EXAMINATION OF MONTEITH'S PARAMETERIZATION OF CANOPY RESISTANCE

J.-P./Lhomme^{a1}, A./Chehbouni^b, E./Elguero^b, and G./Boulet^b ^aORSTOM/Universidad de Sonora, Hermosillo, Sonora, Mexico ^bORSTOM/IMADES, Hermosillo, Sonora, Mexico

INTRODUCTION

For more than twenty 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), in which stomatal resistance is expressed as a minimum resistance multiplied by a series of independent stress functions combined in a multiplicative way (each function representing the influence of one factor). 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. Monteith (1995a,b) showed that the leaf stomatal conductance can be interpreted as a linear decreasing function of transpiration with two empirical parameters: a maximum conductance and a maximum rate of transpiration. He 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. The aim of this paper is to assess and discuss this new formulation of stomatal behaviour proposed by Monteith and to interpret the parameters at canopy scale.

MONTEITH'S FORMULATION

The Penman-Monteith single-source model (Monteith, 1981) gives the flux of evaporation from a fully-covering canopy in the form of the following equation

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

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

¹ Corresponding author: Jean-Paul Lhomme, CICTUS, A.P. 1819, Hermosillo, 83000 Sonora, Mexico; email: Ihommej@rtn.uson.mx.



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 vapour 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 $r_s=0$ in Eq.(1), evaporation can also be expressed as a function of E_p as

$$E = kE_p \qquad \text{with} \quad k = 1/\left(1 + \frac{1}{1 + \varepsilon} \frac{r_s}{r_a}\right) \tag{2}$$

According to Monteith (1995a,b) the canopy surface resistance reads as

$$r_{s} / r_{sn} = E_{x} / (E_{x} - E)$$
 (3)

In this analysis soil evaporation is assumed to be negligible, which means that transpiration rate in Eq.(3) is strictly the same as canopy evaporation in Eq.(1) or (2). Consequently, combining Eq.(2), expressing the thermodynamic dependence of E on r_s , with Eq.(3), expressing the physiological dependence of E on r_s , leads to a quadratic expression for r_s , whose appropriate root is

$$r_{s} = \left[-\Lambda + \sqrt{\Lambda^{2} + 4(1+\varepsilon)r_{a}r_{sn}} \right] / 2$$
with $\Lambda = (1+\varepsilon)r_{a}(1-E_{p}/E_{x}) - r_{sn}$
(4)

When the quadratic equation obtained by combining Eq.(2) with Eq.(3) is solved in E instead of r_s , the appropriate root gives (Monteith, 1995b)

$$E = \left[E_p + \alpha_n E_x - \sqrt{\left(E_p + \alpha_n E_x\right)^2 - 4E_x E_p} \right] / 2$$
(5)
with $\alpha_n = 1 + \frac{1}{\varepsilon + 1} \frac{r_{sn}}{r_a}$

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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 Eq.(5). When atmospheric demand becomes very large, i.e., when Ep tends to infinity (all other parameters being kept constant), it can be shown from Eq.(5) that evaporation tends to E_X . 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. Little is known also on the significance and possible values of rsn.

THE JARVIS TYPE REPRESENTATION

The Jarvis type models (Jarvis, 1976; Stewart, 1988) describe the response of stomata to environmental factors (at leaf scale as well as at canopy scale) in the form of a minimal resistance multiplied by the product of independent stress functions interacting without synergy

$$r_{s} = r_{s\min} F_{1}(S) F_{2}(T) F_{3}(D) F_{4}(\Psi_{l})$$
(6)

Here, r_{Smin} is the minimum stomatal resistance observed in optimal conditions, i.e., if none of the controlling variables is limiting (it is taken to be equal to 40 s m⁻¹ in our analysis). S is the incoming solar radiation, T is the air temperature, D is the water vapour saturation deficit, Ψ_i 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. Each function (F_i) varies from unity to infinity.

The influence of solar radiation can be expressed in terms of a hyperbolic function of the form (Stewart, 1988)

$$F_1(S) = (c+S)/(dS)$$
 (7)

where *d* is obtained from d=1+c/1000. When S is expressed in W m⁻², Stewart and Gay (1989) derived a mean value of about 400 for *c* in the case of the Konsa Prairie in Kansas (FIFE data). The reponse of stomata to temperature is not essential and will be skipped in this analysis. For 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) leading to

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$$F_3(D) = (1 - \alpha D)^{-1}$$
 with $0 < D < 1/\alpha$ (8)

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. However, Lynn and Carlson (1990, p.17) question the real effect of air humidity on stomatal resistance. They think the role played by the saturation deficit is indirect. An increase of D damps the leaf water potential which, in turn, is responsible for an increase of stomatal resistance. As to the dependence of stomatal resistance on leaf water potential it can be expressed in different ways (Jarvis, 1976; Choudhury and Idso, 1985). In their IAGL (Institut d'Astronomie et de Géophysique Georges Lemaître) land surface model, de Ridder and Schayes (1997) employ an hyperbolic dependence of the form

$$F_4(\Psi_l) = (1 - \Psi_l / \Psi_{cc})^{-1}$$
(9)

where Ψ_{CC} represents the value of leaf water potential at which a complete stomatal closure occurs ($\Psi_{CC} \approx 25$ bars).

MATCHING THE TWO FORMULATIONS

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_{S} 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)

$$\Psi_l = \Psi_s - r_{sp} \lambda E \tag{10}$$

where r_{SP} is the total soil-plant resistance and Eis 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). r_{SP} is the sum of a soil-root interface resistance (r_{ST}) and of a root-stem resistance (r_{TS}) : $r_{SP}=r_{ST}+r_{TS}$. The plant component of r_{SP} (r_{TS}) 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_{ST}) expresses the resistance of the flow of liquid water from the soil to the roots. The formulation proposed by Choudhury and Idso (1985) is

$$r_{sr} = 0.0013k_1 / (Z_{ef} K_s) \tag{11}$$

where 0.0013 (m²) 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 (Wm⁻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 $K_S = K_{Sat}(\Psi_{Sat}/\Psi_S)^{3/b+2}$ (Campbell, 1974), where K_{Sat} and Ψ_{Sat} are respectively the conductivity and the water potential at field saturation.

Taking into account Eqs.(9) and (10), Eq.(6) can be rewritten as

$$r_{s} = \frac{r_{13} / (1 - \Psi_{s} / \Psi_{cc})}{1 - (r_{sp} \lambda E) / (\Psi_{s} - \Psi_{cc})}$$
(12)

with $r_{13}=r_{smin}F_1(S)F_3(D)$. Eq.(12) is an expression similar and functionally equivalent to Eq.(5), when rewritten as $r_S=r_{sn}/(1-E/E_x)$. Matching term by term these two equations leads to

$$r_{sn} = \eta_3 / (1 - \Psi_s / \Psi_{cc}) = \eta_3 F_4(\Psi_s)$$
(13)

and

$$\lambda E_x = (\Psi_s - \Psi_{cc}) / r_{sp} \tag{14}$$

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. The two parameters $(r_{Sn} \text{ and } E_X)$ of Monteith's relationship can be interpreted in terms of the parameters and functions making up the Jarvis model and their physical significance appears now clearly. rsn represents the canopy stomatal resistance when the leaf water potential is equal to the soil water potential ($\Psi_{f}=\Psi_{S}$), i.e., at zero transpiration (conditions experimentally encountered at pre-dawn). 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.

The issue that arises now is the dependence of the canopy minimal stomatal resistance r_{SII} upon water vapour saturation deficit. To Monteith's mind, r_{SII} cannot depend upon saturation deficit, since in Eq.(3) 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_{SII} is a function of

 r_{13} and then of $F_3(D)$, as shown by Eq.(13)). It is possible to keep only one dependence (that upon transpiration) by assuming with Lynn and Carlson (1990) that stomata do not respond directly to *D* (but indirectly through Ψ_1) and by putting then $F_3(D)=1$. From a pragmatic viewpoint this idea seems recommendable. 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 Eq.(10) (assuming Ψ_S and r_{SP} to remain constant), which provokes a stronger stomatal closure.



Fig.1- Maximum canopy evaporation λE_X (given by Eq.(14)) versus soil water potential Ψ_S for different values of leaf water potential Ψ_{CC} corresponding to a complete stomatal closure (defined by Eq. (9)).



Fig.2- Maximum canopy evaporation λE_X versus soil water potential Ψ_S for different values of the root-stem resistance r_{CS} .

NUMERICAL RESULTS

For a particular type of soil, characterised by fixed values of K_{sat} , Ψ_{sat} and b, and a given vegetation, characterised by fixed values of Ψ_{CC} , r_{TS} and Z_{ef} , the soil-plant resistance r_{Sp} and then the maximum canopy transpiration λE_X depend only upon the soil water potential Ψ_S . The values of the parameters used in the simulations are those given in the text. For the soil we took: K_{Saf} =6.3 10⁻⁶ m s⁻¹,



Figure 1. Schematic diagram of heat pulse stem flow system used in measurement of riparian trees.

3. MATERIALS AND METHODS

The Lewis Springs study site was located in southeastern Arizona, USA on the San Pedro River just north of where it intersects with state route 90 (31 33'N, 110 07'W), within the San Pedro National Riparian Conservation Area. The elevation of the site was approximately 1250 m. The site was dominated by riparian forest vegetation consisting of Frémont cottonwood as a dominant overstory species and Goodding willow as a subdominant species. Mesquite (*Prosopis velutina*) and seep-willow (*Bacharis glutinosa*) existed in the understory. There was a significant difference in size classes in relation to distance from the current primary channel for both cottonwood and willow with larger trees being located on older, once primary, channels further away from the active channel.

Vegetation surveys were conducted in order to establish stand characteristics such as species composition and vegetation structure. Four transects were laid down on each side of the stream running perpendicular to the stream channel and extending to the limit of the riparian zone. Transects were 30m wide and broken into 10m long sections. Total counts of individual trees, as wells as their corresponding DBH's were recorded for each species. From these data, size class distributions for willow and cottonwood were developed.

Heat pulse velocity probes (Thermal Logic, Pullman WA) were implanted in a range of trees of differing

diameters proportional to size class distributions determined from vegetation surveys of both cottonwood and willow. Nine trees of cottonwood were selected with DBH's ranging from 0.14 to 0.75m. Six trees of willow were selected with DBH's ranging from 0.15 to 0.24m. Each tree, depending on its size, received from three to five probes, placed equidistant around the trunk at breast height (1.5m). Bark was removed until the cambium was exposed and sensors inserted into holes drilled parallel with the grain of the wood. Before insertion, probes were coated with G5 compound to ensure good thermal contact. After insertion, exposed cambium was covered with G5 compound, to reduce evaporation from the wood surface, and then covered with foil to reduce ambient temperature effects.

Thermocouples on probes were connected to multiplexers (AM416, Campbell Scientific, Logan UT) and heating elements were controlled by relay drivers (A21REL-12, Campbell Scientific, Logan UT). Multiplexers and relay drivers were controlled and data was collected using dataloggers (CR10X, Campbell Scientific, Logan UT). Heating elements and dataloggers were powered by standard 12V deep-cycle marine batteries (Fig. 1).

Eight second pulses of heat were generated by the upstream heating elements and three downstream thermocouples (at 10, 20, 30mm deep into the xylem) measured xylem temperature for 60s; the time to maximum temperature rise, as well as the maximum temperature difference, was recorded. Sap velocity V (length per unit time) was calculated using equation (1) derived from Cohen *et al.* (1981):

$$V = r \frac{\sqrt{\left(1 - t_m/t_{mo}\right)}}{t_m} \tag{1}$$

where r is the distance between heater and thermocouple (6mm), t_m is time to maximum recorded temperature, and t_{mo} is the time to maximum temperature at zero flow (assumed to be at pre-dawn, 0200 to 0400 hours). Mass flow of sap J (volume per unit time) was calculated using equation (2) also from Cohen *et al.*, (1981):

$$J = \rho c / \rho_{\rm w} c_{\rm w} \sum V_{\rm i} A_{\rm i}$$
 (2)

where ρc and $\rho_w c_w$ are the volumetric specific heat (density times specific heat) of wet wood and water respectively. V_i and A_i are the sap velocity and the cross sectional area of the I^{h} increment of sapwood being measured by a thermocouple. The volumetric specific heat of wet wood (ρc) was determined during a period of zero flow using the relationship for dissipation of a heat pulse with no fluid correction developed by Campbell *et al.*, (1991) and is shown in equation (3):

Tree	DBH (m)	Sapwood Area (m ²)	Maximum Flow (kg H ₂ O hr ⁻¹)	Maximum Flux (cm ³ cm ⁻² hr ⁻¹)	Total Daily Water Use (kg d ⁻¹)
Cottonwood	0.14	0.009	3.0	32.7	20.4
Contoninood	0.19	0.015	6.6	43.7	50.2
	0.20	0.016	4.7	29.2	35.9
	0.43	0.068	25.1	37.2	219.9
	0.48	0.081	28.2	34.9	256.8
	0.50	0.085	34.4	40.4	308.4
	0.69	0.143	68.5	48.1	574.1
	0.71	0.150	58.8	39.1	520.1
}	0.75	0.162	87.8	54.3	702.9
Willow	0.15	0.002	4.6	42.5	36.7
	0.24	0.027	14.9	66.5	120.7
	0.24	0.027	5.1	19.3	39.7
	0.24	0.027	7.9	29.9	52.1

Table 1. Physical characteristics along with transpiration for 9 cottonwood and 4 willow trees along the San Pedro River. Data are for julian day 223 (August 11). DBH is bole diameter at 1.5m height. Sapwood area = basal area - heartwood area - bark area.

$$\rho c = \frac{Q}{\left(e\pi r^2 \Delta T_{\rm m}\right)} \tag{3}$$

 ΔT_m is the maximum temperature rise recorded by the thermocouple. Q is the heat input (J m⁻¹) of the heat pulse and is calculated using equation (4):

$$Q = tl^2 \left(\frac{R_{\rm h}}{L}\right) \tag{4}$$

t is the heating time (8*s*), *I* is the heater current, and $R_{\rm H}/L$ is the resistance per meter of the heater (1141 Ω/m).



Figure 2. Diumal course of photosynthetic photon flux density (PPFD) and transpiration from a large cottonwood tree (0.71m DBH) for julian days 223-225 (August 11-13).

4. RESULTS

Table, 1 shows all trees measured for sap flux at Lewis Springs during the August 1997 SALSA field campaign. DBH and sapwood area are given for each tree, as well as maximum observed daily transpirational rate (kg H₂O hr⁻¹), maximum flux density (cm³ H₂O cm⁻² sapwood hr1), and the total daily transpiration (kg H2O d⁻¹) for julian day 223 (August 11). Mass flow rate (kg of H,O hr') for a large cottonwood tree (0.71m DBH) is shown in Fig. 2, along with the photosynthetic photon flux density (PPFD, µmol photons m⁻² s⁻¹) for julian days 223-225 (August 11-13). Maximum flow is 58.8kg hr¹ on day 223 (the day with the highest PPFD). Day 224 was mostly cloudy for the entire day and this was reflected in the low transpiration rates for that day. Sap flux on a sapwood area basis (cm³ H₂O cm⁻² sapwood hr⁻¹) is shown (Fig. 3) for a large and small cottonwood tree (0.71 and 0.14m DBH respectively) as well as for two equally sized willow trees (both 0.24m DBH). Maximum flux is similar for both cottonwood trees, but varies considerably between the willow trees. Cottonwood shows little difference in flux between large and small individuals while willow shows a marked difference in flux between two individuals of the same size.

5. DISCUSSION

Diumal variations in whole tree transpiration appear to be strongly influenced by short term fluctuations in photosynthetically active radiation (Fig. 2). Other studies of transpiration (Cohen *et al.*, 1993; Meinzer *et al.*, 1995; Schulze *et al.*, 1985; Smith, 1991) have shown that diurnal patterns of transpiration are highly influenced by solar radiation. Snyder *et al.* (this issue) show that cottonwood is largely phreatophytic.





It appears that cottonwood has a relatively stable water source to drawn on, and consequently patterns of transpiration are driven by climatic conditions (i.e. solar radiation) and less by soil water availability.

Snyder *et al.* (this issue) found that midday plant water potential remained constant for cottonwood over a variety of climatic conditions, suggesting that these plants may be adjusting stomatal aperture to regulate water potential and transpirational flux. The observation that sap flux density is similar between individuals of cottonwood of different size supports the idea that these trees may be operating at some threshold level for transpirational flux.

Position in the canopy may also play an important role in sap flux. Both cottonwood trees in Fig. 3, although of different size, had portions of there crowns located in the overstory. This would put them in a position to receive unobstructed solar radiation throughout the day. Of the willow trees however, only the one with the highest flux shown in Fig. 3 had any portion of its crown located in the overstory. It was located on the western edge of the forest and was in a position to receive unobstructed afternoon sunlight. These differences in overall stand structure may lead to large differences in sap flux, and transpiration for subdominant species or individuals, but relatively small differences for dominant/co-dominant species or individuals.

In conclusion, stand structure and climatic factors both play important roles in controlling riparian water fluxes. Canopy position (dominant, co-dominant, and sub-dominant) affects the amount of solar radiation incident on an individual plant canopy. This information could support the effort to scale the consumptive water use of individual trees to the level of the stand and provides important information about species' roles in ecosystem processes (Williams et al., this issue).

6. ACKNOWLEDGMENTS

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