Water uptake by plants under nonuniform soil moisture conditions: A comprehensive numerical and experimental analysis

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1. Introduction

Water uptake by plants constitutes a major component of the eco-hydrological cycle. It is a vital factor affecting various hydrological and environmental processes such as solute transport and groundwater recharge (Yadav et al., 2009a). Root water uptake (RWU) is also a decisive factor in irrigation planning and management and a major component of various ecosystem models. Therefore, the adequate representation of RWU in these models is essential. RWU is a dynamic process associated with various exogenous and endogenous factors, including soil water status, soil hydraulic properties, plant physiology, and meteorological conditions (Albasha et al., 2015; Thomas et al., 2020). Under non-limiting soil water conditions, plants transpire at the potential demand, and RWU is usually proportional to the root mass distribution and root system properties (Feddes et al., 1978). However, this linear relationship between the root distribution and soil water extraction cannot always be maintained as the soil water content can be heterogeneously distributed in the vadose zone. In such cases, plants rely on strategies to minimize the impact of water stress, with RWU shifting from a plant-atmosphere demand-driven process to a soil water availability-dependent process (Carminati and Vetterlein, 2013). In addition, plants can initiate adaptive water uptake processes such as compensated root water uptake and root-mediated hydraulic redistribution to maintain transpiration at the potential demand (Dawson, 1993; Amenu and Kumar, 2008; Albasha et al., 2015; Dara et al., 2015).

Compensated root water uptake (hereafter CRWU) represents the ability of plants to preferentially extract water from the moist zone to offset a reduction of RWU from the water-stressed zone (Yadav et al., 2009a; Simůnek and Hopmans, 2009; Verma et al., 2014). Thereby, CRWU allows plants to transpire at or closer to the potential transpiration demand, even though some parts of the root system may experience water stress (Thomas et al., 2020). On the other hand, hydraulic...
redistribution (HR) refers to the passive transfer of soil water (following the pressure head gradient) through the root system from a relatively wetter soil zone to drier soil layers under reduced transpiration demand or after rainfall/irrigation (Kitajima et al., 2013; Oliveira et al., 2005; Prieto et al., 2010a,b). HR significantly modulates transpiration, enhances nutrient uptake, and also prevents xylem embolism (Caldwell et al., 1998; Domec et al., 2006; Neumann and Cardon, 2012; Prieto et al., 2012, 2014; Prieto and Ryel, 2014; Thomas et al., 2020). CRWU and HR thus delay the onset of transpiration reduction and allow the plant to survive during prolonged dry periods (Smithwick et al., 2008). In addition, plants develop a highly conducting root system (deep roots) that facilitates CRWU and HR under dry conditions (Da Rocha et al., 2004; Yan and Dickinson, 2014; Baker et al., 2008). Therefore, on an ecosystem scale, the presence of deep roots and these adaptive RWU processes strongly influence various eco-hydrological processes, such as the increased global evapotranspiration rate (Lee et al., 2005; Wang and Dickinson, 2012), declining groundwater tables (Fan and Miguez-Macho, 2010), elevating carbon sequestration (Baker et al., 2008; Scott et al., 2008; Domec et al., 2010, 2012), and reduced rainfall runoff and altered energy partitioning (Zheng and Wang, 2008; Baker et al., 2008). Consequently, the combined effects of CRWU and HR play a crucial role in optimal resource utilization. Hence, it is vital to consider the coexistence and combined impacts of CRWU and HR in various eco-hydrological applications (Simunek and Hopmans, 2009; Yadav et al., 2009a).

Over the last few decades, several modeling studies have been performed to improve our understanding of water acquisition by plants from drying soil (e.g., Feddes et al., 1978; Ojha and Rai, 1996; Li et al., 1999; Jackson et al., 2000; Lai and Katul, 2000; Heinen, 2001; Vrugt et al., 2001; Arnold et al., 2012; Simunek et al., 2013, 2016). Most of the vadose zone models, including the HYDRUS models, use the Richards equation to describe the soil water dynamics, while RWU is accounted for by adding a source/sink term to it (Richards, 1931; Simunek et al., 2013, 2016, 2022; Simunek and Hopmans, 2009). Over the years, various models have been developed for estimating RWU, considering different assumptions, theoretical bases, and dimensionality. Based on the hydrological perspective, these models can be classified as macroscopic or microscopic (Simunek and Hopmans, 2009; Yadav et al., 2009b; Peters et al., 2017). In empirical macroscopic approaches, RWU is represented as a function of potential transpiration, root density, and soil water contents or soil matric pressure heads (van Dam, 2000; Feddes et al., 2001; Homaeae et al., 2002; Skaggs et al., 2006). Few of these models are capable of simulating CRWU and HR, even though these processes may sometimes be considered separately (Ryel et al., 2002; Simunek and Hopmans, 2009; Yadav et al., 2009a), and their integrated role on RWU is largely ignored. The conventional way of expressing empirical CRWU is to use in the definition of RWU an empirical stress function term that ranges from zero to one (e.g., Lai and Katul, 2000; Jarvis, 1989; Li et al., 2001; Yadav et al., 2009a). On the other hand, empirical representations of HR usually consider an approach of interconnected rhizosphere layers, which allow the soil water to flow between the soil layers based on the average root hydraulic conductivity and water potential gradients (e.g., Ryel et al., 2002; Kitajima et al., 2013). However, the concept and parameters used in these RWU models are empirical and, therefore, they cannot be linked to root system properties.

In contrast, microscopic models consider the root system architecture that explicitly reflects their hydraulic properties to simulate root water uptake (de Jong van Lier et al., 2006; Vereeken et al., 2016; Koch et al., 2018; Schnepf et al., 2023). Models such as RootTyp (Pagen et al., 2004), RootBox (Leitner et al., 2010), R-SWMS (Javaux et al., 2008), and SPACSYS (Bingham and Wu, 2011) represent a few examples of these models, which significantly improved our understanding of soil-root interactions and plants responses in heterogeneous environments. While these models can account for the concepts of CRWU and HR, estimating the root hydraulic parameters in real-time under field conditions remains challenging (Lobet and Draye, 2013; Cai et al., 2018a). Moreover, these models require extensive parameterization and complex geometrical and functional operations and demand substantial computational resources (Dunbar et al., 2013).

Some of these microscopic models have been upscaled to simplified mechanistic macroscopic models, which require reduced data input and computational time (e.g., Amenu and Kumar, 2008; de Jong van Lier et al., 2008, 2013; Couvreur et al., 2012, 2014; Vanderborght et al., 2021, 2023). The description of flow through the root systems in the RWU models of Amenu and Kumar (2008) and de Jong van Lier et al., (2008, 2013) is simplified, and a leafy or factor or resistance represents root hydraulic properties. In contrast to these models, the models of Couvreur et al. (2012, 2014) and, more recently, Vanderborght et al. (2021) focused on the root hydraulic properties and derived upscaled or simplified approaches to represent root hydraulic. Finally, Vanderborght et al. (2023) presented an approach that combined the soil and root hydraulic approaches. The semi-empirical models, in empirical forms with added physical parameters, have also gained increased attention (e.g., Jarvis, 2011; Santos et al., 2017). These models are derived from the existing mechanistic models and are simplified to the classical empirical approach while retaining the dynamic functionality of the RWU process.

The availability of various RWU models that can simulate CRWU and HR with different complexities and parameter requirements is potentially confusing when selecting the appropriate model for a given problem. Moreover, the lack of understanding of various models adds uncertainty to interpreting predicted RWU processes, especially when simulated under distinct climates or simulation conditions. Therefore, this study aims to investigate the possibility of simultaneous estimation of CRWU and HR by different types of empirical, semi-empirical, and process-based RWU models and to discuss their advantages and drawbacks. This study also aims to understand how the modeling of soil water dynamics in HYDRUS-1D can be improved while considering CRWU and HR in the RWU term.

To achieve these aims, we revisited the process-based RWU model proposed by de Jong van Lier et al. (2008, 2013), Couvreur et al. (2012), and Nimah and Hanks (1973), and compared their results with the results of two other (standard HYDRUS) RWU models suggested by Feddes et al. (1978) and Jarvis (1989) (hereafter called DJ, CR, NH, DF, and JF, respectively). We compared these models in terms of their ability to predict drought survival, assess the contributions of CRWU and HR towards the transpiration demand, and estimate soil water distributions and RWU dynamics in maize (Zea mays L.). This is achieved by integrating the DJ, CR, and NH models into the HYDRUS-1D platform as a submodule. To validate the performance of these models, we conducted a column lysimeter experiment and compared the soil water dynamics under dry-down conditions with the simulation result. Additionally, we compared the RWU estimates for various scenarios with and without considering CRWU and HR to understand the importance of considering these processes while modeling agricultural, environmental, and eco-hydrological processes.

2. Material and methods
2.1. Model description

The HYDRUS-1D platform, a widely used software package for simulating soil water movement in the vadose zone (Simunek et al., 2013, 2016), is used in this study to conduct a comparative analysis of various RWU models. The standard version of the HYDRUS-1D code numerically solves the Richards equation to simulate the soil water dynamics. The Richards equation includes a macroscopic sink term, which accounts for RWU and lumps all RWU processes into a single term of the governing mass balance equation. An empirical, macroscopic formulations of Feddes (the FD model; Feddes et al., 1978) and Jarvis (the JF model; Jarvis, 1989) are used in HYDRUS-1D to represent RWU.
The empirical Feddes (FD) model (see the mathematical description below) distributes potential transpiration across the root zone based on the roots’ spatial distribution and then reduces it locally due to various environmental (e.g., saturation or salinity) stresses. This reduction is represented using empirical stress response functions. The standard Feddes model does not account for CRWU or HR. Jarvis (1989) modified the FD model by introducing a critical value of the water stress index, a so-called root adaptability factor, representing a threshold value above which root water uptake reduced in stressed parts of the root zone is fully compensated by increased uptake from other parts. Thus, the JF model can account for CRWU but cannot account for HR.

While simple and potentially efficient, these models are often subject to criticism (Couvreur et al., 2012). First, most of the macroscopic parameters require calibration since they cannot be directly measured. Second, these models neglect the effect of root hydraulic properties and architecture (Draye et al., 2010). Third, RWU stops when parameters require calibration since they cannot be directly measured. HYDRUS-1D is written in a modular form so that it allows for replacing empirical descriptions of the sink term with different processed-based descriptions of RWU, enabling us to incorporate the previously reported RWU models of de Jong van Lier et al. (2013), Couvreur et al. (2012), and Nimah and Hanks (1973). Since all three models are processed-based, they can help us overcome some of the disadvantages of the RWU models currently available in HYDRUS-1D and potentially account for both CRWU and HR.

De Jong van Lier et al. (2008, 2013) (the DJ model) derived a macroscopic RWU model from an approximate analytical solution of a detailed RWU model for the 1D radially symmetric Richards equation for water flow around a single root. The final formulation of the macroscopic RWU sink term is the product of the matrix flux potential gradient between the soil and roots and the root function, which accounts for spatial root distribution but does not account for root conductance and, thus, the root system hydraulic architecture, contrary to the model of Couvreur et al. (2012). However, similarly to the NH model driven by the pressure head gradients, the DJ model driven by the matrix flux potential gradients allows for HR and CRWU.

Couvreur et al. (2012, 2014) (the CR model) developed a macroscopic RWU model based on analytical water flow solutions in a simple root system hydraulic architecture and then validated it for more complex hydraulic architectures. In contrast to current RWU models, the CR model decouples water stress and compensatory RWU processes, making it more appropriate for HR simulations. The model is based on upscaling the Doussan model of water flow inside a 3D root system (Doussan et al., 1998a, 1998b) for a given root architecture and root hydraulic properties (i.e., root radial and axial conductances), from which it identifies macroscopic parameters (spatially distributed root parameters, and stress and compensatory RWU functions) controlling the macroscopic uptake process. The CR model thus accounts for water flow from the soil through the 3D root architecture into the atmosphere along potential gradients while considering individual resistances along the path. CRWU and HR naturally arise from this model description since water exchange between soil and roots occurs according to potential gradients, with water entering or leaving the roots according to the sign of the potential gradient.

Finally, Nimah and Hanks (1973) proposed a simple RWU model (the NH model) based on the concept of Gardner (1960), in which the root uptake term is computed as the product of the bulk soil hydraulic conductivity, the normalized root length density, and the difference between the effective water potential in the root at the soil surface ($H_0$) and the soil (Nimah and Hanks, 1973) (see the mathematical description of the NH model below). The value of $H_0$ is obtained by making RWU over the entire soil profile equal to potential transpiration provided the value of $H_0$ is higher than the wilting point ($h_w$). Since the integration of RWU is done over the soil profile regardless of its sign, the model allows for HR and CRWU.

In the following, we describe the five RWU models currently available in the HYDRUS-1D software, including the new numerical implementation of the three processes-based models (the DJ, CR, and NH models) into HYDRUS-1D. The readers are referred to the original literature for the detailed derivation of these models.

### 2.1.1. The DJ model

In the de Jong van Lier et al. (2013) model (or DJ), the soil water movement between soil and root is represented by the radial soil water flow equation considering plant roots as a series of cylinders of radius $r_0$ [L], distributed over the root zone, $T$ [L], as represented below (de Jong van Lier et al., 2006):

$$\frac{\partial H}{\partial r} = -\frac{q}{r} \frac{\partial q}{\partial r}$$

The analytical solution of Eq. (1) can be obtained by relating the soil water flux, $q$ [LT$^{-1}$], with the matric flux potential, $M$ [LT$^{-2}$], as follows:

$$q = -\frac{\partial M}{\partial r}$$

where the matric flux potential is an integral of the water potential, $h$, and hydraulic conductivity, $K(h)$, and can be represented as:

$$M = \int_{h_0}^{h} K(h) dh$$

When $K(h)$ is known, $M(h)$, can be determined either analytically or numerically depending on the complexity of the $K(h)$ function (de Jong van Lier et al., 2009). Thus, the sink term obtained by solving Eq. (1) as a function of $M$ for prevailing boundary conditions at the root-soil interface (de Jong van Lier et al., 2008) can be expressed as:

$$S = \frac{4(M_f - M_0)}{R_{so} - \sigma^2 R_{so}^2 + 2(R_{in}^2 + R_{in}^2)\ln \frac{R_{so}}{2R_{in}}} \rho(M_f - M_0)$$

with $\rho$ [L$^{-2}$] is defined by:

$$\rho = \frac{4}{R_{so}^2 - \sigma^2 R_{so}^2 + 2(R_{in}^2 + R_{in}^2)\ln \frac{R_{so}}{2R_{in}}}$$

where $R_{so}$ [L] is the half mean distance between roots or the rhizosphere radius, $a$ [L] is the distance from the root axis relative to half the mean distance between roots at which the mean (bulk) soil water content occurs ($R_{so}$), and $T_0$ [LT$^{-1}$] is the actual transpiration obtained by integrating the sink term over the root zone as follows:

$$T_0 = \int S(z)dz = \int \rho(M_f - M_0)dz$$

where $M_f$ is the soil matrix flux potential [LT$^{-2}$], $M_0$ is the matrix flux potential at the root-soil interface [LT$^{-2}$], and $\rho$ [L$^{-2}$] is defined in Eq. (5). $M_0$ is also a function of $h_0$ (the pressure head at the soil root interface), which is unknown. $h_0$ can be obtained by solving the continuity equation representing soil water movement within the xylem vessels, assuming a constant water content within the root tissues (de Jong van Lier et al., 2013), i.e.:

$$h_0 + \phi h_0 = h_1 + \frac{T_0}{L_i} + \phi M_0$$

where

$$\phi = \frac{\rho R_{in} \ln \frac{R_{in}}{2K_{root}}}$$

and $h_1$ is the leaf water potential [L], $L_i$ is the conductance over the root-to-leaf pathway [T$^{-1}$], and $K_{root}$ is the root conductivity [LT$^{-1}$] for radial
movement of water from an outer radius to a xylem radius, \( R_x \) [L]. Eq. (7) contains three unknown parameters: \( T_m \), \( h_m \), and \( h_0 \).

The steps to solve the equation are briefly described here (de Jong van Lier et al., 2008). First, calculate the maximum possible transpiration \((T_m)\) assuming \( M_0 = 0 \) in Eq. (6). If \( T_m < T_p \), the plant is under water stress, and actual transpiration equals the maximum possible transpiration \((T_m = T_p)\). Therefore, the sink term can be obtained by substituting \( M_0 = 0 \) in Eq. (7), i.e., \( S_x = \beta \left( M_x - 0 \right) \). If \( T_m > T_p \), the plant transpires at the potential demand and \( T_x = T_p \). In this case, to solve \( M_0 \), we assume a value for \( h_x \) and find \( h_0 \) and \( M_0 \) (a function of \( h_0 \)) using the bracketing (bisection) method, and calculate \( T_x \) using Eq. (6). If \( T_m \) is smaller (or larger) than \( T_p \), we decrease (or increase) the value of \( h_x \), and repeat this until \( T_x \) becomes equal to \( T_p \). The sink term can be estimated by substituting \( M_0 \) obtained from Eq. (6).

2.1.2. The CR model

Couvreur et al. (2012, 2014) divided RWU into two components: 1) water uptake under uniform soil conditions or the standard RWU term \((S_{std})\), and 2) compensatory root water uptake under nonuniform conditions \((S_{comp})\). \( S_{std} \) is a function of space and time and is defined as a product of the normalized root length density \( \beta \) [L⁻¹] and actual transpiration \((T_x)\):

\[ S_{std}(z) = \beta(z)T_x \tag{9} \]

and the compensated water uptake term, \( S_{comp} \), is expressed as:

\[ S_{comp}(z) = K_{comp}(z)\beta(z)(H(z) - H_q) \tag{10} \]

where \( H \) is the hydraulic head, \( H_q \) is the average or effective hydraulic head at the soil-root interface along the rooting depth [L] that can be expressed as:

\[ H_q = \int \beta(z)H(z)dz \tag{11} \]

Thus, the RWU term proposed by Couvreur et al. (2012) can be calculated as:

\[ S(z) = S_{std}(z) + S_{comp}(z) \tag{12} \]

\( T_p \) in Eq. (9) is calculated as a function of the collar water potential \((H_{collar})\) [L] and the root system conductance \((K_{collar})\) as represented below:

\[ T_x = K_{collar}(H_{collar} - H_q) \tag{13} \]

\[ H_{collar} = H_q - T_x/K_{collar} \tag{14} \]

The collar water potential, \( H_{collar} \), is calculated using Eq. (13), assuming the plant is transpiring at the potential rate \((T_p)\). This assumption is valid only if the estimated value of \( H_{collar} \) reaches (or exceeds) a critical leaf hydraulic head \( H_{crit} \), otherwise \( H_{collar} \neq H_{crit} \). For any location with \( H > H_{crit}, \) \( S_{comp} \) is positive and leads to CRWU. When \( h < h_{crit}, \) \( S_{comp} \) becomes negative and \( S \) smaller than \( S_{std} \). When \( S_{comp} \) is negative, and its absolute value is smaller than \( S_{std} \), then negative \( S \) represents HR. Thus, HR can be considered a special case of CRWU (Couvreur et al., 2012).

2.1.3. The NH model

Following the concept of Gardner (1960), Nimah and Hanks (1973) proposed RWU as a function of the soil water potential as follows:

\[ S(z) = -K(z)RDF(z)[H_0 - R_z - h(z)] = -K(z)\beta(z)[H_0 - R_z - h(z)] \tag{15} \]

where \( K(z) \) is the soil hydraulic conductivity [LT⁻¹], \( RDF(z) \) is the function proportional to the total active roots in depth \( z \) [L⁻¹], \( \Delta z \) is the distance between the plant roots at the point in the soil where \( h(z, t) \) is measured (arbitrarily assumed to be one by Nimah and Hanks, 1973), \( \beta \) [L⁻²] is the root distribution function (defined as a ratio of RDF(z) and \( \Delta z \)), \( R_z \) is the root resistance, which is equal to 1 + \( R_x \), and \( R_x \) is the flow coefficient in the root system assumed to be 0.05. Note that the \( \beta \) function [L⁻²] in the NH model has different units than \( \beta \) [L⁻¹] in the CR and FD models. \( H_0 \) is an effective water potential in the root at the soil surface where \( z \) is considered zero, and it can range anywhere between zero and the permanent wilting point \((h_{w_0})\). The value of \( H_0 \) is calculated assuming plant transpiration is at its potential rate, \( T_p \), and thus:

\[ H_0 = \max \left\{ \int \frac{K(z)\beta(z)[H(z) - R_z - h(z)]dz}{K(z)\beta(z)dz}, h_{w_0} \right\} \tag{16} \]

If \( H_0 \) is greater than \( h_{w_0} \), the above assumption is valid, and \( H_0 \) can be estimated from Eq. (16). Otherwise, the transpiration rate is below the potential value and \( H_0 \) is equal to \( h_{w_0} \). The final sink term can be calculated from Eq. (15) by substituting the value of \( H_0 \).

2.1.4. The FD model

In the Feddes et al. (1978) model (FD), potential root water uptake \((S_{p})\) is estimated as a function of potential transpiration \( T_p \) and the normalized root density distribution \( \beta \) [L⁻¹]. Actual root water uptake can then be obtained by multiplying \( S_p \) by a water stress response function, \( \alpha[\cdot] \), that accounts for water/salinity/oxygen stresses (e.g., Feddes et al., 1978; van Genuchten, 1987):

\[ S(z) = \alpha(z)S_p(z) = \alpha(z)\beta(z)T_p \tag{17} \]

The stress response function, \( \alpha[\cdot] \), was defined by Feddes et al. (1978) as a piece-wise linear function of the pressure head and the potential transpiration rate (see also Simunek and Hopmans, 2009; or the HYDRUS manual).

2.1.5. The JF model

To account for CRWU in the FD model, Jarvis (1989) integrated a stress index function, \( \omega[\cdot] \), into the sink term as follows:

\[ \omega = \frac{T_x}{T_p} \int \alpha(h(z), \beta(z))dz \tag{18} \]

\[ S(z) = S_p(z)\alpha(h(z), \beta(z)) \max(\omega, \omega_0) \]

where \( \omega_0 \) is the critical stress index, a threshold value of \( \omega \), above which full compensation for localized water stress occurs (Jarvis, 1989; Simunek and Hopmans, 2009). Note that \( \omega \) is defined using the actual non-compensated transpiration \( T_x \) rather than the final actual compensated transpiration, which is obtained by integrating the second equation in (18) over the entire rooting depth. This integrated approach is already incorporated into the HYDRUS model and has often been used to estimate CRWU.

2.2. Lysimeter experiment and model validation

We evaluated and validated the performance of the selected RWU models by analyzing data collected in a column lysimeter experiment (Thomas et al., 2020). The experimental setup followed the same protocol described by Thomas et al. (2020). The lysimeter had a diameter of 15.24 cm and a height of 55 cm and was planted with fully grown Zea mays (Fig. S1A). The soil water data were collected at four different locations of varying depths, 5 cm (S1), 15 cm (S2), 25 cm (S3), and 35 cm (S4), at 30-minute intervals (Fig. S1B). A control lysimeter experiment was conducted in parallel to estimate actual and potential transpiration at the predefined time intervals (Fig. S1C). Evaporation from the lysimeter was prevented to ensure that any change in soil water content was solely due to RWU. The experiment began with irrigating the lysimeter to its field capacity, followed by nine days of dry-down conditions to attain the wilting point. At the end of the experiment, the lysimeter was segmented into five parts, and roots from each section
were isolated and measured for root length using image analysis (Fig. S1D). The data was then converted into a root length per volume, or root density (RD) (Fig. S1E), as shown in Figure S1F. RWU and soil water dynamics in the column lysimeter were estimated using five different RWU models described in Supplementary Information 1.

2.3. Model performance

To assess the performance of these RWU models, a comparative analysis was conducted by comparing modeling results with the experimentally observed soil water contents (Brocca et al., 2010). Three evaluation metrics were used for this analysis: (i) correlation coefficient \( r \), (ii) index of agreement \( I \), and (iii) root mean square error (RMSE). These metrics were used to quantitatively measure the agreement between the results simulated by the RWU models and the observed soil water dynamics.

\[
r = \frac{\sum_{i=1}^{n} (\theta_{obs,i} - \bar{\theta}_{obs}) (\theta_{sim,i} - \bar{\theta}_{sim})}{\sqrt{\sum_{i=1}^{n} (\theta_{obs,i} - \bar{\theta}_{obs})^2} \sqrt{\sum_{i=1}^{n} (\theta_{sim,i} - \bar{\theta}_{sim})^2}}
\]

\[
I = 1 - \frac{\sum_{i=1}^{n} (\theta_{obs,i} - \theta_{sim,i})^2}{\sum_{i=1}^{n} (\theta_{obs,i} - \bar{\theta}_{obs})^2 + \sum_{i=1}^{n} (\theta_{sim,i} - \bar{\theta}_{sim})^2}
\]

\[
RMSE = \frac{\sum_{i=1}^{n} (\theta_{obs,i} - \theta_{sim,i})^2}{n}
\]

where \( \theta_{obs} \) is the simulated soil water content, \( \theta_{sim} \) is the observed soil water content, \( \bar{\theta}_{obs} \) and \( \bar{\theta}_{sim} \) are the mean absolute values of \( \theta_{obs} \) and \( \theta_{sim} \), respectively, and \( n \) is the number of data points.

2.4. RWU scenarios

Since the column lysimeter experiment limits the representation of extreme climatic conditions and diverse soil properties, we used various additional numerical simulation experiments to evaluate the coexistence of CRWU and HR. The RWU patterns and soil water dynamics were simulated using five RWU models (i.e., DJ, CR, NH, JF, and FD) for heterogeneous root zone parameters. The exponential root distribution by Gale and Grigal (1987) was used as the root density distribution function with a maximum root density of 1.2 cm/cm³. The rooting depth and simulation domain were 100 cm and 130 cm, respectively. The initial soil water potential was set at a constant value of –100 cm. A no-flux boundary condition was specified at the top, which means that evaporation from the soil surface was assumed to be zero.

Reference RWU under simulated soil water conditions was estimated using the FD model. Any increase in RWU above this rate is considered CRWU, while any negative RWU is considered HR. Transpiration due to CRWU (\( T_{comp} \)) is the sum of CRWU over the rooting depth at a particular time interval, and the hydraulically redistributed water (\( T_{diag} \)) is the total HR over the rooting depth during a time period. The degree of CRWU (\( T_{comp}/T_{diag} \)) is used to assess the contribution of CRWU in meeting the transpiration demand. A sensitivity analysis for different parameters involved in the DJ model was also performed.

The following simulation scenarios were considered to investigate the coexistence of CRWU and HR:

Case 1. A drying-out simulation, assuming no irrigation/rainfall throughout the simulation time, representing a summer drought. Three levels of the transpiration demand (\( T_d \)) of 0.75 cm/day, 1.0 cm/day, and 1.5 cm/day (low, medium, and high, respectively) evenly distributed throughout the day for 24, 18, and 12 days, respectively, were considered. This simulation also adopted three different levels of RLD: high (1.2 cm/cm³), medium (0.8 cm/cm³), and low (0.4 cm/cm³). Additionally, in the DJ model, different combinations of \( K_r \), \( R_h \), and \( K_{root} \) were considered to assess the influence of root properties on plant physiological activities (Supplementary Information 2). Different parameters used to simulate RWU using these models are listed in Table 1.

Case 2. This case should explore the possible co-occurrences of CRWU and HR. A constant transpiration demand of 1 cm/day for 18 days was considered, while all other parameters were kept the same as in Case 1. Additionally, a 1 cm/hour rainfall event for 6 h was considered on day 12.

Case 3. While HR is prominent during low transpiration demand periods, i.e., during nighttime, CRWU occurs under high transpiration demand conditions (Siminck and Hopmans, 2009; Prieto et al., 2012). To mimic such conditions, the transpiration demand was set to 1 cm/day for 18 days with a sinusoidal diurnal variation of 0.9 cm/day and a constant nighttime value (10% of daytime transpiration), assuming equal halves of the day-night distribution.

Case 4. Deep-rooted plants/shrubs in arid and semiarid regions mainly survive due to RWU from a deeper root zone in a capillary fringe (Han et al., 2015). Thus, this test was performed to investigate the response of RWU near a groundwater table during meteorological droughts. A no-flux boundary condition was specified at the soil surface, and a zero-pressure head boundary condition was considered at a depth of 130 cm to represent saturated conditions. As in Case 3, the daily transpiration demand followed a sinusoidal variation with a mean value of 1 cm/day.

3. Results

To investigate the possible coexistence of CRWU and HR and their contribution towards meeting the daily transpiration demand, we used four different RWU models (DJ, CR, NH, and JF) with a potential to simulate either CRWU or HR or both, while the FD model was chosen as a baseline. All models were first validated against the soil water content data obtained from the column lysimeter experiment. Soil water content distributions and RWU dynamics simulated by the five models for dry-
down conditions were then compared using four hypothetical scenarios described above.

In the column lysimeter experiment, it was observed that under the optimal soil water conditions, RWU was prominent in the high-density root regions, indicated by the largest drop in the soil water content in these regions (Fig. S1B). Meanwhile, RWU from other regions showed a steady but slow decrease in the soil water content over time. When the highest RLD zone dried up, the roots from the lower compartments were found to facilitate the RWU demand through CRWU (Figs. S1BC), as reported previously (Thomas et al., 2020). This is indicated by a significant reduction in the soil water content in the lower compartment towards the end of the experiment. On the other hand, an increase in the soil water content was not observed, indicating that there was no HR, which is consistent with the findings of Thomas et al. (2020).

The soil water dynamics in the column lysimeter were simulated using the DJ, CR, and JF models. The simulated results were compared with the measured values in Fig. 1. The comparative analysis showed a good correlation between the simulated and experimentally measured values at 5, 15, and 25 cm depths till day 6 (Fig. 1ABC). In contrast, the performance declined in larger soil depths (Fig. 1D). The average r values for observed and simulated soil water contents at four different depths were 0.969, 0.984, and 0.972 for DJ, CR, and JF, respectively, indicating that all RWU models performed considerably well. Similarly, the I values were found to be 0.957, 0.977, and 0.97, while the RMSE values (expressed in %) were 3.7218, 2.972, and 2.788 for the DJ, CR, and JF models, respectively. The detailed comparison of the selected models with the column lysimeter experiment data is summarised in Supplementary Information 1.

3.1. RWU under constant transpiration demand

The simulations performed for Case 1 suggest that accounting for CRWU in RWU models improves the prediction of $T_a$ (De Willigen et al., 2012; Cai et al., 2018b). In the DJ model, RWU was found to be proportional to $RDL$ during the early days of the simulation, with a correlation coefficient of 0.989 and 0.933 on days 1 and 2, respectively (Fig. 2A). Continued RWU from the topsoil resulted in water stress and a subsequent reduction in water uptake (Figs. S2BC). However, this was compensated by increased uptake from deeper layers with sufficient soil water contents (Fig. 2A, S2BC). Between days 2 and 6, $T_{comp}$ continued to increase (Fig. 2B), maintaining the transpiration rate close to its potential rate (Fig. S2A). For given conditions, plants transpired at the potential demand till day 6.5, followed by a rapid reduction in transpiration (Fig. 2B, S2A). On day 6, 75% of total transpiration occurred from the lower half of the root zone, indicating the important role of CRWU in maintaining the transpiration demand. The analysis of RWU using the DJ model for different root densities indicates that the degree of CRWU is positively correlated with $RDL$ and that an increase in $RDL$ delayed the onset of water stress by increasing $T_a$ through increased $T_{comp}$ (Supplementary Information 2). Similarly, an increase in $R_x$ and $R_0$ also improved $T_a$ and $T_{comp}$, indicating that the plants with deep, high density, and large radii roots have a higher potential to survive under water stress conditions due to CRWU (Cai et al., 2018). In contrast, $T_a$ and $T_{comp}$ are independent of $K_{root}$, while the emergence and degree of compensation are highly related to $K_{root}$ (Supplementary information 2).

In the CR model, RWU was directly proportional to the root density distribution during the initial days of simulation (days 0 to 3) (Fig. 2C). CRWU emerged when the plant experienced soil water stress and a
subsequent water uptake reduction occurred in the top soil layer (Fig. 2D, S2EF). As water stress along the rooting depth increased, an abrupt increase in actual transpiration ($T_a$) was observed on day 3 (Fig. 2D). In contrast to the other models, the NH model showed CRWU from day 0, even before the emergence of water stress, and remained high for an extended period (Fig. 2EF). This resulted in the overestimation of CRWU compared to the other models during the early days of simulation and a nearly uniform soil water distribution over the root zone (Figs. S2HI). Similar to the DJ and CR models, the RWU pattern in the JF model was proportional to soil water distribution over the root zone (Figs. S2HI). In response, root water uptake from the wetter top zone to the water-stressed lower zone (Fig. 4CDGH). In the DJ and CR models, 30.9% and 33.5% of the total water extracted from the wet soil layer was released back to the water-stressed zone through HR. Such reverse HR is reported in various studies (e.g., Cai et al., 2018a).

Although RWU from the top root zone increased due to CRWU after the rainfall in the NH and JF models (Fig. 4IM), no HR was detected in these models despite a high water potential gradient (Fig. 4KLOP).

3.3. Combined effects of CRWU and HR under sinusoidal transpiration demand

In the DJ model, $T_{comp}$ was negligible during the initial four simulation days, followed by a gradual increase until day 9, when it peaked, and a reduction after that (Fig. 5C). This model also predicted HR as indicated by negative values of RWU, triggered during the night by nonuniform soil water conditions and a low transpiration demand (Fig. 5A, D). It was observed that under reduced transpiration and water stress, the contribution of CRWU and HR during the daytime decreased significantly after day 10. However, nighttime transpiration was unaffected until day 18, although CRWU and HR were negligible (Fig. 5B).

Similarly, in the CR model, both CRWU and HR were significant when the soil was subjected to localized water stress beginning on day 5 (Fig. 5EGH). This was followed by a gradual increase in CRWU and HR, which peaked on day 11 and declined after that (Fig. 5C). However, CRWU and HR in the CR model were consistently high during the early days of water stress (days 9–12), unlike in the DJ model (Fig. 5G). Also, in the CR model, from day 11 onwards, more than 60% of nighttime RWU contributed to HR (Fig. 5G). As a consequence, higher HR simulated by the CR model compared to the DJ model, the CR model predicted longer drought survival of plants than the DJ model.

3.2. Profiling CRWU and HR after rainfall

In Case 2, the RWU profiles simulated by all models were similar to Case 1 until the occurrence of rainfall (Fig. 4AHI). After the rainfall event, the surface soil water content increased to near-optimum levels (Fig. S3). In response, root water uptake from the wetter top zone increased to compensate for the RWU reduction from the lower water-stressed zone through CRWU, except in the FD model (Fig. 4ADEHILMP). As a result, the transpiration demand was maintained for a few days after the rainfall (Fig. 4BFJN). Notably, in the DJ and CR models, RWU from the top layer increased 3-fold and 2.5-fold, respectively, after the rainfall (Fig. 4AE). The process of HR was also initiated in these models by redistributing the soil water from the wetter top zone to the water-stressed lower zone (Fig. 4CDGH). In the DJ and CR models, 30.9% and 33.5% of the total water extracted from the wet soil layer was released back to the water-stressed zone through HR. Such reverse HR is reported in various studies (e.g., Cai et al., 2018a). Although RWU from the top root zone increased due to CRWU after the rainfall in the NH and JF models (Fig. 4IM), no HR was detected in these models despite a high water potential gradient (Fig. 4KLOP).
In the CR model, the RWU pattern in Case 4 was comparable to Case 3 till day 12 (Fig. 6FG). Likewise, CRWU and HR were relatively low or negligible during the first six simulation days (Fig. 6FG). However, CRWU and HR became predominant when the topsoil experienced water stress. From day 12 to day 18, CRWU and HR contributed to \( T_a \) mainly from the lower root zone and groundwater (Fig. 6FG). Similarly, in the NH model, groundwater played a significant role in daily transpiration through CRWU (Fig. 6IKL). However, similar to Case 3, HR was not visible in the results of the NH model despite having groundwater as the bottom boundary condition (Fig. 6IKL). For the JF model, the contribution of CRWU to daily transpiration was relatively low compared to the DJ and NH models, while HR remained zero.

Comparing Cases 3 and 4 (with groundwater), total \( T_a \) in Case 4 with groundwater as a bottom boundary condition was 17.10, 16.34, 17.47 cm, and 11.69 cm in the CR, DJ, NH, and JF models, respectively, which is 38.9%, 13.7%, 54.5%, and 3.7% more than in Case 3 (Figs. S4AB). This increase in \( T_a \) was due to increased CRWU and HR facilitated by groundwater. Among these models, the DJ and NH models showed a notable increase in cumulative \( T_{comp} \), which was as high as 117% and 167%, respectively, helping to increase the transpiration rate in Case 4 compared to Case 3 (Fig. 5BJ, 6BJ). However, a significant difference in HR was not observed in the DJ model between these two cases. On the other hand, in the CR model, both CRWU and HR increased in the presence of the groundwater table (20.75% and 61.53%, respectively). Compared to the other three models (DJ, CR, and NH), the response of the JF model to the presence of the groundwater table was negligible. Since the JF and FD models do not simulate HR, its contribution to \( T_a \) was zero.

4. Discussion

The present study describes computational modifications and incorporation of previously proposed RWU models, namely DJ, CR, and NH, into the HYDRUS-1D model, in addition to the JF and FD models, to improve the estimation of RWU under varying soil water conditions. Since these five models differ in their input requirements and mathematical formulations, a comparative analysis was conducted to provide a comprehensive outlook. The DJ model was improved by incorporating an efficient iteration step before integrating it as a submodule into HYDRUS-1D. The performance of each RWU model was first evaluated, followed by their experimental validation using the soil water content profile obtained from a column lysimeter. All five models selected for this study have been previously used in the literature for estimating RWU (e.g., De Willigen et al., 2012; Cai et al., 2018a; Brunetti et al., 2019; Lei et al., 2019; Nguyen et al., 2020; De Melo and de Jong van Lier, 2021). The FD model was used as a "negative" control as it does not account for CRWU or HR. The JF model is an empirical model that considers only CRWU and ignores HR. In contrast, mechanistic models, including DJ, CR, and NH, can simulate CRWU and HR simultaneously. Despite this, these models have primarily been used for estimating CRWU while disregarding HR. However, HR can play a significant role in the RWU process and coexist with CRWU (Orellana et al., 2012; Gou et al., 2018). Therefore, this study addresses the simultaneous estimation of CRWU and HR under nonuniform soil water conditions.

The reliability and significance of each model were further studied by considering four hypothetical simulation scenarios that cover a broad spectrum of soil water nonuniformities, which plants may encounter in different geographical habitats. The differences in computational requirements among the CR, NH, JF, and FD models are minimal, as evaluating the sink term in the Richards equation represents only a small fraction of the overall required computational time for solving the Richards equation. In contrast, the DJ model requires significantly more computational time as the model requires two levels of iterations to solve the RWU term. This is further aggravated by the need to evaluate the matrix flux potential for each node, time step, and iteration. However, this step can be significantly speeded up by using the internal
Fig. 4. Root water uptake simulated using the DJ (A-D), CR (E-H), NH (I-L), and JF (M-P) models for a rainfall event on day 12 and the transpiration demand of 1.0 cm/day (Case 2). A, E, I, and M show RWU distributions over the root zone on different days. B, F, J, and N display the transpiration reduction function ($T_a/T_p$). The transpiration demand ($T_p$), actual transpiration ($T_a$), transpiration due to CRWU ($T_{Comp}$), and hydraulically redistributed water ($T_{HR}$) are presented in C, G, K, and O. The RWU profiles for the DJ, CR, NH, and JF models are presented in D, H, L, and P, respectively.

Fig. 5. Root water uptake simulated using the DJ (A-D), CR (E-H), NH (I-L), and JF (M-P) models for a sinusoidal transpiration demand of 1.0 cm/day (Case 3): A, E, I and M show RWU distributions over the root zone on different days. The soil line indicates RWU during mid-day, and solid dotted lines indicate nighttime transpiration. B, F, J, and N show the transpiration reduction function ($T_a/T_p$). The transpiration demand ($T_p$), actual transpiration ($T_a$), transpiration due to CRWU ($T_{Comp}$), and hydraulically redistributed water ($T_{HR}$) are presented in C, G, K, and O. The RWU profiles for the DJ, CR, NH, and JF models are presented in D, H, L, and P, respectively.
interpolation tables, similarly as done for other soil hydraulic properties.

Since the selected RWU models use different sink term formulations and root hydraulic parameters, they tend to generate different RWU dynamics and soil water distribution profiles. Despite its complex formulation and numerical implementation, the DJ model demonstrated more consistent predictions of CRWU and HR under low transpiration demand conditions. This model incorporates important root parameters such as \( RDL, \) \( R_x, \) \( \rho_0, \) and \( K_{root}, \) which play a crucial role in determining CRWU and HR for the accurate estimation of RWU (Bechmann et al., 2014). This contrasts the CR, and JF models, which generated comparable RWU profiles but with varying degrees of CRWU and HR. The differential behavior of RWU models also influenced the soil water content distributions in the root zone under water-stressed conditions. In the DJ and NH models, the soil water content profile did not approach the wilting point, \( \theta_w, \) having a value \( \approx 0.148. \) This contrasts the CR model, which predicted HR into the dry soil layers during the night. This hydraulically redistributed water was then absorbed during the following day, resulting in non-zero RWU from all layers, unlike in the JF model.

The RWU profile simulated by the NH model deviated from \( RDL \) under optimal conditions due to the early emergence of CRWU. Moreover, compared to the other models, the NH model has limitations in its applicability under optimal or near-saturated soil moisture conditions, as well as concerning HR. This is because the NH model estimates RWU based on the water potential gradient between the soil and the root-soil interface and the soil hydraulic conductivity, which is highly influenced by root zone soil conditions. For example, in loam soil, the soil hydraulic conductivity \( (K) \) can vary from 25 cm/day to 1.7e-09 cm/day between saturation and the wilting point, making the RWU profile highly sensitive to soil properties. This may lead to either over-representation or under-representation of water-stress-coping strategies based on the root zone environment. For instance, when the soil water content in the root zone approaches saturation, the RWU profile becomes unrealistic, with a high rate of HR, even with a slight variation in soil water contents. In contrast, in the region with a low water potential, the hydraulic conductivity is at its lowest, restricting the release of water into this region. This limits the applicability of the NH model for the HR simulation and the RWU estimation when the root zone is near saturation. However, under moderate soil moisture conditions, the NH model behaves similarly to the DJ model.

The comparison of transpiration fluxes simulated using the five models in four cases indicates the significance of CRWU and HR in maintaining transpiration. In all four cases, the cumulative actual transpiration simulated using the DJ, CR, NH, and JF models significantly increased compared to the FD model, indicating that ignoring CRWU and HR may cause a significant error in ecological and agricultural models simulating RWU (Deb et al., 2013). Interestingly, when comparing Case 3 and Case 1 with and without HR, significant
differences in cumulative $T_w$ were not observed. This suggests that the effect of HR is negligible under dry-down conditions (as simulated by the DJ and CR models). In contrast, the RWU pattern showed a significant difference in Case 4, which considers HR with a groundwater table. This indicates that the role of HR becomes more pronounced when an external water source, such as groundwater or rainfall/irrigation, is available in the root zone. This may also be prominent for plants with deep roots that can extract water from the deep vadose zone, as applies to CRWU to some extent. This synergy effect can be justified when comparing total transpiration in Cases 3 and 4. In Case 4, total transpiration increased by 13.7% in the CR model, and the plant transpired more, highlighting the importance of CRWU and HR. Thus, for sites without external water sources to the root zone in the form of irrigation/rainfall or groundwater, the CRWU can delay the onset of transpiration reduction (Thomas et al., 2020). However, a significant impact on $T_w$ cannot be expected in the long run, as substantiated by comparing Case 1 vs Case 2 and Case 3 vs Case 4. Likewise, CRWU and HR are predominant under heterogeneous soil water conditions, and therefore, under irrigated agriculture and humid conditions, CRWU and HR are likely less important (Albasha et al., 2015). Moreover, deep-rooted plants with higher axial hydraulic conductance favor CRWU and HR from deeper soil layers compared to plants with finer, shallower roots (Zwieniecki et al., 2002; Simunek and Hopmans, 2009). Thus, when modeling RWU and total transpiration of shallow-rooted agricultural crops such as maize, the impact of CRWU and HR can be neglected unless groundwater is shallow or the site is partially irrigated. Under such conditions, empirical RWU models like JF and FD may perform sufficiently well.

The current study provides a comparative analysis of five well-accepted RWU models and offers insights into their significance in field applications. This study also contributes to the selection of commonly used RWU models with respect to parameter availability, accuracy, and root zone properties.

5. Conclusions

We assessed the performance of five RWU models while considering the combined effect of CRWU and HR. We implemented three additional RWU models (DJ, CR, and NH) in the HYDRUS-1D model. Our findings revealed that the DJ and CR models provided the most realistic predictions of RWU under nonuniform soil water conditions, with the potential to capture both CRWU and HR. Despite differences in the formulation and parameterizations of the sink term in the CR and JF models, these models predicted similar distributions of RWU. However, the NH model was found inadequate to simulate RWU accurately while soil water was near saturation.

In conclusion, the DJ and CR models were found to be effective in quantifying the combined effects of CRWU and HR and better represent the soil water dynamics in the vadose zone than the FD, JF, and NH models. Implementing these models into the HYDRUS platform to simultaneously consider CRWU and HR and making them available to the HYDRUS users will improve RWU predictions by the model and undoubtedly facilitate and encourage future research on water uptake by plant roots using mechanistic models.

CRediT authorship contribution statement

Simunek Jiri: Writing – review & editing. Writing – original draft. Software, Methodology, Conceptualization. Thomas Anoja: Writing – review & editing. Writing – original draft. Visualization, Validation. Software, Methodology, Conceptualization. Yadav Brijesh Kumar: Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Anooja Thomas reports financial support was provided by United States-India Educational Foundation (USIEF)-Fullbright-Nehru Doctoral Fellowship (FNDR). Anooja Thomas reports financial support was provided by Ministry of Human Resource Development (MHRD), Govt. of India.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agwat.2024.108668.

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