Dynamic root growth in response to depth-varying soil moisture availability: a rhizobox study

Cynthia Maan[1], Marie-Claire ten Veldhuis[1], and Bas van de Wiel[1]

[1]Geoscience and Remote Sensing, Delft University of Technology, Stevinweg 1, 2628 CN Delft,The Netherlands

Correspondence: Cynthia Maan (dcmaan@gmail.com)

Abstract. Plant roots are highly adaptable, but their adaptability is not included in crop and land surface models. They rely on a simplified representation of root growth, independent of soil moisture availability. Data of subsurface processes and interactions, needed for model set-up and validation, are scarce. Here we investigated soil moisture driven root growth. To this end we installed subsurface drip lines and small soil moisture sensors (0.2 L measurement volume) inside rhizoboxes (length x width x height, 45 x 10 x 45cm). The development of the vertical soil moisture and root growth profiles are tracked with a high spatial and temporal resolution. The results confirm that root growth is predominantly driven by vertical soil moisture distribution, while influencing soil moisture at the same time. Besides support for the functional relationship between the soil moisture and the root density growth rate, the experiments suggest that vertical root extension only takes place if the soil moisture exceeds a threshold value at the root tip. We show that even a parsimonious one-dimensional water balance model, driven by the measured water input and output fluxes, can be convincingly improved by implementing root growth driven by soil moisture availability.

1 Introduction

Droughts will become more severe and last longer, resulting in increasing (water) stress on plants. However, their dynamic growth provides the plants with a strong ability to adapt and develop resilience to droughts and climate change (Engels et al., 1994; Gao et al., 2014). Especially the flexibility of the root system can be crucial for the plants resilience to droughts and their natural adaptation strategies (King et al., 2003; Ristova and Barbez, 2018; Wasaya et al., 2018; Zhang et al., 2019). However, the flexibility of plant roots, and their ability to adapt to the environment, is badly included in crop and land surface models (Warren et al., 2015). At the same time, climate and ecosystem models poorly represent the fluxes of water and heat to the atmosphere (Giard and Bazile, 2000), are sensitive to the chosen vertical root distribution profiles (Feddes et al., 2001), and commonly underestimate the impact of the rooting depth on climate and climate change (He et al., 2004; van Dam et al., 2011; Warren et al., 2015).

In most crop and land surface models, the vertical root distribution is simply parameterized as an exponentially decaying function with soil depth (Feddes and Rijtema, 1972; Gerwitz and Page, 1974; Jackson et al., 1996; Kroes et al., 2009), while the maximum rooting depth is described by a linearly increasing function with time (Kroes et al., 2009), i.e. both independently of soil moisture. However, many studies indicate that in reality parameters as root length, penetration depth and depletion rate

at depth are dominantly influenced by soil moisture (Barber et al., 1988; Coifman et al., 2005; Zhang et al., 2019), and that deviating functions and trends are commonly found in nature (Fan et al., 2017).

For instance: For maize and rape plants it was found that the plants respond rapidly to drying and re-wetting the topsoil by locally increasing root growth in soil layers with the most favourable conditions (Engels et al., 1994). The same study suggests
that the plasticity in root growth contributes to the maintenance of an adequate nutritional status (Engels et al., 1994). For cotton, Klepper et al. (1973) were able to stimulate a maximum root length density deeper in the soil by altering irrigation schedules. For wheat plants, King et al. (2003) noted that greater density of fine roots at depth increases yields through access to additional resources. Deeper roots lead to higher resilience to subsequent droughts, by increasing the root zone and water accessibility (King et al., 2003).

Models for dynamical root growth have been proposed by Adiku et al. (1996) and Schymanski et al. (2008). Both models allow for enhanced root density growth in areas where soil water is more easily available. The model of Adiku et al. (1996) furthermore includes a proportional dependency of the root growth on the local root length density, while the bulk root growth is linked to the bulk biomass growth (Adiku et al., 1996). The model was (only) qualitatively validated against root density measurements for two different scenarios: (1) for vertically homogeneous and non-limiting soil water conditions, in which case
the model reproduced an exponential decline in root length density with increasing soil depth; and (2) for limiting soil water conditions with downward increasing water content, in which case the patterns of the simulated and observed root growth deviated from a simple exponential function, with more roots in the lower parts of the soil profile.

In the model of Schymanski et al. (2008), the bulk root density growth depends on the difference between the plants water demand and the actual water uptake: growth of the root bulk in case of water shortage and decay of the root bulk in case of
water abundance. The distributions in the vertical are related to the soil moisture profiles. The model was validated against evapotranspiration data and soil moisture at 10 cm depth.

Neither of the dynamic root growth models have been implemented in crop models and land surface models so far. Such an implementation in coupled models would be important for developing a better understanding of the coupled action of plant roots and the subsurface environment, which could for example lead to the development of methods for system manipulation
and boosting the plants climate resilience.

To investigate the dominance of soil moisture driven root growth, we test a similar -but more parsimonious- root system model. The model is parameterized and validated based on data from our experimental set-up. We use a similar root distribution function as Schymanski et al. (2008), but neglect the possible influence of the plants water demand (or biomass growth rate) on the bulk root growth; note that the existing models are not unambiguous about the latter. To apply our experimental set-up for
model calibration and validation, we simulate a single soil-plant system. Thereby, a direct comparison with the experimental data is possible, and the model can be validated against both, measurements of the water balance components and root growth rates. Our model is characterized by simplicity; the number of calibration parameters is limited, and the water balance model only requires the irrigation and (potential) evapotranspiration flux as system drivers, similar to Schymanski et al. (2008).

In the next chapter, we describe our experiments and model formulation. In Section 2.1, the experimental set-up is discussed.
The results are used to define a diagnostic equation between root growth and soil moisture in section 2.2. Secondly, we combine

the diagnostic equation with the Richard's equation to link the variables to independent system drivers, in Section 2.3 and 2.4. In Chapter 3 conclusions are presented.

2 Experiments

2.1 Experimental Set-up

65 We study 50 days of evolution of maize soil-root systems inside a rhizobox (with a length x width x height of 45 x 10 x 45cm, respectively), Figure 1. Irrigation is supplied continuously at a low flow rate through porous drip lines that were installed at five different levels (with $10cm$ intervals). The flow rate is constant throughout the day, but adjusted in steps to follow the plants growth and demand for water (see dashed curve in Figure 2A). The irrigation depth is increased in steps. At the bottom, a drainage reservoir was installed. The top soil was covered with plastic to prevent evaporation from the soil. The

70 rhizobox was filled with sand-potting soil mix (weight ratio 2.7:1). The soil moisture is measured continuously at four depths inside the rhizobox, while the root density growth is tracked daily through the transparent window. The set-up was placed on a $1g$ precision scale to track the overall water balance. It should be noted, however, that the total time series of the system mass, as plotted in Figure 2A, was subjected to multiple extrapolations from shorter time series (with time spans of hours to days), to deal with (daily) interruptions due to measurements. Furthermore, the (increase of the) plants mass was neglected;

75 the overall biomass growth during the whole period was about 100 gram, which is small compared with the total irrigation and evapotranspiration fluxes. At $t = 0$, a maize plant with a maximum root length of $5cm$ and an above ground height of $10 - 15cm$ was placed inside the rhizobox.

2.2 Diagnostic model of root growth: root follows moisture

Time series and correlations

80 The soil moisture development is plotted together with profiles of the soil moisture and root density growth within succeeding periods in figure 2C. Root development is found to be most pronounced at depth intervals with highest soil moisture. These results suggest that soil moisture and root growth distributions are strongly connected.

Model formulation

We test the following diagnostic equation to model the root growth rate distributed as function of the (normalized) soil moisture:

$$85 \quad \frac{\partial R}{\partial t}\frac{1}{r} = \frac{\theta_n}{\int_L^0 \theta_n}, \quad (1)$$

Where $R(z,t)$ (cm/cm^3) is the root density profile, θ_n is the normalized water content

$$\theta_n = \frac{\theta - \theta_r}{\theta_s - \theta_r},$$

(2)

with θ_s the saturated water content and θ_r the welting point.

$r(t)$ in equation 1 is the depth integrated root growth:

90
$$r = \int\limits_{L}^{0} \frac{\partial R}{\partial t} dz,$$

(3)

with $L(t)$ (cm) the vertical root extension, for which a constant growth rate is taken:

$$\frac{\partial L}{\partial t} = u_1$$

(4)

Hence, equation 1 links the local root growth tendency, normalized with the bulk growth tendency, to the local soil moisture, also normalized with the bulk soil moisture.

Model calibration and results

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Modeled root growth profiles are compared with the experimental data for successive time periods, see Figure 3A-E. Note that the two dimensional root length density observed at the window (in cm/cm^2) is used as a direct proxy for the actual root length density $R(z,t)$ (cm/cm^3). By default, for the results in Figure 3, u_1 is taken as $u_1 = 5cm/day$. In Figure 4 the sensitivity to this parameter is investigated. Patterns of root growth are represented fairly well (Figure 3), with the exception

100 of the sharp local peak that occurs within the time slot $40 - 50$ days (at $z = -30$). This latter case is improved by adopting an extra condition for root growth: a threshold requirement is taken at the root tip, i.e. no vertical extension growth takes place if the soil moisture at the root tip is lower than $\theta_n = 0.075$ (see Figure 3 F-J).

2.3 Soil moisture and water uptake model

Model formulation

105 To calculate the evolution of the water content (θ) due to irrigation, soil water flow and plant water uptake, we apply Richards equation:

$$\frac{\partial \theta}{\partial t} = \frac{\partial q}{\partial z} - S + I$$

(5)

with S $(cm^3/cm^3/min)$ the soil water extraction by plant roots, I $(cm^3/cm^3/min)$ the irrigation, z (cm) the vertical coordinate, taken positively upward , and q (cm/min) the soil water flux density (positive upward) . q is given by Darcy's equation:

$$q = K(h)\frac{\partial(h+z)}{\partial z} \qquad , \qquad (6)$$

with K (cm/min) the hydraulic conductivity and $h(cm)$ the soil water pressure head. Following (Clapp and Hornberger, 1978), h is taken as;

$$h = h_s \frac{\theta^{-b}}{\theta_s} \qquad (7)$$

and K is taken as;

$$K = K_s \frac{\theta^{2b+3}}{\theta_s} \qquad (8)$$

with h_s and k_s respectively the soil water pressure head (cm) and conductivity at saturation, θ_s the saturated water content and b an empirical exponent. The values of k_s, θ_s and b are taken from Clapp and Hornberger (1978), and correspond to loamy sand.

Following Adiku et al. (1996), the soil water extraction S is calculated by:

$$S = u_2 R \theta_n \qquad (9)$$

Where u_2 is the water extraction rate *per centimeter of roots* in ideal conditions $(ml/cm/min$ or $cm^3/cm/min)$, S the actual soil water extraction by plant roots per soil volume per minute $(ml/cm^3/min)$, and $R(z,t)$ is the root length density, i.e. roots per soil volume (cm/cm^3) .

Model calibration

u_2 is determined by comparing the soil moisture data with soil moisture simulations driven by the root profile measurements. The sensitivity to a range of tested variations are indicated in Figure 5. By default, for optimum results in Figure 6, different values were used for the subsequent periods: $1.8 \cdot 10^{-2} ml/cm/hr$, $1.2 \cdot 10^{-2} ml/cm/hr$, $0.9 \cdot 10^{-2} ml/cm/hr$ and $1.8 \cdot 10^{-2} ml/cm/hr$ for the time slots in panels A-D in Figure 6 respectively.

Results and discussion

Soil moisture and water uptake simulations were performed for the following settings for the root density profiles: (1) for the measured root profiles, (2) for the calculated root profiles, and (3) for exponential equivalents (most roots in the upper soil), all

with identical (measured) overall root growth rates. Results are indicated in Figure 6. The first 10 days were omitted because of the lack of observable root growth; it takes a couple of days before the roots can be observed at the window.

135   The results indicate that the soil moisture profiles and water uptake profiles derived from the modeled root profiles correspond fairly well with the results obtained from the measured root profiles (comparison solid and dashed lines in Figure 6), whereas the results derived from the exponentially shaped profiles show larger deviations, especially for the periods 30-40 days and 40-50 days.

    Furthermore, the simulations driven by the measured and modeled root profiles correspond better with the measured total

140 uptake rates compared to the simulations driven with the exponentially shaped root profiles, except for the first period in Figure 6 (10-20 days).

    However, the differences between the modeled water components are relatively small, compared with the big differences in the root profiles. Even with the less realistic exponential root profile, rather similar soil moisture profile shapes are found (Figure 6). In each panel, the local peaks in the soil moisture coincide with the depths of irrigation. Smaller local root densities

145 at these depths correspond with higher and wider soil moisture peaks (compare the dashed and dotted profiles in Figure 6), which can simply be explained by the smaller local uptake rates. Note that wider peaks result in a larger area in which uptake by plant roots can occur. Hence, this positive effect on the water uptake rates implies a negative (regulating) feedback loop between these components of the water balance, which keeps the differences limited.

    In spite of the obvious differences, the limited impact of the root density distribution on the water components, together

150 with the big changeability and limited predictability of a standard outside environment, might raise the question whether it is beneficial for the plant to invest in roots at times when the plant experiences drought, as assumed by Schymanski et al. (2008). The smaller the effects of the investment are, the more beneficial it will be for the plant to only invest during periods of abundant resources (as is assumed in most crop and land surface models via a linear dependency of the root growth on the overall biomass growth).

155 **2.4   A prognostic model for coupled soil moisture and root growth**

Model formulation

Soil moisture and root growth are interacting variables. To *prognostically* simulate the time evolution of both variables, we implement the following equation for root density growth in the model described in Section 2.3:

$$\frac{\partial R}{\partial t} = u_3 \theta_n. \tag{10}$$

160   Hence, the local root growth tendency is now normalized by the (static) root density growth in optimal conditions (saturation) u_3 ($cm/cm^3/min$), instead of by the (measurable) bulk root growth tendency in Equation 1. Equation 10 differs from the formulation proposed by Adiku et al. (1996), which includes a proportional dependency of the root growth on the local root length density. The simulations with the exponential equivalent are performed in a similar fashion: After each update of the

root density profile, the exponential equivalent (with identical overall root length) is calculated and used for calculating the
165 plant water uptake. The model is driven by irrigation data and the estimated overall evapotranspiration fluxes.

Model calibration

u_3 is estimated by comparing the simulated root profiles with the data. The sensitivity to the tested variations are indicated in
Figure 7. By default, for the results in Figure 8, u_3 is taken as $u_3 = 0.2 cm/cm^3/day$.

Results and discussion

170 Also in a coupled fashion, driven by irrigation data and the estimated overall evapotranspiration fluxes, the modeled root
profiles are clearly improvements to the exponential profiles (left column in Figure 8), except for the first 20 days during which
the exponential profile seems to be a good approximation. However, this does not result in a convincing improvement in the
simulated soil moisture profiles and overall water extraction rates (comparison of the data points with the dashed and dotted
lines in the middle column of Figure 8). Note that the results for the exponentially shaped estimates are improved in terms of
175 soil moisture and water extraction rates compared with the stand-alone simulations (comparison of the dotted curves in figure
8 with those in figure 6). Although the vertical root profile shape of the exponential equivalent does not depend on the soil
moisture profile, the bulk root growth rate still depends linearly on the vertically integrated soil moisture field via equation
10 (only in a second step, are the roots redistributed in the exponential equivalent): An off-shape profile initially results in
higher vertically integrated soil moisture values, which triggers extra root growth. Hence, from a 'water balance perspective'
180 an inefficient (unrealistic) profile shape gets compensated by extra root growth. The total difference in overall root growth
between the dynamic and exponential root profile shape is indicated as a percentage in the left column. Hence, these results
underline the relevance of including soil moisture depending (bulk) root growth for realistic water balances. This is in contrast
with the linear dependency of the overall root growth on the overall biomass growth (independently of soil moisture), which is
often assumed in crop and land surface models, and also with the assumption that plants invest in roots at times when the plant
185 experiences drought (Schymanski et al., 2008).

3 **Conclusions**

Our results confirm that there is a strong, and dominant, influence of soil moisture on root density growth and vertical root
extension. We show that root profiles can be predicted rather accurately from information on soil moisture profiles only. If soil
moisture driven root growth is coupled to an infiltration model, both root and soil moisture profiles can be obtained fairly well
190 from the water input and (potential) evapotranspiration fluxes, plus a few constants and simple principles.

We also showed that, in our set-up, the effect of unrealistic root profiles on the water balance components is partly compen-
sated by e.g. spatial diffusion and soil pressure driven water flow redistribution. This means that missing information on the
precise root distribution, does not automatically mean that large errors in the water budgets are made. However, in the latter
case the correct water budget results from 'compensating' errors rather than from correct process mechanism.

195   This study treats root growth independent of above ground processes, while such a dependence is plausible. However, our results suggest that soil moisture status is a dominant factor influencing root growth. Underestimation of the impact of soil moisture on root growth rates, will result in underestimated plant resilience to drought and environmental changes. And for plants probably counts; preventing water stress by continuous adequate root growth, during periods of favorable soil moisture conditions, is better than to cure it.

200   *Code and data availability.* The data for producing the graphs and results will be made available at https://doi.org/10.4121/19513957.

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Competing interests. one author is members of the editorial board of journal HESS. The peer-review process was guided by an independent editor, and the authors have also no other competing interests to declare.

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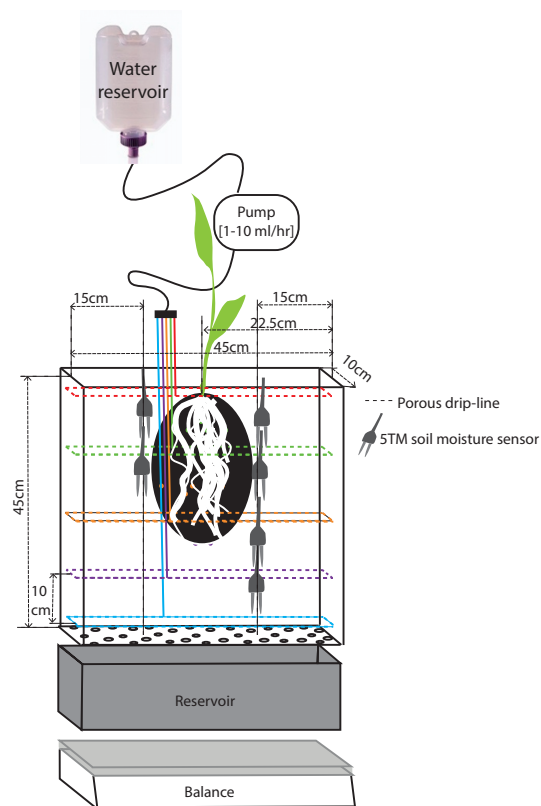
Figure 1. Schematic representation of the experimental setup inside a rhizobox.
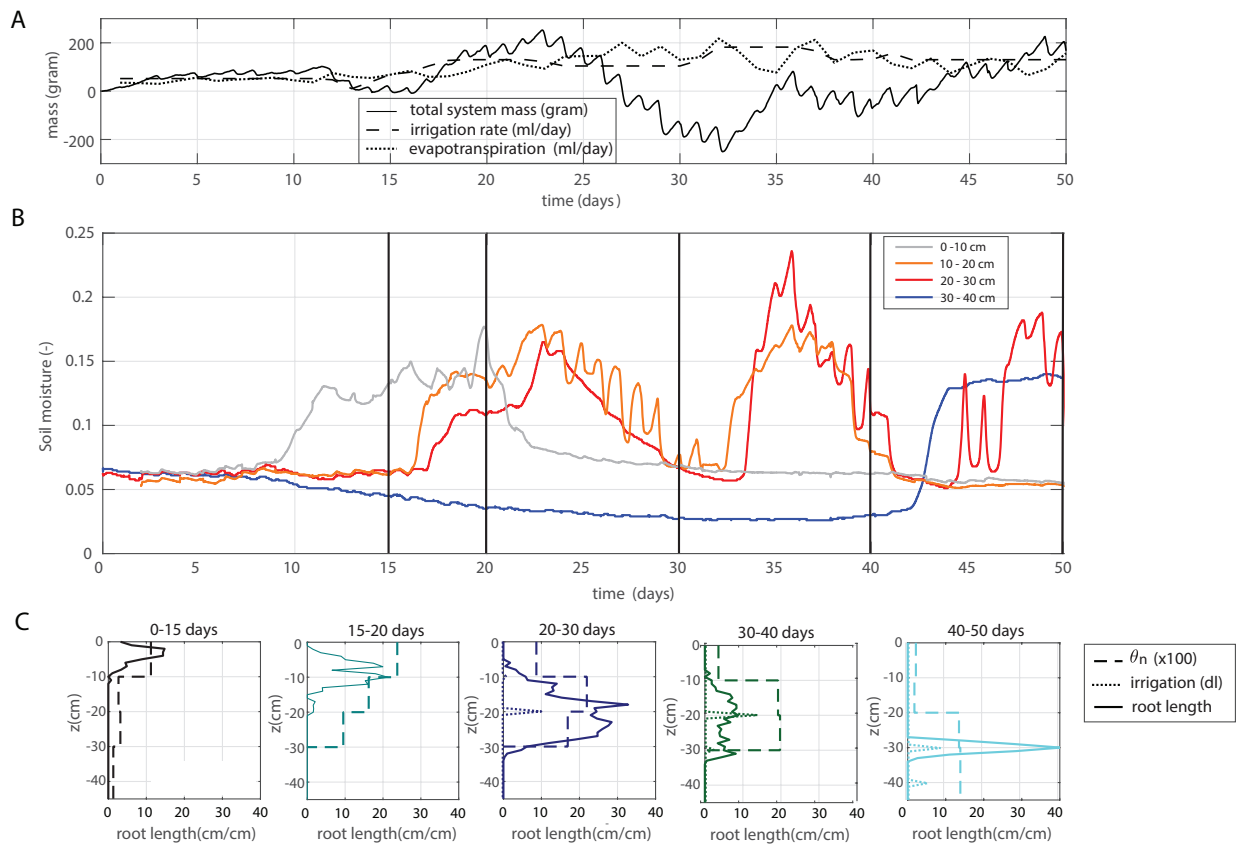
Figure 2. A: time series of the overall system mass, irrigation rate and evapotranspiration. B: time-series of the soil moisture within four different depth intervals. C: root growth (solid lines) profiles within succeeding periods, time-averaged soil moisture profiles (dashed lines) and total applied irrigation volume (dotted lines). Root development is most pronounced in the intervals with largest soil moisture.
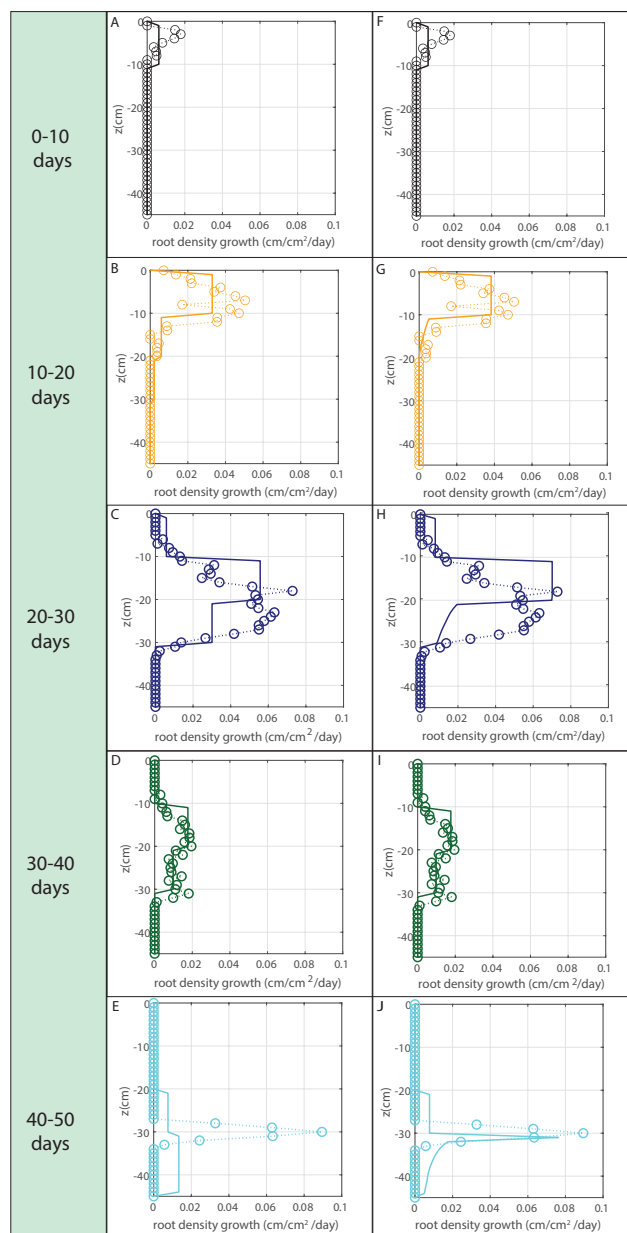
Figure 3. Vertical profiles of averaged root growth rates within succeeding periods as observed (circles) and as diagnostically calculated by equation 1 ('roots follow moisture principle', solid lines), using the measured bulk root growth and soil moisture profiles. Panels F-J show calculations with the extra requirement that root extension growth needs a local minimum soil moisture (threshold) at the root tip: $\theta_n > 0.075$. For both simulations u_1 was taken as $5 cm/day$.
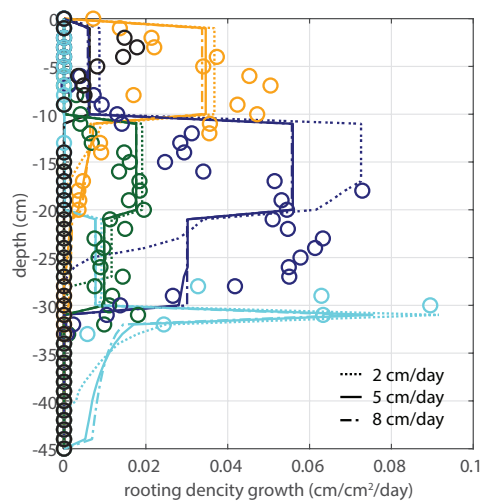
Figure 4. Sensitivity of root growth profiles to different values of the extension rate u_1.
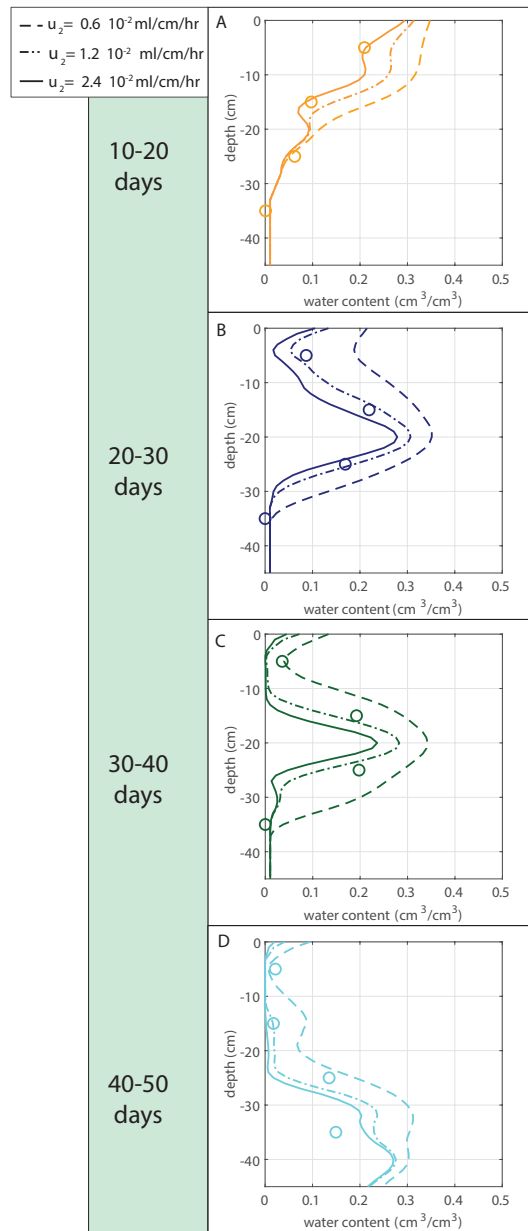
Figure 5. Sensitivity analysis for u_2.
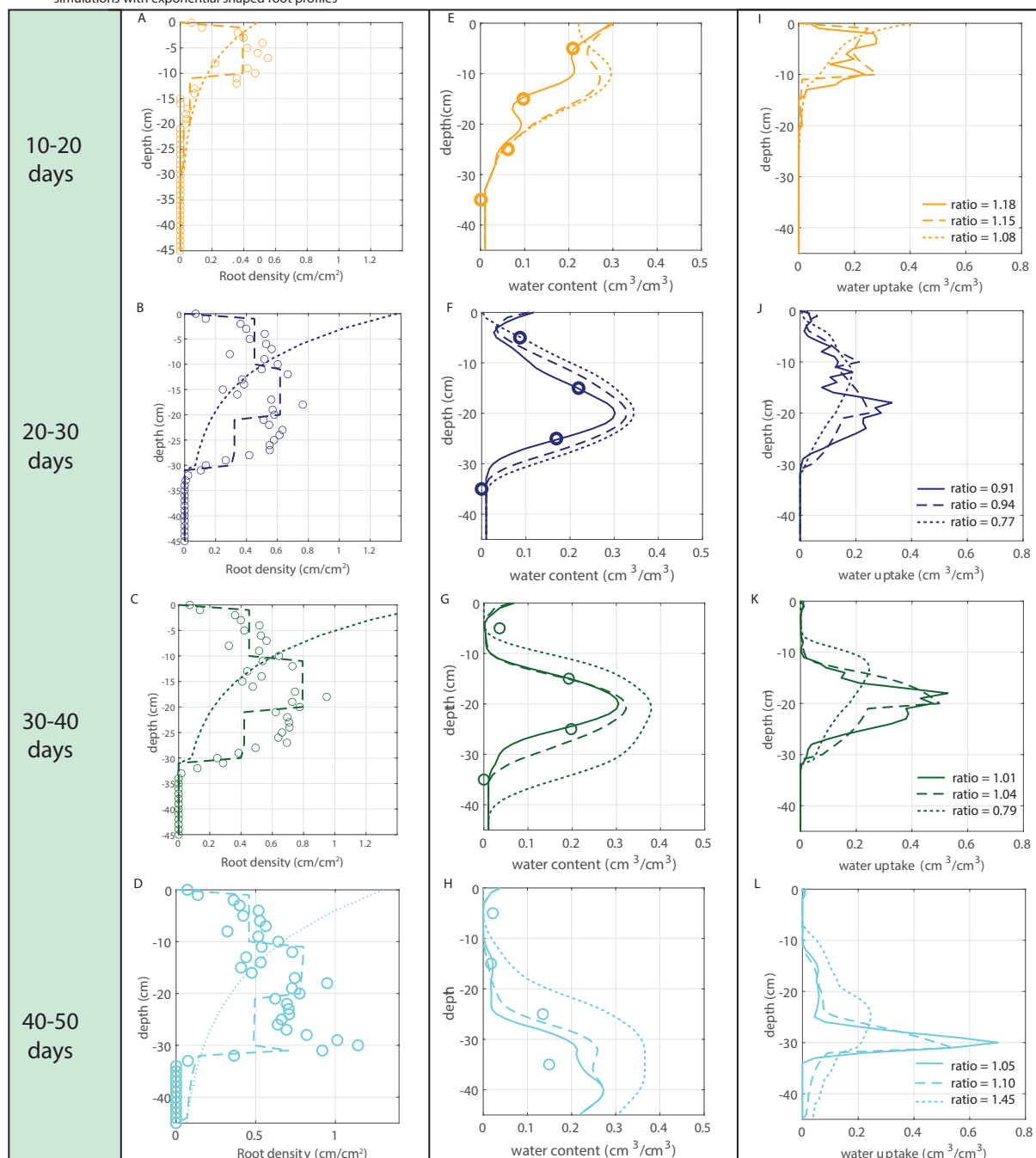
Figure 6. Offline simulations of time averaged soil moisture (middle column) and water uptake (right column) for the measured root profiles at the start of each period, for the calculated root profiles, and for exponential equivalents. The $ratio$ values in panels I-L indicate the ratio's between the modeled and measured bulk (i.e. vertically integrated) water uptake rates.
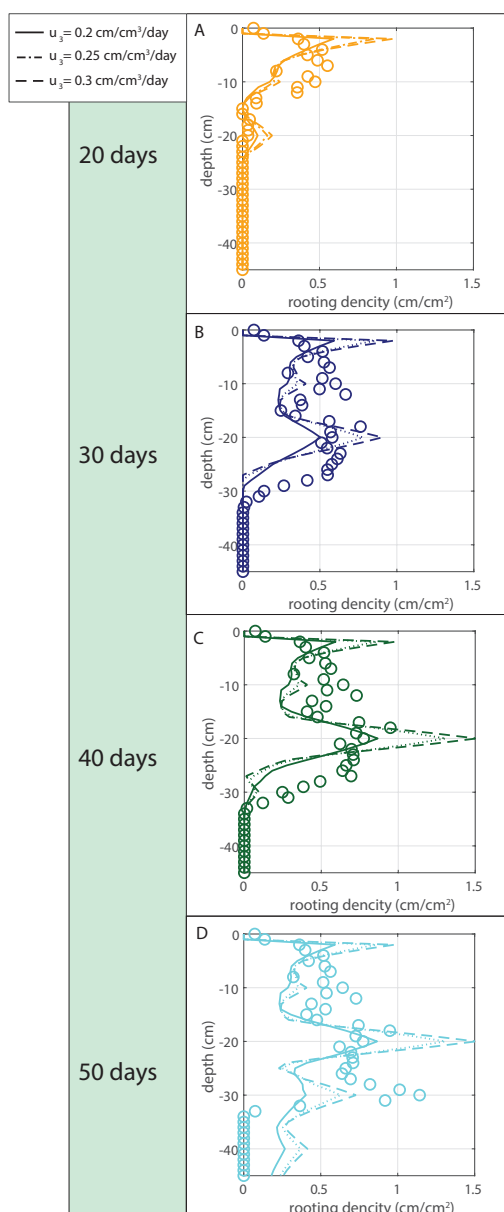
Figure 7. Sensitivity analysis for u_3.
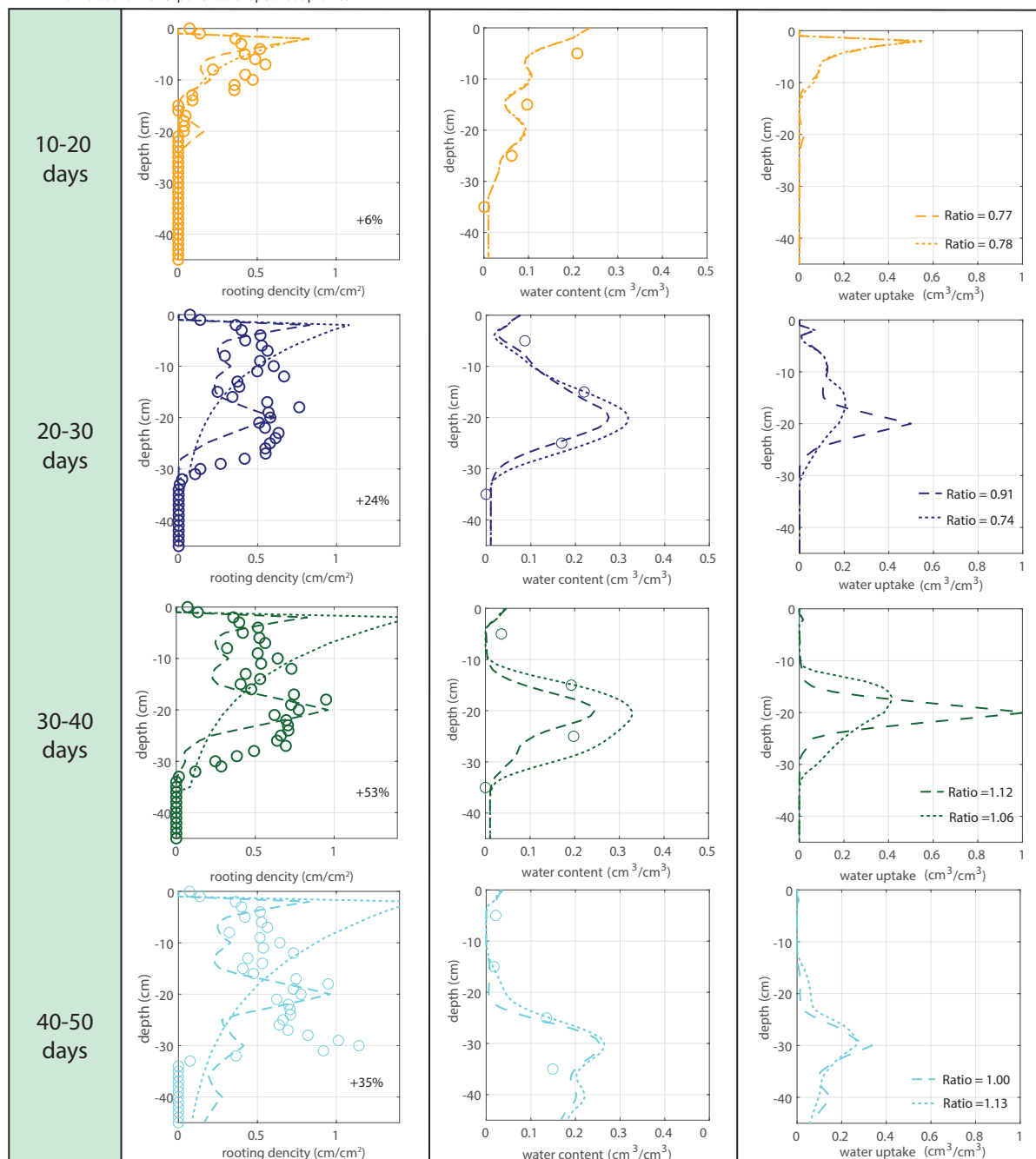
Figure 8. Fully coupled model with irrigation and evaporation as input parameters. Left: Observed (circles), simulated (dashed lines), and exponential (dotted lines) root profiles (at the start of each period). The total difference in overall root growth between the dynamic and exponential root profile shape is indicated as a percentage. Middle: corresponding soil moisture profiles. Right: simulated uptake profiles for simulated and exponentially shaped root profiles.