

## Validation of a root water uptake model to estimate transpiration constraints

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### ABSTRACT

Experimental results obtained from a greenhouse trial with common bean (*Phaseolus vulgaris* L.) plants performed to test model hypotheses regarding the onset of limiting hydraulic conditions and the shape of the transpiration reduction curve in the falling rate phase are presented. According to these hypotheses based on simulations with an upscaled single-root model, the matric flux potential at the onset of limiting hydraulic conditions is as a function of root length density and potential transpiration rate, while the relative transpiration in the falling rate phase equals the relative matric flux potential. Transpiration of bean plants in water stressed pots with four different soils was determined daily by weighing and compared to values obtained from non-stressed pots. This procedure allowed determining the onset of the falling rate phase and corresponding soil hydraulic conditions. At the onset of the falling rate phase, the value of matric flux potential  $M_f$  showed to differ in order of magnitude from the model predicted value for three out of four soils. This difference between model and experiment can be explained by the heterogeneity of the root distribution which is not considered by the model. An empirical factor to deal with this heterogeneity should be included in the model to improve predictions. Comparing the predictions of relative transpiration in the falling rate phase using a linear shape with water content, pressure head or matric flux potential, the matric flux potential based reduction function, in agreement with the hypothesis, showed the best performance, while the pressure head based equation resulted in the highest deviations between observed and predicted values of relative transpiration rates.

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## 1. Introduction

Hydrological models assume root water uptake and plant transpiration to occur at potential rates in the so-called constant rate phase, when soil hydraulic conditions are not limiting (Van den Berg and Driessen, 2002). For water contents below a threshold value  $\theta_l$ , transpiration decreases together with the soil-water content in the falling rate phase (e.g. Palmer et al., 1964; Feddes and Raats, 2004; Kozak et al., 2005). In this phase, actual transpiration and crop growth rates are lower than their potential rates. For water contents below the permanent wilting point, transpiration is supposed to be zero. The shape of the reduction function is often supposed to be linear with water content  $\theta$  (Doorenbos and Kassam, 1986) or with pressure head  $h$  (Feddes et al., 1988), but curvilinear shapes have also been proposed (Metselaar and De Jong van Lier, 2007; De Jong van Lier et al., 2009).

A great number of root water extraction models have been developed aiming to increase insight in the influence of system parameters in the process of plant water uptake. Such models can be empirical (Jarvis, 1989; Li et al., 2001), or describe root water

uptake based on the behavior of a single root, the microscopic approach (Moldrup et al., 1992; Roose and Fowler, 2003; Novák et al., 2005; De Jong van Lier et al., 2006) or of the overall root system, the macroscopic approach (Perrochet, 1987; Dardanelli et al., 2004). An extensive review on the subject can be found in Green et al. (2006).

Mathematical analyses for the microscopic approach have been presented in classical contributions by Philip (1957), Gardner (1960) and Cowan (1965). The use of their results has been extended to the falling rate phase by a sequence of steady rate (or steady state) solutions with iteratively adapted values of the soil physical characteristics (Passioura and Cowan, 1968). Reviews of mathematical analyses are presented in articles by Tinker (1976) and Raats (2006).

Numerical modeling of root water extraction on a microscopic scale has been described by De Jong van Lier et al. (2006). Their simulations showed that expressing the onset of limiting hydraulic conditions in terms of water content, pressure head or hydraulic conductivity is not very effective, as the values depend to a high extent on the soil type and its respective hydraulic properties. Therefore, these authors focused on the matric flux potential as a soil physical property closely related to soil-water movement, root water extraction and limiting hydraulic conditions. Matric flux potential ( $M$ ,  $m^2 d^{-1}$ ) is defined as the integral of unsaturated hydraulic conductivity ( $K(h)$ ,  $m d^{-1}$ ) over pressure head ( $h$ , m), or

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equivalently as the integral of diffusivity ( $D(\theta)$ ,  $\text{m}^2 \text{d}^{-1}$ ) over water content ( $\theta$ ,  $\text{m}^3 \text{m}^{-3}$ ). In order to obtain sensitivity of matic flux potential values in the dry zone, the permanent wilting point in terms of pressure head ( $h_w$ , m) or water content ( $\theta_w$ ,  $\text{m}^3 \text{m}^{-3}$ ) can be chosen as the lower bound of the integral:

$$M = \int_{h_w}^h K(h) dh = \int_{\theta_w}^{\theta} D(\theta) d\theta \quad (1)$$

Matric flux potential at the onset of limiting hydraulic conditions ( $M_l$ ,  $\text{m}^2 \text{d}^{-1}$ ) was shown to be independent of soil type and to depend solely on potential transpiration rate ( $T_p$ ,  $\text{m d}^{-1}$ ) and root length density ( $R$ ,  $\text{m m}^{-3}$ ). According to a numerical analysis neglecting any internal root system resistance to water flow (De Jong van Lier et al., 2006):

$$M_l = T_p r_m^q \quad (2)$$

with  $p = 23.5 \text{ m}^{1-q}$ ,  $q = 2.367$  and  $r_m$  (m), the mean half-distance between roots related to  $R$  by:

$$r_m = \sqrt{\frac{1}{\pi R}} \quad (3)$$

It can be expected that the role of internal root resistance to water becomes more important when the product  $T_p \cdot r_m$  increases and the empirically obtained values for  $p$  and  $q$  may no longer be valid. Under these circumstances, Eq. (2) may underestimate  $M_l$  and, consequently,  $h_l$  and  $\theta_l$ .

Using the same numerical model, Metselaar and De Jong van Lier (2007) showed that, for the falling rate phase:

$$T_R = \frac{T_a}{T_p} = \frac{M}{M_l} \quad (4)$$

where  $T_R$  is the relative transpiration, and  $T_a$  ( $\text{m d}^{-1}$ ) and  $T_p$  ( $\text{m d}^{-1}$ ) are the actual and potential transpiration, respectively. Eq. (4), which states that  $T_R$  decreases linearly with  $M$ , is an alternative to the equations proposed by Doorenbos and Kassam (1986) and Feddes et al. (1988). Using Eq. (4), Metselaar and De Jong van Lier (2007) derived analytical solutions for  $T_R$  as a function of water content for a number of so-called analytical soils (Raats, 2001), among these the soils described by the Brooks and Corey (1964) equation:

$$\Theta = \left( \frac{h_b}{h} \right)^\lambda \quad (5)$$

in which  $\Theta = (\theta - \theta_r)/(\theta_s - \theta_r)$  is the effective saturation,  $\theta$ ,  $\theta_r$  and  $\theta_s$  are water content, residual water content and saturated water content ( $\text{m}^3 \text{m}^{-3}$ ), respectively;  $h$  (m) is the pressure head,  $h_b$  (m) is the air entry pressure head and  $\lambda$  is a shape parameter.

Combining the Burdine (1953) theory to Eq. (5), the following expression for the hydraulic conductivity function  $K(h)$  is obtained:

$$K(h) = K_s \left( \frac{h_b}{h} \right)^{2+3\lambda} \quad (6)$$

Eq. (6) combined to Eq. (1) yields:

$$M(h) = -\frac{K_s h_b}{1+3\lambda} \left[ \left( \frac{h_b}{h} \right)^{1+3\lambda} - \left( \frac{h_b}{h_w} \right)^{1+3\lambda} \right] \quad (7)$$

Combining Eqs. (4) and (7) it can be shown that, in the falling rate phase (Metselaar and De Jong van Lier, 2007):

$$T_R = \frac{\Theta^P - \Theta_w^P}{\Theta_l^P - \Theta_w^P} \quad (8)$$

with  $P = 3 + 1/\lambda$ , and  $\Theta_l$  and  $\Theta_w$  correspond to  $\Theta$  at the onset of limiting hydraulic conditions and at permanent wilting, respectively.

In order to verify these findings, data are needed in which  $T_R$  has been established as a function of pressure head or water

content, and where in addition rooting density and soil physical characteristics are known. No adequate datasets have been found in literature, although experimental implications for the calibration of root water uptake have been discussed (Hopmans and Gutiérrez-Ravé, 1988; Musters and Bouting, 2000); in this paper we describe experimental results obtained from a greenhouse trial with common bean plants performed to test the hypotheses put forward by De Jong van Lier et al. (2006) regarding the onset of limiting hydraulic conditions (Eq. (2)) and by Metselaar and De Jong van Lier (2007) regarding the shape of the reduction curve in the falling rate phase (Eq. (8)).

## 2. Materials and methods

Two greenhouse experiments were performed in Brazil, São Paulo State,  $22^{\circ}42' S$ ,  $47^{\circ}37' W$ , 546 m altitude, at the University of São Paulo campus in Piracicaba. The first experiment (Experiment I) was performed from September to November 2006; the second experiment (Experiment II) was carried out between April and June 2007. The total duration of both experiments was about 70 days.

Plastic garden pots, 0.20 m high and with a volume of approximately 41 were used. In Experiment I, material from two soils (clay texture:  $CL_1$  and sandy loam texture:  $SL_1$ ) was used, six pots per soil. In Experiment II, two other soils (clay texture:  $CL_2$  and sandy loam texture:  $SL_2$ ) were used, 12 pots per soil. Particle size distribution data of these soils are presented in Table 1. Before filling the pots, soil material was air-dried and sieved through a 5 mm mesh. The pots with clay soils ( $CL_1$  and  $CL_2$ ) were filled to a density of  $1200 \text{ kg m}^{-3}$ . The sandy loam soils ( $SL_1$  and  $SL_2$ ) had a density of  $1400 \text{ kg m}^{-3}$  in the pots.

To obtain soil-water retention data, samples were taken from extra pots, filled and treated the same way as the pots with plants. Eight samples per soil were used for standard laboratory methodology with suction funnels and pressure plates. The Brooks and Corey (1964) equation (Eq. (5)) was fitted to these data (Table 1) resulting in  $R^2 > 0.98$  for all cases.

Hydraulic conductivity  $K$  ( $\text{m d}^{-1}$ ) as a function of pressure head was determined by the Wind (1968) evaporation method. Cylinders (103 mm diameter, 80 mm height) were filled with soil material, saturated and equipped with four microtensiometers (3 mm diameter) at four different depths within the cylinder. Tensiometer readings and total mass were registered every 60 min during 2 weeks in the evaporating samples. From these data,  $K-h$  values were obtained by inverse modeling (Van Dam et al., 1994). The following stepwise equation was fitted to the data:

$$K = K_s; \quad |h| < |h_k| \quad (9a)$$

$$K = K_s \left( \frac{|h_k|}{|h|} \right)^b; \quad |h| \geq |h_k| \quad (9b)$$

in which  $K_s$  ( $\text{m d}^{-1}$ ) is the hydraulic conductivity of the saturated soil,  $h_k$  (m) is the pressure head which defines the use of Eq. (9a) or (9b) and  $b$  is a shape factor. Obtained values for  $K_s$ ,  $h_k$  and  $b$  are shown in Table 1. Note that Eq. (9b) equals Eq. (6) if  $b = 2 + 3\lambda$ . Parameter  $\lambda$  can be obtained by fitting Eq. (5) to water retention data, and this Burdine (1953) restriction is often applied to estimate  $K$  when only water retention data and  $K_s$  are determined. In the present case, where hydraulic conductivity is a key parameter to the experimental model verification,  $K(h)$  was determined independently of water retention and  $b$  was obtained experimentally, independent of  $\lambda$ .

Each pot was populated with one common bean plant (*Phaseolus vulgaris* L., cv. "Perola"), transplanted to the pot 2 days after emergence. In order to avoid bare soil evaporation, the soil surface around the seedling was covered with a plastic film and, on

**Table 1**Soil physical parameters for clay and sandy loam soils used in Experiment I (CL<sub>1</sub> and SL<sub>1</sub>) and in Experiment II (CL<sub>2</sub> and SL<sub>2</sub>).

|  | Experiment I           |                        | Experiment II          |                        |
|--|------------------------|------------------------|------------------------|------------------------|
|  | CL <sub>1</sub>        | SL <sub>1</sub>        | CL <sub>2</sub>        | SL <sub>2</sub>        |
| Particle size distribution                                   |                        |                        |                        |                        |
| Sand (kg kg <sup>-1</sup> )                                  | 0.25                   | 0.76                   | 0.39                   | 0.80                   |
| Silt (kg kg <sup>-1</sup> )                                  | 0.12                   | 0.04                   | 0.08                   | 0.06                   |
| Clay (kg kg <sup>-1</sup> )                                  | 0.63                   | 0.20                   | 0.53                   | 0.14                   |
| Brooks and Corey (1964) water retention parameters (Eq. (5)) |                        |                        |                        |                        |
| $\theta_r$ (m <sup>3</sup> m <sup>-3</sup> )                 | 0.186                  | 0.061                  | 0.173                  | 0.128                  |
| $\theta_s$ (m <sup>3</sup> m <sup>-3</sup> )                 | 0.546                  | 0.443                  | 0.536                  | 0.424                  |
| $h_b$ (m)  | -0.244                 | -0.174                 | -0.258                 | -0.167                 |
| $\lambda$  | 0.394                  | 0.392                  | 0.459                  | 0.493                  |
| K-h relation (Eq. (9))                                       |                        |                        |                        |                        |
| $K_s$ (m d <sup>-1</sup> )                                   | $2.396 \times 10^{-3}$ | $64.54 \times 10^{-3}$ | $60.34 \times 10^{-3}$ | $5.803 \times 10^{-3}$ |
| $h_k$ (m)  | -0.748                 | -0.421                 | -1.00                  | -0.902                 |
| $b$  | 3.051                  | 3.000                  | 4.369                  | 2.680                  |
| Exponent R (Eq. (11)) and S (Eq. (14))                       |                        |                        |                        |                        |
| R  | 5.206                  | 5.102                  | 7.340                  | 3.408                  |
| S  | -2.538                 | -2.551                 | -2.179                 | -2.028                 |

top of that, a few millimeters of coarse sand. The pots were randomly distributed, maintaining a distance of 0.35 m between pots, changing places every day in order to minimize any tendency due to different solar radiation intensity and ventilation. The plants were fertilized according to local recommendation and cultivated without water stress until the phenological stage R6 (flowering), when 50% of plants show at least one open flower, at approximately 50 days after emergence. Until this moment, irrigation was performed by the end of every day. Pots were weighed and water was replenished to the previously established water content corresponding to the pot capacity. Pot capacity had been determined previously for each soil as the average water content remaining after 24 h in a non-evaporating pot with respective soil, initially saturated with water and allowed to drain freely. From the phenological stage R6 on, water supply to three (Experiment I) or six (Experiment II) pots per soil type was interrupted (stressed pots), while the other pots continued being watered (non-stressed pots) as before.

Water content  $\theta$  (m<sup>3</sup> m<sup>-3</sup>) per pot was determined daily by weighing to calculate transpiration rates ( $T_a$ , mm d<sup>-1</sup>). Pressure head  $h$  was calculated from  $\theta$  by Eq. (5). The mean daily transpiration rate observed in the non-stressed pots, per soil type, was supposed to be the potential transpiration  $T_p$ . Comparing  $T_p$  to the actual transpiration  $T_a$  from the stressed pots allowed calculation of relative transpiration  $T_R = T_a/T_p$ . Observations continued until complete wilting of the plants, which occurred 12 (Experiment I) and 18 (Experiment II) days after the onset of irrigation cessation.

The following expression for  $M$  can be derived by substitution of Eq. (9) into Eq. (1) and solving the integral:

$$M = \frac{K_s |h_k|^b}{b-1} [|h|^{1-b} - |h_w|^{1-b}]; \quad |h| \geq |h_k| \quad (10a)$$

$$M = \frac{K_s |h_k|^b}{b-1} [|h_k|^{1-b} - |h_w|^{1-b}] + [|h_k| - |h|] K_s; \quad |h| < |h_k| \quad (10b)$$

While Metselaar and De Jong van Lier (2007) used Eq. (7) to derive Eq. (8), the combination of Eqs. (4), (5) and (10), for  $|h| \geq |h_k|$ , yields:

$$T_R = \frac{\Theta^R - \Theta_w^R}{\Theta_l^R - \Theta_w^R} \quad (11)$$

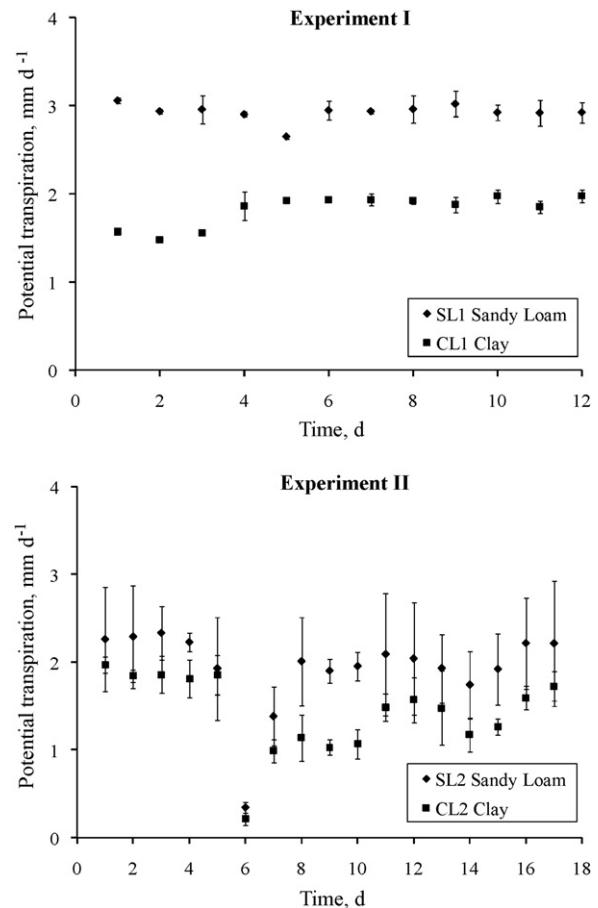
with  $R = (b-1)/\lambda$ .

Values for  $\Theta_l$  and  $\Theta_w$  for each soil were estimated by fitting Eq. (11) to the experimental data pairs ( $\Theta, T_R$ ) with  $R$  known from water retention and hydraulic conductivity analysis (Table 1). Subsequently, the pressure head and matric flux potential at the onset

of limiting hydraulic conditions,  $h_l$  (m) and  $M_l$  (m<sup>2</sup> d<sup>-1</sup>), respectively, were calculated from  $\Theta_l$  by Eqs. (5) and (10).

Alternatives to Eq. (11) are the linear model (Doorenbos and Kassam, 1986):

$$T_R = \frac{\Theta - \Theta_w}{\Theta_l - \Theta_w} \quad (12)$$



**Fig. 1.** Mean values of transpiration as a function of time for the three non-stressed plants in sandy loam and clay soils for Experiments I and II. Error bars indicate one standard deviation.

as well as the model that supposes linearity relative to  $h$  (Feddes et al., 1988):

$$T_R = \frac{h - h_w}{h_l - h_w} \quad (13)$$

By substitution of Eq. (5), the model from Eq. (13) can also be written as:

$$T_R = \frac{\Theta^S - \Theta_w^S}{\Theta_l^S - \Theta_w^S} \quad (14)$$

with  $S = -1/\lambda$ .

Eqs. (11), (12) and (14) are different in their exponents only: exponent  $R$  (Eq. (11)) is positive ( $b > 1$  and  $\lambda > 0$ ), yielding a concave reduction function; in Eq. (12) the exponent implicitly equals 1 for the linear reduction function; exponent  $S$  (Eq. (14)) is negative ( $\lambda > 0$ ) making corresponding reduction functions to be convex. The performance of these three equations was evaluated by comparing predicted values of relative transpiration ( $\hat{T}_R$ ) to the observed ones by means of the Root Mean Square Error (RMSE), the Mean Absolute Error (MAE) and the index of agreement  $d$  (Willmott, 1981), defined as:

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^n (T_{R,i} - \hat{T}_{R,i})^2}{n}} \quad (15)$$

$$\text{MAE} = \frac{\sum_{i=1}^n |T_{R,i} - \hat{T}_{R,i}|}{n} \quad (16)$$

$$d = 1 - \frac{\sum_{i=1}^n (T_{R,i} - \hat{T}_{R,i})^2}{\sum_{i=1}^n (|T_{R,i} - \bar{T}_R| + |\hat{T}_{R,i} - \bar{T}_R|)^2} \quad (17)$$

where  $\bar{T}_R$  is the arithmetic mean of the observed values of relative transpiration and  $n$  is the number of observations. The index of agreement  $d$  is considered to represent an improvement over the coefficient of determination but is sensitive to outliers owing to the squared differences (Legates and McCabe, 1999).

At the end of the experiment, plant leaf area was determined in all plants using a LI-COR® area meter model LI-3100. Roots were separated from the soil by dispersion of soil aggregates and mechanical separation of roots from the soil slurry through a sieve. Root length and root surface area were determined using image analysis software.

**Table 2**

Leaf area, root density (means and standard deviation) and observed potential transpiration (unstressed plants) in both experiments and soils.

|                 | Leaf area $\text{cm}^2$ | Root density $\text{cm cm}^{-3}$ | Observed potential transpiration (unstressed) $\text{mm d}^{-1}$ |
|-----------------|-------------------------|----------------------------------|--|
| Experiment I    |                         |                                  |  |
| Unstressed      |                         |                                  |  |
| CL <sub>1</sub> | 390 ± 64                | 1.310 ± 0.163                    | 2.21 ± 0.05  |
| SL <sub>1</sub> | 425 ± 6                 | 1.623 ± 0.033                    | 3.36 ± 0.33  |
| Stressed        |                         |                                  |  |
| CL <sub>1</sub> | 652 ± 45                | 1.255 ± 0.199                    |  |
| SL <sub>1</sub> | 789 ± 44                | 1.194 ± 0.101                    |  |
| Experiment II   |                         |                                  |  |
| Unstressed      |                         |                                  |  |
| CL <sub>2</sub> | 212 ± 70                | 1.411 ± 0.235                    | 1.68 ± 0.09  |
| SL <sub>2</sub> | 122 ± 82                | 1.265 ± 0.220                    | 2.44 ± 0.31  |
| Stressed        |                         |                                  |  |
| CL <sub>2</sub> | 475 ± 189               | 0.838 ± 0.404                    |  |
| SL <sub>2</sub> | 161 ± 15                | 0.976 ± 0.087                    |  |

### 3. Results and discussion

#### 3.1. Potential transpiration

Mean potential transpiration rates and standard deviations as observed in the non-stressed plants as a function of time are shown in Fig. 1 for both experiments. Standard deviations and temporal variability were smaller in Experiment I than in Experiment II. Meteorological conditions were less stable during the second experimental period, including a rainy day (day 6) with very high relative humidity.

During Experiment I, potential transpiration from the plants in the sandy loam soil was significantly higher than from the clay soil. This higher potential transpiration may be related to differences in root length density and leaf area index (Table 2). Data in this table show stressed plants to have a higher leaf area than unstressed plants at the end of the experiment, which seems contradictory. This is more evident in Experiment I (2 × 3 pots per soil). For the data of Experiment II (2 × 6 pots per soil), values differ by no more than one standard deviation and differences can be supposed not to be significant. It should be remembered that all plants were treated the same way during the initial growth stages, a period of about

**Table 3**

Values of soil hydraulic parameters at the onset of limiting hydraulic conditions and at the wilting point determined in both soils of each experiment: water content ( $\theta_l$ ), pressure head ( $h_l$ ), and matric flux potential ( $M_l$ ).

| Onset of limiting hydraulic conditions |   |           |                                      |   |
|--|---|-----------|--------------------------------------|---|
|  | $\theta_l$ ( $\text{m}^3 \text{m}^{-3}$ ) | $h_l$ (m) | $M_l$ ( $\text{m}^2 \text{d}^{-1}$ ) | $M_l$ ( $\text{m}^2 \text{d}^{-1}$ ) model estimate (Eq. (2)) |
| Experiment I                           |   |           |                                      |   |
| CL <sub>1</sub>                        | 0.251                                     | -19.0     | $0.97 \times 10^{-6}$                | $1.89 \times 10^{-7}$   |
| SL <sub>1</sub>                        | 0.125                                     | -16.3     | $8.52 \times 10^{-6}$                | $3.04 \times 10^{-7}$   |
| Experiment II                          |   |           |                                      |   |
| CL <sub>2</sub>                        | 0.232                                     | -13.6     | $2.62 \times 10^{-6}$                | $2.73 \times 10^{-6}$   |
| SL <sub>2</sub>                        | 0.172                                     | -8.0      | $68.8 \times 10^{-6}$                | $2.99 \times 10^{-6}$   |
| Wilting point                          |   |           |                                      |   |
|  | $\theta_w$ ( $\text{m}^3 \text{m}^{-3}$ ) | $h_w$ (m) | $M_w$ ( $\text{m}^2 \text{d}^{-1}$ ) |   |
| Experiment I                           |   |           |                                      |   |
| CL <sub>1</sub>                        | 0.231                                     | -45.9     | 0 <sup>a</sup>                       |   |
| SL <sub>1</sub>                        | 0.099                                     | -64.6     | 0 <sup>a</sup>                       |   |
| Experiment II                          |   |           |                                      |   |
| CL <sub>2</sub>                        | 0.209                                     | -40.8     | 0 <sup>a</sup>                       |   |
| SL <sub>2</sub>                        | 0.152                                     | -26.4     | 0 <sup>a</sup>                       |   |

<sup>a</sup> By definition.

50 days. The large standard deviations obtained for Experiment II, especially among the six stressed  $CL_2$  plants, indicate that large differences between pots may occur. These large differences may then, possibly, explain the values of Experiment I: the high variability among pots made  $2 \times 3$  pots per experiment too few, increasing the risk of significant differences, as observed in Experiment I.

Despite the observation of large differences in leaf area, transpiration rates were expressed and treated per surface area, not per leaf area. Plant potential transpiration is directly related to absorbed energy (radiation) rather than to leaf area. Absorbed radiation increases with increasing leaf area in a nonlinear way: the higher the leaf area, the lower the increment in absorptivity per increment of leaf area, and a correction for differences in leaf area would have been speculative. Therefore, we considered transpiration rates observed in the irrigated pots as being the potential rates, irrespective of leaf area.

### 3.2. Limiting hydraulic conditions and wilting point

Experimentally estimated values of water content, pressure head and matric flux potential at the onset of limiting hydraulic conditions and at the wilting point are shown in Table 3. The onset of limiting hydraulic conditions corresponds to pressure heads in the order of magnitude of  $-10$  m.

Determination of water content by weighing resulted in average values for water content, disregarding heterogeneities within the pot. Other techniques (tensiometer, TDR) could have been used to obtain values at several depths, but all of these are subject to calibration errors and would probably not be able to detect the small daily variations with sufficient accuracy. Besides of this, distinct information on conditions per layer in the pots would not contribute to the test of the proposed model. Hysteresis in water retention curves, sometimes a concern when transforming observed water contents to pressure heads, is not expected to have been important under these experimental conditions, as drying was the main process during the period of observation of the plants. Some hysteresis may have occurred in day–night cycles close to variably extracting (day) and non-extracting (night) roots.

Except for the  $CL_2$  soil, the matric flux potential at the onset of limiting hydraulic conditions estimated by Eq. (2) was an order of magnitude smaller than the experimental value. In other words, according to the model limiting hydraulic conditions are reached at a lower value of  $M$ , consequently at a lower water content than verified experimentally. This is probably due to the fact that the model used to parameterize Eq. (2) supposes a perfectly distributed root system composed of roots that all have the same radius, no internal resistance to water flow and with an ideal soil–root contact. In real root systems, heterogeneity is enhanced by the tendency of roots to follow pre-existing channels like biopores or cracks in the soil (Tardieu and Manichon, 1986; Wang et al., 1986). Another factor not considered by the model of De Jong van Lier et al. (2006) is the reduction in root–soil contact area, especially under conditions of water shortage due to radial root shrinkage which may lead to the formation of air gaps between root and soil (Faiz and Weatherley, 1982; Nobel and Cui, 1992; Carminati et al., 2009). Therefore, limiting conditions may appear under wetter conditions than those predicted by the model and an empirical correction factor is needed to apply Eq. (2) to a root system with a heterogeneous geometry.

The experimentally determined wilting point corresponded to pressure heads ranging from  $-26$  to  $-64$  m, less negative than the commonly used value of  $-150$  m.

Concerning the reduction curves, the statistical performance of fits to observed values evaluated by indexes RMSE (Eq. (15)), MAE (Eq. (16)) and  $d$  (Eq. (17)) assuming linear reduction of  $T_R$  with  $M$  (Eq. (11)), with  $\theta$  (Eq. (12)) and with  $h$  (Eq. (14)), decreases in this order for both experiments and both soils (Figs. 2 and 3). Besides

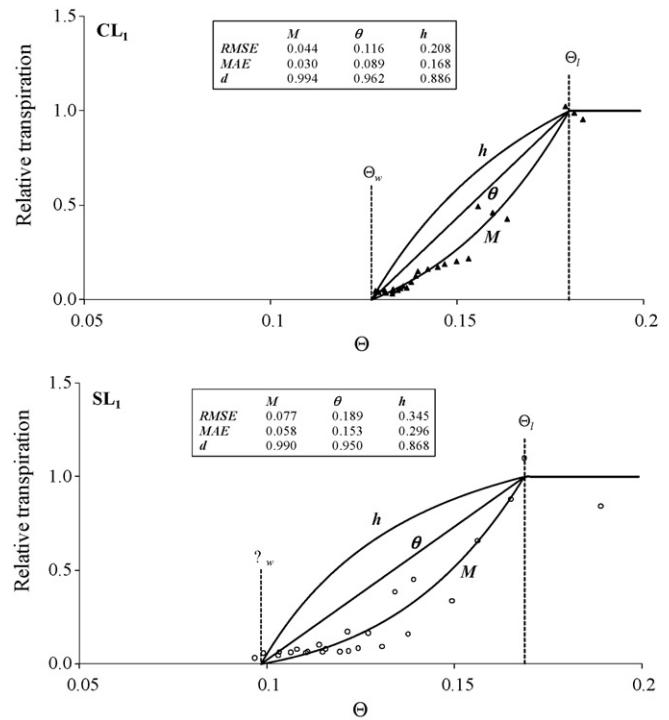


Fig. 2. Relative transpiration as a function of effective saturation ( $\Theta$ ), observed during Experiment I in both soils and predicted assuming linear reduction with  $M$  (Eq. (11)), with  $\theta$  (Eq. (12)) and with  $h$  (Eq. (14)), and respective statistical indexes RMSE (Eq. (15)), MAE (Eq. (16)) and  $d$  (Eq. (17)).

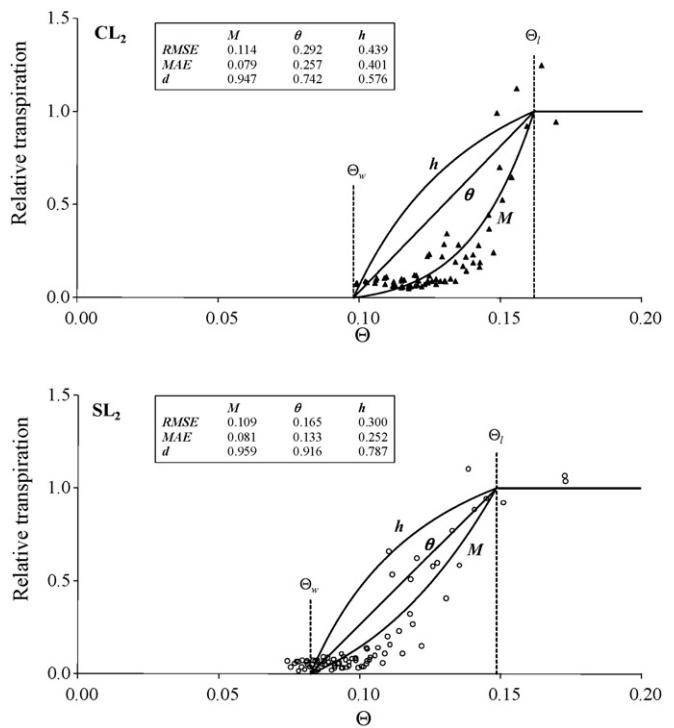
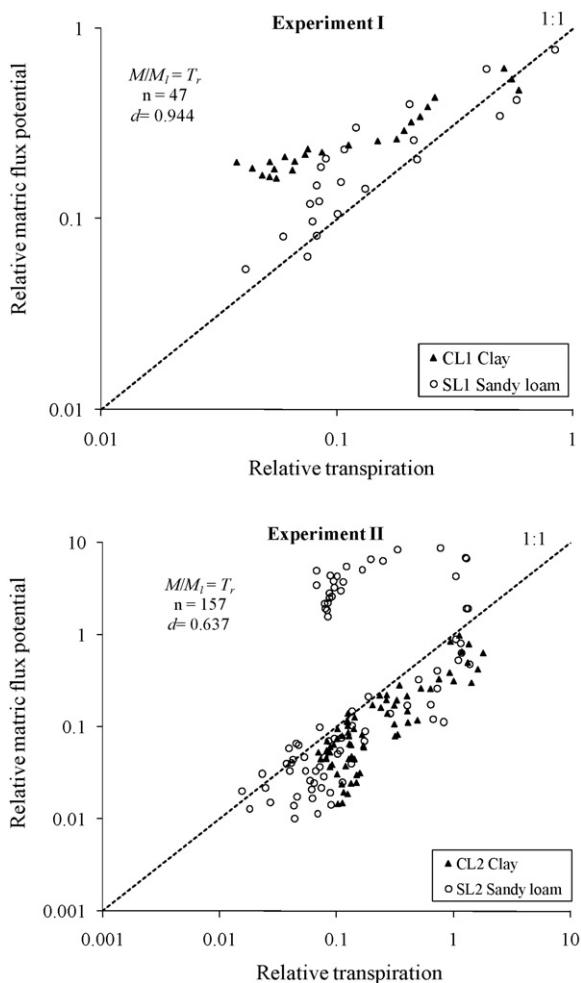


Fig. 3. Relative transpiration as a function of effective saturation ( $\Theta$ ), observed during Experiment II in both soils and predicted assuming linear reduction with  $M$  (Eq. (11)), with  $\theta$  (Eq. (12)) and with  $h$  (Eq. (14)), and respective statistical indexes RMSE (Eq. (15)), MAE (Eq. (16)) and  $d$  (Eq. (17)).



**Fig. 4.** Relative matric flux potential as a function of relative transpiration for both soils from Experiments I and II. Data from the falling rate phase of all stressed plants (3 per soil in Experiment I; 6 per soil in Experiment II).

the statistical parameters, a visual comparison between observed values and the three proposed shapes of the reduction function shows a concave behavior, in agreement with a positive exponent as in Eq. (11).

### 3.3. Relative transpiration versus matric flux potential

Plotting measured relative matric flux potential ( $M/M_i$ ) during the falling rate phase versus relative transpiration (Fig. 4) shows for both experiments that the experimentally obtained data in both soils are in good agreement with Eq. (4). For Experiment I, 47 values were available and comparison with the 1:1 line gives an index of agreement  $d = 0.944$ ; Experiment II yielded 157 values and  $d = 0.637$ . Performing a linear regression  $T_r = A + B \cdot M/M_i$ , the 95% prediction interval of coefficient  $B$  included the value 1 in both experiments; the prediction interval of  $A$  did not include 0, being slightly higher ( $0.06 < A < 0.17$  in Experiment I;  $0.08 < A < 0.16$  in Experiment II).

## 4. Conclusions

(1) At the onset of the falling rate phase, the value of matric flux potential  $M_i$  showed to differ in order of magnitude from the value predicted by an upscaled single-root approach (De Jong van Lier et al., 2006) in three out of four soils.

- (2) The difference between predicted and observed values of  $M_i$  can be explained, among other factors, by the heterogeneity of the root distribution which is not considered by the model. An empirical factor to deal with this heterogeneity should be included in the model to improve predictions. This may be an object of future research.
- (3) Comparing the predictions of relative transpiration in the falling rate phase using a linear shape with  $\theta$ ,  $h$  or  $M$  (the latter proposed by Metselaar and De Jong van Lier, 2007), the matric flux potential ( $M$ ) based reduction function showed the best performance, while the  $h$ -based equation resulted in the highest deviations between observed and predicted values of relative transpiration rates.

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