture is described by replacing $F_s(\Psi)$ by a similar function involving soil water potential instead of $\Psi$. The global effect of soil water potential is similar to the feedback case.

3. In feedback conditions, Jarvis' and Monteith's formulations of canopy resistance are equivalent. Combining the Penman-Monteith model of transpiration with Monteith's parameterization of canopy resistance provides a general expression for the transpiration rate (23), which is a simple and explicit formulation of the climatic demand $E_p$, the soil water extractability $E_s$, and the decoupling factor $\Omega_p$. In strict feedforward conditions, Monteith's formulation does not hold, and neither does this general expression for $E$.

Appendix A: Parameterization of Stress Functions in Jarvis' Scheme

The four major stress functions making up the Jarvis-type formulation of canopy resistance are reviewed in this appendix. Function $F_s(C)$ related to CO$_2$ concentration is deliberately disregarded.

Solar radiation plays an important role in the general formulation of canopy resistance. Fisher et al. [1981] employs an exponential function for $F_s$, but the hyperbolic form recommended by Jarvis [1976] or Stewart [1988] is the most often used:

$$F_s(S) = (c + S)/dS.$$  

(A1)

The values of the two coefficients $c$ and $d$ obtained by Stewart and Gay [1989] for the Konza Prairie in Kansas (First International Satellite Land Surface Climatology Project (ISLSCP) Field Experiment (FIFE) data) are used in this analysis: $c = 400$ and $d = 1 + c/1000$, $S$ being expressed in W m$^{-2}$. The response of stomata to temperature has been represented by an exponential function [Jarvis, 1976] or a power function

$$E = \Omega_p E_p = \frac{\varepsilon A + \rho \lambda D r_s}{\lambda (e + 1 + r_s r_a)}.$$  

(25)
have been determined by

\[ F_2(T) = (1 - k_T(T_s - T)^2)^{-1} \]  

(A2)

with \( k_T = 0.0016 \) and \( T_s = 298 \) K. In many parameterizations, however, the effect of temperature is neglected [Dear-dorf, 1978; Stewart and Gay, 1989; Lynn and Carlson, 1990; Mascart et al., 1991; de Rudder and Schayes, 1997]. The two functions \( F_1 \) and \( F_2 \) have no direct relevance in the analysis performed, but they intervene in the numerical simulations through \( r_{12} = r_{\text{soil}}F_1(S)F_2(T) \).

The most relevant functions with respect to the analysis performed in this paper are those related to environmental humidity: \( F_3 \) and \( F_4 \). For the dependence upon saturation deficit the common form generally adopted is a linear decrease of stomatal conductance with \( D \) [Jarvis, 1976; Stewart, 1988; Jones, 1992], which implies that canopy resistance \( r_c \) can be expressed as a hyperbolic function

\[ F_4(D) = (1 - D/D_c)^{-1} 0 < D < D_c \]  

(A3)

In our analysis, \( D_c \) is taken to be equal to 0.042 kg kg\(^{-1}\), as derived for the Konza Prairie in Kansas (FIFE data) by Stewart and Gay [1989]. The dependence of stomatal resistance on leaf water potential can take various mathematical forms, more or less complicated [Jarvis, 1976; Choudhury and Idso, 1985]. Nevertheless, it seems that the hyperbolic form [Jones, 1992; de Rudder and Schayes, 1997] encapsulates fairly well the general behavior of stomatal resistance in relation to leaf water potential:

\[ F_3(\Psi) = (1 - \Psi/\Psi_{cc})^{-1} \quad \Psi_{cc} < \Psi < 0 \]  

(A4)

where \( \Psi_{cc} \) represents the value of leaf water potential at which a complete closure of stomata occurs. Lhomme et al. [1998, p. 2303] discussed the adequacy of this type of representation retained in the present analysis.

### Appendix B: Calculating the Soil-Plant Resistance \( r_{sp} \)

The soil-plant resistance is calculated following Lynn and Carlson [1990] and Lhomme et al. [1998]. Here \( r_{sp} \) is the sum of a soil-root interface resistance \( r_r \), and of a root-stem resistance \( r_{sr} \): \( r_{sp} = r_r + r_{sr} \). The plant component of \( r_{sp} \) \( (r_{sr}) \) remains relatively constant over a large range of leaf water potential: a typical value is 0.047 (\( \Psi \) being expressed in bars and \( \Delta E \) in W m\(^{-2}\)). The soil component of \( r_{sp} \) \( (r_r) \) expresses the resistance of the flow of liquid water from the soil to the roots. Choudhury and Idso [1985] adapted a formulation from a model originally proposed by Feddes and Rijtema [1972]:

\[ r_r = 0.0013k_{\text{soil}}(Z_{\text{cf}}K) \]  

(B1)

where 0.0013 (m\(^3\)) is the ratio of a parameter relating root distance and geometry to the reciprocal of the effective rooting depth; \( k_{\text{soil}} \) is a conversion factor equal to 0.4 \( \times \) 10\(^{-10}\), when \( r_r \) is expressed in bars (W m\(^{-2}\))\(^{-1}\); \( Z_{\text{cf}} \) is the effective rooting depth (m), assumed to be 1 m in our analysis; \( K \) is the soil hydraulic conductivity (m s\(^{-1}\)), related to soil water potential by \( K_s = K_{\text{sat}}(\Psi_{\text{sat}})^{3.25} \) [Campbell, 1974], where \( K_{\text{sat}} \) and \( \Psi_{\text{sat}} \) are the conductivity and the water potential at field saturation, respectively. Soil hydraulic parameters \( (K_{\text{sat}}, \Psi_{\text{sat}}, \text{and } b) \) have been determined by Clapp and Hornberger [1978] for the 11 soil types of the U.S. Department of Agriculture textural classification. The values retained in our simulations and shown in Table 1 are those corresponding to sandy clay loam.

### Appendix C: Variation of \( \Psi_c \) as a Function of \( D \) and \( \Psi_s \)

**C1. Demonstrating \( \partial \Psi_s/\partial D < 0 \)**

Deriving the expression of \( \Psi_s \) given by (8) with respect to \( D \) leads to

\[ \frac{\partial \Psi_s}{\partial D} = \frac{\partial \Gamma}{\partial D} - \frac{2\partial X_p/\partial D}{\Gamma^2 - 4(X_p + \mu \Psi_s/\Psi_{cc})} \]  

(C1)

Taking into account the definition of \( \Gamma \) given by (8) and noticing that \( \partial X_p/\partial D = \partial X_p/\partial D \), (C1) transforms into

\[ \frac{\partial \Psi_s}{\partial D} = \frac{\partial X_p}{\partial D} \left[ \frac{2 - \Gamma}{\sqrt{\Gamma^2 - 4(X_p + \mu \Psi_s/\Psi_{cc})}} \right] \]  

(C2)

As \( \Psi_{cc} < 0 \) and \( \partial X_p/\partial D = -\rho k_{sp}(r_{sp} + \epsilon) \) strictly positive, \( \partial \Psi_s/\partial D < 0 \) implies that the term in parentheses in (C2) is strictly positive, which is equivalent to

\[ \Gamma - 2 < \sqrt{\Gamma^2 - 4(X_p + \mu \Psi_s/\Psi_{cc})} \]  

(C3)

If this inequality were not verified, the development of the contrary inequality \( (\Gamma - 2 > \sqrt{\Gamma^2 - 4(X_p + \mu \Psi_s/\Psi_{cc})}) \) leads to \( \Psi_s/\Psi_{cc} > 1 \), which is impossible since soil water potential should always be lower than leaf potential (in absolute value) to maintain transpiration. Consequently, we have to admit that (C3) is verified and that \( \partial \Psi_s/\partial D \) is strictly negative.

**C2. Demonstrating \( \partial \Psi_s/\partial \Psi_s > 0 \)**

To obtain a simple and straightforward demonstration, it is necessary to assume that the soil-plant resistance \( r_{sp} \) is independent of soil water potential. This assumption is acceptable as a first approximation since the range of variation of \( r_{sp} \) is much smaller than for \( \Psi_s \) (over the range of \( \Psi_s \), \( [0, -20 \text{ bars}] \) the value of \( r_{sp} \) varies only from 0.05 to 0.11). Without this simplification the demonstration appears to be particularly cumbersome. Following the same steps as above yields

\[ \frac{\partial \Psi_s}{\partial \Psi_s} = \frac{1}{2} \left[ 1 - \frac{\Gamma - 2(1 + \mu)}{\sqrt{\Gamma^2 - 4(X_p + \mu \Psi_s/\Psi_{cc})}} \right] \]  

(C4)

Also, \( \partial \Psi_s/\partial \Psi_s > 0 \) implies that the term in parentheses in (C4) is strictly positive, which is equivalent to

\[ \Gamma - 2(1 + \mu) < \sqrt{\Gamma^2 - 4(X_p + \mu \Psi_s/\Psi_{cc})} \]  

(C5)

If this inequality were not verified, the development of the contrary inequality \( (\Gamma - 2(1 + \mu) > \sqrt{\Gamma^2 - 4(X_p + \mu \Psi_s/\Psi_{cc})}) \) leads to \( \Psi_s/\Psi_{cc} > 0 \), which is impossible since \( r_{sp} \) and \( \Delta E_p \) are strictly positive and \( \Psi_{cc} \) is strictly negative. Consequently, we have to admit that (C5) is verified and that \( \partial \Psi_s/\partial \Psi_s \) is strictly positive.

### Notation

- \( A \) total available energy (W m\(^{-2}\))
- \( D \) vapor pressure deficit at reference height (kg kg\(^{-1}\))
- \( E \) evaporation rate from the canopy (equal to transpiration) (kg m\(^{-2}\) s\(^{-1}\))
- \( E_{sp} \) potential evaporation from the canopy (kg m\(^{-2}\) s\(^{-1}\))
\[ E_s \] maximum transpiration from the canopy in Monteith’s formulation (kg m\(^{-2}\) s\(^{-1}\)).  
\[ g_s \] canopy surface conductance (m s\(^{-1}\)).  
\[ q \] specific humidity at reference height (kg kg\(^{-1}\)).  
\[ q_s \] saturation specific humidity (kg kg\(^{-1}\)).  
\[ r_a \] canopy aerodynamic resistance (s m\(^{-1}\)).  
\[ r_c \] canopy surface resistance (s m\(^{-1}\)).  
\[ r_{s\text{ min}} \] minimum canopy resistance in Jarvis’ formulation (s m\(^{-1}\)).  
\[ r_{s \text{ min}} \] minimum canopy resistance (at zero transpiration) in Monteith’s formulation (s m\(^{-1}\)).  
\[ r_{s \text{ root}} \] root-stem resistance (bars W m\(^{-2}\)).  
\[ r_{s \text{ soil}} \] soil-root resistance (bars W m\(^{-2}\)).  
\[ r_{s \text{ p}} \] plant resistance (bars W m\(^{-2}\)).  
\[ \Delta \] incoming solar radiation (W m\(^{-2}\)).  
\[ T \] air temperature at reference height (°C).  
\[ T_s \] leaf surface temperature (°C).  
\[ \varepsilon \] slope of the saturation specific humidity (dimensionless).  
\[ \lambda \] latent heat of vaporization (J kg\(^{-1}\)).  
\[ \rho \] density of air (kg m\(^{-3}\)).  
\[ \Psi_f \] leaf water potential (bar).  
\[ \Psi_r \] root water potential (bar).  
\[ \Psi_s \] soil water potential (bar).  
\[ \Omega \] decoupling factor (dimensionless).

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