Replies to comments on: From hydraulic root architecture models to macroscopic representations of root hydraulics in soil water flow and land surface models.

Below you find our replies to the comments of the two reviewers and our suggestions for changes to our paper. The comments of by the reviewers are given in black text, our replies in blue and suggestions for changes in blue italic.

Reviewer 1

General comments

This article describes how water flow within a root system which can be described in a global matrix form, can be decomposed into different matrix representing different processes: distribution of contribution of total uptake of each root segments, redistribution of water flow within the root system (in case of heterogeneous soil water potential). This can be done if root system is represented as a set of resistive links (radial and axial) for water flow. If this set of links is supposed to represent the root system hydraulics, then it can be applied at any scale from a fine description of root system architecture (microscopic) to very coarse 1D ' a priori' description of root system (macroscopic), compatible with 1D description of water flow in soil, as done in surface model schemes. This work extends previous works of authors. I found very interesting this work, which rigorously provides a "natural" upscaling of root system hydraulic properties. It will be very useful for modelers to go deeper in the necessary use of root properties in sounded "effective" representation of root systems for water transfer and uptake in soil.

Thank you for this excellent summary of the paper.

I think however, that the paper is a bit hard to follow at some times, even if the authors try to explain their derivation. The matrix notation (in particular for range indices) shall be explained.

Also in response to comments by the second reviewer, we changed the notation to a more conventional notation:

We will change the notation and propose the following:

The ith element of vector $\mathbf{J_x}$ is $J_x[i]$.

The element of the ith row and jth column of matrix $\mathbf{C}$ is $C[i,j]$

The submatrix $\mathbf{C_2}$ that consists of the first N_{root} rows and the second to N_{root} +1 columns of $\mathbf{C}$ is $\mathbf{C}_2 = C\left[i,j\right] for \quad i=1,...,N_{root}, j=2,...,N_{root}+1$

The central notion of Heff must be better explained. As presented, it appears as an added variable to the system.

We include the definition of H_{eff} directly after the equation where it is first used. This should make clear that H_{eff} is not an additional variable but is obtained directly from the soil water potential distribution and the **SUF**.

In the appendix, we derive that H_{eff} corresponds with the SUF weighted average of H_{soil}:

$$H_{eff} = \mathbf{SUF}^T \mathbf{H}_{\mathbf{soil}} \quad [1]$$

I found that section 4.1 was lengthy, and also rather difficult to follow as notation of different "equivalent" root systems is not "fixed" and references to figures and tables to be better done. This could be rearranged according to type of studied model. Some explanations on differences of behavior between models (in section 4) are a bit confusing. I found much more interesting section 4.3 compared to 4.1 + 4.2.

Answering the detailed questions about these part helped us to make sections 4.1 and 4.2 clearer. Since we considered two different parameterizations of the parallel root model, we explained better how we parameterized this model and explained why we call one parameterization a bottom up parameterization and the other parameterization a top down parameterization. In the text and figures we then refer to the bottom up parallel root model and the top down parallel root model.

In all the examples shown, I questioned myself if conclusions would be the same if an imposed water outflow (transpiration) had been used in place of xylem potential collar, as often the case in a 1D model. Could this possibly impact the derivation of equations and water redistribution? A few words about this (in conclusion) would be welcome.

When formulating the model using graph theory, we included an extra equation for the collar node that includes the transpiration rate. In the appendix we added a sentence on how the problem can be solved when the transpiration rate is used as a boundary condition. We noted that using a the relation between the transpiration rate, the root system conductance, the effective soil water hydraulic head and the hydraulic head at the root collar, the hydraulic head at the root collar can be calculated directly from the transpiration rate without having to solve for the xylem water potentials. This means that Hcollar can be used as a boundary condition to solve for Hx and to determine the distribution of the water uptake.

When the transpiration T and $\mathbf{H}_{\mathbf{soil}}$ are known, H_{collar} and $\mathbf{H}_{\mathbf{x}}$ can be obtained by solving the first Nroot +1 equations of Eq. [7]. Alternatively, H_{collar} can be obtained directly from Eq. ***Error! Reference source not found.****. From H_{collar} and $\mathbf{H}_{\mathbf{soil}}$, $\mathbf{H}_{\mathbf{x}}$ can be derived from solving the 2^{nd} to N_{root} +1 equations in Eq. [7].*

Always in the conclusion, regarding "bottom-up" approach, I fully agree concerning integrating better knowledge of root architecture, but this should be balanced by the fact that

(i) it is difficult to get distribution of root conductance (axial and radial) for a range of species, (ii) what about root growth/decay and associated parameterization

We listed a few methods that could be used to determine the conductances of root segments:

This information could be derived either from: direct measurements on root segments (Schneider et al., 2017;Zhu and Steudle, 1991;Meunier et al., 2018b); using information on water fluxes in the soil-plant system (e.g. water contents, collar water hydraulic heads, stable water isotopes in the soil and plant xylem) in combination with inverse modelling (Rothfuss and Javaux, 2017;Cai et al., 2018;Meunier et al., 2018a;Couvreur et al., 2020), or using anatomical information about root tissues in combination with flow modelling (Couvreur et al., 2018;Heymans et al., 2020). Overviews of hydraulic properties of crops, herbaceous species and trees are given in (Bouda et al., 2018;Draye et al., 2010).

Concerning the distribution with depth of the root conductances with depth, root architecture models could be used which are parameterized based on measurements of root densities but also other information. We added:

However, root distributions could be used to constrain parameters (Garré et al., 2012;Vansteenkiste et al., 2014) or parameters groups (Pages et al., 2012;Morandage et al., 2019) of RSA models. When information about distributions of root types with depth is available, this information could be used as well to parameterize root architecture models, which provides additional information about the distribution of root segment hydraulic properties when different root types can be associated with different hydraulic properties (De Bauw et al., 2020). Since root architecture models also simulate root growth, they provide information about root segment age, which is related to root hydraulic properties and how they change over time. Root growth but also decay can be modeled as a function of soil properties and soil conditions (e.g. water content) so that the adaptation of root systems to environmental conditions and two-way feedbacks between root system dynamics and soil water content could be represented (Somma et al., 1998).

and, finally (iii) if LSM (land surface models) are to deal with a mix of species, types of vegetation (e.g. grass, trees…), what would be needed ?

We added in the discussion part the following

The upscaled root water uptake model was derived for a RSA of a single plant or species. The uptake by several plants from the same or from different species of which the roots share the same soil profile with the same $\boldsymbol{H_{soil}}$ *could be represented by summing up the uptake profiles of the individual plants. When the uptake can be described by a parallel root model, Eq.* ***Error! Reference source not found.****, the uptake by a mixture of plants can also be described by an equivalent parallel root model when the* ***SUF****s of the different plants are the same. From Eq.* ***Error! Reference source not found.****, it follows that the equivalent* K_{rs} *for the mixture corresponds with the sum of the* K_{rs} *values of the individual plants and the equivalent collar hydraulic head with the* K_{rs} *weighted* H_{collar} *of the different plants. The joint distribution of Krs and Hcollar or of Krs and the plant transpiration are required to calculate this weighted mean. For a mixture of plants with a different* ***SUF****, it is not possible to derive* *such an equivalent parallel root model that describes the root water uptake profile of the mixture. In that case, the root water uptake profile should be calculated separately for each species, or 'plant functional' type which is characterized by a specific **SUF**.*

Specific comments

L21 … "the big root model" : not very clear for an abstract

This is a term that was used on some papers in which the entire root system was represented by one single vertical 'big-root'. It has some similarities with the 'big leaf' model.

L54-57 axial and radial conductivity and "the root radial conductance per root surface area; the axial conductivity per root cross sectional area" are essentially the same, may be better to express that root conductance are scaled to root surface area and root cross sectional area

We changed as follows:

The axial big-root hydraulic conductance, which determines head losses due to flow in the root system, and the radial big-root conductance, which determines the exchange between the soil and the root, were obtained by scaling intrinsic root segment conductances with the cross sectional and surface area of the root segments in the soil profile, respectively; and the unsaturated soil hydraulic conductivity (Amenu and Kumar, 2008;Quijano and Kumar, 2015).

L50-65: precise how is defined a root system in the big and parallel root approaches: a root density as a function of depth ?

I could add the following but I do not think it fits:

The model is parameterized by the distribution of absorbing root surface with depth and the conductances of the root branches that connect these surfaces with the root collar.

L94 the axial conductance may limit the water absorption at the distal ends of roots: could be not clear for the reader : do you mean that water uptake is limited to the distal end or that water uptake decrease from proximal to distal part

Changed to:

Analytical solutions of water uptake by single roots, which are represented as 'porous pipes' with uniform radial and axial conductances, demonstrated that water uptake takes place along the entire root length but that due to limiting axial conductance, uptake may decrease from the proximal to the distal part of roots (Landsberg and Fowkes, 1978).

L98 water absorbance : water uptake ? Changed

Following the suggestion of the second reviewer, we will change the first part of the methods section until line 170.

L137 hydraulic head, Hcollar: specify unit of Hcollar : (L) OK

L140 Normaly, if considering water head unit for xylem potential, units for Kx should be L3/T and for Kr 1/T – May be specify that conductance doesn't consider here surface and length of root segments

We start now with the continuum equation that uses the intrinsic properties kx and kr with the dimension given here. Then we will derive the extensive conductances that are used on the network equations and that depend on the length and radius of the segments used in the network

Eq5: specify for vector [0 Q] that 0 is N+1, and Q is N length:.OK

L161 may be specify that diag(K) stands for showing a diagonal matrix, based on a vector K where the N first elements are Kx(i) and the others Kr(i): OK

L161 add a dot before diag(K)=> IMT (2Nroot x 2Nroot+1). diag(K) OK

L173 specify that SUF[i]=Q[i]/Qtot

We wrote in the paper we submitted: ***SUF****(i) represents the fraction of the total uptake by a certain root node for a uniform soil water hydraulic head.* We would like to keep it with this since SUF[i]=Q[i]/Qtot is only true when the water hydraulic head is uniform in the soil profile. Otherwise, Q[i] depends also on the distribution of the soil water hydraulic head.

L173 Specify what means Heff : what is an "effective" soil water potential around roots ?

We defined H_{eff} earlier in the text.

In the appendix, we derive that H_{eff} corresponds with the SUF weighted average of H_{soil}::

$$H_{eff} = \mathbf{SUF}^T \mathbf{H}_{\mathbf{soil}} \qquad [2]$$

Eq. [2] implies that the effective soil water hydraulic head depends more strongly on soil water hydraulic heads where the root system takes up more water when the soil water hydraulic head is uniform.

L175-180: the aim of deriving the equations shall be given before (eg after eq 6), introducing the idea of defining Heff whether Hsoil is constant or not. As presented now the derivation is not very easy to understand…

The aim of transforming Eq. 6 is to represent it in terms of effective root system parameters like Krs and SUF. We defined these parameters now first before introducing them in the reformulated equation.

This equation can be written in another form that uses macroscopic characteristics of the root system: the root system conductance, K_{rs} (L^2 T^{-1}), and the standard uptake fraction ***SUF*** *of the root system that were introduced by Couvreur et al. (2012). K_{rs} relates the total root water uptake to the difference between an average or effective soil water hydraulic head, H_{eff} (L) and H_{collar}:*

$$T = \sum_i \mathbf{Q} = K_{rs}\left(H_{eff} - H_{collar}\right) \qquad [3]$$

and SUF[i] represents the fraction of the total uptake by the i^{th} root node for a uniform H_{soil}.

L178.. write the equation of the weighted average: OK

L179-180 the sum of the fluxes of the second term…: not easy to understand, may be add : sum_i (C4(I,j) (Hs(i)-Hef(i)) =0

It is unfortunately more complex than that. We added a reference to the equation in the appendix.

L180 .. "The second term on the right-hand side represents the amount of water that is taken up more (less) by a certain root node than in case the soil water….. " : may be rephrase for more clarity with something like : on right-hand side represents the increase (decrease) in amount of water that is taken up by a root node when Hsoil is higher (lower) relative to Heff

We rephrased to:

The second term on the right-hand side represents the increase (decrease) in amount of water that is taken up by a root node that is connected to soil node where H_{soil} is higher (lower) relative to H_{eff}

L211 conductance form root node i => conductance from node: OK

L203-212 : not easy to follow…

We add why we show and derive these equations:

To explain the meaning of K_{comp} and how it is related to K_{rs} in the parallel root system model, we consider a soil water hydraulic head distribution that is uniform except for one node i where the hydraulic head is ΔH higher than in all other nodes ($H_{soil}[j] = H_{soil}[i] - \Delta H$ for all j ≠ i).

L217-221 : not easy to follow… Useful here ?

We now moved the text that was originally in the appendix to the main body:

For the general root system, we find that $K_{comp}[i]$ is larger than K_{rs}. This means that for a certain ΔH between soil node i and all other nodes, there is more redistribution in the general root system than in the parallel root system. In the general root system, the flow from one soil-root interface to another soil-root interface does not always have to pass through the collar but can take a shorter way. A negative value of $C_7[i,j]$ means that for a given hydraulic head difference between two nodes i and j, there is more redistribution between node i and j than the average redistribution for this head difference between node i and another node than node j of the network. This means that node i is stronger than average connected to node j.

Figure 3: Possibly, add in the figure the limits of soil layers in order for the reader to make a link between subfigures and number / distribution of hydraulic resistances.

We added the soil nodes and defined the number of soil depths in the figure.

L271 : precise that your figure 3 shows some equivalent, upscaled root system where root are distributed along 4 soil layers.

We added 'soil depths' to the text:

Error! Reference source not found. *a) shows the hybrid parallel-big root system that consists of three primary root branches of different length which take up water from up to 4 different depths. This root system was scaled up to a model that describes uptake from the 4 depths assuming that the soil water hydraulic head is uniform at a given depth (the exact model) and that was approximated by upscaled parallel and big root systems.*

L276 "comes down to a top down parameterization" : ? meaning ?

We explain what we mean with top-down parameterization

Since we assume a-priori a certain topology of the root segments and parameterize the model directly based on the number of root segments in a soil layer and their properties (radial and axial conductances), we called this a top down parameterization.

L281 “Parallel root … parameters… is equal to ndepths+1” : (i) isn’t it ndepth? Why +1 ? (ii) There are 2 parallel root models , could you annotate them differently, e.g. parallel –axial and parallel-no-axial (or parallel –Kx and parallel-Inf) to differentiate them. We often get lost in your description of different models…

Indeed, it shoud be ndepths parameters for the parallel root model. We updated:

For the upscaled parallel root model, the number of parameters that needs to be defined is equal to the number of soil layers, ndepths : ndepths $K_{x,eff}$ *values or Krs and ndepths-1 SUF values (sum of SUF =1).*

In fact, for the parallel root model, it does not matter whether Kx is finite or infinite. Since the model is defined by the total conductance from the root tip to the collar, any combination of Kx and Kr for a certain depth that gives the same total conductance will result in the same uptake. So defining the two parallel root models in terms of the Kx they used is maybe confusing. Therefore, we propose to change to: parallel root model bottom up vs parallel root model top down. We added the nomenclature to figure 3 and changed it in the other figures.

L282 “requires 2ndepth parameters”: requires 2 ndepth parameters: OK

Table2 Why 4 digit for SUf except for Parallel root system, which does not exactly sum(s) to 1; eg SUFupscale of hybrid-parallel-big at the first depth is 0.406, not 0.3988. Specify in the legend that root hydraulic conductances are constant along roots

We added for the parallel root model top down 4 digits. We also noticed a typo that we corrected.

Table 3 in the legend specify that Kr=0.1 along roots except at root tip Kr=1: OK

Figure 2: change the place of the legend box: OK

L299-300: add a reference to table 2, this is true for the constant conductance example, not the other.

The top-down parallel root model overestimates the SUF for the shallow depth and underestimates it for the deeper depths in the two cases.

L303-304 No real underestimation of uptake figure 2 on proximal segments but rather overestimation at distal end from fig 2 ! please check.

The fact that we were referring here to uptake in case of a uniform soil water hydraulic head whereas figure 2 shows uptake for a non-uniform hydraulic head was confusing. Therefore, we changed uptake to SUF.

L304-305: On fig 3 this follows more less the same pattern as figure 2 but with less discrepancy.

We are discussing the SUF in Table 2 and 3 here and not the uptake for a non-uniform hydraulic head distribution that is shown in figure 3and 4.

L305-306: Is it useful here? where do we see this equality which is not the really the case from table 2.

We moved this sentence to the beginning of the discussion of Table 2 and 3. We corrected an entry of Table 2 so that the sum matches now.

L314 implies that redistribution flow => implies that redistribution of flow

We changed to: *redistribution of water*

L325 in these layers soil => soil layers: OK

L324-327: hard to follow…..

We changed to:

The higher radial root segment conductances near the root tips make that water transfer between two soil layers through root tips in these soil layers, which passes via the root collar, is more efficient than water transfer between a root tip segment and a root segment with lower radial conductance that is directly connected to it.

L354-355: conductance have now units which differ from their previous definition. It would be good to clarify the text with more adequate and explained words: conductance: when there is no normalization by geometry (ie length or area), conductivity when geometry normalized (as the case of these lines). "Intrinsic" conductivity is, classically in the field of porous media flow, related to conductivity of the matrix only, independently of the fluid…

We start the set up of equations part now with defining the intrinsic root segment hydraulic properties where we introduce the porous pipe model. Intrinsic properties refer here to properties of the root *segments* which are independent of the axial discretisation that we use to solve the equation. But these root segment properties are still not fully 'intrinsic' properties or conductivities since they still depend on the radius of the segments. The 'intrinsic' axial and radial *segment* conductances depend on the root tissue conductivities which need to be scaled with the root radius and root cross sectional area (the root segment axial conductance must be divided by the xylem cross sectional area to obtain the xylem conductivity and the root segment radial conductance needs to be multiplied by the radius of the root to obtain the radial conductivity of the root tissue. We propose to add:

Intrinsic conductances refer here to properties of the root segments which are independent of the axial discretisation that we use to solve the equation.

For the hybrid parallel-big root model, we used a dummy parameterization with dummy units. But, this does not mean that we used intrinsic parameters or dimensionless parameters. Since we use a discretized network model, the parameters are extensive properties that depend on the size of the elements that were considered.

We used a dummy parameterization of the root hydraulic properties and of the vertical distribution of the soil water hydraulic heads (i.e. the parameters were chosen to represent certain differences but the actual values of the parameters and their units were not of interest).

L357-358 the roots was assumed… with 1 cm long… : => rather the "reference " exact model was based on a root 50 cm long discretized with 1 cm long root segments of uniform… OK

L358 The soil collar potential: ??? the water potential of root collar: OK

L361 As to be expected => As expected, due to the series-pathway of water,

Figure 6a: distribution of hydraulic condutances is given as function of age, but in the text and result a distribution as function space (depth) is considered. A distribution of conductance as function or root collar distance would be rather needed here

We changed the x-axis and plotted conductances versus depth for the single root system. For the realistic root architecture, we kept root segment age.

Figure 7 : Sink term (in legend and axis) => Root sink term: OK

Figure 8 Specify for which model are these figures (parallel—Kx): OK

L364-376: That the parallel model with distribution fluxes behaves well, and better than parallel infiny is not really surprising. And all this section could be shorten…

We agree that this was not surprising. What we did not expect was that the top-down parameterized parallel root model would overestimate the uptake compensation since a parallel root model underestimates Kcomp. But, neglecting axial resistance leads to an overestimation of the water uptake from the distal ends of the roots.

L396 Why did you choose these 3 root systems ? which main differences ? add a reference to figure 9 here

We added:

*The grass root system with several primary roots and few laterals may represent a parallel root system. The maize root system with several primary roots that each take up water along their axis by lateral roots may represent a hybrid parallel big root system whereas as the sunflower root system with a single main root and several lateral roots might rather represent a big root system (**Error! Reference source not found.**).*

L410 cross the layer is calculated… => cross the layer *i* is calculated: OK

L415 …as above…, as in section 4.1 ? This was changed

*For the parallel root system with bottom up parameterization, we used the **SUF** and K_{rs} values of the exact upscaled model.*

L417-418 of the radial root segment conductance… => radial root segment conductance upscaled as in the big root model OK

L421 to parameterize hydraulic root water uptake => to parameterize hydraulic macroscopic root water uptake OK

L431 but is more outspoken => ?? but the difference is amplified: We skipped this.

L433 add a reference to figure 10 here: OK

L434 an overestimation … distal ends of roots=> (i) there is no distal end of roots here but rather only soil depths, (ii) there is only a slight overestimation at depth, overestimation occurs at shallower to mid depth for maize and sunflower and seem not be related to a variation in distribution of roots in figure 9…

We rewrote this as:

*For the maize and sunflower root systems, the parallel root system using a top down parameterization and assuming no axial resistance to flow underestimated the **SUF** at shallower depths and overestimated it at intermediate (maize) and deeper (sunflower and maize) depths (**Error! Reference source not found.** a,c).*

We related the overestimation to the combination of high radial conductance and low axial conductance at lateral root tips and made a reference to the single root case with varying conductances along the root (figure 7b).

*Not considering axial resistance to flow leads to an overestimation of the uptake capacity of the distal ends of roots, especially when the axial conductivity decreases and the radial conductance increases towards the root tip (see also **Error! Reference source not found.** b). Depths where the **SUF** is strongly overestimated correspond with depths with high densities of younger lateral roots.*

L435 opposite was observed => mostly for sunflower, for other plants only slight variations

We first included that the big root model reproduced the exact SUF better.

*The **SUF** of the big root model corresponded better with the exact **SUF**. But, in the big root model, the axial resistance to flow from the distal ends of the deep primary roots to the collar is apparently overestimated and the SUF in the deeper soil layer underestimated.*

L435-444 May be a more straightforward and concise interpretation, given the difference between the maize and sunflower, would be that as root act in parallel in a layer , and that most roots are laterals of lower conductance, this leads to higher SUF at shallower depth compared to greater depth

We agree that the lateral roots within a layer act in parallel. But, they are still connected to a primary root in series. For the parameterization of the big root model, it was assumed that all roots in a layer act in parallel. We rewrote as follows:

In the big root model, the xylem water potentials in the secondary and primary roots in a certain layer are assumed to be equal since it is assumed that all root segments in a layer act in parallel. However, because of the lower axial conductance of secondary roots (see ***Error! Reference source not found.****) which are connected in series to primary roots, the xylem water heads can be considerably higher in the secondary than in the primary roots in a certain layer. Assuming similar xylem water heads in secondary and primary roots in a certain soil layer reduces the xylem heads in the secondary roots and generates too much uptake by the secondary roots in that layer. An overestimation of uptake in a more 'downstream' or shallower soil layer will lead to an underestimation in the more 'upstream' or deeper layers*

Figure 11 to which model (big root ?) refer these figures? We added to the figure caption that these C7 and Kcomp/Kres are for the exact model.

L452 The parallel root model => Which one, the parallel with Kx ?

We added:

The parallel root model with bottom up parameterization that uses the exact K_{rs} and ***SUF*** *profile but approximates K_{comp} by K_{rs} and* $\mathbf{C_7}$ *by the identity matrix, predicts almost the same sink term distribution profile as the exact model. This bottom up parallel root model slightly underestimates the compensatory root water uptake, i.e. too much uptake near the soil surface and too little deeper in the soil profile.*

L453 – 455 I can' understand the meaning of this sentence, which model is on figure 11?

The exact K_{comp}/K_{rs} trace and $\mathbf{C_7}$ matrix of the root systems are shown in Figure 11.

L455 impact of approximations of Kcomp and the C7 matrix… of the parallel Kx model?

We specified now always the parameterization of the parallel root model that is discussed.

L472 RSA is not defined… OK

L491 LSM is not defined.. OK

Appendix

Eq A3 and connectivity matrix: may be state that IM(i,j)=0 if I and j are not connected and what about IM(I,j) if j is a proximal node of I ?

We redefined the incidence matrix in the main text. The rows refer to the nodes and the columns to elements.

IM[i,j]=1 when node i is a distal node of element j, IM[i,j] = -1 when i is proximal node of element j and IM[i,j]=0 otherwise.

Eq A10 verify indices of matrix C that should be C[Nr+1:2Nr, 2Nr+1]

It should be the last Nroot rows of the C matrix and all the columns

Eq A14 verify indices of CL3 matrix, this rather be CL3[N+1:2N, N+2,2N+1]: OK

L603 in "Considering Eq. [A 31], we can write:", may be better "indeed, when considering…" OK

In A38 What is ones ? where **ones** is the Nroot all-ones vector.

L638 add also that SUF_T Heff= Heff to get A40: OK

L656 What means "are connected more strongly"

We moved this part to the main text and explain now what we mean with node i being stronger connected to node j.

For the general root system, we find that $K_{comp}[i]$ is larger than K_{rs}. This means that for a certain ΔH between soil node i and all other nodes, there is more redistribution in the general root system than in the parallel root system. In the general root system, the flow from one soil-root interface to another soil-root interface does not always have to pass through the collar but can take a shorter way. A negative value of $C_7[i,j]$ means that for a given hydraulic head difference between two nodes i and j, there is more redistribution between node i and j than the average redistribution for this head difference between node i and another node than node j of the network. This means that node i is stronger than average connected to node j.

Reviewer 2:

The paper presents a model of root water uptake based on a distributed root architecture system and tries to perform upscaling to make the proposed approach suitable for land-surface models.

This interesting paper focuses on a topic of great interest to the hydrological community. However I have a number of reservations on the current manuscript and thus I suggest some revisions that I consider necessary for a better collocation of the research.

Thank you for your comments and suggestions. They helped us to make the paper clearer by providing a link to graph theory and improving the notation.

Here is the (unordered) list of comments that should be addressed by the authors.

1. Notation. I do not like the non-standard Matlab-like notation. I think it is confusing and misleading, taking away the attention from the essntial components of the model. I had a hard time reading through it . The paper feels more like a cut-and-paste from the matlab code (see supplementary information) rather than the description of a model.
We changed the notation and propose the following:

The ith element of vector $\mathbf{J}_\mathbf{x}$ is $J_x[i]$.

The element of the ith row and jth column of matrix **C** is $C[i,j]$

The submatrix $\mathbf{C}_2$ that consists of the first N_{root} rows and the second to N_{root} +1 columns of **C** is The submatrix $\mathbf{C}_2$ that consists of the first N_{root} rows and the second to N_{root} +1 columns of **C** is $\mathbf{C}_2 = C[i,j] \, for \quad i = 1,...,N_{root}, j = 2,...,N_{root} + 1$

In the main part of the paper, we focus on the results of the derivations that are given in the appendix. In the appendix, we explain how the root system scale properties like Krs and SUF are obtained, how the equation for the general root system and the parallel root systems are obtained and we derive some properties of the equation matrices that are important to interpret the main equations.

In order to improve the readability, we rewrote equations so that the form (order of terms and factors) is repeated through the manuscript and appendix.

For example, if we read through the indices of eq. [5], this is nothing else than a weighted graph Laplacian defined on the graph with wich the root system is discretized. It took me a long time to understand this, also because of the uncommon wording (e.g., the connectivity matrix is typically called the incidence matrix in graph theory).

We changed the start of the setup of equation section. We start now from the continuum equation for flow in a porous pipe, discretize it on a network of root and soil nodes and derive the equations in line with the formalisms of graph theory. However, after having setup the equations, we do not use graph theory further: i) to derive root system characteristics such as Krs and SUF, ii) to prove that these two characteristics are sufficient to describe total root water uptake as a function of soil water potential distributions, iii) to prove that redistribution of uptake when soil water hydraulic heads vary in space is independent of the transpiration rate (a finding that is in contradiction to how root water uptake compensation is implemented in a few macroscopic root water uptake models), iv) to derive upscaled root water uptake models, and v) to compare solutions for more complex root architectures with simplified models such as the parallel root and big root models. All these derivations are presented in the Appendix.

The flow into and within a single root can be described using the porous pipe model (Landsberg and Fowkes, 1978) with the following equation:

$$\frac{d}{d\ell} k_x \frac{dH_x}{d\ell} = -2\pi r k_r \left(H_{soil} - H_x \right) \qquad [4]$$

where ℓ [L] is the local axial coordinate of the root, k_x ($L^3\ T^{-1}$) and k_r (T^{-1}) are the intrinsic axial and radial root segment conductances, r [L] is the root segment radius, and H_x (L) and H_{soil} (L) are the hydraulic heads of the water in, respectively, the xylem and the soil in contact with the root, which include both the pressure potential and the elevation potential. Intrinsic conductances refer here to properties of the root segments which are independent of the axial discretisation that we use to solve the equation. We can discretize this equation for a root system network that consists of Nroot root segments (edges) that are connected with each other in nodes (vertices). These root nodes are connected by Nroot soil-root segments to Nroot soil nodes. The entire system is connected to an extra outlet node that represents the root collar where the hydraulic head, H_{collar}, or the flux boundary condition is defined. Since branches of a root architecture do not re-join distally (further away from the collar), there is only one segment that connects a certain node with the proximal (closer to the collar) part of the root system or each node is the distal node of only one element (except for the collar node). The total number of segments (root segments connecting root nodes and soil-root segments connection root with soil nodes) is 2Nroot. The total number of nodes in this system, including the collar node, is 2Nroot+1. Each root node (expect the collar node) can be linked uniquely to two segments: a root segment that connects the node to the proximal part of the root system and a soil-root segment that connects the node to the soil. The axial conductance $K_x[i]$ ($L^2\ T^{-1}$) of the proximal root segment and the radial conductance of the soil-root segment $K_r[i]$ ($L^2\ T^{-1}$) connected to the i^{th} root node are defined as:

$$K_x[i] = \frac{k_x[i]}{l[i]} \qquad [5]$$

$$K_r[i] = 2\pi r[i] l[i] k_r[i] \qquad [6]$$

where l[i] (L) is the length and r[i] (L) the radius of the proximal root segment connected to the i^{th} root node. The transpiration stream to the collar, T ($L^3\ T^{-1}$), the xylem hydraulic heads, and the fluxes from the soil to the root nodes Q ($L^3\ T^{-1}$) are obtained from solving the Laplacian on the weighted directed graph of soil and root nodes, which is the discrete representation of the flow equation in the leaky root system:

$$\left[\mathbf{IM} \cdot diag(\mathbf{K}) \cdot \mathbf{IM}^{\mathbf{T}}\right] \begin{bmatrix} H_{collar} \\ \mathbf{H_x} \\ \mathbf{H_{soil}} \end{bmatrix} = \begin{bmatrix} -T \\ \mathbf{0} \\ \mathbf{Q} \end{bmatrix} \quad [7]$$

*where **IM** is the (2Nroot +1 x 2Nroot) incidence matrix of the graph with 2Nroot +1 nodes and 2Nroot segments. The rows of the incidence matrix represent the nodes of the graph and the columns the segments. The first row represents the root collar, the next Nroot rows the root nodes and the last Nroot rows the soil nodes. The first Nroot columns represent the root segments and the last Nroot columns soil-root elements. IM[i,j]=1 when node i is a distal node of element j, IM[i,j] = -1 when i is proximal node of element j and IM[i,j]=0 otherwise.* $\mathbf{H_x}$ *is the Nroot vector with xylem hydraulic heads in the root nodes and* $\mathbf{H_{soil}}$ *the Nroot vector with the soil water hydraulic heads in the soil nodes. diag(**K**) is a diagonal conductivity matrix with the first Nroot diagonal elements representing the xylem conductivities and the last Nroot elements the radial conductances. **0** is an Nroot vector with zeros and **Q** is the Nroot vector with fluxes from the soil nodes to the root nodes. The derivation of Eq. ?? is demonstrated in the appendix. The first equation represents the total transpiration stream out of the network as a function of the hydraulic heads in the root nodes connected to the collar and in the root collar and the axial conductances of the root segments connected to the root collar. The next Nroot equations close the water balances in root nodes and from solving these, the xylem water potentials in the root nodes are obtained. The last Nroot equations yield the fluxes Q from the soil nodes to the root nodes.*

The use of standard mathematical (linear algebra) notation is welcome.

See proposal above

(in line 160 the product between IM^Tdiag(K) is not diagonal. May be the authors refer only to diag(K). Please correct.)

In the previous version, we had missed a comma in between. In the new version, this sentence was changed to:

*diag(**K**) is a diagonal conductivity matrix with the first Nroot diagonal elements representing the xylem conductivities and the last Nroot elements the radial conductances.*

2. The authors describe a discrete model without ever looking at the continuous counterpart. Thus, one is forced to wonder how the discretization affects the parametrization and the solution. There is no answer to this question and it should be discussed at least in the numerical experiments.

We included now the continuous equation. In the part on the single root simulations, we add a comment on the discretization. We do not consider the discretization of the flow equation in the root system to be a topic of this paper but we analyzed this in other studies to which we refer here. Spatial variations and gradients in soil water potentials might as well be the limiting factor that determine the spatial discretization of the root network.

The deviations are due to the upscaling and the variations of soil water and xylem hydraulic heads along a root segment that is represented by a single node (Bouda, 2019). Nevertheless, the close agreement indicates that the 1cm discretisation of the root approximates the exact solution of the flow equation in the single root well. Details on the convergence of this discretization and on exact solutions for arbitrary root segment sizes (given that the soil water potentials do not vary along the root segments) are given by Meunier et al. (2017a);(Meunier et al., 2017b). For large root segment sizes or small K_x*, when the discrete approximation becomes inaccurate, exact solutions can be implemented in a complex root architecture but this leads to a different coefficient matrix* ***C4*** *and* ***C5*** *vector (see Bouda (2019)).*

3. The distinction between parallel/big root systems and the proposed model really boils down to parametrization of the same model: all of them are based on a linear diffusion-like equation, making the assumption that a potential function exists, and then proceed to upscaling in order to find the K-Q relationship. For example, the parallel root system makes the assumption that resistance inside the root system is negligible with respect to resistance at the soil-root interface and use it throughout to solve (exact upscaling) the related mass conservation equation (i.e. the diffusion-like equation). In this case, the approach is exactly the approach proposed in this paper, as argued also by the authors themselves in a simpler case. Isn't then the difference only related to a different paramterizations of the same model?

We are not sure whether we understood this comment. It is unclear to us what is meant by 'model'. If the model refers to a network of resistances (which are independent of the potential) and if the connection of these resistances are interpreted as a 'parameterization' of the network, then the complex root network model, the big root and parallel root models are all different parameterizations of the same model. However, we considered the way the segments were connected to each other as a 'model' of the root system. In that sense, we have an 'exact' model (representing the connections of a true root architecture), a parallel root system model, and a big root model. In the introduction part, we can add:

A first approach to model this system is to start with a simplified concept of the root system or its topology. Although the topology of the root system may also be considered as a parameterization of a model that describes water flow in the soil-root system, we consider the root topology here as specific 'model' that is fixed a-priori in a kind of top-down approach and that is subsequently parameterized based on measurements of soil water potential, leaf water potential, transpiration fluxes and information about the root system such as the root density distribution and hydraulic properties of root segments. Two a-priori proposed root system topologies can be distinguished: big root and parallel root models.

For the parallel root model, we have two 'parameterizations': one that assumes infinite axial conductances and that derives the radial conductances from the root segment radial conductances (which are all scaled by the same factor to obtain the same root system conductance as the 'exact' model), and one that adapts axial conductances for each soil depth so that the SUF of the parallel root model matches with the SUF of the exact model.

It must be noted that the parallel root model does not presume a priori an infinite axial conductance. It assumes that all nodes are directly connected to the collar. Furthermore, the upscaling of the exact model does not make any assumptions or simplifications about the connections of the segments. For the upscaled exact model, we did not derive an 'upscaled' network model. The parallel and big root models are network models that approximate the exact upscaled model, but they are not exact analogues. We had already in the appendix:

We call this root system the 'parallel root system'. The radial and axial resistances for each soil node can however be different. Also a root system in which there is no resistance to axial flow can be considered as a system in which all soil nodes are connected directly to the root collar. But, it is important to keep in mind that systems with a significant axial root resistance can also be considered, as long as there is a direct connection between the soil node and the root collar without additional intermediate nodes that connect to the soil. For instance, fibrous root systems with only primary roots, in which uptake takes only place near the root tip but not at the more basal ends, can also be represented by this root system model.

Note that the assumption of existence of a potential is reasonable in the linear regime but is prone to fail in a nonlinear regime, not addressed here. The authors at some point comment on linear vs nonlinear models, but they should elaborate more on this. In addition, it is linearity that allow the upscaling, which can be done equivalently (from the mathematical point of view) using a "series/parallel resistance" analogy or inverting the resulting weighted graph-Laplacian (the diffusion-like equation enforcing mass conservation of the system).

Assuming that Kx and Kr do not depend on the hydraulic heads leads to linear equations which simplify the problem considerably. Nonlinearity would make the diagonal matrix diag(**K**) a function of the H_{collar}, H_x and H_{soil}. This would imply that the full set of (non-linear) equations must be solved iteratively and upscaling would be of limited use since the upscaled equations would have to be changed every time H_{collar}, H_x and H_{soil} change. We elaborate in the discussion why the root system can be assumed to behave as a linear system in many cases. But, the soil-root resistance is non-linear when the soil resistance becomes limiting. We are currently developing an upscaling approach that consider this non-linearity.

We found that the linearity of the root system can be used quite elegantly to scale up the linear root-system part first which can subsequently be coupled to non-linear soil system part. This upscaling of the linear part first makes that the non-linear part needs to be solved for much less equations. Given the length of the current paper we would like to keep the focus on the linear flow equation in the root system and how it can be scaled up and represented by a parallel root system model that parameterized based on the upscaled equations.

We propose to add the following in the conclusion part of the paper:

*The nonlinearities render the diagonal conductivity matrix diag(**K**) a function of the hydraulic heads H_{collar}, H_x and H_{soil}. This implies that the full set of (non-linear) equations must be solved iteratively to derive 'exact' upscaled root system properties, K_{rs}, **SUF** every time H_{collar}, H_x and H_{soil} change. For large root systems, this approach would be unfeasible so that approximations are required. One approach would be to derive functional relations between the upscaled properties and hydraulic head distributions, root and soil hydraulic properties, and root architectures based on a large set of simulations and advanced data analytics. Another approach would be to start with simplifying assumptions that reduce the complexity* *of the system. A simplification that we are currently testing exploits the linear behavior of the root hydraulics for upscaling RSA first, using the approach developed in this paper, and couple the upscaled equations subsequently to a non-linear rhizosphere flow model.*

We indeed scaled up the inverted Laplacian. Then we rewrote this inverted Laplacian into a form from which root system characteristics such as the root system conductance, the standard uptake fraction and the root water uptake compensation could be derived. This form was then further analyzed to come to a form that shows similarities with the parallel root model analogy. However, this parallel root model analogy is not an exact representation of the upscaled root model but a quite good approximation. This is different for upscaled root models that use the parallel or series (big root) analogies that are parameterized directly (in a top down approach) based on root segment conductances.

In addition, linearity is the main limitation of the proposed approach, as it cannot be extended to the nonlinear case since there is no analytically expressable upscaling and numerics (Newton method) has to be used everytime parameters are changed.

Yes, that is correct. See our reply to the previous comment

-

4. Appendix: I don't understand the wording "distal" and "proximal" that have a relative meaning. Eq. [A1] is just the sum of the fluxes entering/exiting node i, i.e., div q =0. Also I do not understand the change in sign convention for the first term. Also eq. [A2] has a different sign convention. Then, one has to be overly careful in assembling all the fluxes.

Distal and proximal are anatomical terms with proximal referring to closer to the collar and distal referring to further away from the collar. Concerning the sign, the first term is what flows out of the node towards the collar. The other terms is what flows towards the node from the distal parts. Fluxes in the network are positive when they are towards the collar.

Again, I think it wouldn't be bad to use standard linear algebra (graph theory) notation and call IM the incidence matrix of the graph instead of the connectivity matrix. Then it becomes obvious that [A4] is just Darcy's (Ohm) law and [A3] is the mass balance (-div k grad h=q).

Thank you for the suggestion. We renamed IM to incidence matrix and we added the collar node to the set of nodes in the graph (so we don’t have a distinction between IM_{collar} and IM anymore)

The developments starting after equation [A5] seems just an application of Gaussian elimination. Is this needed? I am in favor of summarizing the model with some basic equations and then describe the steps used to solve it (finding the K-Q relationship) giving some physical meaning to intermediate steps is necessary only after the full algorithm description is reported. Or the authors could add to all this lengthy (and to me useless) equations a summary of the basic idea (solve for Q when H is known to get the effective conductivity).

We tried to make the summary of these equations in the main text. In fact, the 'effective conductivity' that we find is the root system conductance: K_{rs} and Eq. 8 (or Eq. A 24) represents the K-Q relation for the entire root system.

The following equations are used to develop characteristic properties of the root system: Krs and SUF which have a clear meaning. We also develop these equations to show that these are the two characteristics that fully characterize a parallel root system. What we derive is how these two characteristics are implemented in a general root architecture and how the formulation for the general root architecture differs from the formulation of the parallel root system. By casting the exact solution (or its finite difference approximation) in the same form as the solution for the parallel root model (Eq. A41), we can identify the nature of these differences. We find that this difference can be brought back to a difference in how the water uptake compensation is described.

Amenu, G. G., and Kumar, P.: A model for hydraulic redistribution incorporating coupled soil-root moisture transport, Hydrology and Earth System Sciences, 12, 55-74, 10.5194/hess-12-55-2008, 2008.

Bouda, M., Brodersen, C., and Saiers, J.: Whole root system water conductance responds to both axial and radial traits and network topology over natural range of trait variation, J. Theor. Biol., 456, 49-61, 10.1016/j.jtbi.2018.07.033, 2018.

Bouda, M.: A Big Root Approximation of Site-Scale Vegetation Water Uptake, Journal of Advances in Modeling Earth Systems, 11, 4597–4613, 10.1029/2019ms001806, 2019.

Cai, G. C., Vanderborght, J., Couvreur, V., Mboh, C. M., and Vereecken, H.: Parameterization of Root Water Uptake Models Considering Dynamic Root Distributions and Water Uptake Compensation, Vadose Zone J., 17, 10.2136/vzj2016.12.0125, 2018.

Couvreur, V., Vanderborght, J., and Javaux, M.: A simple three-dimensional macroscopic root water uptake model based on the hydraulic architecture approach, Hydrol. Earth Syst. Sci., 16, 2957-2971, 10.5194/hess-16-2957-2012, 2012.

Couvreur, V., Faget, M., Lobet, G., Javaux, M., Chaumont, F., and Draye, X.: Going with the Flow: Multiscale Insights into the Composite Nature of Water Transport in Roots, Plant Physiol., 178, 1689-1703, 10.1104/pp.18.01006, 2018.

Couvreur, V., Rothfuss, Y., Meunier, F., Bariac, T., Biron, P., Durand, J. L., Richard, P., and Javaux, M.: Disentangling temporal and population variability in plant root water uptake from stable isotopic analysis: when rooting depth matters in labeling studies, Hydrology and Earth System Sciences, 24, 3057-3075, 10.5194/hess-24-3057-2020, 2020.

De Bauw, P., Mai, T. H., Schnepf, A., Merckx, R., Smolders, E., and Vanderborght, J.: A functional-structural model of upland rice root systems reveals the importance of laterals and growing root tips for phosphate uptake from wet and dry soils, Ann. Bot., 126, 789-806, 10.1093/aob/mcaa120, 2020.

Draye, X., Kim, Y., Lobet, G., and Javaux, M.: Model-assisted integration of physiological and environmental constraints affecting the dynamic and spatial patterns of root water uptake from soils, J. Exp. Bot., 61, 2145-2155 10.1093/jxb/erq077, 2010.

Garré, S., Pagès, L., Laloy, E., Javaux, M., Vanderborght, J., and Vereecken, H.: Parameterizing a Dynamic Architectural Model of the Root System of Spring Barley from Minirhizotron Data, Vadose Zone J., 11, 10.2136/vzj2011.0179, 2012.

Heymans, A., Couvreur, V., LaRue, T., Paez-Garcia, A., and Lobet, G.: GRANAR, a Computational Tool to Better Understand the Functional Importance of Monocotyledon Root Anatomy, Plant Physiol., 182, 707-720, 10.1104/pp.19.00617, 2020.
Landsberg, J. J., and Fowkes, N. D.: WATER-MOVEMENT THROUGH PLANT ROOTS, Ann. Bot., 42, 493-508, 10.1093/oxfordjournals.aob.a085488, 1978.
Meunier, F., Couvreur, V., Draye, X., Zarebanadkouki, M., Vanderborght, J., and Javaux, M.: Water movement through plant roots - exact solutions of the water flow equation in roots with linear or exponential piecewise hydraulic properties, Hydrol. Earth Syst. Sci., 21, 6519-6540, 10.5194/hess-21-6519-2017, 2017a.
Meunier, F., Draye, X., Vanderborght, J., Javaux, M., and Couvreur, V.: A hybrid analytical-numerical method for solving water flow equations in root hydraulic architectures, Appl. Math. Model., 52, 648-663, 10.1016/j.apm.2017.08.011, 2017b.
Meunier, F., Rothfuss, Y., Bariac, T., Biron, P., Richard, P., Durand, J. L., Couvreur, V., Vanderborght, J., and Javaux, M.: Measuring and Modeling Hydraulic Lift of Lolium multiflorum Using Stable Water Isotopes, Vadose Zone J., 17, 10.2136/vzj2016.12.0134, 2018a.
Meunier, F., Zarebanadkouki, M., Ahmed, M. A., Carminati, A., Couvreur, V., and Javaux, M.: Hydraulic conductivity of soil-growth lupine and maize unbranched roots and maize root-shoot junctions, J. Plant Physiol., 227, 31-44, 10.1016/j.jplph.2017.12.019, 2018b.
Morandage, S., Schnepf, A., Leitner, D., Javaux, M., Vereecken, H., and Vanderborght, J.: Parameter sensitivity analysis of a root system architecture model based on virtual field sampling, Plant Soil, 10.1007/s11104-019-03993-3, 2019.
Pages, L., Bruchou, C., and Garre, S.: Links Between Root Length Density Profiles and Models of the Root System Architecture, Vadose Zone J., 11, 10.2136/vzj2011.0152, 2012.
Quijano, J. C., and Kumar, P.: Numerical simulations of hydraulic redistribution across climates: The role of the root hydraulic conductivities, Water Resour. Res., 51, 8529-8550, 10.1002/2014wr016509, 2015.
Rothfuss, Y., and Javaux, M.: Reviews and syntheses: Isotopic approaches to quantify root water uptake: a review and comparison of methods, Biogeosciences, 14, 2199-2224, 10.5194/bg-14-2199-2017, 2017.
Schneider, H. M., Wojciechowski, T., Postma, J. A., Brown, K. M., Lücke, A., Zeisler, V., Schreiber, L., and Lynch, J. P.: Root cortical senescence decreases root respiration, nutrient content and radial water and nutrient transport in barley, Plant, Cell & Environment, 40, 1392-1408, https://doi.org/10.1111/pce.12933, 2017.
Somma, F., Hopmans, J. W., and Clausnitzer, V.: Transient three-dimensional modeling of soil water and solute transport with simultaneous root growth, root water and nutrient uptake, Plant Soil, 202, 281-293, 1998.
Vansteenkiste, J., Van Loon, J., Garre, S., Pages, L., Schrevens, E., and Diels, J.: Estimating the parameters of a 3-D root distribution function from root observations with the trench profile method: case study with simulated and field-observed root data, Plant Soil, 375, 75-88, 10.1007/s11104-013-1942-3, 2014.
Zhu, G. L., and Steudle, E.: Water Transport across Maize Roots, Simultaneous Measurement of Flows at the Cell and Root Level by Double Pressure Probe Technique, 95, 305-315, 10.1104/pp.95.1.305, 1991.