Hydrology and Earth System Sciences, 2(1), *31–40* (1998) © EGS

Hydrology & Earth System Sciences

Formulation of root water uptake in a multi-layer soil-plant model: does van den Honert's equation hold?

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Abstract

The withdrawal of water from soil by vegetation, which in steady state conditions is equivalent to the transpiration rate, can be written in terms of water potential in the form of an Ohm's law analogy, known as van den Honert's equation: The difference between an effective soil water potential and the bulk canopy water potential is divided by an effective soil-plant resistance. This equation is commonly used, but little is known about the precise definition of its parameters. The issue of this paper is to bridge the gap between the bulk approach and a multi-layer description of soil-plant water transfer by interpreting the bulk parameters in terms of the characteristics of the multi-layer approach. Water flow through an elementary path within the soil or the root is assumed to follow an Ohm's law analogy, and the soil and root characterisics are allowed to vary with depth. Starting from the basic equations of the multi-layer approach, it is proved that the total rate of transpiration can also be expressed in the form of an Ohm's law analogy. This means that van den Honert's equation holds at canopy scale, insofar as the assumptions made on the physics of root water uptake hold. In the bulk formulation derived, the effective soil-plant resistance appears as a combination of the elementary resistances making up the multi-layer model; and the effective soil water potential is a weighted mean of the water potentials in each soil layer, the weighting system involving the complete set of elementary resistances. Simpler representations of soil-plant interaction leading to Ohm's law type formulations are also examined: a simplified multi-layer model, in which xylem (root axial) resistance is neglected, and a bulk approach, in which soil-root interaction is represented by only one layer. Numerical simulations performed in different standard conditions show that these simpler representations do not provide accurate estimates of the transpiration rate, when compared to the values obtained by the complete algorithm.

Introduction

It is difficult to describe accurately the withdrawal of water by plant roots because of the complexity of root systems. To bypass this complexity, a bulk approach is generally used which ignores details of the various paths of water movement. In this approach it is assumed that, under steady state conditions, the flux of water from soil to canopy, i.e. the transpiration rate Tr, can be expressed following an Ohm's law analogy in the form

$$Tr = (\Psi_s^e - \Psi_c)/r_{sp}^e \qquad (1)$$

Ψ_s^e is an effective soil water potential, representing an average value of soil water potential, Ψ_c is an average leaf water potential and r_{sp}^e is an effective bulk resistance to water transfer from soil to canopy. This equation, which is often referred to as van den Honert's equation (van den Honert, 1948), has gained wide acceptance amongst plant scientists (Cowan, 1965; Feddes and Rijtema, 1972; Katerji *et al.*, 1983; Lynn and Carlson, 1990), although little is known about the precise definition and calculation of the terms making up this equation.

In many models of soil-vegetation-atmosphere water transfer, the soil-root interaction is represented by a set of parallel layers, each one assumed to be horizontally homogeneous and characterised by mean properties such as water content, water potential, root density, root potential and resistance to water transfer from soil to root, etc. In each layer, the Ohm's law approximation is used to describe horizontal transfer of water from soil to xylem and vertical transfer through the xylem (Cowan, 1965; Hillel *et al.*, 1976; Taylor and Klepper, 1978). The total root extraction term (equal to the transpiration rate Tr when there is no water storage in the vegetation) is computed as the sum of the contributions from each layer.

May Eqn. (1) be used legitimately in a vertically heterogeneous soil? In other words, can an Ohm's law analogy for canopy transpiration be derived from a multi-layer description of the soil-root interaction? And if that is the case, how are Ψ_s^e and r_{sp}^e expressed in terms of the characteristics of each layer? These questions will be the topic of the study and the plan will be as follows. The first section details the basic equations of the multi-layer approach, specifying how each type of elementary resistance can be expressed. The second section presents the derivation of van den Honert's equation with its effective parameters in the general case. Also presented are additional simpler formulations of these parameters obtained when certain approximations are made. The third section compares numerically the performance of these simpler expressions with respect to the exact solution.

Soil-root water transfer basic equations

THE MULTI-LAYER APPROACH: AN ELECTRICAL ANALOGUE

Assuming horizontal homogeneity, the soil is divided into several parallel layers, each with a thickness δz_i, where subscript i refers to the layer number, counted from 1 to n from the soil surface to the deepest layer explored by the roots (Fig.1); the sum of the δz_i is z_r, the rooting depth. $\Psi_{s,i}$ is the mean water potential of soil layer i and $\Psi_{r,i}$ is the mean water potential of root xylem within the same layer. The whole system is depicted as an electrical circuit where the flux of water replaces current and the driving force is water potential (Cowan, 1965; Hillel *et al.*, 1976; Taylor and Klepper, 1978). The elementary flux of water extracted by the roots in each layer (the properties referring to a layer are termed 'elementary' as opposed to 'bulk') can be written as

$$\delta Tr_i = (\Psi_{s,i} - \Psi_{r,i})/r_{sr,i} \quad \text{with} \quad \Psi_{s,i} > \Psi_{r,i} \qquad (2)$$

$r_{sr,i}$ is the soil-root resistance in layer i, considered to be the sum of a soil resistance $r_{s,i}$ (from the soil matrix to the root surface) and of a root radial resistance $r_{r,i}$ (from the root surface to the root xylem through the root cortex)

$$r_{sr,i} = r_{s,i} + r_{r,i} \qquad (3)$$

The vertical flux through the root xylem emanating from soil layer i is written as

$$Tr_i = (\Psi_{r,i} - \Psi_{r,i-1})/r_{x,i-1} \qquad (4)$$

where $r_{x,i-1}$ is the root axial resistance (or xylem resistance) to vertical water transfer within layer $i-1$. Assuming there is no water storage in the plant, the total flux of water which enters the shoot above the soil surface (denoted by Tr_0) can be expressed as the sum of the elementary fluxes emanating from each layer

$$Tr_0 = \sum_{i=1}^{n} \delta Tr_i \qquad (5)$$

In the electrical analogue shown in Fig. 1 Ψ_c represents the water potential in the stem right below the first leaves of the canopy in order to avoid the additional complexity generated by the foliage architecture.

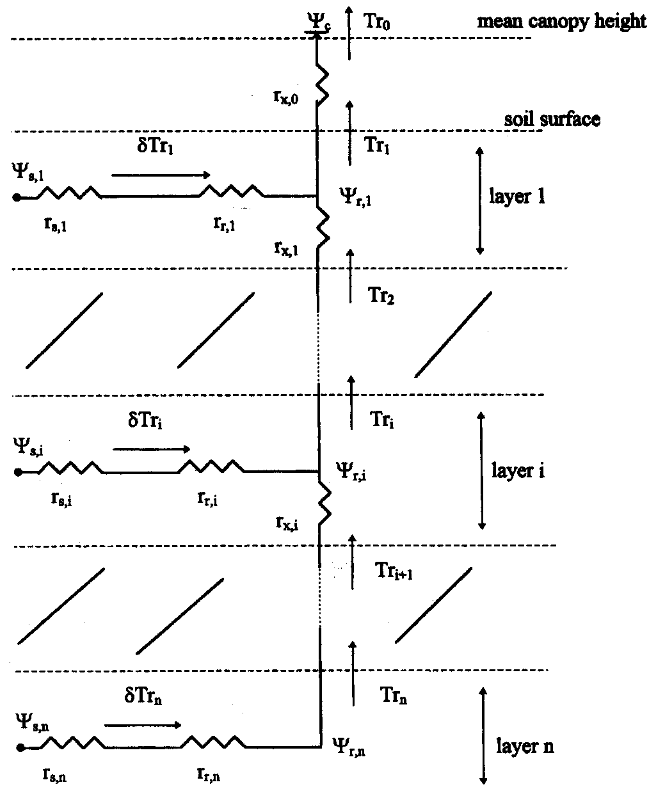

Fig. 1. *Electrical analogue of water transfer processes within the soil-root system: general case of the multi-layer approach.*

EXPRESSING SOIL RESISTANCE $r_{s,i}$

The rate of water uptake per unit length of root can be expressed as

$$q = \Delta\Psi/\rho_s \qquad (6)$$

where $\Delta\Psi$ represents the difference of potential (expressed in MPa) between the bulk soil and the root surface and ρ_s is the corresponding resistance per unit root length with units of $MPa\ s\ m^{-2}$ (because q represents a flux of water per unit length of root expressed in m^3 (of water) s^{-1} m^{-1} (of root)). Root length density in layer i is denoted by RD_i (expressed in m (of root) per m^3 of soil), and L_i is the total root length within the same layer per unit area. Both entities are linked by $L_i = RD_i\delta z_i$. The total water flow Q_i entering the roots in layer i is calculated as the integral of q over the total root length and is then given by

$$Q_i = \int_0^{L_i} q\,dl = (\Delta\Psi/\rho_s)L_i = \Delta\Psi/r_{s,i} \text{ with } r_{s,i} = \rho_s/(RD_i\delta z_i) \qquad (7)$$

The elementary resistance ρ_s has been inferred from physical models. In the model of Gardner (1960), a single root is taken to be a hollow, infinitely long cylinder of uniform radius r_1, extracting water at a constant rate from an infinite volume. Under steady state conditions, with water flowing from a distance r_2, ρ_s is expressed as a function of soil hydraulic conductivity K (assumed to be constant) as

$$\rho_s = ln(r_2/r_1)/(2\pi K) \quad (8)$$

Cowan (1965) developed a similar model, assuming that the constant flux of water entering the root comes from the volume surrounding the root (defined by $r_1 < r < r_2$), and derived an expression for ρ_s which is different from that of Gardner. Hydraulic conductivity K is expressed as a function of soil water potential Ψ_s as (Campbell, 1974)

$$K = K(\Psi_s) = K_{sat}(\Psi_{sat}/\Psi_s)^{3/b+2} \quad (9)$$

where Ψ_{sat} is the soil water potential at field saturation and K_{sat} is the corresponding maximum conductivity. Assuming that r_2 is linked to root density RD by $r_2=(\pi RD)^{-1/2}$, the volume v of root per unit volume of soil is given by $v=\pi\ r_1^2 RD=(r_1/r_2)^2$. Taking into account Eqns. (7) and (8) the soil resistance can be rewritten in terms of v as (Reicosky and Ritchie, 1976; Abdul-Jabbar *et al.*, 1984)

$$r_{s,i} = -ln(\pi r_{1,i}^2 RD_i)/(4\pi K_i RD_i \delta z_i) = -ln v_i/(4\pi K_i RD_i \delta z_i) \quad (10)$$

The units of $r_{s,i}$ are $MPa\ s\ m^{-1}$ when K_i is expressed in $m^2\ MPa^{-1}\ s^{-1}$. Zur *et al.* (1982), working on field soybeans with limiting soil moisture, found that soil resistances calculated from experimental results were four to six orders of magnitude higher than theoretically calculated using the Gardner model. They attributed this result to the fact that the unsaturated hydraulic conductivity of soil adjacent to the roots may be several orders of magnitude lower than that of the bulk soil.

EXPRESSING ROOT RADIAL RESISTANCE $r_{r,i}$

The radial movement of water from soil to xylem occurs through the cortical tissue, partly in the water-filled free space of the cell wall, and partly within the symplasm, which is the connected protoplasm within the cell membrane (Jones,1983). A unit radial resistance, ρ_r, can be defined as the root cortex resistance per unit length of root (with the same units as ρ_s), linked to the radial resistivity ρ_r^0 (resistance per unit area of root) by $\rho_r=\rho_r^0/(2\pi r_1)$, r_1 being the root radius. The flux of water entering the root per unit root length is given by an equation similar to (6): $q=\Delta\Psi/\rho_r$, where $\Delta\Psi$ represents the potential difference between the surface of the root and the xylem, assumed to be constant for a given layer. In a very similar way to the previous section, it can be shown that the total water flow Q_i entering the roots from soil layer i is written as

$$Q_i = \int_0^{L_i} q dl = \Delta\Psi / r_{r,i} \text{ with}$$

$$r_{r,i} = \rho_r/(RD_i \delta z_i) = \rho_r^0/(2\pi r_{1,i} RD_i \delta z_i) \quad (11)$$

$r_{r,i}$ has the same units as $r_{s,i}$ (MPa s m^{-1}). Herkelrath *et al.* (1977) give an average value for ρ_r of 1.2 × 10^{10} MPa s m^{-2}. For young maize plants Steudle *et al.* (1987) evaluated the radial resistivity (ρ_r^0) of excised main roots and found an average value of about 2 × 10^9 MPa s m^{-1} (which means that ρ_r = 3 × 10^{11} MPa s m^{-2} for a root radius of 1 mm). In the case of onion roots grown hydroponically Melchior and Steudle (1993) found a value of about 7 × 10^6 MPa s m^{-1} for ρ_r^0 at distances between 30 and 150 mm from the root tip: In this case ρ_r = 10^{10} MPa s m^{-2} for a onion root radius of 0.1 mm. These authors, however, specified that ρ_r^0 was considerably larger in more basal root zones.

EXPRESSING ROOT AXIAL RESISTANCE (XYLEM RESISTANCE) $r_{x,i}$

The pathway for axial or longitudinal flow is the xylem. The conducting elements are primarily the non-living and lignified tracheides and xylem vessels (Jones, 1983). It is assumed that the flux, q, of liquid water between two points along a set of xylem elements in a primary root (defined as a root which crosses a layer from bottom to top, i.e. which transfers water vertically) can be expressed in the form of an Ohm's law analogy (Denmead and Millar, 1976; Taylor and Klepper, 1978)

$$q = \Delta\Psi/r \quad \text{with} \quad r = \rho_x d \quad (12)$$

$\Delta\Psi$ is the potential difference and d the distance between the two points; ρ_x is the resistance of xylem elements per unit length expressed in MPa s m^{-4} (because q is expressed in m^3 (of water) s^{-1}, $\Delta\Psi$ in MPa and d in m (of root)). Let m_i be the number of primary roots which cross the soil layer i of thickness δz_i per unit surface and Q_i the total water flow through the roots for the elementary volume (1 × δz_i). Applying Eqn. (12) to each primary root crossing the layer (counted from $j=1$ to $j=m_i$) and considering that $\Delta\Psi$ is the same for all the roots leads to

$$Q_i = \sum_{j=1}^{m_i} q_j = \frac{\Delta\Psi}{\rho_x} \sum_{j=1}^{m_i} \frac{1}{d_j} \quad (13)$$

For the sake of convenience the primary roots are assumed to cross layer i with a mean angle ω_i to the vertical. This means that $d_j=\delta z_i/\cos\omega_i$, and Q_i can be rewritten as

$$Q_i = \Delta\Psi/r_{x,i} \quad \text{with} \quad r_{x,i} = \rho_x \delta z_i/(m_i \cos\omega_i) \quad (14)$$

Introducing the primary root density function, denoted by $RD_{p,i}$, which represents the length of primary root per unit volume (m m^{-3}) in layer i, the following relationship can be written

$$RD_{p,i}\delta z_i = \sum_{j=1}^{m_i} d_j = m_i \delta z_i / \cos\omega_i \quad (15)$$

which means that $m_i=RD_{p,i}\cos\omega_i$. This leads to the following expression for $r_{x,i}$

$$r_{x,i} = \rho_x \delta z_i/(RD_{p,i}\cos^2\omega_i) \quad (16)$$

with the dimensions of MPa s m^{-1}. Denmead and Millar (1976) studied water transport in the xylem elements of wheat stems and determined the average value of the stem resistance per unit length (ρ_x). The value found was 1.6 × 10^{10} MPa s m^{-4}. Melchior and Steudle (1993) measured the axial resistance of onion roots grown hydroponically and found an average value of 10^{10} MPa s m^{-4}. Yamauchi *et al.* (1995) measured the axial resistance to water flow along a cotton taproot of 70–120 days old plants and found a value for ρ_x of about 10^9 MPa s m^{-4}, stipulating that this value is near the lower limit of other reported values for cotton as well as other species.

It should be noted that the values of ρ_x and ρ_r cannot be compared directly because they represent different processes (Melchior and Steudle, 1993): ρ_x is the axial resistance per unit length of root expressed in MPa s m^{-4}, whereas ρ_r is the root radial resistance per unit length of root expressed in MPa s m^{-2}. Only $r_{r,i}$ and $r_{x,i}$, which have the same units, can be compared (cf. the section devoted to numerical results).

Formulation of water withdrawal by roots

MULTI-LAYER APPROACH: GENERAL CASE

The mathematical algorithm which follows solves the problem of deriving an Ohm's law type expression for the transpiration rate in the general case of a multi-layer model represented by Fig. (1). This algorithm was developed by Lhomme (1988a,b) for application to multi-layer micrometeorological models describing the vegetation-atmosphere interaction. It can be extended to multi-layer models of soil-plant water transfer in the way detailed below.

For each node in the electrical circuit, assuming no water storage, the following conservation equation can be written

$$Tr_i - Tr_{i+1} = \delta Tr_i \qquad (17)$$

where Tr_i is the upper vertical flux, Tr_{i+1} is the lower vertical flux and δTr_i is the lateral flux which enters the roots. Expressing the fluxes in Eqn. (17) in terms of driving potentials and resistances, following Eqns. (2) and (4), leads to

$$\Psi_{r,i+1} = a_i\Psi_{r,i} + b_i\Psi_{r,i-1} + c_i\Psi_{s,i} \qquad (18)$$

with

$$\begin{aligned} a_i &= 1 - b_i - c_i \\ b_i &= -r_{x,i}/r_{x,i-1} \\ c_i &= -r_{x,i}/r_{sr,i} \end{aligned} \qquad (19)$$

From this recurrent formula it can be proved (see Appendix B) that the following relation holds for any subscript i

$$\Psi_{r,i} = \alpha_i\Psi_c + \beta_i(r_{x,0}Tr_0) + \sum_{j=1}^{i-1}\varepsilon_i^j\Psi_{s,j} \qquad (20)$$

where the coefficients α_i, β_i and ε_i^j are calculated by means of the recurrent formulae given in Appendix B (Eqn. B7).

Substituting Eqn. (20) into Eqn. (2) and putting $\varepsilon_i^i = -1$ leads to

$$\delta Tr_i = -(\alpha_i / r_{sr,i})\Psi_c - (\beta_i / r_{sr,i})(r_{x,0}Tr_0) - \sum_{j=1}^{i}(\varepsilon_i^j / r_{sr,i})\Psi_{s,j} \qquad (21)$$

Introducing Eqn. (21) into Eqn. (5) yields

$$Tr_0\left(1 + r_{x,0}\sum_{i=1}^{n}\beta_i / r_{sr,i}\right) = -\left(\sum_{i=1}^{n}\alpha_i / r_{sr,i}\right)\Psi_c - \sum_{i=1}^{n}\sum_{j=1}^{i}(\varepsilon_i^j / r_{sr,i})\Psi_{s,j} \qquad (22)$$

Noticing the following formal identity between coefficients ε (see Appendix C)

$$\sum_{i=1}^{n}\sum_{j=1}^{i}(\varepsilon_i^j / r_{sr,i})\Psi_{s,j} = \sum_{i=1}^{n}\sum_{j=i}^{n}(\varepsilon_j^i / r_{sr,j})\Psi_{s,i} \qquad (23)$$

and defining

$$A = \sum_{i=1}^{n}\alpha_i / r_{sr,i} \quad B = \sum_{i=1}^{n}\beta_i / r_{sr,i} \quad E_i = -\sum_{j=i}^{n}\varepsilon_j^i / r_{sr,j} \qquad (24)$$

the total flux of transpiration can be rewritten as

$$Tr_0(1 + r_{x,0}B) = \sum_{i=1}^{n}E_i\Psi_{s,i} - A\Psi_c \qquad (25)$$

Parameters A, B and E involve only the elementary resistances ($r_{s,i}$, $r_{r,i}$ and $r_{x,i}$). They have the dimensions of a conductance (reciprocal of a resistance). We will put

$$r_{sp}^e = (1 + r_{x,0}B) / A \quad \Psi_s^e = \sum_{i=1}^{n}E_i\Psi_{s,i} / A \qquad (26)$$

r_{sp}^e has the dimensions of a resistance and Ψ_s^e represents a weighted mean of the water potentials of each layer because $A = \Sigma_{i=1}^{n}E_i$. This last relation can be easily proven by giving the same value to all the driving potentials in Eqn. (22). In this case Tr_0 is equal to zero, which implies the above equality. Therefore, Eqn. (25) can be rewritten as

$$Tr_0 = (\Psi_s^e - \Psi_c)/r_{sp}^e \qquad (27)$$

Consequently the total transpiration rate can effectively be expressed in the form of an Ohm's law analogy, which confirms the legitimacy of van den Honert's equation in a multi-layer representation of root water uptake. The effective soil-plant resistance r_{sp}^e and the effective soil potential Ψ_s^e do exist and are calculable by means of the recurrent formulae derived above, which are fairly easy to implement on a computer. The coefficients α_i, β_i and ε_i^j are calculated by the recurrent algorithm (B.7), and A, B and E_i by Eqn. (24).

However, it is worthwhile considering the possibility of deriving approximate expressions for the effective parameters, because, in the practice of soil-plant-atmosphere water transfer modelling, simpler models are often used to describe the soil-root interface.

APPROXIMATE EXPRESSIONS

For instance, in the SiSPAT model (Braud *et al.*, 1995), xylem resistance $r_{x,i}$, which is smaller than root radial resistance $r_{r,i}$ by about two orders of magnitude (cf. section devoted to Numerical Results), is neglected and the water transfer occurs through parallel resistors. Other models are based upon a bulk approach in which the soil root interface is represented by only one layer with the mean properties of the entire soil-root profile (Rose *et al.*, 1976; Lynn and Carlson, 1990).

(i) Multi-layer approach: case of parallel resistors

If xylem resistance is disregarded, all the root potentials $\Psi_{r,i}$ are equal to $\Psi_{r,1}$, and the whole circuit is equivalent to parallel resistors. In this case derivation of effective parameters is straightforward. Combining Eqn. (5) with Eqn. (2) leads to

$$Tr_0 = \sum_{i=1}^{n} (\Psi_{s,i} - \Psi_{r,1}) / r_{sr,i} = \sum_{i=1}^{n} \Psi_{s,i} / r_{sr,i} - \Psi_{r,1} \sum_{i=1}^{n} 1 / r_{sr,i} \quad (28)$$

which can be transformed into

$$Tr_0 = \left[\left(\sum_{i=1}^{n} \Psi_{s,i} / r_{sr,i} \right) \Big/ \left(\sum_{i=1}^{n} 1 / r_{sr,i} \right) - \Psi_{r,1} \right] \sum_{i=1}^{n} 1 / r_{sr,i} \quad (29)$$

Tr_0 being also equal to $(\Psi_{r,1} - \Psi_c)/r_{x,0}$, this means that

$$r_{sp}^e = r_{x,0} + r_{sr}^e \quad \text{with} \quad r_{sr}^e = 1 \Big/ \sum_{i=1}^{n} 1 / r_{sr,i} \quad (30)$$

and

$$\Psi_s^e = \left(\sum_{i=1}^{n} \Psi_{s,i} / r_{sr,i} \right) \Big/ \left(\sum_{i=1}^{n} 1 / r_{sr,i} \right) \quad (31)$$

(ii) One-layer or bulk approach

When the soil-root system is represented by only one layer, the equivalent electric circuit consists of four bulk resistances (r_s^b, r_r^b, r_x^b and $r_{x,0}$) put in series between an effective soil water potential Ψ_s^e and a canopy water potential Ψ_c (Fig. 2). The transpiration rate is written as

$$Tr_0 = (\Psi_s^e - \Psi_c)/r_{sp}^e \quad \text{with} \quad r_{sp}^e = r_s^b + r_r^b + r_x^b + r_{x,0} \quad (32)$$

These resistances can be easily calculated from the formulae derived above (Eqns. (10), (11) and (16)). Using the same symbols, the bulk soil resistance reads as

$$r_s^b = -ln(\pi r_1^2 RD)/(4\pi K^b RD z_r) \quad \text{with}$$

$$K^b = K_{sat}(\Psi_{sat}/\Psi_s^e)^{3/b+2} \quad (33)$$

K^b being the bulk hydraulic conductivity of the soil layer. The bulk root and xylem resistances read as

$$r_r^b = \rho_r/(RD z_r) \quad \text{and} \quad r_x^b = \rho_x z_r/(RD_p \cos^2 \omega) \quad (34)$$

When the root density and soil water potential profiles are known, the effective soil water potential can be logically expressed as a weighted mean of the soil water potential of each layer in the following form

$$\Psi_s^e = \left(\sum_{i=1}^{n} RD_i \delta z_i \Psi_{s,i} \right) \Big/ \left(\sum_{i=1}^{n} RD_i \delta z_i \right) \quad (35)$$

The soil water potential is weighted by the root density mutliplied by the layer thickness (Federer, 1979; Jones *et al.*, 1982; Zur *et al.*, 1982).

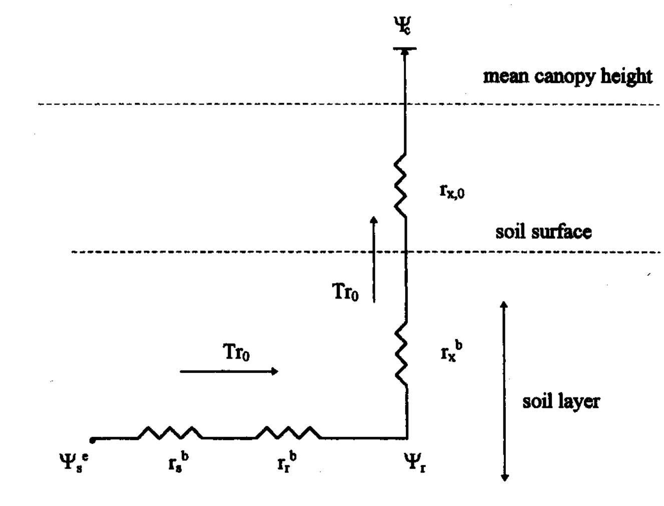

Fig. 2. *Electrical analogue of water transfer processes within the soil-root system: particular case of the bulk (or one-layer) approach.*

Numerical results

The purpose of this section is to evaluate numerically, with respect to the true solution given by the general algorithm, the performance of the approximate expressions of the transpiration rate presented in the previous section: (i) the parallel resistors approach, (ii) the bulk approach. The following standard conditions have been chosen to carry out this assessment. The root depth z_r is 2 m. The number of layers n is 20 with a constant thickness $\delta z_i = 0.10$ m. The canopy water potential Ψ_c (in fact the stem potential) has a constant value of −1.2 MPa and the stem resistance is neglected ($r_{x,0} = 0$). The root characteristics (r_1, ρ_r and ρ_x) and the soil characteristics (K_{sat}, Ψ_{sat} and b) are assumed to be known with constant values that do not vary with depth. They are given in Table 1: the root radius

Table 1. Base values of the variables and coefficients used in the numerical simulations (see Appendix A for the significance of each symbol).

K_{sat}	Ψ_{sat}	b	r_l	ρ_r	ρ_x	ω	$r_{x,0}$
6.3×10^{-4} $m^2 s^{-1} MPa^{-1}$	–0.003 MPa	7.1	10^{-4} m	5×10^{10} MPa s m^{-2}	10^{10} MPa s m^{-4}	0 degree	0 MPa s m^{-1}

r_l is 0.1 mm (value given by Abdul-Jabbar *et al.* (1984) for alfalfa); ρ_r and ρ_x are taken to be respectively equal to 5×10^{10} MPa s m^{-2} and 10^{10} MPa s m^{-4}, which correspond roughly to the average of the values encountered in the literature. The values retained for the soil hydraulic parameters K_{sat}, Ψ_{sat} and b are those corresponding to a sandy clay loam in the classification given by Clapp and Hornberger (1978).

In the simulations only root density (RD_i) and soil water potential ($\Psi_{s,i}$) vary with depth. The root density profile is described by a polynomial function of depth z

$$RD(z) = d_n z^n + \ldots + d_1 z + d_0 \qquad (36)$$

where d_i (i = 1 to n) are adjusted coefficients. Two simple cases are considered in the simulation process: (i) the root density profile is constant from the soil surface to the rooting depth z_r with a value of 10^4 m root/m^3 soil; (ii) the root density profile decreases with depth from $RD(0) = 2 \times 10^4$ m m^{-3} to $RD(z_r) = 0$. (In both cases this means that $d_{n>1} = 0$, $d_1 = (RD(z_r) - RD(0))/z_r$ and $d_0 = RD(0)$). These values of root density are in agreement with the experimental data given by Jones *et al.* (1982) for soybean or Abdul-Jabbar *et al.* (1984) for alfalfa. For the sake of convenience, the density function of primary root RD_p (Eqn. 16) is arbitrarily taken as half the value of the root density function ($RD_p = RD/2$) and the primary root angle to the vertical ω is set to 0. The vertical distribution of soil water potential is also parameterized in the form of a polynomial function of depth z

$$\Psi_s(z) = e_n z^n + \ldots + e_1 z + e_0 \qquad (37)$$

Only two linear cases are analysed here: (i) a linear decreasing profile from $\Psi_s(0) = -0.1$ MPa to $\Psi_s(z_r) = -1.0$ MPa, and (ii) a linear increasing profile from $\Psi_s(0) = -1.0$ MPa to $\Psi_s(z_r) = -0.1$ MPa. This means in both cases that $e_{n>1} = 0$, $e_0 = \Psi_s(0)$ and $e_1 = (\Psi_s(z_r) - \Psi_s(0))/z_r$. These conditions are summarised in Table 2. With the units chosen (MPa for water potential and *MPa s* m^{-1} for the elementary resistances $r_{s,i}$, $r_{r,i}$ and $r_{x,i}$) the flux of transpiration is expressed per unit area of soil as m^3 m^{-2} s^{-1}. To obtain the flux in *W* m^{-2} (the most commonly used units in micrometeorology) it must be multiplied by the latent heat of vaporization (2.4×10^9 *J* m^{-3}). Figs. 3 and 4 show the variation with depth of elementary resistances $r_{s,i}$, $r_{r,i}$ and $r_{x,i}$ in two different conditions (case 1 and case 2, Cf. Table 2). Xylem resistance $r_{x,i}$ is generally two orders of magnitude lower than root resistance $r_{r,i}$. Both increase when root density decreases. Soil resistance $r_{s,i}$ varies with soil moisture and root density, and is one to three orders of magnitude lower than $r_{r,i}$.

The results of the numerical simulations are shown in Table 3 for the four cases considered in this analysis. The method denoted by A is the complete multi-layer approach which takes into account the three types of elementary resistance: soil resistance, root radial resistance and root axial resistance (Eqns. 26 and 27). Method B is the simplified multi-layer approach which does not take into account root axial resistance (Eqns. 30 and 31). Method C is the bulk or one-layer approach (Eqns. 32 and 35). For the standard conditions simulated methods B and C provide estimates of the effective soil water potential which are fairly close to the true value given by method A, but

Table 2. Root density and soil water potential profiles for each of the four cases considered in the numerical simulations.

	Case 1	Case 2	Case 3	Case 4
Root density profile ($m\ m^{-3}$)	Constant profile $RD(0) = RD(z_r) = 10^4$		Decreasing linear profile $RD(0) = 2 \times 10^4$, $RD(z_r) = 0$	
Soil water potential profile (MPa)	Decreasing linear profile $\Psi_s(0) = -0.1$ $\Psi_s(z_r) = -1.0$	Increasing linear profile $\Psi_s(0) = -1.0$ $\Psi_s(z_r) = -0.1$	Decreasing linear profile $\Psi_s(0) = -0.1$ $\Psi_s(z_r) = -1.0$	Increasing linear profile $\Psi_s(0) = -1.0$ $\Psi_s(z_r) = -0.1$

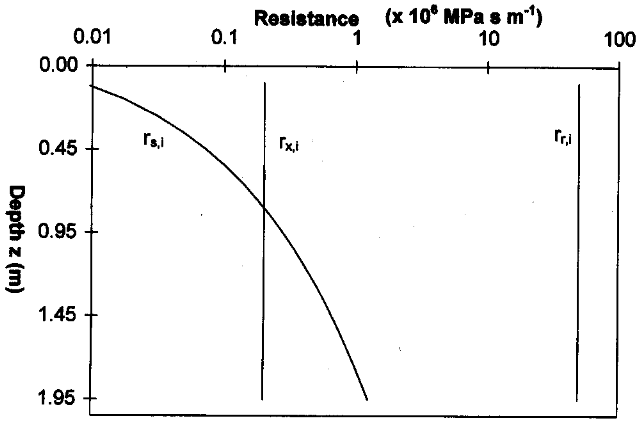

Fig. 3. *Variation of soil, root and xylem elementary resistances* $r_{s,i}$, $r_{r,i}$ *and* $r_{x,i}$ *(Eqns. (10), (11) and (16)) as a function of depth in the conditions corresponding to case 1.*

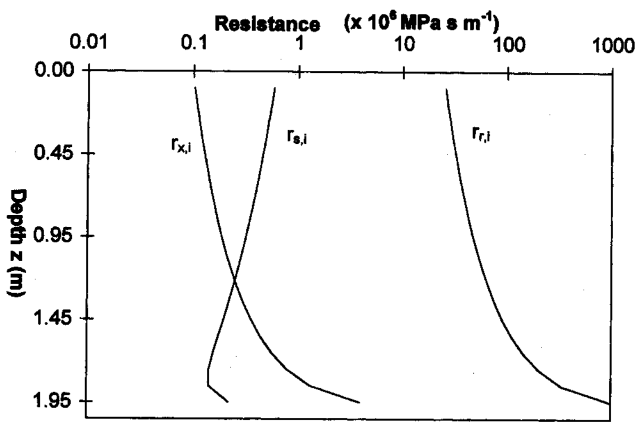

Fig. 4. *Variation of soil, root and xylem elementary resistances* $r_{s,i}$, $r_{r,i}$ *and* $r_{x,i}$ *as a function of depth in the conditions corresponding to case 4.*

the estimates of the effective soil-plant resistance r_{sp}^e are not as good. Method B underestimates the soil-plant resistance, which leads to a systematic overestimation of the transpiration rate (up to 48%), whereas method C overestimates r_{sp}^e, which generates a systematic underestimation of Tr (up to 59%). Consequently, neither the parallel resistors model, which neglects xylem resistance in the multi-layer approach, nor the bulk model, which considers only one soil layer, can offer reliable alternatives to the complete algorithm of method A.

Conclusion

Starting from a multi-layer description of the soil-plant interaction, which accounts for soil, root and xylem elementary resistances, it has been proved that the total flux of water withdrawn from the soil by the roots (i.e. the transpiration rate of the plant canopy) can be expressed in the form of an Ohm's law. This means that the van den Honert equation holds at canopy scale. Explicit mathematical expressions have been obtained for the effective resistance r_{sp}^e and the effective soil water potential Ψ_s^e (see Eqn. 1): r_{sp}^e is a combination of the elementary resistances making up the multi-layer model and Ψ_s^e is a weighted mean of the water potentials in each soil layer, the weighting system involving the complete set of elementary resistances. Simpler representations of soil-plant interaction leading to Ohm's law type formulation of the transpiration rate have been examined: a simplified multi-layer representation (B), in which xylem resistance is neglected, and a bulk approach (C), in which soil-root interaction is represented by only one layer; and numerical simulations have been carried out to assess the performance of these simpler models. It appears that both approaches do not provide the values obtained from the correct algorithm. Model B substantially overestimates transpiration, which means that xylem resistance cannot be neglected, even if it is two

Table 3. Estimates of the effective parameters (Ψ_s^e and r_{sp}^e) and of the transpiration rate (Tr) obtained by different methods (A, B, C) in the four experimental conditions detailed in Table 2. Ψ_s^e is the effective soil water potential and r_{sp}^e is the effective soil-plant resistance. (A) is the reference method based on a complete multi-layer approach; (B) is the method based on a simplified multi-layer approach with parallel resistors; (C) is the bulk (or one-layer) approach. The canopy water potential Ψ_c is set to be equal to –1.2 MPa.

		Case 1	Case 2	Case 3	Case 4
Ψ_s^e	A	–0.49	–0.56	–0.37	–0.65
(MPa)	B	–0.55	–0.55	–0.40	–0.70
	C	–0.55	–0.55	–0.40	–0.70
r_{sp}^e	A	3.6×10^6	3.6×10^6	2.9×10^6	2.9×10^6
(MPa s m^{-1})	B	2.5×10^6	2.5×10^6	2.5×10^6	2.5×10^6
	C	6.5×10^6	6.5×10^6	6.5×10^6	6.5×10^6
Tr	A	469	419	686	451
(W m^{-2})	B	621 (+32%)*	621 (+48%)	765 (+12%)	476 (+6%)
	C	239 (–49%)	239 (–43%)	295 (–57%)	184 (–59%)

* Between brackets is the relative error made on the estimation of the transpiration rate, method A providing the reference value.

orders of magnitude lower that root radial resistance. Model C systematically underestimates the transpiration rate (of about 40–60%), which implies that the one-layer approach is not an accurate model of water transfer by roots either.

As a concluding remark, and at the risk of denegrating the significance of the results obtained, it is worthwhile pointing out that the legitimacy of this analysis rests essentially on the current understanding of the physics of water uptake by the roots. This understanding assumes that water transfer, through an elementary path within the soil, the root cortex or the root xylem, follows an Ohm's law analogue. There is still debate in the literature on the true nature of the elementary processes involved, and many cases of non-linearities between flow and driving forces have been encountered: e.g. osmotic effects in root water uptake, flux-dependent root resistances (Passioura, 1984; Steudle, 1994). A physically-correct model of elementary water transfer within the roots may ultimately differ from Ohm's law analogy and invalidate the analysis performed.

Appendix A: definition of symbols

- A parameter representing a combination of elementary resistances (m MPa^{-1} s^{-1})
- a_i dimensionless parameter defined by Eqn. (19)
- B parameter representing a combination of elementary resistances (m MPa^{-1} s^{-1})
- b dimensionless parameter in the relation $K = f(\Psi_s)$ (Eqn. (9))
- b_i, c_i dimensionless parameters defined by Eqn. (19)
- E_i parameter representing a combination of elementary resistances (m MPa^{-1} s^{-1})
- K soil hydraulic conductivity (m^2 s^{-1} MPa^{-1})
- K_{sat} soil hydraulic conductivity at field saturation (m^2 s^{-1} MPa^{-1})
- m_i number of primary roots crossing soil layer i per unit area
- Q_i water flow entering the roots in layer i per unit area ($=\delta Tr_i$) (m^3 m^{-2} s^{-1})
- r_1 root radius (m)
- r_2 distance from which water flows to the roots (in Eqn. 8) (m)
- $r_{s,i}$ soil resistance (from the soil matrix to the root surface) of layer i (MPa s m^{-1})
- $r_{r,i}$ root radial resistance (through the root cortex) of layer i (MPa s m^{-1})
- $r_{sr,i}$ $= r_{s,i} + r_{r,i}$ (MPa s m^{-1})
- $r_{x,i}$ root axial resistance (through the root xylem) of layer i (MPa s m^{-1})
- $r_{sp}{}^e$ effective resistance to water transfer from soil to canopy (MPa s m^{-1})
- RD_i root length density in layer i (m m^{-3})
- $RD_{p,i}$ primary root length density in layer i (m m^{-3})
- Tr_i vertical flux of water which leaves layer i through primary roots (m^3 m^{-2} s^{-1})
- Tr_0 total root water uptake (m^3 m^{-2} s^{-1})
- α_i, β_i dimensionless parameters calculated by Eqn. (B.7)
- δz_i thickness of soil layer i (m)
- δTr_i flux of water extracted by the roots in soil layer i per unit area (m^3 m^{-2} s^{-1})
- ε_i^j dimensionless parameter calculated by Eqn. (B.7)
- v volume of root per unit volume of soil (dimensionless)
- ρ_s soil resistance per unit root length (MPa s m^{-2})
- ρ_r root cortex resistance per unit root length (MPa s m^{-2})
- ρ_x xylem resistance per unit root length (MPa s m^{-4})
- Ψ_c canopy water potential (in the stem below the first leaves) (MPa)
- Ψ_s soil water potential (MPa)
- Ψ_r water potential of root xylem (MPa)
- Ψ_s^e effective soil water potential (MPa)
- Ψ_{sat} soil water potential at field saturation (MPa)
- ω mean angle of the primary roots to the vertical (degree)

Appendix B: derivation of eqn. (20)

The root water potential in the first layer $\Psi_{r,1}$ is linked with the bulk canopy water potential Ψ_c by

$$\Psi_{r,1} = \Psi_c + r_{x,0}Tr_0 \qquad \text{(B.1)}$$

where Tr_0 is the total transpiration rate which passes through the shoot and $r_{x,0}$ is the xylem resistance of the stem. $\Psi_{r,2}$ and $\Psi_{r,3}$ are easily calculated from Eqn. (17) as

$$\Psi_{r,2} = (1 - c_1)\,\Psi_c + a_1(r_{x,0}Tr_0) + c_1\Psi_{s,1} \qquad \text{(B.2)}$$

$$\Psi_{r,3} = [a_2(1 - c_1) + b_2]\Psi_c + (a_2a_1 + b_2)(r_{x,0}Tr_0) + a_2c_1\Psi_{s,1} + c_2\Psi_{s,2} \qquad \text{(B.3)}$$

Eqns. (B1), (B2) and (B3) suggest that $\Psi_{r,i}$ can be written in the general form

$$\Psi_{r,i} = \alpha_i\Psi_c + \beta_i(r_{x,0}Tr_0) + \sum_{j=1}^{i-1}\varepsilon_i^j\Psi_{s,j} \qquad \text{(B.4)}$$

To prove the validity of this relationship we suppose that Eqn. (B4) is true for i and i–1 and we demonstrate it also holds for i+1. Using Eqn. (18) $\Psi_{r,i+1}$ can be written as

$$\Psi_{r,i+1} = (a_i\alpha_i + b_i\alpha_{i-1})\Psi_c + (a_i\beta_i + b_i\beta_{i-1})(r_{x,0}Tr_0) + \sum_{j=1}^{i-2}(a_i\varepsilon_i^j + b_i\varepsilon_{i-1}^j)\Psi_{s,j} + a_i\varepsilon_i^{i-1}\Psi_{s,i-1} + c_i\Psi_{s,i} \qquad \text{(B.5)}$$

which means that $\Psi_{r,i+1}$ can be written in the same form as $\Psi_{r,i}$

$$\Psi_{r,i+1} = \alpha_{i+1}\Psi_c + \beta_{i+1}(r_{x,0}Tr_0) + \sum_{j=1}^{i}\varepsilon_{i+1}^j\Psi_{s,j} \qquad \text{(B.6)}$$

and that Eqn. (B4) holds whatever the value of i. The coefficients α, β and ε, which are dimensionless, are calculated by means of the following recurrent formulae

$$
\begin{aligned}
\alpha_{i+1} &= a_i\alpha_i + b_i\alpha_{i-1} \\
\beta_{i+1} &= a_i\beta_i + b_i\beta_{i-1} \\
\varepsilon_{i+1}^{j<i-1} &= a_i\varepsilon_i^j + b_i\varepsilon_{i-1}^j \\
\varepsilon_{i+1}^{i-1} &= a_i\varepsilon_i^{i-1} + a_i c_{i-1} \\
\varepsilon_{i+1}^{i} &= c_i
\end{aligned}
\quad (B.7)
$$

the first coefficients being defined as

$$
\begin{aligned}
&\alpha_1 = 1 \qquad \beta_1 = 1 \\
&\alpha_2 = 1 - c_1 \qquad \beta_2 = a_1 \qquad \varepsilon_2^1 = c_1
\end{aligned}
\quad (B.8)
$$

Appendix C: derivation of eqn. (23)

We define

$$X_i^j = (\varepsilon_i^j / r_{sr,j})\Psi_{s,j} \quad (C.1)$$

The terms X_i^j (with $j \le i$) can be arranged in the form of the following ($n \times n$) triangular square matrix, i referring to the row and j to the column

X_1^1	0	....	0	....	0
X_2^1	X_2^2	....	0	....	0
....	....	....	....	....	....
X_i^1	X_i^2	....	X_i^i	....	0
....	....	....	....	....	....
X_n^1	X_n^2	....	X_n^i	....	X_n^n

The double sum which appears in the left hand side of Eqn. (23) can be rewritten as

$$SS = \sum_{i=1}^{n} S_{r,i} \quad \text{with} \quad S_{r,i} = \sum_{j=1}^{i} X_i^j \quad (C.2)$$

SS represents the sum of all the elements of this matrix and $S_{r,i}$ is the sum of the elements of row i. The same summation can be performed by summing the elements by column instead of row. In this case we have

$$SS = \sum_{i=1}^{n} S_{c,i} \quad \text{with} \quad S_{c,i} = \sum_{k=i}^{n} X_k^i \quad (C.3)$$

Since the summation by row should give the same result as the summation by column, the following equality holds

$$SS = \sum_{i=1}^{n}\sum_{j=1}^{i} X_i^j = \sum_{i=1}^{n}\sum_{k=i}^{n} X_k^i \quad (C.4)$$

which means that

$$\sum_{i=1}^{n}\sum_{j=1}^{i} (\varepsilon_i^j / r_{sr,i})\Psi_{s,j} = \sum_{i=1}^{n} \Psi_{s,i} \sum_{k=i}^{n} (\varepsilon_k^i / r_{sr,k}) \quad (C.5)$$

References

Abdul-Jabbar, A.S., Lugg, D.G., Sammis, T.W. and Gay, L.W., 1984. A field study of plant resistance to water flow in alfalfa. *Agron. J.*, **76**, 765–769.

Braud, I., Dantas-Antonino, A.C., Vauclin, M., Thony, J.L. and Ruelle, P., 1995. A simple Soil-Plant-Atmosphere Transfer model (SiSPAT): development and field verification. *J. Hydrol.*, **166**, 213–250.

Campbell, G.S., 1974. A simple method for determining unsaturated conductivity from moisture retention data. *Soil Sci.*, **117**, 311–314.

Clapp, R.B. and Hornberger, G.M., 1978. Empirical equations for some soil hydraulic properties. *Wat. Resour. Res.*, **14**, 601–604.

Cowan, I.R., 1965. Transport of water in the soil-plant-atmosphere system. *J. Appl. Ecol.*, **2**, 221–239.

Denmead, O.T. and Millar, B.D., 1976. Water transport in wheat plants in the field. *Agron. J.*, **68**, 297–303.

Feddes, R.A., and Rijtema, P.E., 1972. Water withdrawal by plant roots. *J. Hydrol.*, **17**, 33–59.

Federer, C.A., 1979. A soil-plant-atmosphere model for transpiration and availability of soil water. *Wat. Resour. Res.*, **15**, 555–562.

Gardner, W.R., 1960. Dynamic aspects of water availability to plants. *Soil Sci.*, **89**, 63–73.

Herkelrath, W.N, Miller, E.E., and Gardner,W.R., 1977. Water uptake by plants: II. The root contact model. *Soil Sci. Soc. Am. J.*, **41**, 1039–1043.

Hillel, D., Talpaz, H., and van Keulen, H., 1976. A macroscopic-scale model of water uptake by a nonuniform root system and of water and salt movement in the soil profile. *Soil Sci.*, **121**, 242–255.

Jones, H.G., 1983. *Plants and microclimate: a quantitative approach to environmental plant physiology*. Cambridge University Press, Cambridge, UK.

Jones, J.W., Zur, B., Boote, K.J., and Hammond, L.C., 1982. Plant resistance to water flow in field soybeans: I. Non-limiting soil moisture. *Agron. J.*, **74**, 92–98.

Katerji, N., Hallaire, M., Perrier, A. and Durand, R., 1983. Transfert hydrique dans le végétal. *Acta Oecologica*, **4**, 11–26.

Lhomme, J.P., 1988a. Extension of Penman's formulae to multi-layer models. *Boundary-Layer Meteorol.*, **42**, 281–291.

Lhomme, J.P., 1988b. A generalized combination equation derived from a multi-layer micrometeorological model. *Boundary-Layer Meteorol.*, **45**, 103–115.

Lynn, B.H. and Carlson, T.N, 1990. A stomatal resistance model illustrating plant vs. external control of transpiration. *Agric. For. Meteorol.*, **52**, 5–43.

Melchior, W. and Steudle, E, 1993. Water transport in onion (*Allium cepa L.*) roots. *Plant Physiol.*, **101**, 1305–1315.

Passioura, J.B., 1984. Hydraulic resistance of plants. I. Constant or variable ? *Aust. J. Plant Physiol.*, **11**, 333–339.

Reicosky, D.C. and Ritchie, J.T., 1976. Relative importance of soil resistance and plant resistance in root water absorption. *Soil Sci. Soc. Am. J.*, **40**, 293–297.

Rose, C.W., Byrne, G.F. and Hansen, G.K., 1976. Water transport from soil through plant to atmosphere: a lumped-parameter model. *Agric. For. Meteorol.*, **16**, 171–184.

Steudle, E., 1994. Water transport across roots. *Plant and Soil*, **167**, 79–90.

Steudle, E. Oren, R., and Schulze, E.D., 1987. Water transport in maize roots. *Plant Physiol.*, **84**, 1220–1232.

Taylor, H.M. and Klepper, B., 1978. The role of rooting characteristics in the supply of water to plants. *Adv. Agronomy*, **30**, 99–128.