Response RC1

Dear reviewer,

Thank you for your constructive comments. Please find our reply to your remarks below.

The authors investigated soil moisture-driven root growth using a rhizobox experiment. Their results confirm that vertical soil moisture distribution regulates the root growth profile, while at the same time, the soil moisture dynamics are impacted by the root growth. This study is mainly supported by the parsimonious one-dimensional water balance model they developed, with the functional relationship between the soil moisture and the root density growth rate being its key. The manuscript is well organized and well written.

- Thank you for the positive response

However, despite this reviewer's great interest in this study, he found there is still some room to extend this study for real case applications (if not at the global scale, then at the regional scale, or at least using a range of in-situ sites). This reviewer will motivate his comments as below:

- *This reviewer agrees with the authors that the current LSM should consider the dynamic root growth model, which should take into account the impact of soil moisture.*

- We agree that there is room for extension to real case applications. However, we think that the results presented here – the parsimonious model with very direct relationships between the two state variables (soil moisture and root density) and the experimental setup for validation (including `constant' and highly controlled flow rates through the drip lines) can by itself already be shared with the public.

- *The parsimonious model as the author developed sounds ok, and the current toy example is good for raising the awareness of LSM community on this point. Nevertheless, this is not new. For example, NoahMP[1] has a dynamic root growth module, which considers its dependence on soil moisture and soil temperature. The recently published STEMMUS-SCOPE[2] model also considers the dynamic root growth as a function of air temperature, soil temperature (via water stress factor) and net assimilation.*
- The authors agree that the proposed model is not the first one considering dynamic root growth. However, only few models take *soil moisture driven root growth* into account. STEMMUS scope considers the effect of the total root zone soil moisture availability, but does not consider vertical variations in the soil moisture profile.

The authors are aware (now) of only the coupled NoahMP/VOM-ROOT that considers the impact of the vertical soil moisture profile on the root growth profile. Last model makes another assumption about the bulk root growth: Whereas the bulk growth in NoahMP/VOM-ROOT is demand driven (bulk grows when the plant is in a demand for water, to minimalize costs related to the maintenance) , we here propose a supply driven relationship (soil moisture enhances both, the bulk and local root growth). Hence that existing dynamic root growth models are unambiguous about first principles. E.g. should the bulk root growth rate be related to the biomass growth rate, as Adiko et al. suggest, to the difference between the water demand and the actual water uptake (Schymanski et al./ NoahMP/VOM-ROOT; growth of the root bulk in case of water shortage), or could it be related to the soil water status directly/only (in combination with a maximum root growth for ideal conditions) as proposed here.

When coupling the model with a full plant growth model it would be possible (necessary) to link to or limit root growth by total biomass growth. However, this experiment shows that this very simple supply-driven model seems to work surprisingly well .

- *With the above, this reviewer is trying to search for the unique contribution from this study.*

Unique about this study is the following:

- In the last version of the model we propose to link the (local) root growth rate very directly to the local soil moisture, with no other (e.g. above ground or biomass growth) dependencies. Although this hypothesis seems too simple, it works surprisingly well to model observed root growth.

- In our experiment we maintain the water flow relatively constant. In other studies irrigation is concentrated in short periods of irrigation or rain, which makes it more difficult to distinguish between signals of the forcing and of the response of the plant. By applying constant `irrigation forcing' it is easier to recognize the adjustment processes to constant irrigation forcing.

- Also by simulating a single plant and perform direct measurements on both the soil moisture and root density growth rates simultaneously, i.e. it gives more insight in the direct interactions between the two variables. This information is missing when root densities/weights are measured after the soil moisture measurements. Also we measure both variables (roots densities and soil moisture) directly instead of indirect proxies (like evaporation or temperature) that depend on a translation by more complicated models with more assumptions.

- *The reviewer is not clear or the authors did not show how the current approach can be applied elsewhere in the field.* We propose two different model-versions for root growth that can be applied in different settings/situations:

- The first one is *only the relationship between (vertical varying) soil moisture and root density growth*. This part of the model is easy to couple with a LSM, because the *vertical extension velocity u1* is a parameter that is already included in many LS models including root growth (albeit excluding soil moisture driven root growth), and is therefore already estimated/determined for different plants and crops. The most easy way to implement our model in the most basic form (only the impact of vertical varying soil moisture) is to incorporate only equation 1 (possibly in combination with adding a threshold value at the root tip as we also propose), and leave the bulk (depth integrated) root growth of the LSMs intact.

*The water extraction rate per centimeter of roots in saturated condition*s *u2* was only introduced to make a simple translation between the vertical root profiles and the (measureable) soil moisture. Most existing LSMs contain a much better described and well validated module to calculate water extraction from given root profile and soil moisture profiles. So this part of the model is not meant for incorporation or practical application.

- In the second version we propose to link the root growth rate directly to the normalized soil moisture. This is a new proposal/hypothesis. We however fully agree that further measurements and experiments are needed to test this hypothesis (for identical plant types), and to determine *the root density growth rate in optimal conditions (saturation) u3* for different plant types. Note however, that we make use of only one and the same value to simulate the root growth in all time spans and at each level in Figure 8 . In practical applications, to implement this model in LSMs, it will be necessary to maximize the total root growth to (a part of) the total biomass growth. The results suggest, however, that this dependency might not be dominant (i.e. the experiment suggests that the root growth is dominantly driven by soil moisture).

Particularly, the most important parameters (e.g., u2/u3) are determined via sensitivity analysis, which makes this reviewer wonder how to obtain these parameters in the field, and further at regional/global scale?

Parameters u1 and u3 could be determined by repeating experiments and should be extensively tested in regional/global scale models. Note that differences in modeled root distributions (derived by the tested parameters values) are much smaller compared with the difference with the exponential distribution, so results from preliminary experiments could already make an improvement in the root distributions compared with the exponential functions.

- *Please find attachment with some minor comments.*

Please see the other 'Reply to reviewer' file to see our reply on the minor comments in the attachment.

References:

1. Gayler, S., Wöhling, T., Grzeschik, M., Ingwersen, J., Wizemann, H.-D., Warrach-Sagi, K., Högy, P., Attinger, S., Streck, T., and Wulfmeyer, V. (2014), Incorporating dynamic root growth enhances the performance of Noah-MP at two contrasting winter wheat field sites, Water Resour. Res., 50, 1337– 1356, doi:10.1002/2013WR014634.

2. Wang, Y., Zeng, Y., Yu, L., Yang, P., Van der Tol, C., Yu, Q., Lü, X., Cai, H., and Su, Z.: Integrated modeling of canopy photosynthesis, fluorescence, and the transfer of energy, mass, and momentum in the soil–plant–atmosphere continuum (STEMMUS–SCOPE v1.0.0), Geosci. Model Dev., 14, 1379–1407, https://doi.org/10.5194/gmd-14-1379-2021, 2021

Response RC2

Dear reviewer,

Thank you for your constructive comments. Please find our reply to your remarks below.

- *This work investigates the driven factor of root growth. It provide a simply but practical method to model root growth.*

Thank you for this positive response

Here the manuscript needs some improvements to enhance its clarity and readability. The specific comments are as follows.

Specific comments:

- *L 21-24: some models described the maximum rooting depth by a linearly increasing function with accumulated temperature.*

The authors agree that temperature can be a dominant driving factor. We added the following line in the MS (see line 25):

> "Some exceptional models treat root growth more dynamically by relating root growth to soil related parameters as accumulated temperature or root zone soil moisture. Models that take the vertical profiles of soil moisture into account, however, are scarce."

- *L47 : As I know, Some crop (e.g. Spacsys and STICS) and land surface models (e.g. CLM 5.0) have implemented dynamic root growth.*

These models have indeed a dynamic root growth component, but do not include a dependency on the vertical variation in soil moisture.

- *L 85: equation (1): the theta_n in bottom right should be followed by 'dz'*

Thank you, this has been adjusted in the MS (see equation 1)

- *L 142-144: The relative insensitive soil moisture should be the reason why exponential root profile is widely used in crop models and land surface models*

Our data indeed suggests that roots do not only `follow moisture', but the moisture also `finds roots' if roots are locally not present (by diffusion), reducing the resulting error made by assuming exponential profiles. However, the experimental setup in an enclosed box favors this process unrealistically. At a larger scale the ‘root follows moisture routine’ is expected to have a more pronounced effect on the soil moisture.

- *Fig. 7 and Fig. 8: “rooting dencity” should be “root density”.*

Thank you. This has been adjusted in the manuscript

1. The reviewer comments that some models described the maximum rooting depth by a linearly increasing function with accumulated temperature.

Response RC3

Dear reviewer, dear dr. Schymanski

Thank you for your constructive comments. Please find our reply to your remarks below.

The manuscript by Maan et al. describes an experiment where a maize plant was grown in a transparent rhizobox and root growth was monitored along with soil moisture in the vertical soil profile. The authors compare different model simulations with the observations, one with a prescribed exponential root distribution, and several simulations based on dynamic root distributions with different levels of observation data assimilated into the simulations. The authors find that root growth rates follow the soil moisture distribution, and that this could be simulated by assuming that root growth rate is a function of soil moisture and only happens at a normalized water content greater than 0.075.

- *The results presented are interesting and potentially insightful, but unfortunately, the paper is not well organized and lacks details and clarity. Therefore I found the results difficult to interpret and the conclusions difficult to verify. The paper consists of essentially three separate methods and results sections, one for each model version. It is not clear which parameters were calibrated in each model run and how, e.g. whether in 2.4 only u3 was calibrated, or also u2, and on what data precisely.*

The Manuscript has been adjusted. In lines 118 and 149 the words " and for the further experiments" were added to clarify that the obtained value for the considered calibration parameter– calibrated with the considered data in that section – is also applied in the subsequent runs and sections.

Hence, in each section, one extra parameter is calibrated, while the other is taken from the previous step:

- In section 2.2 ('root follows moisture' model) *the vertical extension velocity u1* is calibrated on the measured root growth profile/distribution. Note however that the results are not that sensitive to this parameter (figure 4)
- In section 2.3 (soil moisture and water uptake model) *The water extraction rate per centimeter of roots in saturated condition*s *u2* is calibrated based on the soil moisture data, while u1 is taken from section 2.2 (based on the root growth data)
- In section 2.4 (the prognostic model) *the root density growth in saturated (assumed to be ideal) conditions u3* is calibrated on the root density data. u1 (calibrated against the same root growth data) and u2 are taken directly from the previous sections and thus not calibrated for the `updated'

version of the model. We fully agree that it would be necessary to repeat these experiments for different datasets, in order to get more confidence about the parameter values.

- *It is also not clear in which soil depth how much irrigation was applied when,* The authors adjusted the MS to make the levels of irrigation visible in figure 2 D (red line). The irrigation depth was increased in steps (but normally remained constant in the order of days to weeks). We also noticed that the dotted lines in the first two panels in figure 2 C were missing by omission, this has been corrected in the manuscript (Figure 2 C).

At each moment only one level is irrigated, this has now been clarified in the MS in line 79.

- *and whether the vertical soil moisture differences were induced by differential irrigation or root water uptake.*

The vertical soil moisture is determined by both processes, differential irrigation and root water uptake. In the MS we conclude that there is a strong correlation between the soil moisture field and root growth field, see e.g. line 101.

- *The main conclusion is that root growth is strongly determined by soil moisture, with high soil moisture promoting root growth. However, since irrigation was "adjusted in steps to follow the plants growth and demand for water" (L68), and the soil moisture increases over time in the deeper soil (Fig. 2C), I am a bit confused in how far the vertical soil moisture distribution was controlled and if it really triggered differential root growth. More information about the experimental strategy would be helpful.*

The vertical soil moisture differences were induced by a combination of differential irrigation and differential water uptake. The irrigation supply, controlled at (relatively constant) low rates during the experiment. Although we adjusted the irrigation amount and depth in steps, we see the irrigation as (relatively independent) system driver, since it is not directly controlled by soil moisture or root growth.

Note that the irrigation depth was generally adjusted only after the rooting depth seemed to stabilize (e.g. the depth was increased between day 15 and 17 after the maximum root length was constant for a week; the depth was adjusted on day 38, after weeks of constant maximum root length). Between day 17 and 21 the irrigation depth has been modified several times because the plant was unable to absorb the water because there were only few roots at the deeper irrigation depth (the system weight increased, see panel A, because the water uptake rate decreased) . Hence, the soil moisture was the first factor that changed, followed by active root growth). The spatial correlation between the water content and the root density growth rates (figure 2) suggests a causal relationship.

- *I would propose to consolidate the methods and results in two separate sections as per standard convention, and include sufficient details about the experimental and modelling methods to enable reproduction of the experiment and analysis.*

The authors fully agree that sufficient details should be given to enable reproduction. However, the authors think that sufficient clarity can be given without changing the structure of the paper. The review process helped the authors to identify the missing information in the paper. Details about the experimental and modelling methods have been added in the MS in the following paragraphs and figures:

- Section 2.1. many details about the experimental methods were added, including information about the sensor types and the applied software.
- Figure 2. Panel D has been added give clarity about the irrigation depth and observed maximum rooting depth.
- For all the Figures that test the sensitivity to the calibration parameters (Figures 4, 5 and 7) a description of the calibration parameter has been added to the captions.

- *The authors promise to publish the data for producing the plots and results in the future, and provided links for the referees, but unfortunately, the links did not work for me, so I was not able to assess if the promised material will be indeed adequate to enable reproducibility of results.*

The authors are very sorry that the data has not been visible before. The data is accessible via the following link: https://figshare.com/s/f206405c95ebfbbf9bf7 , and we can soon also active the DOI.

- *I added detailed comments in an annotated pdf-file, as they are too many to list here. Some of the equations provided are incorrect, but I cannot tell if they were correct in the analysis. For linguistic glitches, I just highlighted bits of text in yellow. I hope that my review will help to revise the manuscript and add more clarity about the methods and results.*

The authors revised the equations in the code, and were delighted to find that the indicated errors were omissions in the text (not in the code). However, the remarks led us to discover another omission in the code; the `effective saturation van Genuchten' (equation 2) was used instead of `soil wetness' in equation 6 and 7. This has been corrected and the results were analyzed. Fortunately, the resulting differences in the graphs are small and do not affect the main results and conclusions of the paper. All the figures and calibration values that are affected have been updated in the manuscript.

Thank you very much for all the helpful comments. Please see the other ‘Reply to reviewer’ file for the annotated pdf file and a reply to all the detailed comments.

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

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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

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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

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 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; 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

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:

$$\frac{\partial R}{\partial t}\frac{1}{r} = \frac{\theta_n}{\int_L^0 \theta_n}, \tag{1}$$

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

$$\theta_n = \frac{\theta - \theta_r}{\theta_s - \theta_r}, \tag{2}$$

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

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

$$r = \int_L^0 \frac{\partial R}{\partial t} dz, \tag{3}$$

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

$$\frac{\partial L}{\partial t} = u_1 \tag{4}$$

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

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 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

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

$$\frac{\partial\theta}{\partial t} = \frac{\partial q}{\partial z} - S + I \tag{5}$$

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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:

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

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

$$h = h_s\frac{\theta^{-b}}{\theta_s} \tag{7}$$

and K is taken as;

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

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:

$$S = u_2 R\theta_n \tag{9}$$

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.

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 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 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 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).

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:

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

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

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root density profile, the exponential equivalent (with identical overall root length) is calculated and used for calculating the 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 $u_3 = 0.2cm/cm^3/day$.

Results and discussion

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 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’ 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 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 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 compensated 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.

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.

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

Author contributions. Cynthia Maan: conceptualization, experiments, code- and model design, writing - original draft, data curation. Marie-Claire and Bas van de Wiel: funding acquisition, supervision, writing - Review & Editing

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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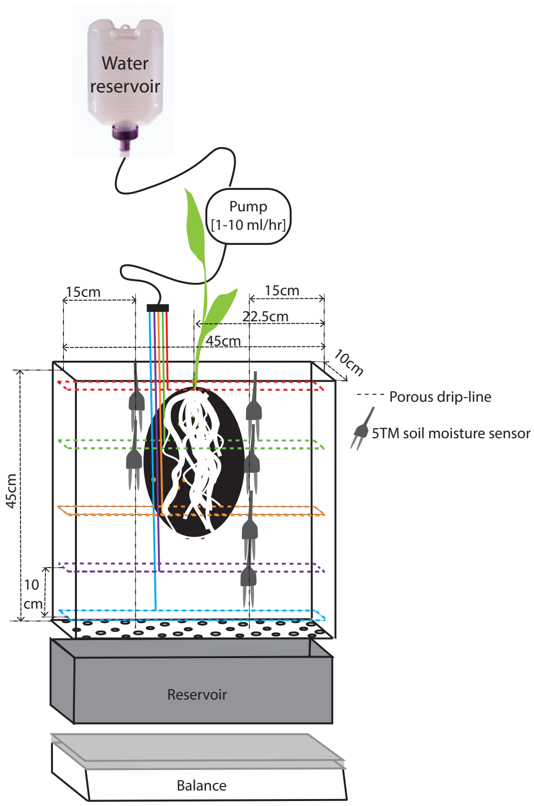

Figure 1. Schematic representation of the experimental setup inside a rhizobox.

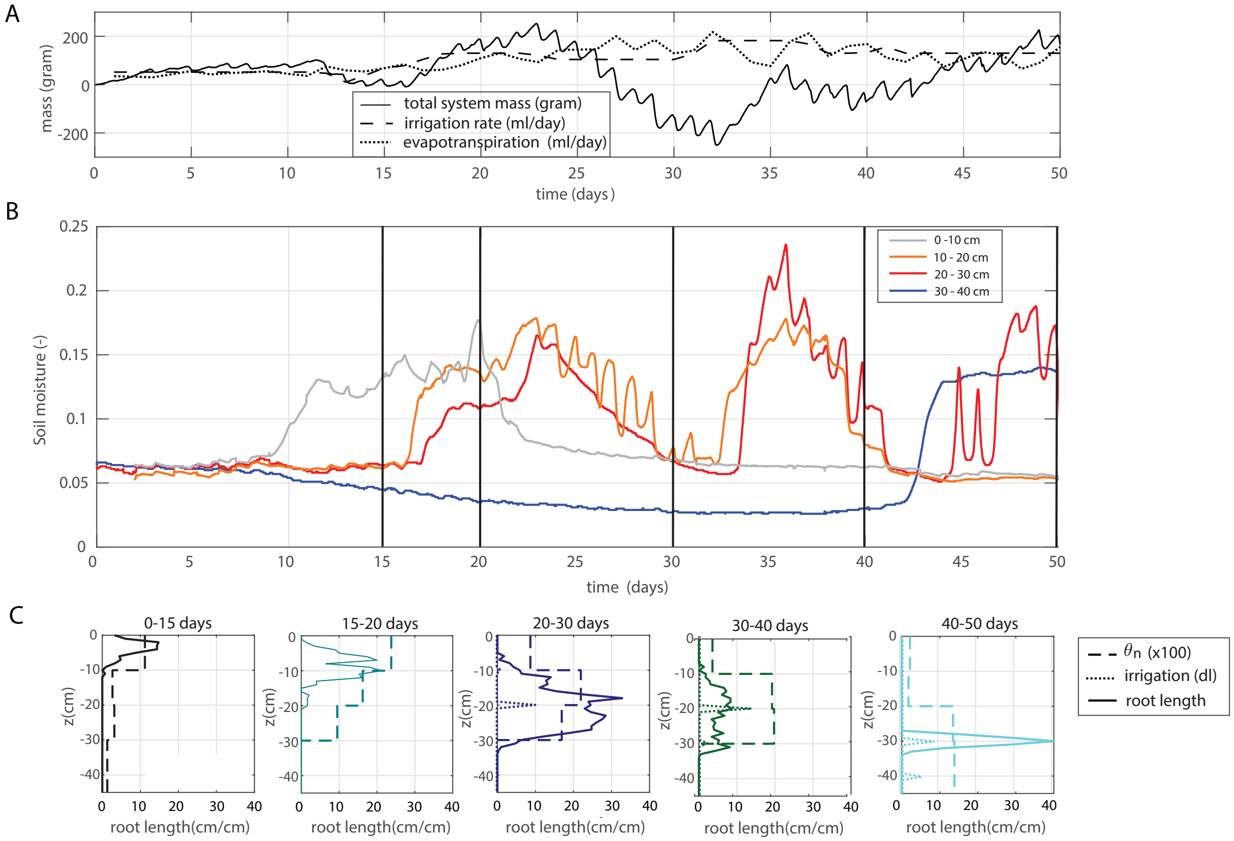

Figure 2. A: time series of the overall system mass, irrigation rate and evapotranspiration. B: time-series of the soil moisture within four different depth intervals. C: root growth (solid lines) profiles within succeeding periods, time-averaged soil moisture profiles (dashed lines) and total applied irrigation volume (dotted lines). Root development is most pronounced in the intervals with largest soil moisture.

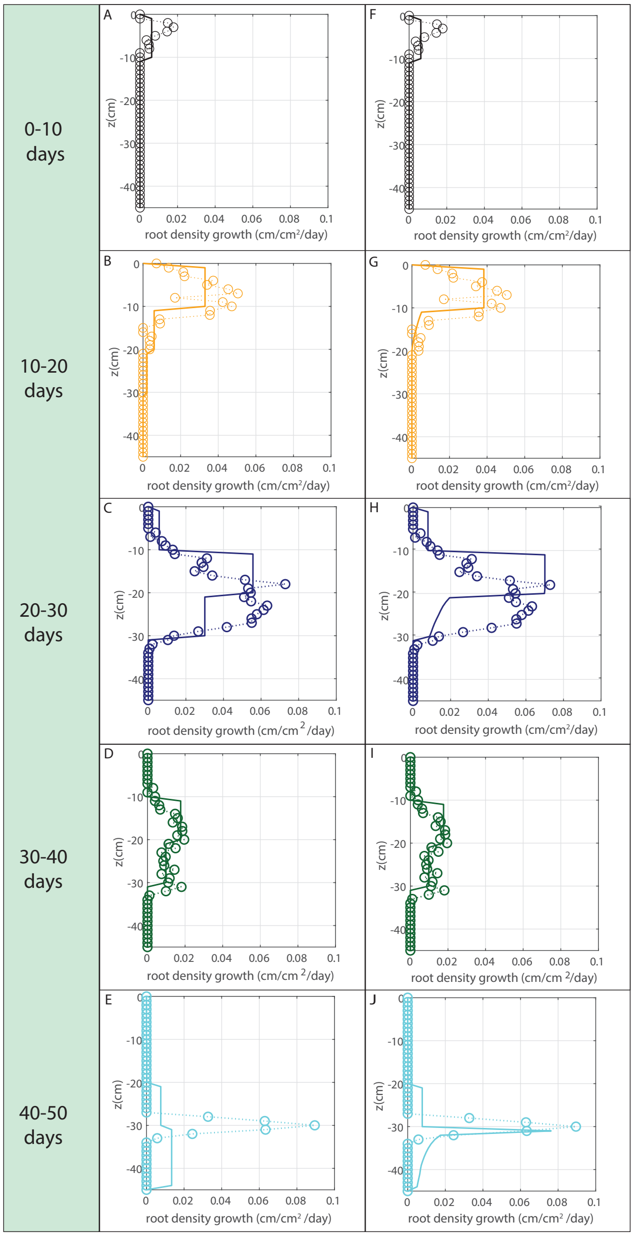

Figure 3. Vertical profiles of averaged root growth rates within succeeding periods as observed (circles) and as diagnostically calculated by equation 1 (‘roots follow moisture principle’, solid lines), using the measured bulk root growth and soil moisture profiles. Panels F-J show calculations with 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 $5cm/day$.

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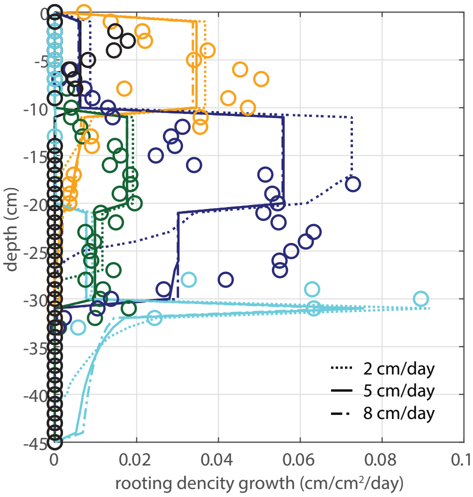

Figure 4. Sensitivity of root growth profiles to different values of the extension rate u_1.

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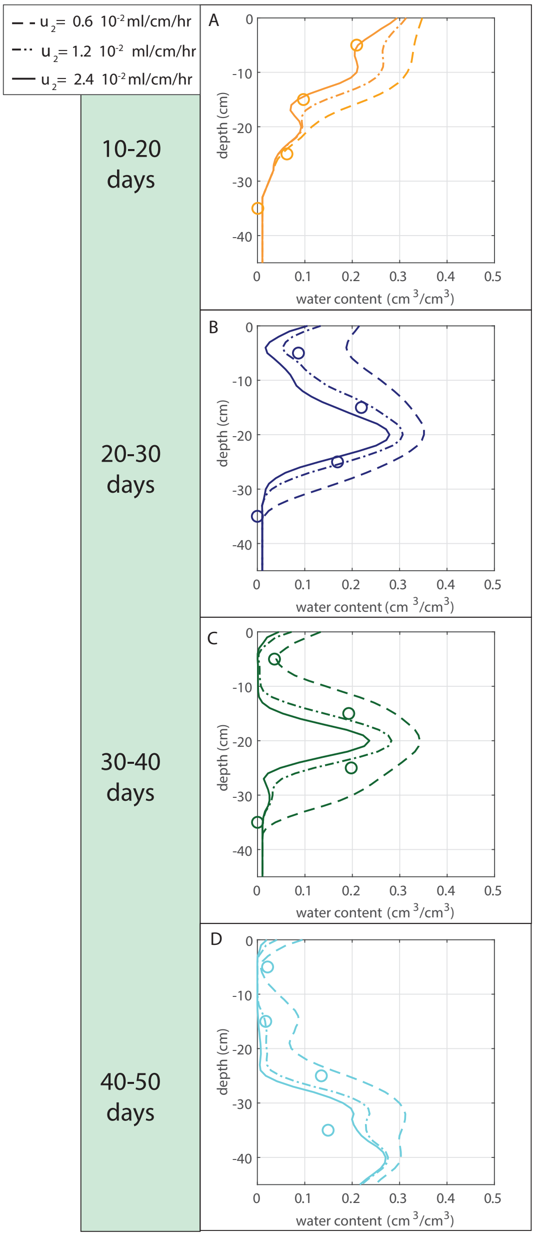

Figure 5. Sensitivity analysis for u_2.

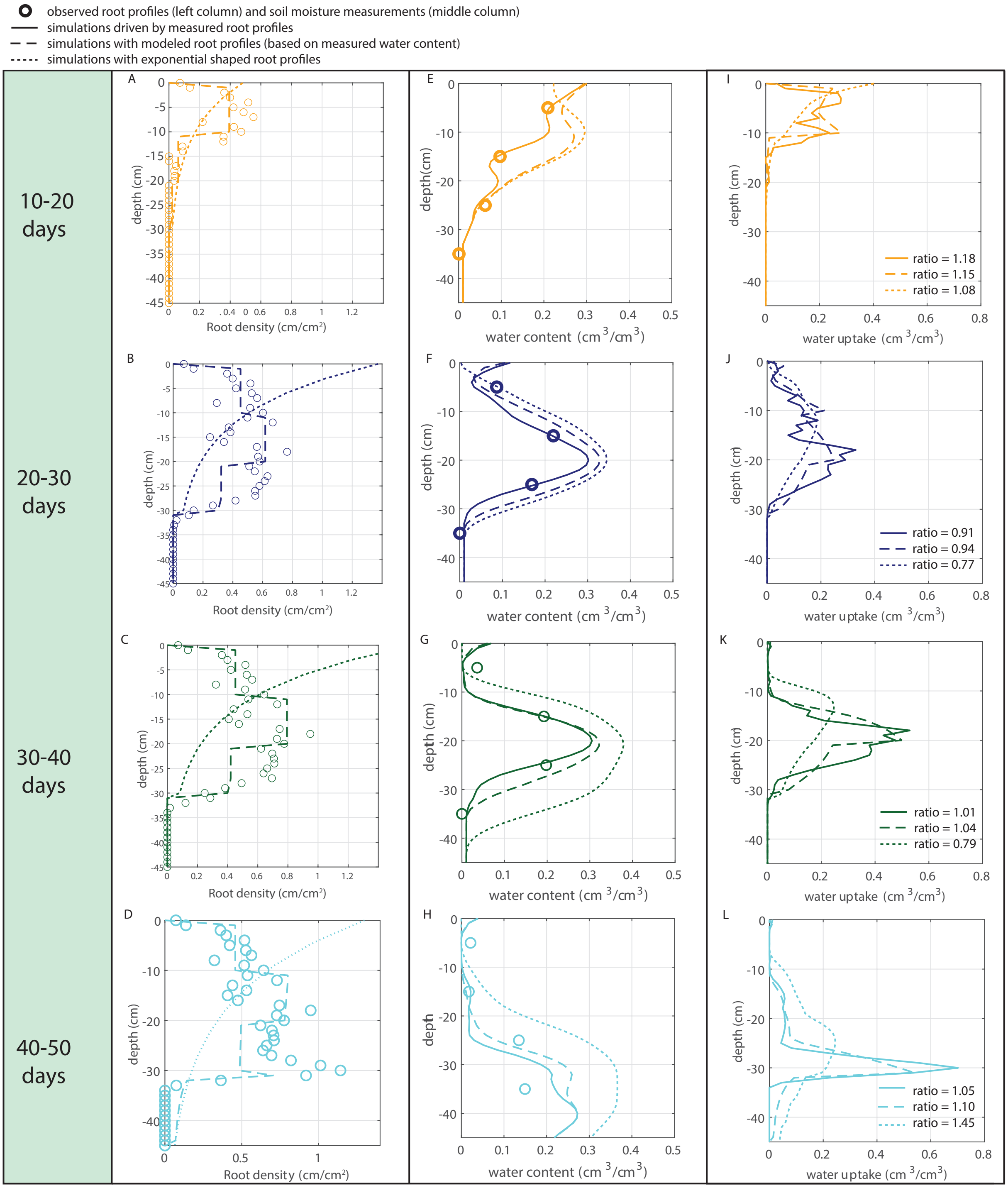

Figure 6. Offline simulations of time averaged soil moisture (middle column) and water uptake (right column) for the measured root profiles at the start of each period, for the calculated root profiles, and for exponential equivalents. The *ratio* values in panels I-L indicate the ratio's between the modeled and measured bulk (i.e. vertically integrated) water uptake rates.

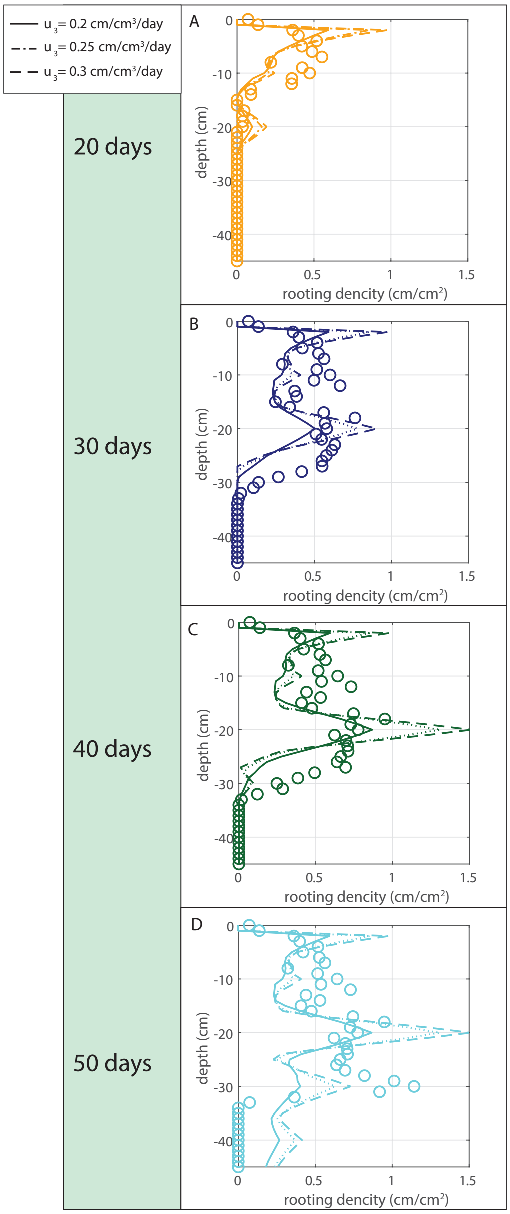

Figure 7. Sensitivity analysis for u_3.

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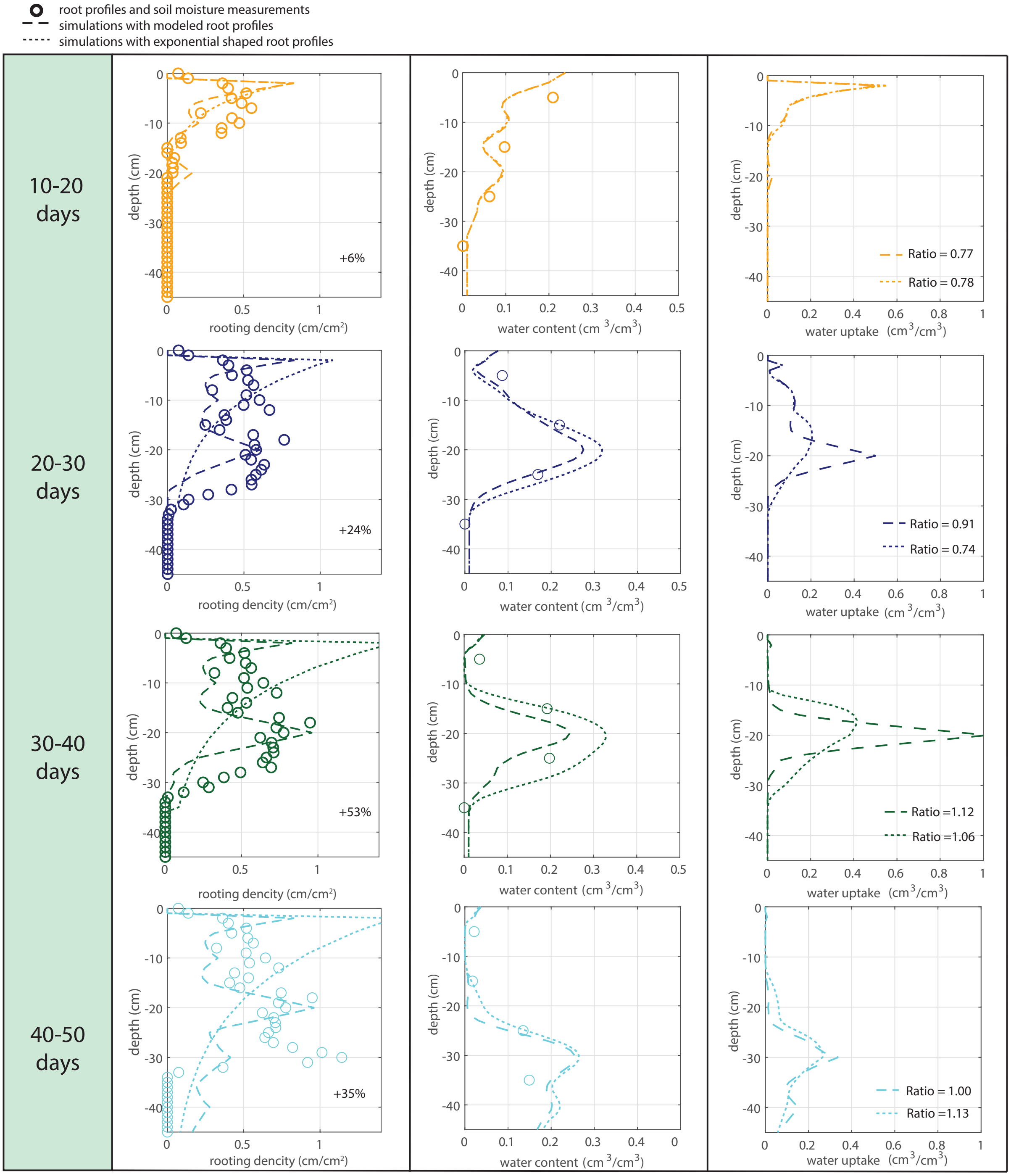

Figure 8. Fully coupled model with irrigation and evaporation as input parameters. Left: Observed (circles), simulated (dashed lines), and exponential (dotted lines) root profiles (at the start of each period). The total difference in overall root growth between the dynamic and exponential root profile shape is indicated as a percentage. Middle: corresponding soil moisture profiles. Right: simulated uptake profiles for simulated and exponentially shaped root profiles.

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

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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

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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

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 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; 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

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:

$$\frac{\partial R}{\partial t}\frac{1}{r} = \frac{\theta_n}{\int_L^0 \theta_n}, \tag{1}$$

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

$$\theta_n = \frac{\theta - \theta_r}{\theta_s - \theta_r}, \tag{2}$$

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

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

$$r = \int_L^0 \frac{\partial R}{\partial t} dz, \tag{3}$$

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

$$\frac{\partial L}{\partial t} = u_1 \tag{4}$$

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

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 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

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

$$\frac{\partial \theta}{\partial t} = \frac{\partial q}{\partial z} - S + I \tag{5}$$

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:

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

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

$$h = h_s\frac{\theta^{-b}}{\theta_s} \tag{7}$$

and K is taken as;

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

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:

$$S = u_2 R\theta_n \tag{9}$$

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.

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 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 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 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).

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:

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

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 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 $u_3 = 0.2cm/cm^3/day$.

Results and discussion

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 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’ 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 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 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 compensated 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.

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.

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

Author contributions. Cynthia Maan: conceptualization, experiments, code- and model design, writing - original draft, data curation. Marie-Claire and Bas van de Wiel: funding acquisition, supervision, writing - Review & Editing

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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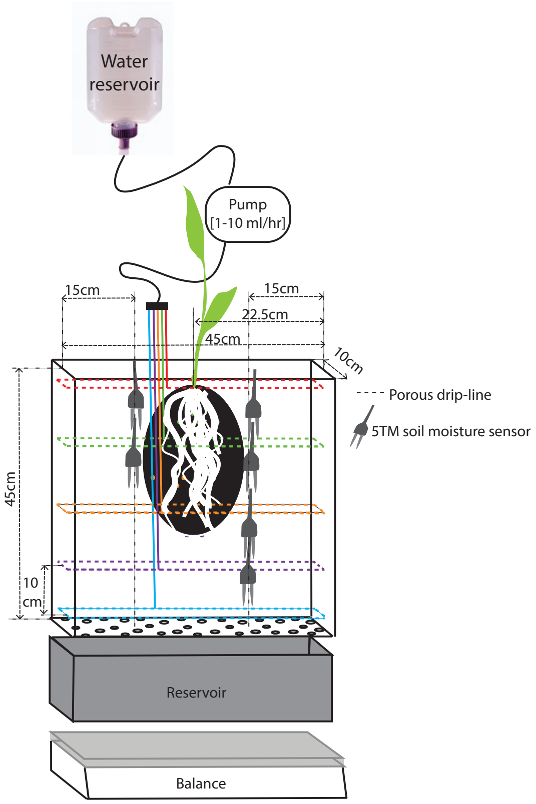

Figure 1. Schematic representation of the experimental setup inside a rhizobox.

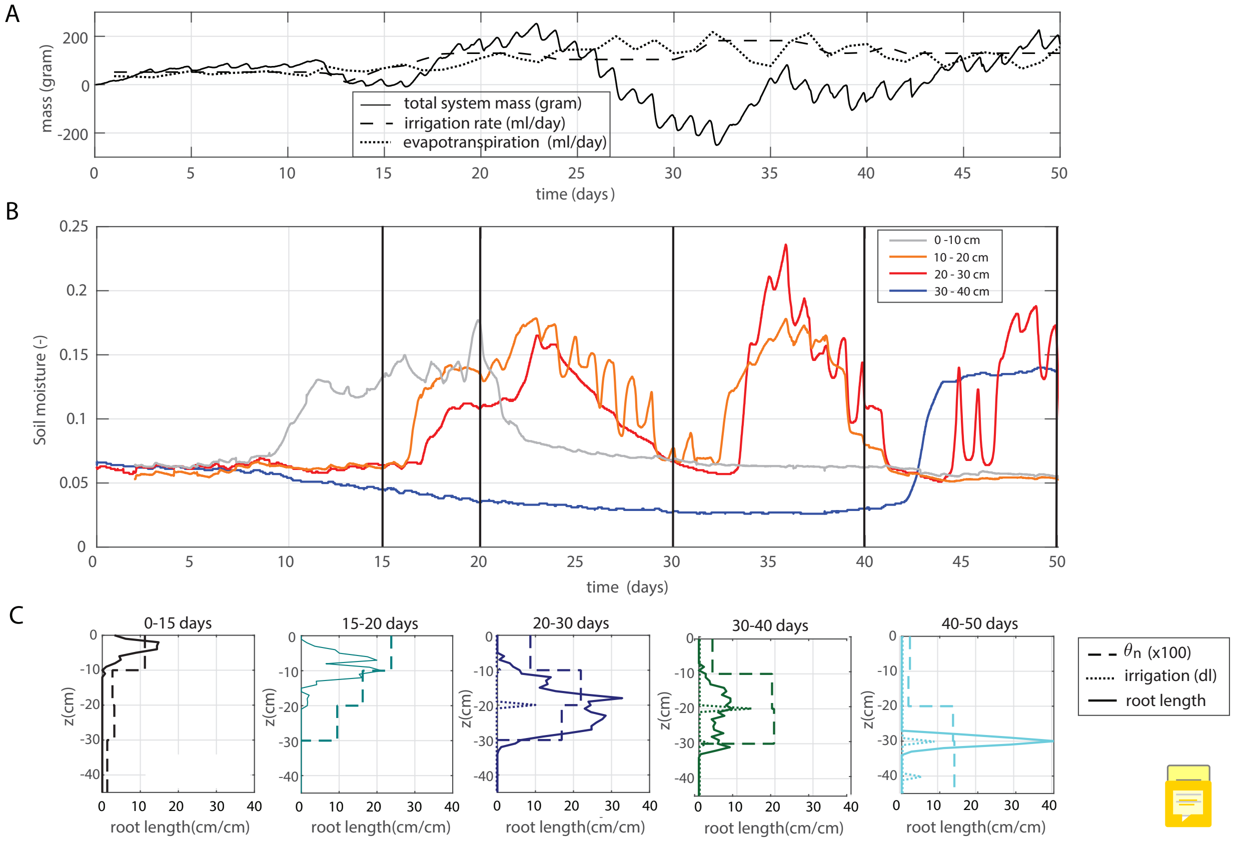

Figure 2. A: time series of the overall system mass, irrigation rate and evapotranspiration. B: time-series of the soil moisture within four different depth intervals. C: root growth (solid lines) profiles within succeeding periods, time-averaged soil moisture profiles (dashed lines) and total applied irrigation volume (dotted lines). Root development is most pronounced in the intervals with largest soil moisture.

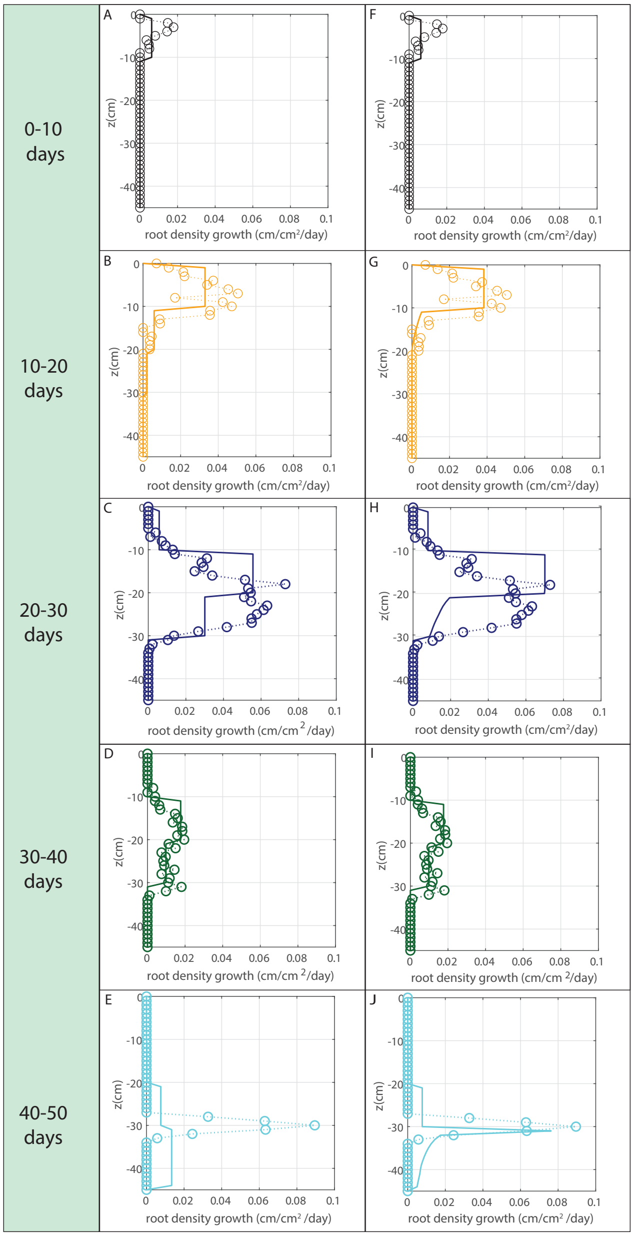

Figure 3. Vertical profiles of averaged root growth rates within succeeding periods as observed (circles) and as diagnostically calculated by equation 1 (‘roots follow moisture principle’, solid lines), using the measured bulk root growth and soil moisture profiles. Panels F-J show calculations with 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 $5cm/day$.

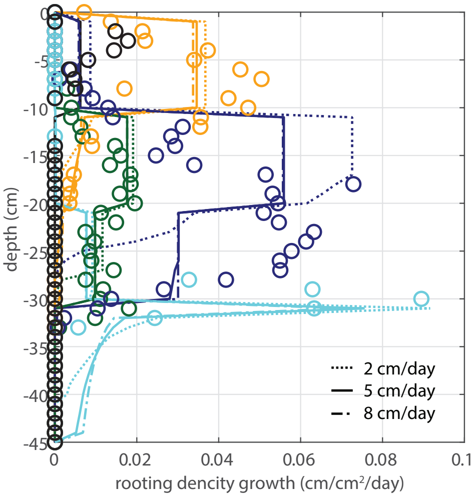

Figure 4. Sensitivity of root growth profiles to different values of the extension rate u_1.

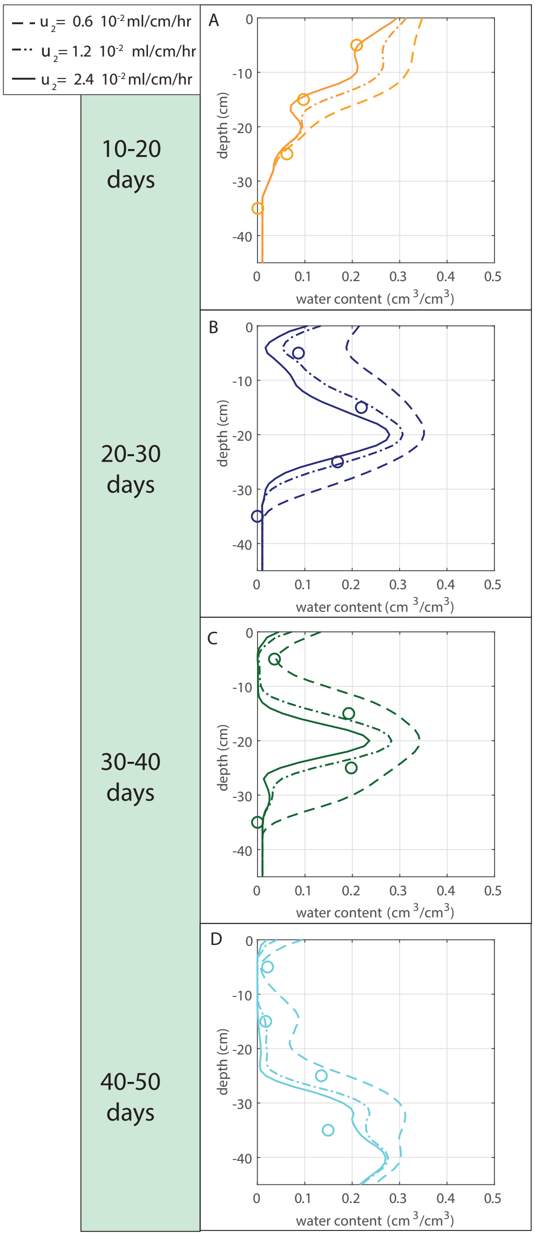

Figure 5. Sensitivity analysis for u_2.

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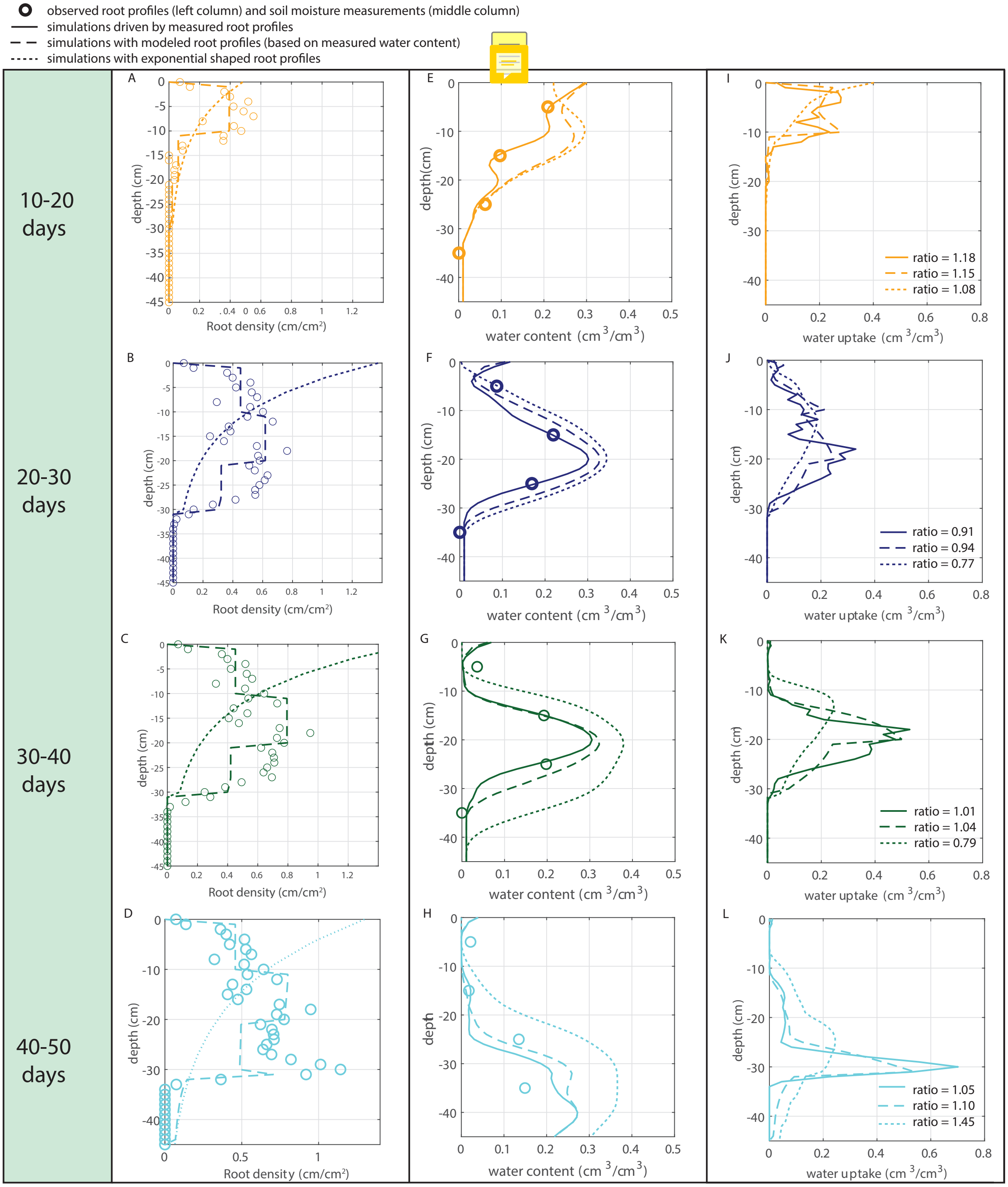

Figure 6. Offline simulations of time averaged soil moisture (middle column) and water uptake (right column) for the measured root profiles at the start of each period, for the calculated root profiles, and for exponential equivalents. The *ratio* values in panels I-L indicate the ratio's between the modeled and measured bulk (i.e. vertically integrated) water uptake rates.

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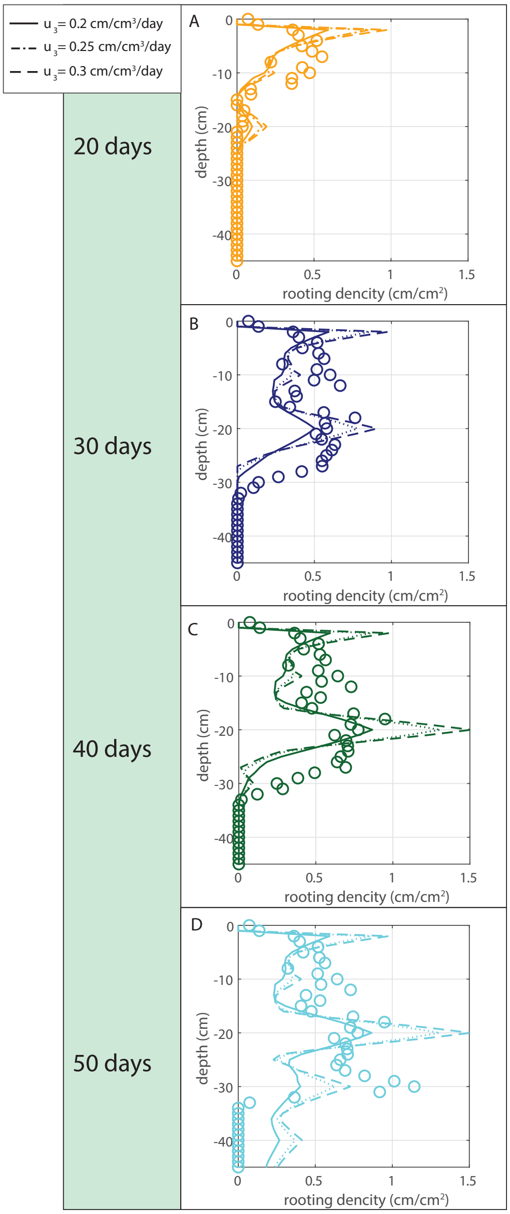

Figure 7. Sensitivity analysis for u_3.

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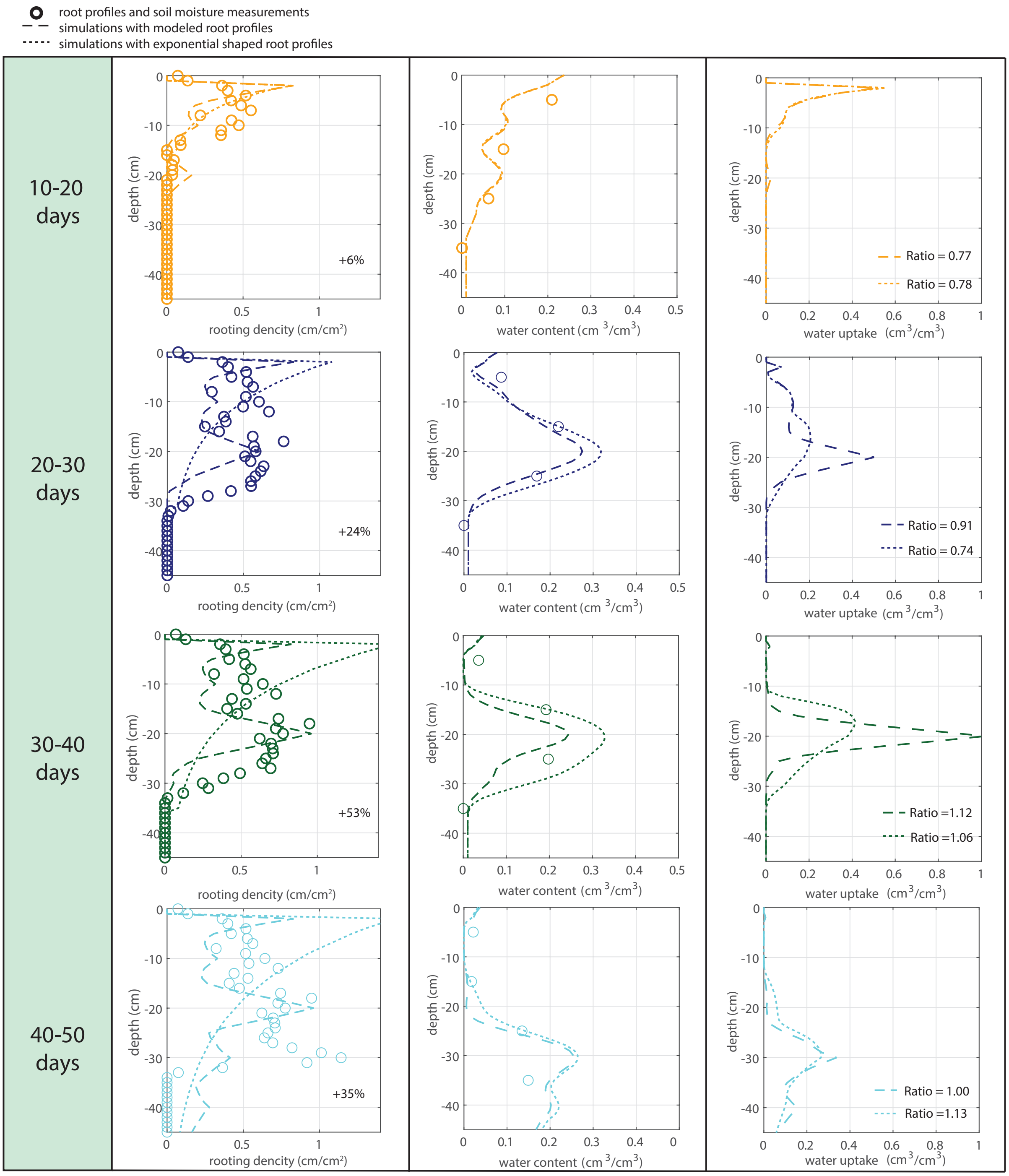

Figure 8. Fully coupled model with irrigation and evaporation as input parameters. Left: Observed (circles), simulated (dashed lines), and exponential (dotted lines) root profiles (at the start of each period). The total difference in overall root growth between the dynamic and exponential root profile shape is indicated as a percentage. Middle: corresponding soil moisture profiles. Right: simulated uptake profiles for simulated and exponentially shaped root profiles.