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Modeling compensated root water and nutrient uptake

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ABSTRACT

Plant root water and nutrient uptake is one of the most important processes in subsurface unsaturated flow and transport modeling, as root uptake controls actual plant evapotranspiration, water recharge and nutrient leaching to the groundwater, and exerts a major influence on predictions of global climate models. In general, unsaturated models describe root uptake relatively simple. For example, root water uptake is mostly uncompensated and nutrient uptake is simulated assuming that all uptake is passive, through the water uptake pathway only. We present a new compensated root water and nutrient uptake model, implemented in HYDRUS. The so-called root adaptability factor represents a threshold value above which reduced root water or nutrient uptake in water- or nutrient-stressed parts of the root zone is fully compensated for by increased uptake in other soil regions that are less stressed. Using a critical value of the water stress index, water uptake compensation is proportional to the water stress response function. Total root nutrient uptake is determined from the total of active and passive nutrient uptake. The partitioning between passive and active uptake is controlled by the a priori defined concentration value c_{max}. Passive nutrient uptake is simulated by multiplying root water uptake with the dissolved nutrient concentration, for soil solution concentration values below c_{max}. Passive nutrient uptake is thus zero when c_{max} is equal to zero. As the active nutrient uptake is obtained from the difference between plant nutrient demand and passive nutrient uptake (using Michaelis–Menten kinetics), the presented model thus implies that reduced passive nutrient uptake is compensated for by active nutrient uptake. In addition, the proposed root uptake model includes compensation for active nutrient uptake, in a similar way as used for root water uptake. The proposed root water and nutrient uptake model is demonstrated by several hypothetical examples, for plants supplied by water due to capillary rise from groundwater and surface drip irrigation.

1. Introduction

Root surfaces represent one of the most important phase boundaries in nature since most mineral nutrients essential for life enter the biosphere and the food chains of the animal world through the roots of higher plants (Nissen, 1991). Similarly, root water and nutrient uptake is one of the most important processes considered in numerical models simulating water content and fluxes in the subsurface, thus controlling water flow (recharge) and nutrient transport (leaching) to the groundwater, and exerting a major influence on predictions of climate change impacts (Feddes and

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Raats, 2004) on terrestrial ecological systems, driving new research at understanding roots and their functioning (Skaggs and Shouse, 2008).

There are two major approaches generally used for the simulation of root water uptake in vadose zone hydrological models, to be applied at the plot or field scale (Hopmans and Bristow, 2002). Early detailed quantitative studies of water extraction by plant roots were based on a *microscopic* or *mesoscopic* (Feddes and Raats, 2004) approach that considered a single root to be an infinitely long cylinder of uniform radius and water-absorbing properties (Gardner, 1960). Water flow to a root was described using the Richards equation formulated in radial coordinates, with flow into the root driven by water potential gradients between the root and surrounding soil and proportional to the hydraulic conductivity of the soil surrounding the root (Mmolawa and Or, 2000) or the root radial water conductivity parameter (Roose and Fowler, 2004). Recent numerical modeling studies are increasingly applying the integrated plant root–soil domain approach, whereby total plant transpiration is computed from solution of water potential in the combined soil and root domain, solving for both root and soil water potential (e.g., Doussan et al., 2006; Javaux et al., 2008). Several models have been suggested that simulate individual roots and overall plant root architecture (e.g., Clausnitzer and Hopmans, 1994; Kastner-Maresch and Mooney, 1994; Brown et al., 1997; Grant, 1998; Somma et al., 1998; Biondini, 2001). These models often consider specific processes such as biomass allocation to individual roots (e.g., Kastner-Maresch and Mooney, 1994; Grant, 1998; Somma et al., 1998; Biondini, 2001), root growth redirection to areas with high soil nutrient concentrations (e.g., Somma et al., 1998; Biondini, 2001), linking of functioning of microbial ecosystems (Brown et al., 1997) and mycorryzal growth (Grant, 1998) to spatial structure of roots, or competition of different plant species for nutrients (e.g., Biondini, 2001; Raynaud and Leadlley, 2005). In addition to being more realistic in simulating soil-root interactions at the individual rootlet scale, the main advantage of this approach is that it automatically allows for compensation of soil water stress, as root water uptake is controlled by computed local water potential gradients and root conductivity for the whole root system. However, because of the lack of relevant soil and root data and the huge computational requirements for simulation purposes at this microscopic scale, soil water flow models that consider flow to each individual rootlet or plant root architecture have been limited to applications at a relatively small scale of a single plant.

Most vadose zone models that are used at the plot or field scale (e.g., Jarvis, 1994; Flerchinger et al., 1996; van Dam et al., 1997; Fayer, 2000; van den Berg et al., 2002; Šimůnek et al., 2008) utilize the *macroscopic* approach, whereby the potential transpiration is distributed over the root zone proportionally to root density, and is locally reduced depending on soil saturation and salinity status (Molz, 1981). This much more widely used approach (e.g., Feddes et al., 1974; Bouten, 1995) neglects effects of the root geometry and flow pathways around roots, and formulates root water uptake using a *macroscopic* sink term that lumps root water uptake processes into a single term of the governing mass balance equation. A wide variety of root water uptake reduction functions have been suggested, ranging from a simple two-parameter threshold and slope function

(Maas, 1990) or an S-shaped function (van Genuchten, 1987), to more complex functions that can include up to 5 fitting parameters such as suggested by Feddes et al. (1978). We refer readers to the review paper by Feddes and Raats (2004) for more details.

Usually, a *compensation* mechanism to balance reduced water uptake from one part of the rhizosphere by increased uptake in another less-stressed region of the rooting zone, while simulated in microscopic models, is neglected in vadose zone models. There is, however, growing experimental evidence that plants, especially non-cultural plants, can compensate for water stress in one part of the root zone by taking up water from parts of the root zone where water is available (e.g., Taylor and Klepper, 1978; Hasegawa and Yoshida, 1982; English and Raja, 1996; Stikic et al., 2003; Leib et al., 2006). The MACRO model (Jarvis, 1994) is an exception among the more widely used models as it uses a critical value of the water stress index, or root adaptability factor, to allow for compensated root water uptake. This factor represents a threshold value above which root water uptake that is reduced in stressed parts of the root zone is fully compensated for by increased uptake from other parts. Among the research models, in their ENVIRO-GRO model, Pang and Letey (1998) used a similar threshold value to compute partial root water uptake compensation. Similarly, Li et al. (2001) and Bouten (1995) distributed the potential transpiration across the root zone according to a weighted stress index, which was a function of both root distribution and soil water availability or water saturation fraction, respectively. A different approach was used by Adiku et al. (2000), who assumed that plants seek to minimize the total rate of energy expenditure during root water uptake. They formulated the root water uptake problem as a minimization problem and solved it using a dynamic program framework. Their optimized model simulated patterns of water extraction from uniformly wet soil profiles, with highest water extraction rates in the section where the root length density was also highest. For conditions with a dry soil surface, a reduction of root water uptake from the drier near soil surface zone was compensated for by an increased root activity at greater soil depths, irrespective of root distribution. A review of compensatory modeling approaches was recently presented by Skaggs et al. (2006).

Plant nutrient availability and uptake is controlled by both soil transport and plant uptake mechanisms. A detailed description of nutrient uptake is often included in agronomic models that simulate differentiation of plant nutrient demand during various physiological growth stages (e.g., Parton et al., 1987; Jones and Ritchie, 1990). These models, however, typically greatly simplify soil water flow and nutrient transport towards the root–soil interface. In contrast, vadose zone models greatly simplify root nutrient uptake, often considering only its passive component and neglecting plant growth dynamics (e.g., Jarvis, 1994; Flerchinger et al., 1996; van Dam et al., 1997; Fayer, 2000; van den Berg et al., 2002; Šimůnek et al., 2008).

Solute transport in soils occurs by both mass flow and molecular diffusion. In the case of non-adsorbing nutrients, nutrient uptake is controlled mainly by mass flow, as is the case of nitrate-N (e.g., Barber, 1995). In some cases, mass flow of specific nutrients (e.g., Ca^{2+} and Mg^{2+}) may exceed the plant

requirements, resulting in accumulation of particular ions or even precipitation of corresponding solids (e.g., $CaSO_4$) at the root surface (Neumann and Römheld, 2002). Alternatively, nutrients that exhibit low solubility in soil solutions, such as P, K, NH_4^+, and most micronutrients, are rapidly depleted by root uptake in the soil solution (Neumann and Römheld, 2002), since roots absorb nutrients only in the dissolved state. A resulting concentration gradient causes nutrient diffusion from the bulk soil toward the root surface. A decrease in the solution concentration also disturbs the equilibrium between the nutrients in solution and those bound to the solid soil phase, resulting in their release from the solid phase and replenishing of the solution concentration (Jungk, 2002). Plants may utilize various additional strategies to mobilize nutrients, i.e., to release them from their association with the solid phase, such as modification of the chemical composition or association of roots with micro-organisms (Neumann and Römheld, 2002).

There are many physical, biological, and physiological mechanisms that are involved in the nutrient uptake by plant roots (e.g., Jungk, 2002; Hopmans and Bristow, 2002; Darrah et al., 2006). These can be broadly divided into passive and active components. While the passive component represents the mass flow of nutrient into roots with water, the active component represents a very diverse range of various biological energy-driven processes (e.g., Luxmoore et al., 1978; Jungk, 2002; Neumann and Römheld, 2002; Silberbush, 2002; Hopmans and Bristow, 2002) that affect the movement of specific nutrients from the root's free space (cell walls) into the plant. The term passive nutrient uptake is thus defined here as the movement of nutrients into the roots by convective mass flow of water, directly coupled with root water uptake. The term active nutrient uptake then represents the movement of nutrients into the roots induced by other mechanisms than mass flow. These other mechanisms include, for example, specific ion uptake by electro-chemical gradients, ion pumping and uptake through ion channels.

Different fractions of different nutrients are supplied by active and passive mechanisms (Jungk, 2002; Neumann and Römheld, 2002). Shaner and Boyer (1976) demonstrated that the nitrate xylem concentration varied inversely with transpiration rate, and that nitrate uptake is mostly a function of metabolic rate rather than transpiration rate. Active nitrate uptake is considered to occur via NO_3^-/H^+ cotransport, or NO_3^-/H^+ counter transport via carriers (Haynes, 1986), with the electrochemical gradient generated by proton pumping. Although not strictly proven, it is generally proposed that active uptake dominates in the low supply concentration range and under stress conditions, whereas passive uptake becomes more important at higher soil solution concentrations, via mass flow driven by root water uptake and transpiration (see also Porporato et al. (2003)). Rather than a priori defining the nutrient uptake mechanism, Somma et al. (1998) assumed that passive and active uptake can be considered as additive processes, and allowed for a flexible partitioning between active and passive uptake, with the relative contribution of each to be determined by the model user, and total nutrient uptake controlled by plant nutrient demand (Hopmans, 2006). A similar approach was adopted by Porporato et al. (2003) in their modeling study to evaluate the

influence of soil moisture control on soil carbon and nitrogen cycling.

In addition to soil transport mechanisms, nutrient uptake is controlled by the spatial distribution of roots, as influenced by its architecture, morphology and presence of active sites of nutrient uptake, including root hairs (e.g., Somma et al., 1998; Biondini, 2001; Javaux et al., 2008). For nutrients that are immobile (e.g. P) or slowly mobile (ammonium), a root system must develop so that it has access to the nutrients, by increasing their exploration volume. Alternatively, the roots may increase its exploitation power for the specific nutrient by local adaptation of the rooting system, allowing for increased uptake efficiency of the nutrient. When considering the rhizosphere dynamics of water and nutrient uptake, many more mechanisms may have to be considered, including rhizosphere acidification (Pierre and Banwart, 1973) and nitrogen mineralization (Bar-Yosef, 1999).

The root water and nutrient uptake model presented in this manuscript links soil physical principles with plant physiological concepts, thereby providing for an improved integration of scientific principles as needed for an interdisciplinary ecological approach, as compared to most other approaches. We understand that such integration may polarize different view points between scientific fields, and create misunderstandings of notation and concepts that are unique within each discipline. However, the mathematical model introduced here is an honest attempt to cross disciplinary boundaries as required for advancing the science for the broad and complex study field of ecology. The presented subsurface modeling approach will greatly improve scenario testing for soil–plant systems, by including plant uptake mechanisms such as compensated root water and active root nutrient uptake. As we demonstrate in the example simulations, soil nutrient concentrations are controlled by the magnitude of partitioning between passive and active plant nutrient uptake. This is especially important for natural ecosystems, where soil nutrient concentrations are generally much lower for most plant nutrients than in agricultural systems. In addition, natural ecosystems often suffer from environmental stresses (water, nutrient, temperature), and the plant responses to such limiting factors are highly relevant for understanding their functioning and survival strategies. We note that comparison of model results as shown here at the single-plant scale is much more difficult for larger ecosystem models, because of inherent soil heterogeneities, thereby complicating model input requirements and model calibration (Wegehenkel and Mirschel, 2006). Alternatively, less data-intensive and simpler water- and nutrient uptake models may be warranted for ecosystem-scale analysis of soil environmental constraints (De Barros et al., 2004; van den Berg et al., 2002).

The objective of the presented study is to reformulate the mathematical and numerical model of root water and nutrient uptake, as commonly implemented in vadose zone flow and transport models (e.g., Jarvis, 1994; Bouten, 1995; Flerchinger et al., 1996; van Dam et al., 1997; Fayer, 2000; van den Berg et al., 2002; Šimůnek et al., 2008), by including compensation of local water and nutrient stresses, and partitioning between passive and active nutrient uptake. The model should be as general as possible so that it can be applied to an arbitrary nutrient (either adsorbing or non-adsorbing) without any further

modifications by simply selecting the relevant model parameters, while at the same time simple enough so that it can be readily implemented in vadose zone flow and transport models. Therefore, we do not strive to simulate individual roots or plant root architecture (e.g., Biondini, 2001 and similar references given above), biomass allocation to roots (e.g., Grant, 1993; Kastner-Maresch and Mooney, 1994), or dynamics of the soil microbial system and the carbon, nitrogen and phosphorus cycles in the soil (e.g., Parton et al., 1987; Wegehenkel and Mirschel, 2006). The new root uptake model is implemented into the HYDRUS software packages (Šimůnek et al., 2006, 2008) and several examples are given demonstrating the effects of the water and nutrient uptake compensation and active nutrient uptake on root zone soil moisture and nutrient distribution.

2. Theory

2.1. *Water flow and nutrient transport*

Water flow and nutrient transport in variably saturated porous media are usually described using the Richards (1931) and convection–dispersion equations (CDE), respectively:

$$\frac{\partial \theta(h)}{\partial t} = \frac{\partial}{\partial x_i}\left[K(h)\left(K_{ij}^A \frac{\partial h}{\partial x_j} + K_{iz}^A \right) \right] - s^*(h) \tag{1}$$

$$\frac{\partial \rho_b \bar{c}}{\partial t} + \frac{\partial \theta c}{\partial t} = \frac{\partial}{\partial x_i}\left(\theta D_{ij} \frac{\partial c}{\partial x_j} \right) - \frac{\partial(q_i c)}{\partial x_i} - \phi - r_a(c, h) \tag{2}$$

In the Richards equation (1), θ is the volumetric water content [$L^3 L^{-3}$], h is the soil water potential expressed by pressure head [L], K is the unsaturated hydraulic conductivity [LT^{-1}], K_{ij}^A are components of a dimensionless anisotropy tensor $\mathbf{K}^A$ (which reduces to the unit matrix when the medium is isotropic), t is time [T], x_i are the spatial coordinates [L], and s^* is the sink/source term [$L^3 L^{-3} T^{-1}$], accounting for root water uptake (transpiration). The sink term, s^*, represents the volume of water removed per unit time from a unit volume of soil due to plant water uptake. In this paper, s^* can represent either uncompensated (s) or compensated (s_c) root water uptake.

In the CDE, ρ_b is the bulk density [ML^{-3}], $\bar{c}$ [MM^{-1}] and c [ML^{-3}] are concentrations in the solid and liquid phases, respectively; D_{ij} are components of the effective dispersion tensor [$L^2 T^{-1}$], q_i is the volumetric flux density [LT^{-1}], ϕ is the rate of change of mass per unit volume by chemical or biological reactions or other sources (negative) or sinks (positive) [$ML^{-3} T^{-1}$]. For example, nitrification and denitrification are typical examples of reactions that can be represented by the ϕ-term. Finally, r_a represents the root nutrient uptake [$ML^{-3} T^{-1}$], which is the sum of the actual (subscript a) passive (p_a) and active (a_a) root nutrient uptakes. The sink terms r_a, p_a, and a_a represent the mass of nutrient (nutrients) removed per unit time from a unit volume of soil due to the total, passive and active plant nutrient uptake, respectively. The solid phase concentration, $\bar{c}$, accounts for nutrient either sorbed to the solid phase or precipitated in various minerals. This term is usually mathematically described using linear or nonlinear

sorption isotherms describing instantaneous sorption of the nutrient, or various kinetic equations describing rate limited sorption/desorption or precipitation/dissolution. For example, when the solid phase concentration is expressed by an adsorption isotherm, the left hand side of Eq. (2) can be reformulated as follows:

$$\frac{\partial \rho_b \bar{c}}{\partial t} + \frac{\partial \theta c}{\partial t} = \frac{\partial \theta R c}{\partial t}, \qquad R = 1 + \frac{\rho_b}{\theta}\frac{\partial \bar{c}}{\partial c} \tag{3}$$

where R is the retardation factor [−], defining the partitioning of nutrient between the solid and liquid phases. The retardation factor is closely related to the buffering factor, a term often used in literature dealing with root uptake. Notice that in both Eqs. (1) and (2), lower case symbols describing root water and nutrient uptake represent local values, while upper case symbols (defined below) represent global values, that is, local values integrated over the root zone.

2.2. *Root water and nutrient uptake*

In the following we will formulate our root water (s^*) and nutrient uptake (r_a) terms using the *macroscopic* approach (Fig. 1). We will formulate it for a two-dimensional problem, although both one- or three-dimensional formulations are trivial simplification or expansion of this two dimensional formulation, respectively. Fig. 1 presents a schematic diagram that illustrates various stressed and unstressed, compensated and uncompensated, active and passive root water and nutrient uptakes discussed in the following sections.

2.2.1. *Root water uptake*
First, we must define the magnitude of potential root water uptake rate, s_p, corresponding to the potential transpiration rate, T_p. Typically, the root water uptake is distributed over the root zone according to the spatial root distribution (for example, see Skaggs et al., 2006). The potential transpiration is determined by the atmospheric demand, as controlled by meteorological variables, such as net radiation, air temperature, wind speed, and relative humidity, but does not consider the plant and soil environment. The potential transpiration rate can be calculated from the meteorological variables using various process-based or empirical formulas, such as the FAO-recommended Penman–Monteith combination equation (FAO, 1990) or the Hargreaves formula (e.g., Jensen et al., 1997), respectively.

When distributing the potential water uptake rate equally over a two-dimensional rectangular root domain, s_p becomes:

$$s_p(x, z, t) = \frac{1}{L_x L_z} L_t T_p(t) \tag{4}$$

where s_p is the potential root water uptake rate [T^{-1}] at location (x, z) and time t, T_p is the potential transpiration rate [LT^{-1}], L_z is the depth [L] of the root zone, L_x is the width [L] of the root zone, L_t is the width [L] of the soil surface associated with the transpiration process, and x and z are spatial coordinates. The distinction between L_t and L_x is needed for partially plant-covered soil surfaces, and s_p reduces to T_p/L_z when $L_t = L_x$. Eq. (4) may be generalized by introducing
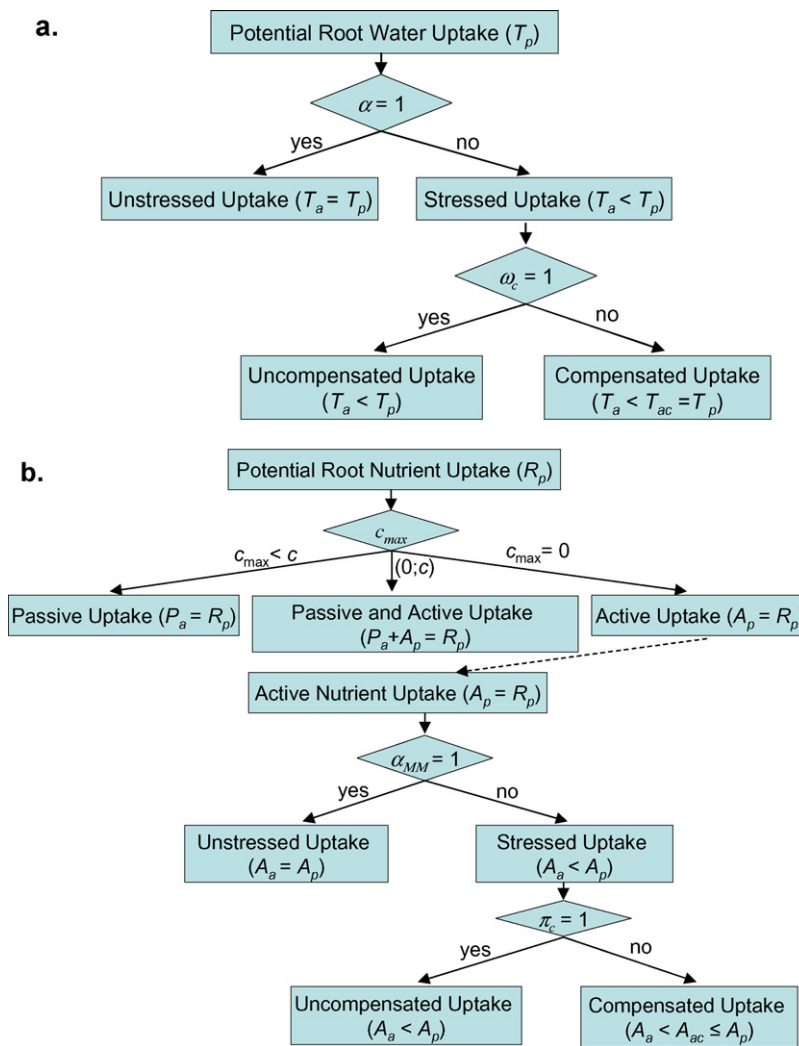
a.

b.

Fig. 1 – Schematic diagram that illustrates the presented root water (a) and nutrient (b) uptake mechanisms (T_p, T_a, T_{ac} – potential, actual non-compensated, and actual compensated root water uptake rate, respectively; α – water stress response function; ω_c – water stress index; R_p – potential root nutrient uptake rate; P_a – passive root nutrient uptake rate; A_p, A_a, A_{ac} – potential, actual non-compensated, and actual compensated root nutrient uptake rate, respectively; α_{MM} – nutrient stress response (Michaelis–Menten) function; π_c – nutrient stress index).

a non–uniform distribution of the potential water uptake rate over a root zone with an arbitrary shape (Vogel, 1987):

$$s_p(x, z, t) = b(x, z, t)L_t T_p(t) \qquad (5)$$

where $b(x, z, t)$ is the normalized water uptake distribution [L^{-2}] (Fig. 2). Note that $b(x, z, t)$ is a function of space and time, allowing for plant root growth. The functional description is flexible, and can accommodate known root distribution functions, such as linear (Feddes et al., 1978), exponential (Raats, 1974), or can be more general (Vrugt et al., 2001a,b). The function $b(x, z, t)$ must be normalized to ensure that $b(x, z, t)$ integrates to unity over the flow domain, i.e.:

$$\int_{\Omega_R} b(x, z, t)\, d\Omega = 1 \qquad (6)$$

where Ω_R represents the root zone [L^2]. From (5) and (6) it follows that S_p is related to T_p by the expression:

$$T_p(t) = \frac{1}{L_t} \int_{\Omega_R} s_p(x, z, t)\, d\Omega \qquad (7)$$

Notice that the formulation above is given for a two-dimensional problem. A similar expression can be derived, with L_t equal to 1 [−] and the soil surface area [L^2] associated with the transpiration process, for one- and three-dimensional formulations, respectively. Similarly, the normalized water uptake distribution is equal either to $b(z, t)$ [L^{-1}] or $b(x, y, z, t)$ [L^{-3}] for one- and three-dimensional problems, respectively.

2.2.1.1. *Uncompensated root water uptake.* For the non-compensated root water uptake model, the actual root water
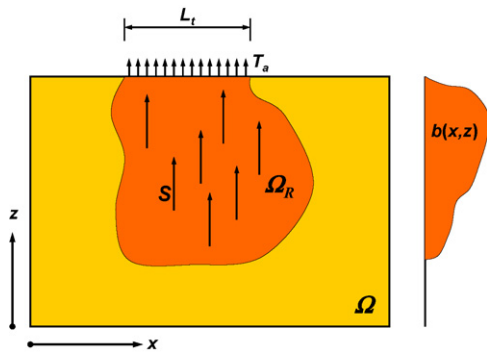
Fig. 2 – Schematic of the potential water uptake distribution function, $b(x, z, t)$, in the soil root zone.

uptake, s, is obtained from the potential root water uptake, s_p, through multiplication with a stress response function (Feddes et al., 1978), α, as follows:

$$s(h, h_\phi, x, z, t) = \alpha(h, h_\phi, x, z, t)\, s_p(t) \tag{8}$$

where the stress response function $\alpha(h, h_\phi)$ is a prescribed dimensionless function of the soil water (h) and osmotic (h_ϕ) pressure heads ($0 \leq \alpha \leq 1$). The stress response function reduces the potential root water uptake due to the moisture and salinity stress. Since extensive literature is devoted to various formulations of the water stress response function (e.g., Cardon and Letey, 1992; Feddes and Raats, 2004; Skaggs et al., 2006), we will not discuss these here in detail. For example, effects of the pressure head and osmotic stresses can be considered to be either additive or multiplicative (van Genuchten, 1987; Cardon and Letey, 1992; Feddes and Raats, 2004) or various functions (e.g., an S-shape function (van Genuchten, 1987) or a threshold and slope function (Maas, 1990)) representing these stresses can be used. While some functions require only two parameters (Maas, 1990; van Genuchten, 1987), the more complex functions, such as that suggested by Feddes et al. (1978), require five parameters.

The presented examples will use the stress response function of Feddes et al. (1978) (Fig. 3). Notice that water uptake is assumed to be zero close to saturation (i.e., wetter than some arbitrary "anaerobiosis point", h_1). For $h < h_4$ (the wilting point
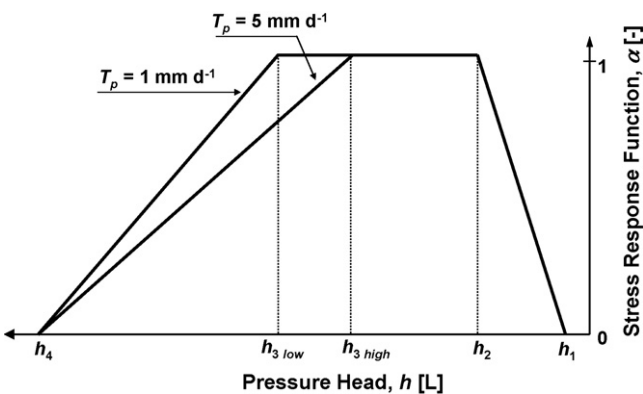

Fig. 3 – Schematic of the plant water stress response function, $\alpha(h)$, as used by Feddes et al. (1978).

pressure head), water uptake is also zero. Water uptake is considered optimal between pressure heads h_2 and h_3, whereas for soil water pressure head values between h_3 and h_4 (or h_1 and h_2), water uptake decreases (or increases) linearly with h. For phreatic plants and trees that are able to extract water from below the groundwater, values of h_1 and h_2 can be adjusted, or set to zero in which case the Feddes' function is similar to the Maas (1990) model. Parameters of the stress response function for a majority of agricultural crops can be found in various databases (e.g., Taylor and Ashcroft, 1972; Wesseling et al., 1991) and are directly implemented into the GUI of HYDRUS. As is apparent from inspection of Eq. (7) the actual root water uptake is equal to potential uptake (and potential transpiration) during periods of no water stress ($\alpha(h) = 1$).

The actual local uncompensated root water uptake, s, is obtained by substituting (5) into (8), or

$$s(h, h_\phi, x, z, t) = \alpha(h, h_\phi, x, z, t) b(x, z, t) L_t T_p(t) \tag{9}$$

so that the actual transpiration rate, T_a [LT^{-1}], is obtained by integrating (9) over the root domain Ω_R, or

$$
\begin{aligned}
T_a(t) &= \frac{1}{L_t} \int_{\Omega_R} s(h, h_\phi, x, z, t)\ d\Omega \\
&= T_p(t) \int_{\Omega_R} \alpha(h, h_\phi, x, z, t) b(x, z, t)\ d\Omega
\end{aligned}
\tag{10}
$$

2.2.1.2. Compensated root water uptake. The ratio of actual and potential transpiration of uncompensated root water uptake is defined as

$$
\begin{aligned}
\frac{T_a(t)}{T_p(t)} &= \frac{1}{T_p(t) L_t} \int_{\Omega_R} s(h, h_\phi, x, z, t)\ d\Omega \\
&= \int_{\Omega_R} \alpha(h, h_\phi, x, z, t) b(x, z, t)\ d\Omega = \omega(t)
\end{aligned}
\tag{11}
$$

where ω is a dimensionless water stress index (Jarvis, 1989, 1994). Following Jarvis (1989, 1994), we introduce a critical value of the water stress index ω_c, or the so-called root adaptability factor. It represents a threshold value, above which the root water uptake reduced in stressed parts of the root zone is fully compensated for by uptake from other, less-stressed parts (Fig. 4). Below this critical value, there is a certain reduction of the potential transpiration, although smaller than in uncompensated root water uptake.

Defining compensated actual transpiration rate, T_{ac}, as the ratio of T_a/ω, the ratio of the actual to potential transpiration becomes for the water stress range above the critical water stress index (i.e., $\omega > \omega_c$):

$$\frac{T_{ac}(t)}{T_p(t)} = \frac{T_a(t)}{T_p(t)\omega(t)} = \frac{\int_{\Omega_R} \alpha(h, h_\phi, x, z, t) b(x, z, t)\ d\Omega}{\omega(t)} = \frac{\omega(t)}{\omega(t)} = 1,$$

$$s_c(h, h_\phi, x, z, t) = \alpha(h, h_\phi, x, z, t) b(x, z, t) L_t \frac{T_p(t)}{\omega(t)} \tag{12}$$
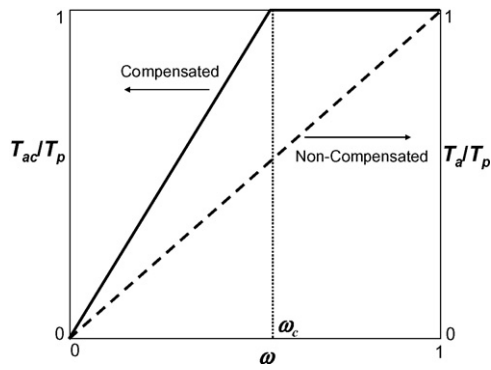
Fig. 4 – Ratio of the actual to potential transpiration as a function of the stress index ω (arrows point towards the corresponding axis; the left axis is for compensated uptake, while the right axis is for uncompensated uptake).

For the water stress range below the critical water stress index (i.e., $\omega < \omega_c$) we define $T_{ac} = T_a/\omega_c$, so that

$$\frac{T_{ac}(t)}{T_p(t)} = \frac{T_a(t)}{T_p(t)\omega_c(t)} = \frac{\int_{\Omega_R} \alpha(h, h_\phi, x, z, t)b(x, z, t)\ \mathrm{d}\Omega}{\omega_c} = \frac{\omega(t)}{\omega_c} < 1,$$

$$s_c(h, h_\phi, x, z, t) = \alpha(h, h_\phi, x, z, t)b(x, z, t)L_t\frac{T_p(t)}{\omega_c} \qquad (13)$$

where s_c is the compensated root water uptake $[T^{-1}]$. For $\omega_c = 1$ and 0, root water uptake is either uncompensated or fully compensated, respectively. We note that division by zero in (13) is theoretically not-defined. Uncompensated root water uptake is thus a special case of compensated root water uptake when $\omega_c = 1$ (Fig. 1a). Combined, both uncompensated and (fully or partially) compensated models can be defined by

$$\frac{T_{ac}(t)}{T_p(t)} = \frac{\int_{\Omega_R} \alpha(h, h_\phi, x, z, t)b(x, z, t)\ \mathrm{d}\Omega}{\max[\omega(t), \omega_c]} = \frac{\omega(t)}{\max[\omega(t), \omega_c]} \leq 1,$$

$$s_c(h, h_\phi, x, z, t) = \alpha(h, h_\phi, x, z, t)b(x, z, t)L_t\frac{T_p(t)}{\max[\omega(t), \omega_c]} \qquad (14)$$

so that the total actual compensated plant transpiration is equal to

$$T_{ac}(t) = \frac{1}{L_t} \int_{\Omega_R} s_c(h, h_\phi, x, z, t)\ \mathrm{d}\Omega$$

$$= \frac{T_p(t)}{\max[\omega(t), \omega_c]} \int_{\Omega_R} \alpha(h, h_\phi, x, z, t)b(x, z, t)\ \mathrm{d}\Omega \qquad (15)$$

Using this approach, water uptake compensation is proportional to the water stress response function. Water uptake increase (compensation) is maximum in parts of the root zone where the root water uptake is optimal (i.e., not reduced), equal to zero in parts of the root zone where the pressure head is below the wilting point or above the anaerobiosis point; and proportional to the water stress response for other pressure head values. In this way, the proposed compensation model is closely related to models based on minimizing energy of root water uptake (e.g., Adiku et al., 2000; Van Wijl and Bouten,

2001). We note that this compensation mechanism spatially redistributes root water uptake from stressed to less-stressed regions of the root zone, where water is held with smaller capillary forces and thus more easily available for the plant. This is very different than simply modifying the stress response function by expanding the pressure head intervals for both unlimited and limited uptake across the whole rooting zone.

However, as pointed out by Skaggs et al. (2006), the presented compensation is conceptually unsound, if the whole root domain is equally stressed. For example, the model will predict a full compensation of root water uptake when the root zone has the uniform pressure head for which the water uptake is reduced by less than the critical water stress index. The predicted root water uptake, which is uniform under such conditions throughout the root zone, will then deviate, due to compensation, from the value predicted by the stress response function. To overcome this conceptual problem one can, for example, consider compensation of root water uptake to occur (a) only from parts of the root zone which are not stressed at all or (b) from zones which are stressed less than ω. After such modification, the updated compensated root water uptake model will follow the thick line from Fig. 4 only when the pressure head in a part of the root zone is below the wilting point and the rest is either non-stressed or stressed less than ω, respectively. For all other conditions, the model will be between theoretical lines for non-compensated and compensated root water uptake.

The compensated root water uptake model requires as input the potential evapotranspiration rate T_p, the spatial root distribution function $b(x, z, t)$, the water stress response function α, and the critical water stress index ω_c. Therefore, the additional new input variable, as compared to traditional uncompensated root water uptake is the critical water stress index, ω_c. It can be expected that cultural (i.e., agricultural) plants have a relatively high ω_c and thus their ability to compensate natural stresses is limited, as compared to natural plants, especially desert species, that have a low ω_c and correspondingly high ability to compensate for natural stresses (i.e., to only take up water and nutrients from those parts of the root system where they are most available).

2.2.2. Root nutrient uptake

The presented model allows for both passive and active root nutrient uptake. Whereas passive uptake describes the mass flow and root uptake of nutrients dissolved in water taken up by plant roots, we define active uptake as all other possible nutrient uptake mechanisms, including energy-driven processes against electrochemical gradients. The term "passive uptake" is used here, and throughout the manuscript, to represent flow of nutrients into roots associated with flow of water supplying the plant transpiration demand. Since transpiration flow is an active process, the mass nutrient flow is also a process that is actively regulated by plants. The terms "passive" and "active" are used here mainly to distinguish between these two mechanisms of root nutrient uptake.

Similarly, as for root water uptake, we define a potential nutrient demand, R_p $[ML^{-2}T^{-1}]$, that depends on the plant physiological growth stage, supplied by both passive and active nutrient uptake. Daily nutrient consumption rates are known for various field crops as a function of their growth

stage (after emergence or planting), for example as reported by Bar-Yosef (1999) for N, P, and K nutrients.

We further assume that passive uptake is the primary mechanism of supplying plants with nutrients, and that active uptake is initiated only if passive uptake is inadequate. For their physiological development, plants need to take up water from the root zone, and as nutrients are dissolved in soil water they can enter the plant by the dissolved water phase pathway. The active uptake will then provide additional nutrients that are required beyond what is supplied by passive uptake. In general, the presented model allows for both passive and active nutrient uptake mechanisms to occur separately or simultaneously, as described below. The relative significance of active and passive nutrient uptakes in supplying various agricultural crops with nutrients can be found in the literature. For example, values for N, P, and K in maize are given by Jungk (1991).

2.2.2.1. Uncompensated nutrient uptake model. To clearly differentiate between point and root domain nutrient uptake rate values, we define lower case variables to represent point root nutrient uptake rates $[ML^{-3}T^{-1}]$, while upper case variables represent nutrient uptake rates $[ML^{-2}T^{-1}]$ over the entire two-dimensional root zone domain, Ω_R. Both point and root domain nutrient uptakes are assumed to be the sum of their passive and active components, or

$$r_a(x, z, t) = p_a(x, z, t) + a_a(x, z, t) \tag{16}$$

$$R_a(t) = P_a(t) + A_a(t) \tag{17}$$

where r_a, p_a, and a_a define total actual (subscript a) passive and active root nutrient uptake rates $[ML^{-3}T^{-1}]$, respectively, at any point, and R_a, P_a, and A_a denote actual total, passive and active root nutrient uptake rates $[ML^{-2}T^{-1}]$, respectively, for the root zone domain.

Passive nutrient uptake is simulated by multiplying root water uptake (compensated or uncompensated) with the dissolved nutrient concentration, for concentration values below a priori defined maximum concentration (c_{max}), or

$$p_a(x, z, t) = s^*(x, z, t) \min[c(x, z, t), c_{max}] \tag{18}$$

where c is the dissolved nutrient concentration $[ML^{-3}]$ and c_{max} is the maximum allowed solution concentration $[ML^{-3}]$ that can be taken up by plant roots during passive root uptake. All nutrient dissolved in water is taken up by plant roots when c_{max} is large (larger than the dissolved concentration c), while no nutrient is taken up when c_{max} is equal to zero, with only active uptake remaining in that case (Fig. 1b). The maximum solution concentration for passive root uptake, c_{max}, thus controls the relative proportion of passive root water uptake to total uptake. Using this flexible formulation, uptake mechanisms can vary between specific nutrients. For example, Na uptake can be excluded by setting c_{max} equal to zero, passive Ca uptake can be limited by defining a finite c_{max} value, or all soil solution available P or N is allowed to be taken up passively, by setting c_{max} to a very large value. Note that the c_{max} parameter is introduced as a control model parameter that does not necessarily have a physiological meaning.

Passive actual root nutrient uptake for the whole root domain, P_a $[ML^{-2}T^{-1}]$, is calculated by integrating the local passive root nutrient uptake rate, p_a, over the entire root zone, or after applying Eq. (14):

$$\begin{aligned} P_a(t) &= \frac{1}{L_t} \int_{\Omega_R} p_a(x, z, t) \ d\Omega \\ &= \frac{1}{L_t} \int_{\Omega_R} s^*(x, z, t) \min[c(x, z, t), c_{max}] \ d\Omega \\ &= \frac{T_p(t)}{\max[\omega(t), \omega_c]} \int_{\Omega_R} \end{aligned}$$

$$\alpha(h, h_\phi, x, z, t) b(x, z, t) \ \min[c(x, z, t), c_{max}] \ d\Omega \tag{19}$$

Defining R_p as the potential (subscript p) nutrient demand $[ML^{-2}T^{-1}]$, the potential active nutrient uptake rate, A_p $[ML^{-2}T^{-1}]$, is computed from:

$$A_p(t) = \max[R_p(t) - P_a(t), 0] \tag{20}$$

Thus, using this formulation, we assume that active nutrient uptake will be invoked only if the passive root nutrient uptake term does not fully satisfy the potential nutrient demand of the plant. However, as was discussed earlier, the passive uptake can be reduced or completely turned off ($c_{max} = 0$), thus allowing the potential active nutrient uptake (A_p) to be equal to the potential nutrient demand (R_p). Once A_p is known, the point values of potential active nutrient uptake rates, a_p $[ML^{-3}T^{-1}]$, are obtained by distributing the potential root zone active nutrient uptake rate, A_p $[ML^{-2}T^{-1}]$, over the root zone domain, using a predefined spatial root distribution, $b(x, z, t)$, as was done for root water uptake in Eq. (5), or

$$a_p(x, z, t) = b(x, z, t) L_t A_p(t) \tag{21}$$

Using Michaelis–Menten kinetics (e.g., Jungk, 1991) provides for actual distributed values of active nutrient uptake rates, a_a $[ML^{-3}T^{-1}]$, allowing for nutrient concentration dependency, or

$$\begin{aligned} a_a(x, z, t) &= \frac{c(x, z, t) - c_{min}}{K_m + c(x, z, t) - c_{min}} a_p(x, z, t) \\ &= \frac{c(x, z, t) - c_{min}}{K_m + c(x, z, t) - c_{min}} b(x, z, t) L_t A_p(t) \end{aligned} \tag{22}$$

where K_m is the Michaelis–Menten constant $[ML^{-3}]$ and c_{min} is the minimum nutrient concentration required for active uptake to take effect $[ML^{-3}]$ (Jungk, 1991), thus assuming that active nutrient uptake will occur only if the dissolved nutrient concentration in the soil solution is sufficiently high. Other approaches have been suggested to deal with the concentration threshold (Silberbush, 2002). The Michaelis–Menten constants for selected nutrients (e.g., N, P, and K) and plant species (e.g., corn, soybean, wheat, tomato, pepper, lettuce, and barley) can be found in the literature (e.g., Bar-Yosef, 1999). Though not in agreement with the presented concept of distinguishing between passive and active uptake, the formulation could be easily modified so that the Michaelis–Menten kinetics is applied to the sum of the active and passive nutrient
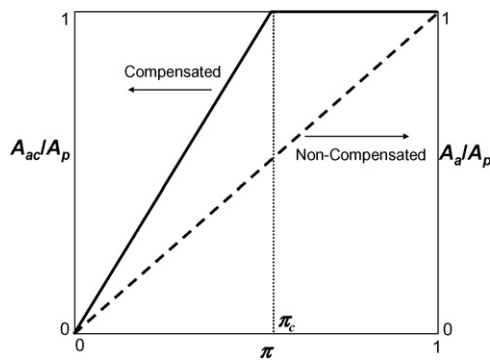
Fig. 5 – Ratio of actual to potential active nutrient uptake as a function of the stress index π (arrows point towards the corresponding axis; the left axis is for compensated uptake, while the right axis is for uncompensated uptake).

uptake as it is usually used in the literature (Silberbush, 2002).

Finally, total active uncompensated root nutrient uptake rate, A_a [$ML^{-2}T^{-1}$], is calculated by integrating the actual active root nutrient uptake rate, a_a, at each point, over the root domain Ω_R, in analogy with the non-compensated root water uptake term in Eq. (10), or

$$A_a(t) = \frac{1}{L_t} \int_{\Omega_R} a_a(x, z, t) \ d\Omega$$

$$= A_p(t) \int_{\Omega_R} \frac{c(x, z, t) - c_{min}}{K_m + c(x, z, t) - c_{min}} b(x, z, t) \ d\Omega \qquad (23)$$

2.2.2.2. *Compensated nutrient uptake model.* The above nutrient uptake model includes compensation of the passive nutrient uptake, by way of the root water uptake compensation term, s_c, and root adaptability factor, ω_c, in Eq. (19). A similar compensation concept as used for root water uptake in Eqs. (11) and (12), was implemented for active nutrient uptake rate, by invoking a so-called nutrient stress index π:

$$\pi(t) = \frac{A_a(t)}{A_p(t)} \qquad (24)$$

After substitution of the active total root nutrient uptake rate value from Eq. (23) above, this newly defined nutrient stress index (π) is equal to

$$\pi(t) = \int_{\Omega_R} \frac{c(x, z, t) - c_{min}}{K_m + c(x, z, t) - c_{min}} b(x, z, t) \ d\Omega \qquad (25)$$

After defining the critical value of the nutrient stress index π_c (Fig. 5), above which value active nutrient uptake is fully compensated for by active uptake in other more-available (less stressed) soil regions, the local compensated active root nutrient uptake rate, a_{ac} [$ML^{-3}T^{-1}$], is obtained by including the nutrient-stress index function in the denominator of Eq. (22), or

$$a_{ac}(x, z, t) = \frac{c(x, z, t) - c_{min}}{K_m + c(x, z, t) - c_{min}} b(x, z, t) L_t \frac{A_p(t)}{\max[\pi(t), \pi_c]} \qquad (26)$$

from which the total compensated active root nutrient uptake rate, A_{ac} [$ML^{-2}T^{-1}$] in the two-dimensional root domain, Ω_R, is calculated, in analogy with the compensated root water uptake term in Eq. (15), as follows:

$$A_{ac}(t) = \frac{1}{L_t} \int_{\Omega_R} a_{ac}(x, z, t) \ d\Omega$$

$$= \frac{A_p(t)}{\max[\pi(t), \pi_c]} \int_{\Omega_R} \frac{c(x, z, t) - c_{min}}{K_m + c(x, z, t) - c_{min}} b(x, z, t) \ d\Omega \qquad (27)$$

Eq. (20) implies that reduction in root water uptake will decrease passive nutrient uptake, thereby increasing active nutrient uptake proportionally. In other words, total nutrient uptake is not affected by soil water stress, as computed by the proportion of actual to potential root water uptake. This is not realistic since one would expect that plant nutrient requirements will be reduced for water-stressed plants. For that reason, the uptake model includes additional flexibility, by reducing the potential nutrient demand R_p [$ML^{-2}T^{-1}$], in proportion to the reduction of root water uptake, as defined by the actual to potential transpiration ratio, or

$$A_p(t) = \max\left[R_p(t) \frac{T_{ac}(t)}{T_p(t)} - P_a(t), 0 \right] \qquad (28)$$

In summary, the presented root nutrient uptake model with compensation requires as input the potential nutrient uptake rate (demand), R_p, the spatial root distribution function $b(x, z, t)$ as needed for the water uptake term, the Michaelis–Menten constant K_m, the maximum nutrient concentration that can be taken up passively by plant roots c_{max}, the minimum concentration c_{min} needed to initiate active nutrient uptake, and the critical nutrient stress index π_c. The passive nutrient uptake term can be turned off by selecting c_{max} equal to zero. Moreover, active nutrient uptake can be eliminated by specifying a zero value for R_p in Eq. (20), or by selecting a very large c_{min} value in Eq. (22). It is likely that values of these parameters are nutrient- and plant-specific. Similarly as for root water uptake, it can be expected that π_c for agricultural crops is relatively high when compared to natural plants that are likely to have more ability to compensate for soil environmental stresses. Other parameters, such as c_{max} will likely need to be calibrated to specific conditions before the model can be used for predictive purposes.

3. Numerical implementation

Both the Richards equation (1) and the convection–dispersion equation (2) are solved in HYDRUS code (Šimůnek et al., 2006, 2008) using the finite element method in the spatial domain and the finite differences method in the temporal domain. Implementation of the compensated root water and nutrient uptake routines did not require changing the numerical approach to solve these governing equations. However, a two- or three-step approach was needed to calculate the compensated root water and nutrient uptake with passive and active components, respectively, for each time step.

In the root water uptake module, the uncompensated root water uptake (9) and the dimensionless water stress index ω (11) are evaluated in the first iteration step, which is the only step needed when compensated root water uptake is not considered. The compensated root water uptake (13) is evaluated in the second step, prior to solving the Richards equation (1).

A multiple-step approach was required to evaluate the root nutrient uptake term. Only one step is needed, when only passive or no root nutrient uptake is considered. If non-compensated active root nutrient uptake is considered, a two-step approach is required. In this case, passive nutrient uptake (18) and potential active nutrient uptake rate A_p (20) are evaluated in the first step, whereas uncompensated active root nutrient uptake (22) is evaluated during the second step. The additional third step is needed if compensated active root water uptake is considered. In that case, the nutrient stress index π (24) is first evaluated during the second step, so that the compensated active root nutrient uptake (26) can be evaluated in the third step, prior to solving the convection–dispersion equation (2).

4. Examples

The functioning of compensated root water uptake is demonstrated for three examples. While the first example considers a simple one-dimensional soil profile, the second example applies to an axi-symmetrical three-dimensional water flow and nutrient transport domain. In the third example we demonstrate the consequences of the various presented nutrient uptake models, including both passive and active nutrient uptake, with and without compensation. All examples apply to the same loamy soil, for which the soil hydraulic properties were taken from Carsel and Parrish (1988). Also, the same soil water stress response function of Feddes et al. (1978) in Fig. 3 was used for all examples, with $h_1 = -10$ cm, $h_2 = -25$ cm, $h_{3,high} = -200$ cm, $h_{3,low} = -800$ cm, and $h_4 = -8000$ cm. The true h_3 parameter is interpolated from $h_{3,high}$ and $h_{3,low}$ and T_p (see Fig. 3), as done in the SWATRE code (e.g., Wesseling et al., 1991).

4.1. Root water uptake in a one-dimensional soil profile with groundwater table

The first example applies to a one-dimensional 120-cm soil profile with a 90-cm root depth and the root distribution linearly decreasing with depth. The bottom of the soil is bounded by a ground water table that is in hydrostatic equilibrium with the soil profile at the start of the simulation (initial condition). The hypothetical plant is assumed to transpire with a potential transpiration rate, T_p, of 0.4 cm/day, while the water stress index ω_c is varied with values of 1.0 (corresponding to uncompensated root water uptake), 0.75 and 0.5, with the latter two values corresponding with increasing compensated root water uptake as the index decreases. Since this set of model simulations does not include precipitation or irrigation, water required for transpiration will deplete the soil water profile so that the resulting soil water potential (h) gradient will partially supply the root zone with water, driven by capillary rise from the shallow groundwater. Simulations were carried out for a total period of 50 days.
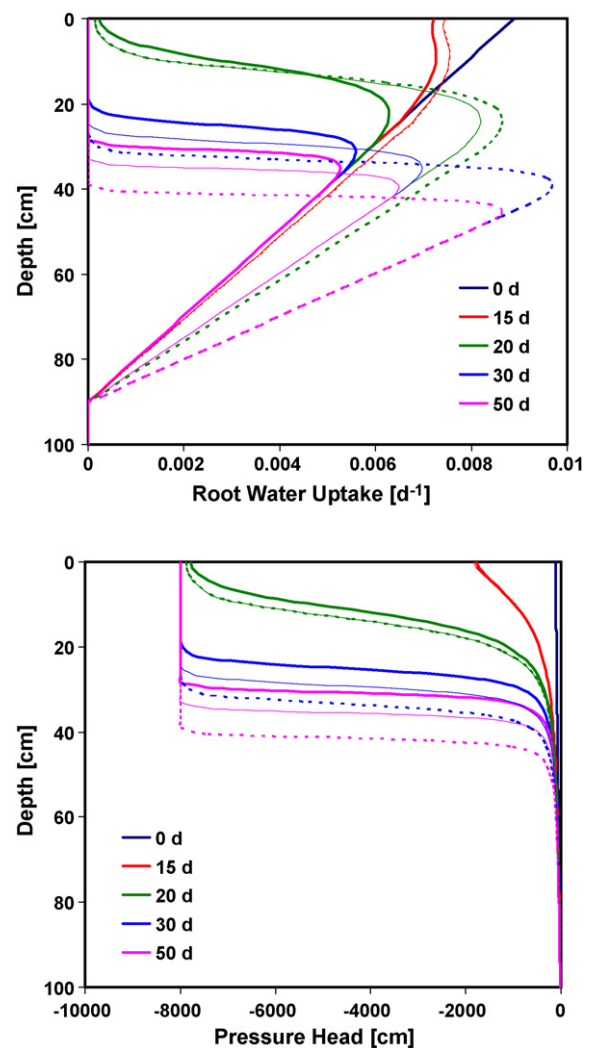

Fig. 6 – Example 1. Root water uptake (top) and soil water pressure head (bottom) profiles for uncompensated (solid thick lines) and compensated root water uptake with values of $\omega_c = 0.75$ (solid thin lines) and 0.5 (dashed thick lines).

Fig. 6 presents the depth distribution of root water uptake, s^* (day^{-1}) and soil water pressure head, h (cm), along the soil profile for the uncompensated ($\omega_c = 1.0$) and compensated ($\omega_c = 0.75$ or 0.5) root water uptake scenarios, whereas Fig. 7 is a plot of both actual (cm/d) and cumulative values (cm) of the potential (T_p) and actual (T_a) transpirations, and water flux at the groundwater table for the three corresponding scenarios during the 50-day simulation period. As Figs. 6 and 7 show, the *non-compensated* root water uptake starts to decrease around the 10th day (Fig. 6) as a result of water stress, with the top 20 cm of the soil profile being fully depleted of water (Fig. 7) after about 20 days of plant transpiration. For the 30–90 cm soil depth, capillary rise provides for sufficient water supply towards the rooting zone, thus allowing the lower root domain to remain unstressed with root water uptake at the normal unstressed uptake rate. Root water uptake rates after about 10 days are always either equal or lower than the root water uptake at the beginning of the simulations.
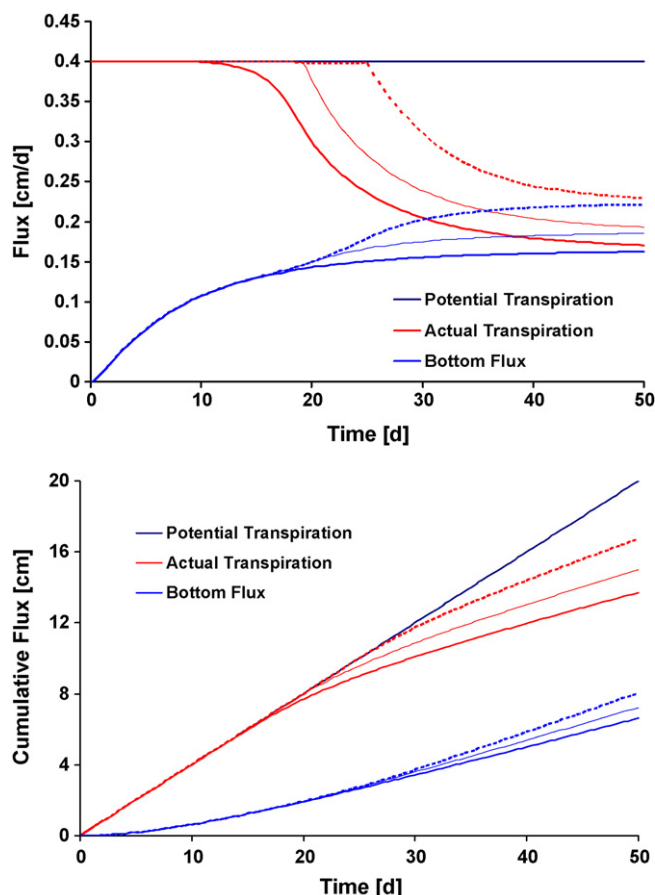
Fig. 7 – Example 1. The potential transpiration (black), the actual transpiration (red), and the bottom flux (blue) (top) and their cumulative values (bottom) for uncompensated (solid thick lines) and compensated ($\omega_c = 0.75$, solid thin lines; $\omega_c = 0.5$, dashed thick lines) root water uptake scenarios. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

For the scenarios that considered *compensated* root water uptake, a reduction in the uptake from the upper part of the profile is initially fully compensated by uptake from the deeper part of the soil profile. Root water uptake rates gradually increase in deeper parts of the soil profile as the upper part of the root zone becomes more stressed. The compensation from larger soil depths is larger for lower values of ω_c. As a result, the root water uptake distribution in Fig. 6 moves to the right as time increases; and increasingly so for the more compensated uptake ($\omega_c = 0.5$) scenario. Since compensated root water uptake is greater than the uncompensated root water uptake at the bottom of the root zone, a larger fraction of the soil profile is water-depleted, thus capillary rise will need to supply a smaller fraction of the root zone.

As a result of water stress, Fig. 7 shows that actual transpiration (T_a) starts to deviate from T_p already after 10 days for the uncompensated scenario, whereas compensated root water uptake continues to be at a potential rate until days 20 and 27 for scenarios with values of $\omega_c = 0.75$ and 0.5, respectively.

During this time period, a reduced uptake from the upper part of the soil profile is fully compensated for by an increased uptake from deeper soil profile. Root water uptake remains significantly higher for the compensated scenarios even when it is reduced from its potential values at later times. Cumulative actual transpiration during the 50 day period increases from about 13.7 to 15.0 and 16.7 cm for the uncompensated and compensated ($\omega_c = 0.75$ and 0.5) root water uptake scenarios, respectively. Daily values of T_a at the end of the simulation period increase from 0.17, to 0.19, and 0.235 cm/day for these three scenarios, resulting in an increase in cumulative plant transpiration by almost 40%. Neglecting root water uptake compensation by plant roots in water-stressed soil conditions would thus result into significant errors in plant transpiration and the soil water balance. The presented interactions of root water uptake and soil moisture and their spatial variations confirm experimental studies by Green and Clothier (1995) and Andreu et al. (1997), with the shifting of preferential root water uptake to the wetter parts of the soil system after irrigation or the development of water uptake fronts moving downwards as the soil dries (Doussan et al. (2006). Irrespective of the selected scenario, near steady-state conditions were attained at the end of the 50-day simulation period, with actual transpiration fully supplied by the capillary rise from the ground water table. Similar results were obtained when considering more realistic diurnal plant transpiration variations similar to natural conditions (0.24 T_p during night time (6 pm to 6 am) and $2.75 T_p \sin(2\pi t/t_{\text{Period}} - \pi/2)$ during the day).

4.2. Root water uptake for an axi-symmetrical three-dimensional profile with irrigation

In the second example we considered an axi-symmetrical flow domain for which both depth and radius values are equal to 100 cm. The initial pressure head ($t = 0$) was −400 cm throughout the soil profile and the potential transpiration rate was 0.04 cm/h. While water needed for transpiration was supplied by capillary rise from the shallow water table in the first example, water was supplied by irrigation for the example two scenarios. Irrigation water application was confined to a 50-cm radius around the center of the simulation domain, at a constant rate of 0.16 cm/h. Since this irrigated area is 4 times smaller than the flow domain, the irrigation flux of four times the value of T_p was exactly equal to the transpiration demand. Root density was assumed to decrease linearly from its maximum value to zero at the 50 cm soil depth, but to be constant in the radial direction. The water stress index ω_c was varied from 1.0 to 0.4, using increments of 0.2.

Fig. 8 presents both actual and cumulative values of the potential and actual transpiration rates. While only a limited reduction in transpiration (0.038 cm/h) was attained for the compensated root water uptake scenario with $\omega_c = 0.4$, root water uptake for the uncompensated scenario was reduced by exactly one half (0.020 cm/h). For the other scenarios with ω_c values of 0.6 and 0.8, T_a was reduced to 0.29 and 0.24 cm/h, respectively. With the uncompensated root water uptake scenario being reduced immediately as the initial pressure head was already on the declining part of the water stress response function (Fig. 3), plant water uptake for the compensated root water uptake scenarios started to decrease
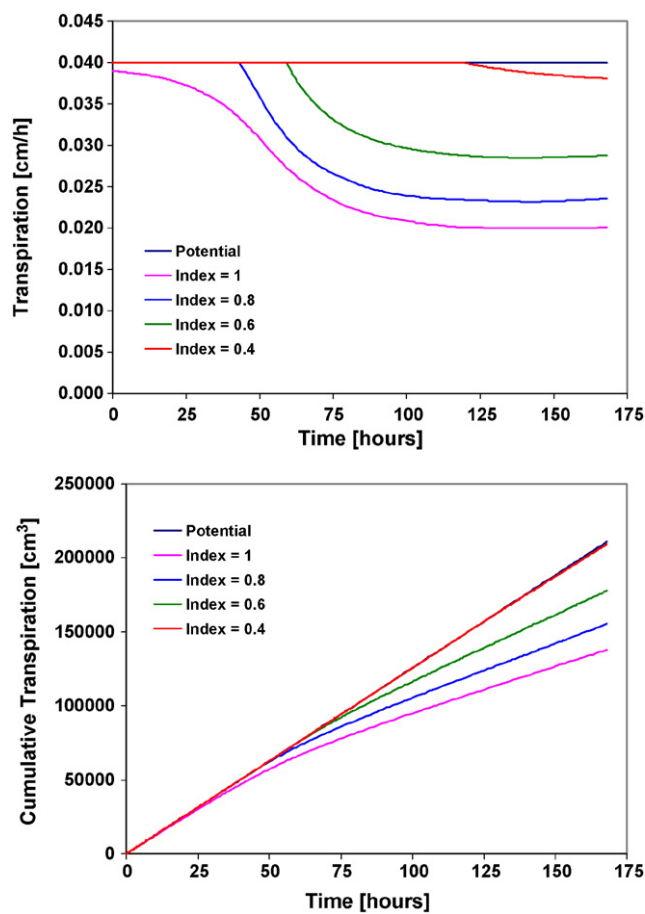
Fig. 8 – Example 2. The potential (black line) and actual transpirations for scenarios with the water stress index ω_c equal to 1.0 (pink), 0.8 (blue), 0.6 (green), and 0.4 (red). Actual values are shown at the top, while cumulative values at the bottom. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)
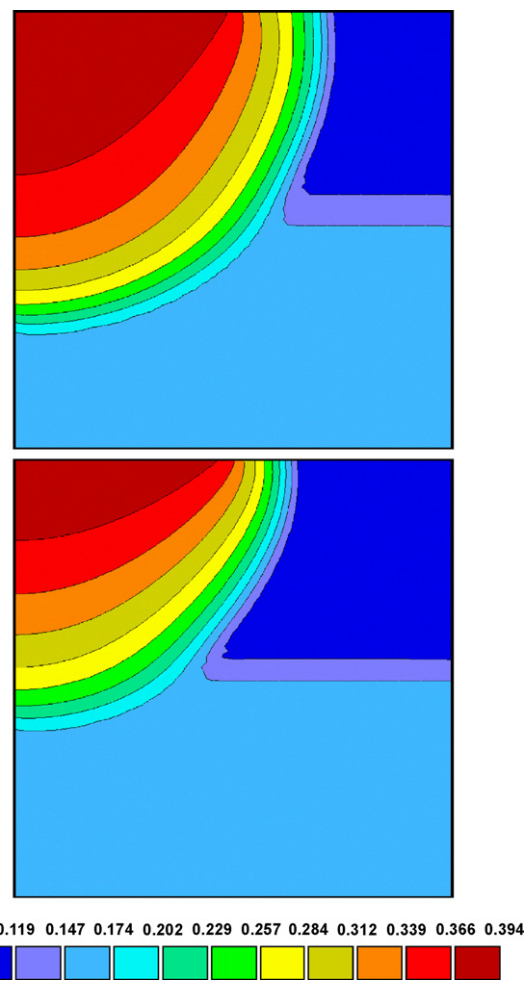

Fig. 9 – Example 2. Water content profiles for scenarios with uncompensated (top) and compensated (bottom) ($\omega_c = 0.4$) root water uptake at the end of the simulation period.

from potential values after 44, 60, and 120 h for scenarios with ω_c equal to 0.8, 0.6 and 0.4, respectively.

Fig. 9 shows water content profiles at the end of the simulation period for scenarios with uncompensated and compensated root water uptake ($\omega_c = 0.4$). Note that the volumetric soil water content corresponding with an initial h-value of -400 is equal to $0.156\,\mathrm{cm^3\,cm^{-3}}$. The portion of the root zone that is not irrigated (right side in Fig. 9) is near the wilting point for both scenarios. Since the water supply rate by irrigation is identical for both scenarios, whereas the root water uptake is significantly larger for the compensated scenario, much more water is present in the soil profile for the uncompensated root water uptake scenario. As a result, the moisture front for this scenario reached a depth of 75 cm, while it propagated only to the 60 cm soil depth for the compensated root water uptake scenario. Water also moved further laterally in the scenario with uncompensated root water uptake. Although more water was taken up from the soil profile with compensated root water uptake, a larger fraction of the root zone was active in the scenario with uncompensated root water uptake since

more water was available in the larger part of the soil profile.

This example with partial root zone wetting by irrigation demonstrated that potential plant water demand can be satisfied when compensated root water uptake is considered. Therefore, spatial root distribution is expected to have a significant effect on T_a predictions if uncompensated root water uptake is considered. Insufficient knowledge of the spatial root distribution may lead to large errors in actual transpiration calculations. However, spatial root distribution effects may be much less important if compensated root water uptake is considered. The compensated root water uptake thus confirms with recent findings (e.g., Roose and Fowler, 2004) that root water uptake is not solely proportional to root density.

4.3. Coupled root water and nutrient uptake in a one-dimensional soil profile with groundwater table and no irrigation

The first example with compensated root water uptake is further expanded in this third example to evaluate the associated impacts on root nutrient uptake, including passive and active

considerations. To simplify this analysis, nutrient transport and uptake was coupled with the example 1 scenario that considered uncompensated root water uptake only (thick solid lines in Figs. 6 and 7 with $\omega_c = 1.0$). We compared six root nutrient uptake scenarios: (a) no nutrient uptake, (b) only passive nutrient uptake (i.e., no active uptake), (c) passive and uncompensated active nutrient uptake, (d) passive and compensated active nutrient uptake, (e) uncompensated active nutrient uptake (i.e., no passive uptake), and (f) compensated active nutrient uptake (i.e., no passive uptake).

Calculations were carried out in relative concentrations. The initial nutrient concentrations in the soil profile and in the ground water were both assumed to be equal to one. The potential nutrient demand, R_p, for scenarios that involved active root nutrient uptake was assumed to be equal to 1 ($-/cm^2$ day) as well, whereas its value was set to zero for the example scenarios without an active root nutrient uptake. For scenarios that excluded passive root nutrient uptake, the c_{max} was set equal to 0, while its value was set to 10 (larger than any simulated dissolved soil solution concentration) for scenarios that include passive root nutrient uptake. The critical value of the nutrient stress index, π_c, was assumed equal to 0.5 for scenarios that allowed compensated active root nutrient uptake. The Michaelis–Menten constant, K_m, was set to 0.1, whereas the minimum concentration, c_{min}, was assumed zero.

While Figs. 10 and 11 shows concentration profiles for the various root nutrient uptake scenarios, the actual and cumulative nutrient uptake rates as a function of simulation time are presented in Fig. 12. It is specifically noted that scenarios without any nutrient uptake lead to an increase in nutrient concentrations in the root zone (Fig. 10, top), and that scenarios that allow active nutrient uptake will lead to a decrease in soil nutrient concentration (Figs. 11) as time progresses. Dissolved soil solution concentrations gradually increase in the root zone for the scenario that neglects nutrient uptake (Fig. 10, top), as caused by decreased volumetric water content by root water uptake. Since water content gradually decreases while the amount of dissolved ions in the root zone remains constant, the resulting soil solution concentrations will gradually increase. Concentrations increase initially fastest close to the soil surface, because the root water uptake is highest in this region. Concentrations in this zone tend to not further increase, after the soil water content is depleted, thus limiting root water uptake by soil water stress. However, as root water uptake continues from deeper soil regions, concentrations will continue to increase there. The increase in nutrient concentrations might eventually affect the soil's osmotic potential and thus cause salinity stress, in addition, thereby further reducing root water uptake.

As expected, there will be no change in soil nutrient concentrations when nutrient uptake is only passive (Fig. 10, bottom), since there are no mechanisms in place that would cause concentration gradients in the soil profile to develop, thus eliminating diffusion/dispersion to occur. Since the c_{max} value was set to be above soil solution concentrations, water removed from the root zone by root uptake takes along all dissolved ions, while water left behind in the root zone will remain at constant concentrations. Yet, the total soil nutrient mass will decrease, because of the passive nutrient uptake and reduction in water contents.
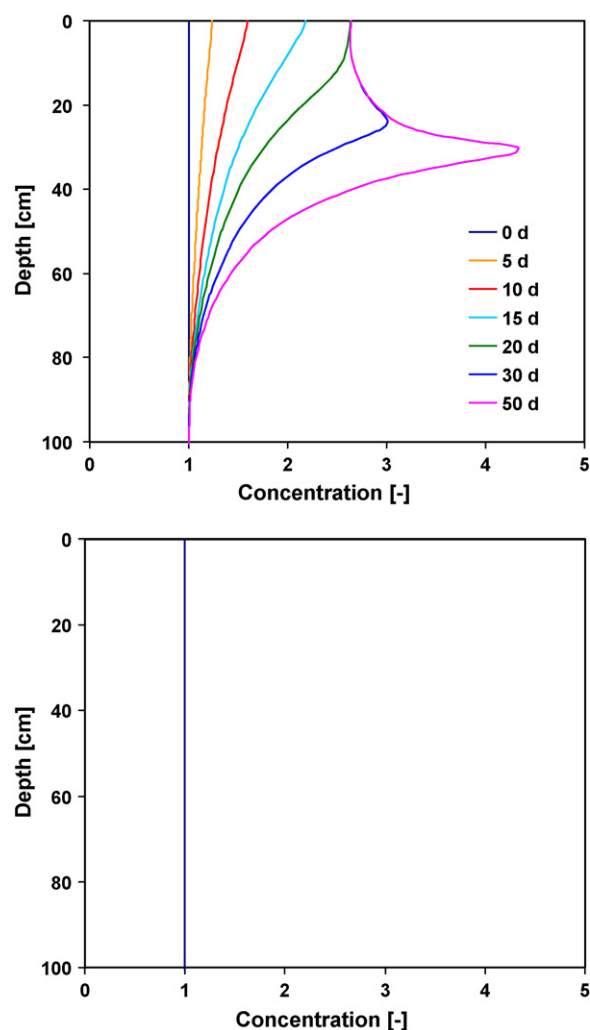

Fig. 10 – Example 3. Depth distribution of nutrient concentration for nutrient uptake scenarios considering (a) no nutrient uptake (top) and (b) passive nutrient uptake only (bottom).

Soil solution nutrient concentrations will gradually decrease throughout the soil profile for those scenarios with active nutrient uptake (Fig. 11), leading to early nutrient depletion in the near soil surface regions of the profile. This depletion is faster for scenarios with compensated root nutrient uptake. We note that there is only a small difference in the depth distribution of nutrient concentration for scenarios that consider (both uncompensated and compensated) active nutrient uptake, irrespective of whether passive nutrient uptake is allowed.

It is important to realize that the absence of nutrient uptake will result in an increase in soil solution concentration as a consequence of root water uptake. No concentration changes were computed for those scenarios where nutrient uptake is solely by passive nutrient uptake, whereas all scenarios that involved active nutrient uptake led to a significant decrease in soil solution nutrient concentration.

Fig. 12 presents the actual and cumulative total plant nutrient uptakes for scenarios where nutrient uptake was
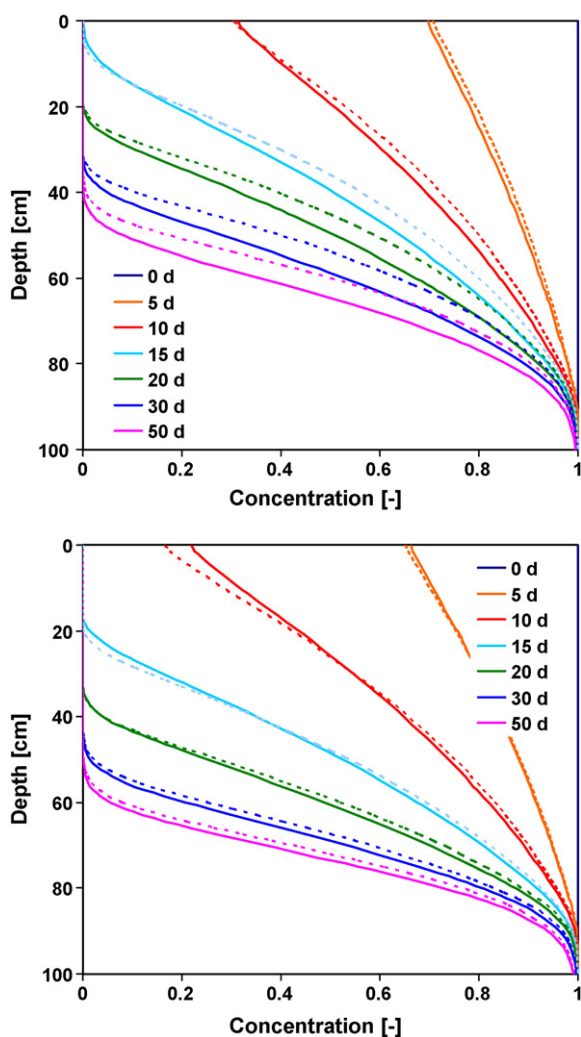
Fig. 11 – Example 3. Depth distribution of nutrient concentration for nutrient uptake scenarios considering either uncompensated (top) or compensated (bottom) active nutrient uptake with (solid line) or without (dashed line) passive nutrient uptake.
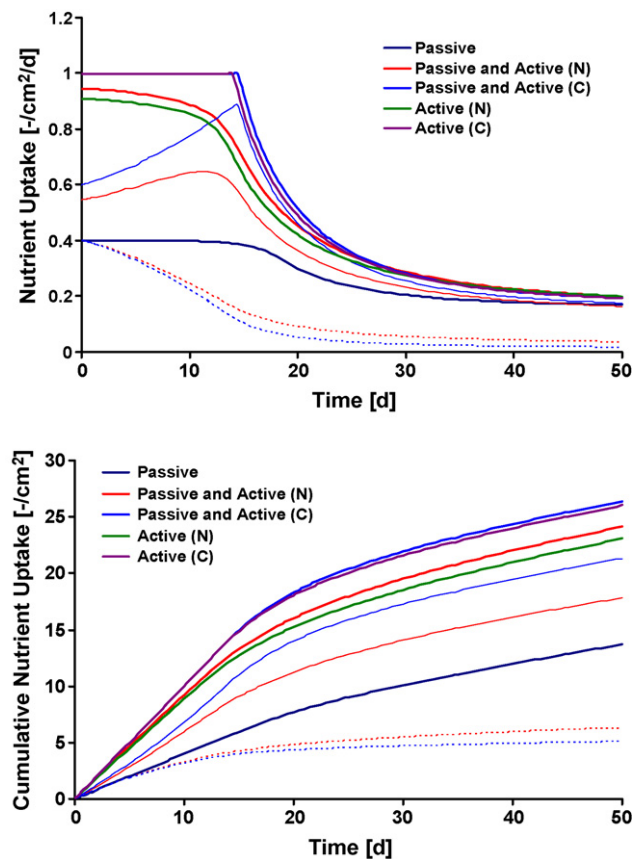

Fig. 12 – Example 3. The actual (top) and cumulative (bottom) nutrient uptakes for scenarios considering (a) only passive nutrient uptake (black line), (b) passive and uncompensated active nutrient uptake (red lines), (c) passive and compensated active nutrient uptake (blue lines), (d) uncompensated active nutrient uptake (green line), and (e) compensated active nutrient uptake (brown line). Thin and dashed lines represent active and passive nutrient uptake components, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

considered. For scenarios where active and passive nutrient uptakes were simultaneously considered, Fig. 12 additionally also shows both active and passive components of the nutrient uptake. When only the passive nutrient uptake is considered, total nutrient uptake is directly proportional to root water uptake as the dissolved soil solution concentrations remain constant. When both active and passive root nutrient uptakes are considered, the total uptake is significantly larger than when only the passive component is allowed. The total root nutrient uptake is initially equal to the potential nutrient demand, if nutrient uptake from regions with sufficient nutrients present can compensate for uptake from nutrient-depleted soil depths. The passive nutrient uptake is significantly smaller when also active uptake is considered, since active uptake leads to lowering of dissolved concentrations that are involved in the passive uptake. The total nutrient uptake is relatively similar for scenarios that consider the

active uptake, irrespectively if the passive uptake is active or not. When the passive nutrient uptake is neglected, the active uptake correspondingly increases, resulting to similar results. As groundwater is the only source of water and nutrients, the root nutrient uptake eventually decreases with time, similarly as the root water uptake. Additional irrigation and fertigation would be needed to sustain water and nutrient uptake at its potential values.

The presented modeling results conform to many experimental nutrient uptake data that show compensation and enhanced nitrate uptake responses by differential nitrate supply (Robinson, 1994, 1996). Moreover, enhanced local nutrient uptake to meet total plant nutrient demand supports the notion that local root uptake rate is not only dependent on the local environment, but also on the environmental conditions of the whole root system (Dunbabin et al., 2002).

5. Summary and conclusions

A compensated root water and nutrient uptake model is presented that is highly flexible. It can accommodate various root spatial distribution functions, including their temporal variations due to root growth. The water uptake model can be used for any stress response function accounting for the reduction of the potential root water uptake due to the soil water pressure and osmotic potential stresses.

The root nutrient uptake model considers either active or passive nutrient uptake or both, is similarly flexible. Few model parameters will allow for a large number of modeling options. The model allows for the absence of nutrient uptake, only passive or active nutrient uptake (each uncompensated or compensated), and any combinations of uncompensated or compensated passive nutrient uptake with either uncompensated or compensated active nutrient uptake (Fig. 1). While the c_{max} parameter activates the passive root nutrient uptake, the potential nutrient demand R_p initiates the active nutrient uptake. Finally, critical values of the water stress index ω_c and the nutrient stress index π_c activate compensation for root water uptake and nutrient uptake, respectively.

Presented examples demonstrated several important characteristics of the compensated root water and nutrient uptake model. Flexibility in modeling compensation of water and nutrient uptake, as presented here, generally reduces plant stress and allows the plant to meet potential transpiration and nutrient demands, irrespective of local soil water and nutrient stresses. Neglecting the possibility of compensation may cause significant errors in the water and nutrient balances, thus affecting biomass production and predicted crop yields.

Root water uptake is closely related to the spatial root distribution function when uncompensated water uptake is considered. However, a much weaker correspondence between the spatial root distribution and root water uptake exists for compensated water uptake. Therefore, spatial root distribution has a significant effect on the prediction of actual plant transpiration when uncompensated root water uptake is considered. The effect of the spatial root distribution is much less significant when compensated root water uptake is allowed. We conclude that a priori knowledge of the spatial root distribution in the soil profile is important when root water uptake is considered to be uncompensated.

Widely different dynamics of nutrient concentrations in the soil profile were simulated when a wide range of root nutrient uptake models were applied. While the scenario without nutrient uptake led to the increase in solution concentrations, the scenario with only passive nutrient uptake maintained constant soil solution concentrations, whereas all scenarios that involved active nutrient uptake led to nutrient concentration reductions.

Only small differences in the depth distribution of nutrient concentrations were determined for scenarios that considered active nutrient uptake, irrespective of whether passive nutrient uptake was involved. This result indicates that soil nutrient concentration measurements are unlikely to provide evidence about the relative importance of active and passive nutrient uptakes.

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