# A new model for optimizing the water acquisition of root hydraulic architectures over full crop cycles

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***Abstract* — Drought stress is one of the most significant environmental stress in agriculture worldwide and is even expected to become more and more severe in many regions of the globe. In this context, the concept of ideotypes (plant with ideal traits that is expected to yield a greater quantity or quality of product when developed as a cultivar) opens new avenues for breeding as shown by the results of plant model simulations. However currently root system ideotypes lack quantitative traits and moreover cannot perform optimally in every single environment. We present here a physically-based model of the water flow in the soil-plant-atmosphere continuum working at the plant scale capable of efficiently simulating the root water uptake of growing crops over full crop cycles as well as other environmental flow (rain, irrigation, evapotranspiration). It is adapted to discriminate genotypes/ideotypes performance in any environment. In a simulation study we analyze the ability of maize root cultivars to maintain their transpiration under two management practices in two different environments.**

***Keywords — Root water uptake; Full crop cycle; Plant performance; genotype x environment x management interaction***

## I. Introduction

Drought stress is among the dominant yield limiting factors worldwide for global crop production [1], [2]. Plant transpiration is driven by water potential gradients between soil and atmosphere, and mainly controlled by stomata regulation, and soil and root hydraulic resistances [3]. Improving the root system (RS) ability to extract soil water has been defined as potential focus for breeding because of its close connection with improved yield, and its high natural diversity within species [4],[5].

Although it is recognized that a RS ideotype cannot perform optimally under all environmental conditions [6], several organ, tissue and cellular level traits have been associated with increased productivity under drought. Xylem conductance, root length or root diameter have been proposed as target traits for breeders [7]. All these RS traits have in common that they will either impact the root system structure (root length, root angle) or the root hydraulic function (aquaporin activity, apoplastic barriers). In this context many authors (see for example Lynch [5] for maize or Wasson et al. [7] for wheat) suggested root system ideotypes. An ideotype was first defined by Donald as a plant model expected to yield a greater quantity or quality of product when developed as a cultivar [4]. Yet, beyond qualitative characterization, quantitative assessment of root trait effects on plant ability to extract water is currently impossible [6]. Several reasons explain this gap: (1) the link between structural and functional properties is not always known at the local scale; (2) functional and structural traits are hard to characterize in real conditions and (3) a general framework to combine structural and functional traits at the plant scale is still missing.

Recently, Couvreur et al. (2012) developed a physically-based plant-scale model for characterizing plant ability to extract water [6]. In this approach, RS hydraulic architecture is characterized via two macroscopic parameters: the global hydraulic conductance of the root system and the relative distribution of water uptake under uniform soil water potential. These two plant-scale parameters define how easily water flows through a root system and the spatial extent of the uptake, and could be used as structural-functional hydraulic RS. Yet, these characteristics do not assess whether a given RS is optimal under a certain environment, which can only be evaluated taking into account the environmental constraints (evaporative demand, rainfall, soil properties, etc.) and the crop management practices (irrigation volume and time, sowing date, etc.).

The objective of this paper is to investigate *in silico* how root structural and/or hydraulic functions on plant stress and ability to maintain transpiration with a physical model. Establishing relations between root local properties and plant performance would allow breeders to quantify how local properties may improve plant scale uptake potentials or physiologists to define quantitative (and not only qualitative) optimal plant root traits for given environmental conditions.

To achieve this, several assumptions are needed. First we define a cultivar as a combination of architectural and hydraulic local root and a species as a specific set of possible such combinations. Among a species thus, there is a genetic variation of a series of local traits which leads to different macroscopic parameters, behaviors and performances. We identify potentially useful traits and generate various cultivars of the considered species. In an ultimate stage, we compare the cultivars macroscopic parameters and their field performances with 3D simulations of water flow in the soil-plant-atmosphere continuum considering root growth and development under different management practices, soil and climate conditions. This procedure takes us one step forward in detangling the relation between drought traits, environment, and crop performances.

This paper is divided in four sections: the model description, the simulation study details used to illustrate the model potential, a presentation of the main outputs of the model and a discussion on the simulation study results and on the model.

## II. Water flow model

The soil water flow in a vegetated soil can be described using the Richards equation [8] including a three-dimensional volumetric sink term S $[L^3L^{-3}T^{-1}]$ for root water uptake:

$$\frac{\partial\theta}{\partial t} = \nabla.(K\nabla\Psi) - S \quad (1)$$

where $\theta$ $[L^3L^{-3}]$ is the volumetric water content, t [T] is time, K $[L^2P^{-1}T^{-1}]$ is the unsaturated hydraulic conductivity tensor, and $\Psi$ [P] is the total soil water potential. To describe the sink term of this equation, we adopted the model of Couvreur et al. for isohydric plants [8], [9]. At the root segment scale, we consider that root water uptake is the sum of two processes: the water uptake in homogeneous conditions and the compensatory uptake due to heterogeneous soil water potential:

$$Q_{r,i} = \left(T_{act} + K_{rs}\left(\Psi_{rs,i} - \Psi_{rs,eq}\right)\right) SUF_i \quad (2)$$

where $Q_{r,i}$ $[L^3T^{-1}]$ is the water flow entering (if positive) or leaving (if negative) the root segment i, $T_{act}$ $[L^3T^{-1}]$ the actual transpiration rate, $K_{rs}$ $[L^3P^{-1}T^{-1}]$ the root system conductance (= first macroscopic parameter), $SUF_i$ $[-]$ the Standard Uptake Fraction of segment i (= second macroscopic parameter), $\Psi_{rs,i}$ [P] the potential at the root-soil interface of this segment and $\Psi_{rs,eq}$ [P] a weighted root-soil interface potential. The first macroscopic parameter is defined as the transpiration rate of a root system per unit of water potential difference between the root collar and the soil potential in homogeneous conditions. The second macroscopic parameter is the fraction of the transpiration taken up by the considered segment in homogeneous soil conditions. It is also an intrinsic property of the cultivar and does not depend on the environment (the soil-type for example). This Standard Uptake Fraction is also used to weight the root-soil interface potentials and define the equivalent soil water potential sensed by the plant:

$$\Psi_{rs,eq} = \sum_j SUF_j \Psi_{rs,j}$$

It is worth noting that Equation (2) is Equation (7) in Couvreur et al. [8] where we assumed $K_{comp} = K_{rs}$ with $K_{comp}$ $[L^3P^{-1}T^{-1}]$ the root system compensatory water uptake conductance, which is a reasonable hypothesis according to Couvreur et al. [10]. Just as in Couvreur et al. [9], the actual transpiration is the least of water demand (set by the atmospheric conditions and the leaf area) and water supply (maximum flow rate made available by the soil-root system). The former is calculated using a Penman-Monteith -like equation under the form of a potential transpiration $T_{pot}$ $[L^3T^{-1}]$ and the latter is the maximal water flow brought to the leaves by the root system without exceeding (in absolute value) a minimal collar potential $\Psi_{lim}$ [P] (as we assume a isohydric behavior). The actual transpiration is then given by:

$$T_{act} = \min\left(T_{pot}, K_{rs}\left(\Psi_{rs,eq} - \Psi_{lim}\right)\right) \quad (3)$$

This transpiration rate is inserted in the stress function of Couvreur et al. to obtain the root collar potential $\Psi_{collar}$ [P] [8]:

$$\Psi_{collar} = \Psi_{rs,eq} - \frac{T_{act}}{K_{rs}} \quad (4)$$

Combining (2) and (3), we obtain the local water flow under water stress condition ($\Psi_{collar} = \Psi_{lim}$) or when no stress is felt by the plant ($\Psi_{collar} \geq \Psi_{lim}$):

$$Q_{r,i} = \begin{cases} K_{rs}\left(\Psi_{rs,i} - \Psi_{collar}\right)SUF_{i,} & \Psi_{collar} = \Psi_{lim} \\ \left(T_{pot} + K_{rs}\left(\Psi_{rs,i} - \Psi_{rs,eq}\right)\right)SUF_i, & \Psi_{collar} \geq \Psi_{lim} \end{cases} \quad (5)$$

Equations (5) allow calculating water flow in the whole root system and consequently deriving the sink term in the k^th^ soil element $S_k$ $[L^3L^{-3}T^{-1}]$:

$$S_k = \frac{1}{V_k}\sum_i \varepsilon_{ik} Q_{r,i} \quad (6)$$

where $V_k$ $[L^3]$ is the volume of this element and $\varepsilon_{ik}[-]$ is a factor which is 1 when the $k^{th}$ soil element contains the $i^{th}$ root segment and else 0. The sum is over all root segments i. These equations are encoded in RSWMS (Root-Soil Water Movement and Solute transfer, [11]) where they are solved numerically using an iterative scheme between the soil and the root modules for each time step. The root-soil water interface potential is defined as the mean potential of the soil node potential surrounding the root. The macroscopic parameters SUFi and Krs depend on the root system hydraulic architecture and the hydraulic properties of the root segments (radial and axial root hydraulic conductivity). The root architecture and the hydraulic properties and hence the macroscopic root parameters vary with time as the root grows and develops. The macroscopic parameters are calculated using the hydraulic-tree approach of Doussan et al. [12].

## III. Simulation Study

### A. Cultivars

Each cultivar is considered as a combination of local hydraulic and architectural trait chosen in a range of natural inner-species variation (see Appendix A for the ranges of changes and the parameters changed). The structural parameters which were varied were: the inter-branch distance of primary roots and the radius, initial elongation rate and maximal length of lateral roots. The hydraulic parameters considered for genetic variations were the axial conductivity values of primary root and the radial and axial conductivity values of lateral roots as well as the transient ages for these properties. The hydraulic properties of root segments were considered to vary with root age in a stepwise shape [13]. All other growth and hydraulic parameters were kept constant including the minimal collar potential value $\Psi_{lim}$ (meaning that the stomatal regulation was kept the same for all cultivars).

3D Root system architectures were generated using Root Typ [14] parametrized for maize by Couvreur et al. [8]. The macroscopic parameters of each cultivar were calculated using similar (in shape) local hydraulic conductivity functions than the ones obtained by Doussan et al. [13] for maize.

In an exploratory virtual experiment, 250 maize root systems were generated with randomly chosen parameters in ranges typically observed in the literature for the structural traits while one order of magnitude was chosen as limit for the hydraulic values. This choice was also dictated by typical variabilities observed in these properties [15], [16]. To limit the computational expense and for sake of clarity, the 250 created root system were then grouped into categories according to their final macroscopic parameters: root system conductance ($K_{rs}$) and normalized depth of the water uptake in standard conditions ($z_{SUF}$ [L]) defined as:

$$z_{SUF} = \sum_i SUF_i \, z_i \tag{7}$$

Where $z_i$ [L] is the z-position of the root segment i. In each category a root system representative of the group was selected on the basis of the minimal distance to the center of mass.

### *B. Environment and management practices*

Each category of plant was subject to four combinations of management and environmental conditions. The environment was defined as a combination of evaporative demand and soil properties) and the management practices by the sowing date and the irrigation treatment. Two environments and two management practices were considered in the simulation study. They correspond to two experimental fields of the DROPS project (FP7-244374) located in Nerac, France and in Karl, Germany in well-watered conditions (= wet conditions) and under drought stress (= dry conditions). The potential evaporative demand was calculated according to Penmanth-Montheith equation based on temperature, wind velocity and relative humidity measurements. The simulated management practices (sowing date, irrigation timing and volumes) correspond to the actual ones performed on these fields.

The soil is silty loam in the French site and varies between a loam (topsoil) and a fine sand (bottom layers) in the German location. The soil hydraulic parameters of the water retention curve were derived from simultaneous measurements of water potential and water content on undisturbed samples of $100cm^3$. The soil hydraulic conductivity curve parameters were fitted for each soil horizon using results of a MultiStep Outflow experiment on undisturbed samples of $1000cm^3$.

The potential evaporative demand was calculated according to Penmanth-Montheith equation based on temperature, wind velocity and relative humidity measurements. The simulated management practices (sowing date, irrigation timing and volumes) correspond to the actual ones performed on the field. The simulation duration was fixed to 90 days with uniform pressure head as initial condition corresponding to al pF of 2.5 (field capacity) where pF is the logarithm of the soil water potential in centimeters:

$$pF = \log_{10}(|\Psi|_{cm})$$

We use free drainage bottom boundary conditions for a soil domain whose dimensions are: 75cm x 15cm x 126cm. A periodic domain was set to mimic crop field comportment and limit the computational requirements.

### *C. Plant water uptake and performance*

To understand the plant water uptake location and performance, we propose several indices reflecting its behavior. We define the actual mean depth of the root water uptake $z_{Sink}$ [L] as the sink-weighted depth:

$$z_{Sink} = \frac{\sum_k S_k \, z_k}{\sum_k S_k} \tag{8}$$

where $z_k$ [L] is the mean z-position of the soil element k and the sum is over all soil elements. It is worth noting that $z_{Sink}$ differs from $z_{SUF}$ because of soil heterogeneity.

The $\Delta t$ –averaged average potential sensed by the plant $\bar{\Psi}_{rs,eq}$ [P] is defined as the temporal mean of the equivalent potential over a period $\Delta t$ [T]:

$$\bar{\Psi}_{rs,eq}(t) = \frac{1}{\Delta t}\int_{t-\Delta t/2}^{t+\Delta t/2} \Psi_{rs,eq}(t')\,dt' \tag{9}$$

It can be used to understand what is the mean root-soil water potential felt by the plant during the last 24 hours for example when the period is fixed to one day. The cumulative transpiration $T_{cum}$ [$L^3$] is simply the integral of the instantaneous transpiration:

$$T_{cum}\,(t) = \int_0^t T_{act}\,(t')\,dt' \tag{10}$$

which is of course strongly correlated to plant yield [15].

Finally, the $\Delta t$ –averaged transpiration $\bar{T}_{\Delta t}$ [$L^3$] is defined as the integral value of the actual transpiration over $\Delta t$ [T]:

$$\bar{T}_{\Delta t}\,[L^3]\,(t) = \int_{t-\Delta t/2}^{t+\Delta t/2} T_{act}\left(t'\right)dt' \tag{11}$$

## IV. RESULTS

This section is divided in three parts. First the generated cultivars are presented in terms of macroscopic parameters. Secondly, some of the produced outputs are shown. Finally main outputs of the simulation study are provided.

### A. *Cultivar macroscopic parameters*

Out of the 250 generated root systems, eleven different categories (= representative cultivars) were finally selected on the basis of their different $K_{rs}$ and $z_{SUF}$ using k-means clustering. The evolution of the macroscopic parameters of the eleven selected root systems is presented in Fig. 1 as they change over time: from the origin, the distance between two successive points is five days. The top panel shows the mean depth of the normalized water uptake as a function of the root system conductance as the plant grows and develops. For all cultivars the water uptake depth ($z_{SUF}$) increases with time. It means that if the water potential remains homogeneous with time, the root system takes up the necessary water deeper and deeper. In addition for many cultivars (except for the red and cyan cultivars) the root system conductance reaches a maximal value before decreasing. The bottom panel represents the global conductances of the same cultivars as a function of the root system volume with the same color legend. A volume increases means overall RS growth while a decrease is due to death, senescence or tissue maturation.

If we consider that the root system volume is a proxy for the carbon spent in the roots, it can be directly seen from the second subplot of Fig. 1 that some root systems are much more efficient to increase their ability to take up water per gram of carbon invested in the root systems. It is also observed that this efficiency (the slope of the curves) changes with time.

Fig. 1 must be put in relation with Fig. 2 where the root local traits are represented for the eleven cultivars. The top panel of this figure represents the axial intrinsic conductances of the primary roots $k_{x,I}$ $[L^4P^{-1}T^{-1}]$ in log-scale as a function of root segment age. This local hydraulic property is responsible for conducting the water along the main root towards the root collar. This water is essentially collected by the lateral roots all along the primary root. In the middle panel the lateral root conductances $K_{lat}$ $[L^3P^{-1}P^{-1}]$ are plotted according to their age. These lateral roots are the main location of water uptake in the maize RS. The third subplot shows the number of laterals for each cultivar $N_{lat}$ $[-]$. The number of lateral roots is mainly determined by the internodal distance between two successive laterals on the primaries which is a critically parameter together with the local hydraulic properties of the laterals for determining the macroscopic parameters.

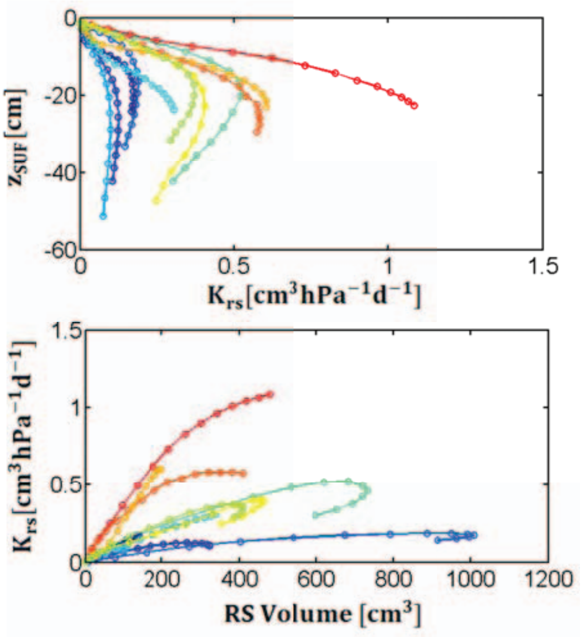


**Fig. 1. Root systems macroscopic parameters of the eleven selected cultivars :** Root system conductances *vs* depths of the normalized water uptake in standard conditions (top panel); Root systems conductance as a function of the root system volume (bottom panel). Each single scatter is a specific age of the root system cultivar (time between two succesive points is five days). Each color represent one of the 11 representative cultivars.

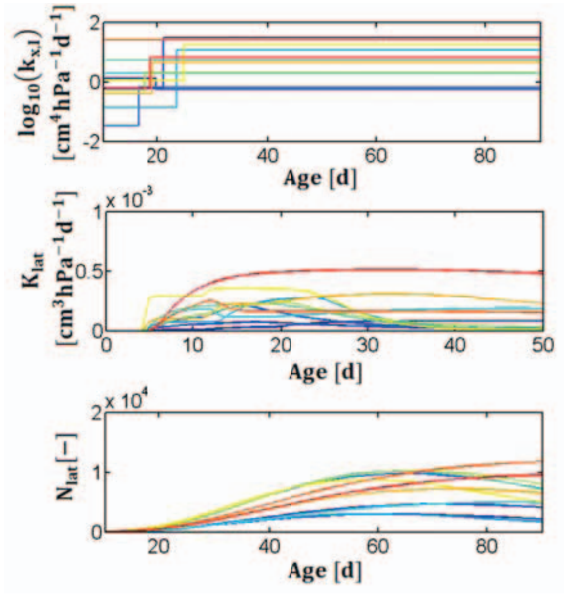


**Fig. 2. Root system local traits of the eleven selected cultivars:** root primary axial conductivity as a function of the root segment age (top); root lateral conductance according to root age (middle); number of laterals $N_{lat}$ as a function of the root system age (bottom).

These local properties are the explanatory variables of the macroscopic parameters shown in figure 1. The large conductance of the red to yellow cultivar for relatively small volumes is explained by a large number of lateral roots combined with high radial and axial conductivities of these lateral roots which lead to large lateral conductances. At the opposite, the small global conductances of the dark blue cultivars are clearly due to the tiny lateral conductances and the little number of laterals. The root system conductances first increase because the young laterals have high conductances and then decrease because of tissue maturation and a progressively reduced number of laterals due to root senescence. The mean depth of the water uptake decreases also because the maximal lateral conductance is reached in general for relatively young roots. Thanks to the gravitropism of the primary roots, the laterals are progressively generated deeper in soil leading to more uptake in deep soil layers.

The number of lateral roots is mainly determined by the internodal distance between two successive laterals on the primaries which is a critical parameter together with the local hydraulic properties of the laterals for determining the macroscopic parameters.

*B. Model outputs*

Solving the Richards equation allows obtaining the soil water potential distribution everywhere in the domain which enables to calculate the water flux and potential distributions over the whole soil-plant system. This is illustrated in Fig. 3 where the soil pF generated by the uptake of two cultivars (the red and the darkest blue) are represented for the site of Nerac and the two treatments (well-watered condition and drought stress) after 80 days of simulation. Under dry conditions different water distributions appear between both root systems. The root system 1 (red cultivar) has always the highest conductance leading to the minimal water content in the soil domain. The root system 2 (darkest blue) illustrated here has always one of the lowest conductance. This leads to much higher water content at the end of the simulation which could then play a major role for water availability later on if there is no rainfall and no scheduled irrigation. On the contrary under irrigation, no clear differences exist between the two cultivars. The figure also suggests that the root hydraulic architecture is playing a role essentially in dry conditions as we will make it even clearer in the next illustrations. From Fig. 3, it is also clear that the irrigation makes the water content higher everywhere in the soil domain, especially in the topsoil layers as compared to dry conditions (bottom line *vs* top line). Fig. 3, it is also clear that the irrigation makes the water content higher everywhere in the soil domain, especially in the topsoil layers as compared to dry conditions (bottom line *vs* top line).

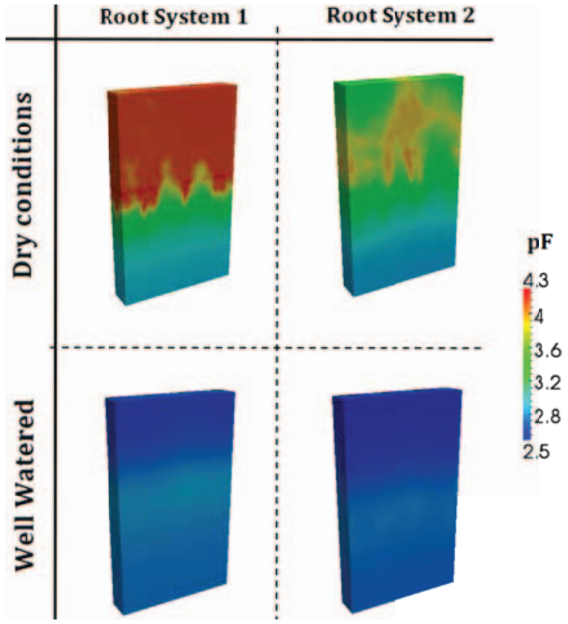


**Fig. 3. Example of three-dimensional simulation results:** soil pF distribution for two cultivars after 80 days of water uptake. The two root systems (columns) have been selected because of their different behaviors. The lines depict the treatment: the irrigation mangement is the bottom line while the dry condition is represented in the top line. No clear differences of water content distribution appears in wet soils unlike in drought conditions.

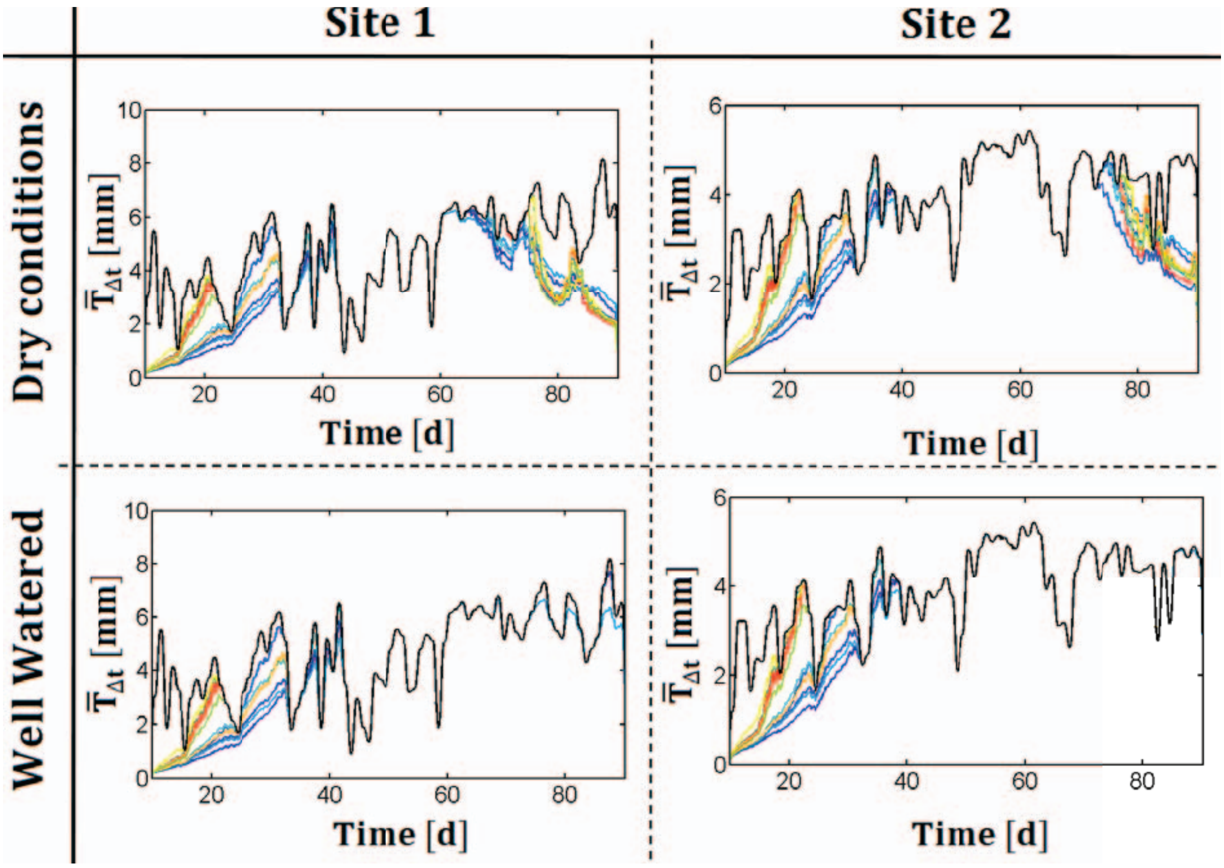


**Fig.4. Instantaneous cumulative transpiration of the last day:** as calculated using (8) with $\Delta t = 1d$ for the eleven selected cultivars (the colors correspond to Figures 1 and 2) in dry (top panels) and wet (bottom panels) conditions for the two simulated sites (corresponding columns). The black solid lines represent the potential instantaneous cumulative transpiration of the last day.

*C. Root water uptake and performance*

Fig. 4 shows the cumulative transpiration of the last day at any time and for the eleven cultivars as calculated by (11) (normalized by the soil surface) with a period of one day for the two sites and the two treatments. The colors represent the same cultivars as the ones used in the previous figures. The black lines are the day-averaged transpirations of the last day at any time and for each scenario: it is consequently the maximal potential transpiration. In general, three stages can be highlighted in each case: the initial phase during which the root system cannot provide the water requested by the leaves due to the limited size of the root system, an intermediate stage when the demand is successfully met and the final stage where a drought potentially appears. The final stress appearance concerns all cultivars for the drought conditions (top line) while only few reach this state under wet conditions (bottom line). When comparing treatments for the same site it clearly appears that the performance ranking greatly depends on the management practices. For example at the end of the simulation the darkest blue and the cyan cultivars perform the best for the first site in dry conditions while they are the only ones to experience water stress under irrigation treatment. This highlights the fact that a cultivar cannot perform ideally in all situations. Here again we demonstrate that the root cultivar greatly affects the plant performances under water limited conditions while the results are much more uniform when there is no water scarcity. It is worth noting that the best cultivars in terms of averaged transpiration after 80 days of simulation under dry conditions have surprisingly small root system conductance over the full crop cycles. On the contrary, the cultivars with high conductances over the season perform the worst under these conditions. The former save water at the beginning of the crop season that will remain available in case of severe stress later. The latter consume all the available water at any time and rely on new inflow of water from rainfall events or irrigation to keep transpiring. Two strategies clearly appear here: water saving *vs* water spending. There is no *a-priori* better strategy: it always depends on the cultivar per environment per management interaction. In some cases there is no way to discriminate a better strategy: they perform equally well such as in well-watered conditions in the second site after day 40. But we can find situations where the water savers experience less (end of simulation in dry conditions) or more (beginning of the simulation in any scenario, end of simulations in well-watered conditions for site 1) severe stress than the water spenders.

We now focus on the evolution of the water uptake mean depth $z_{Sink}$ for each scenario using Equation (8). The resulting curves are plotted in Fig. 5 for days of simulation 40 to 90. The general trend for each cultivar in any scenario is downwards (the water uptake goes deeper and deeper in the soil with time): we observe a downwards moving front of

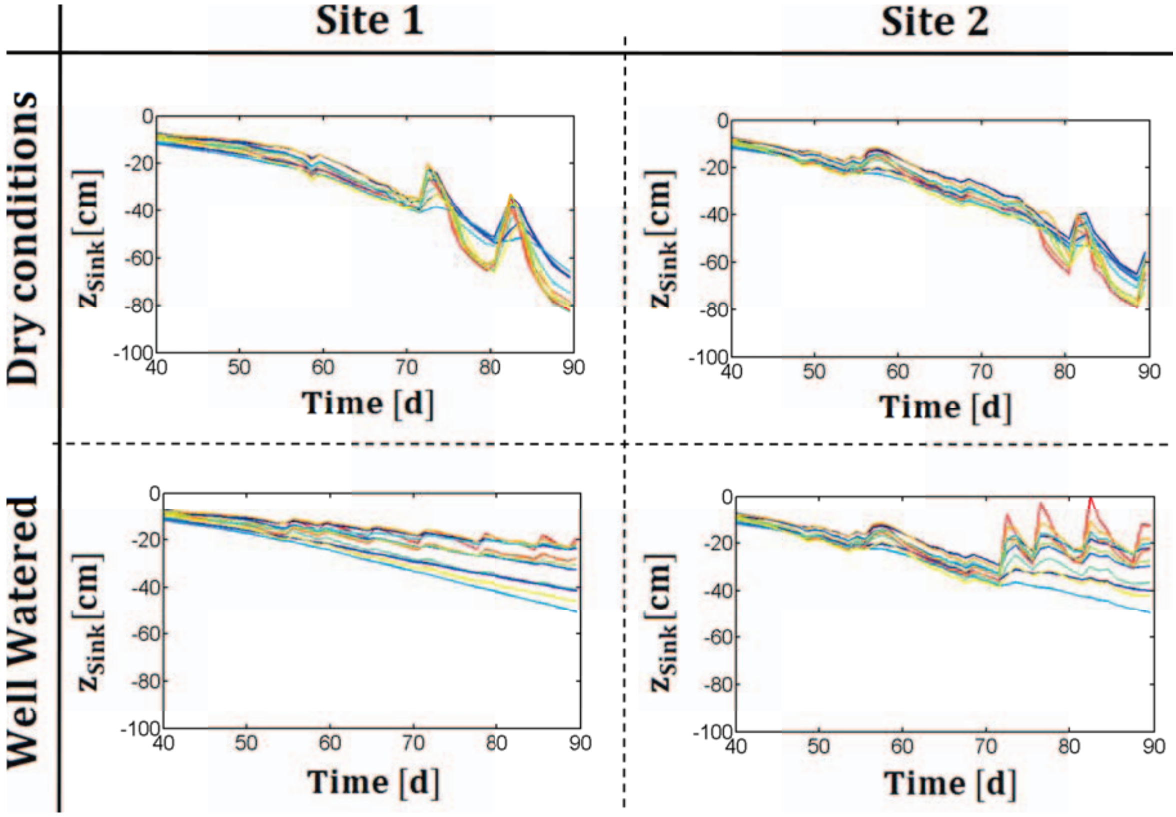


**Fig.5. Changes in water uptake averaged depth:** Sink-weighted depths $z_{Sink}$ as a function of the time for all the considered cultivars (the colors correspond to Figures 1 and 2) in dry (top panels) and wet (bottom panels) conditions and for the two environments (corresponding columns). The root system water uptake goes deeper when the water content decreases and generally ascends in case of rain or irrigation.

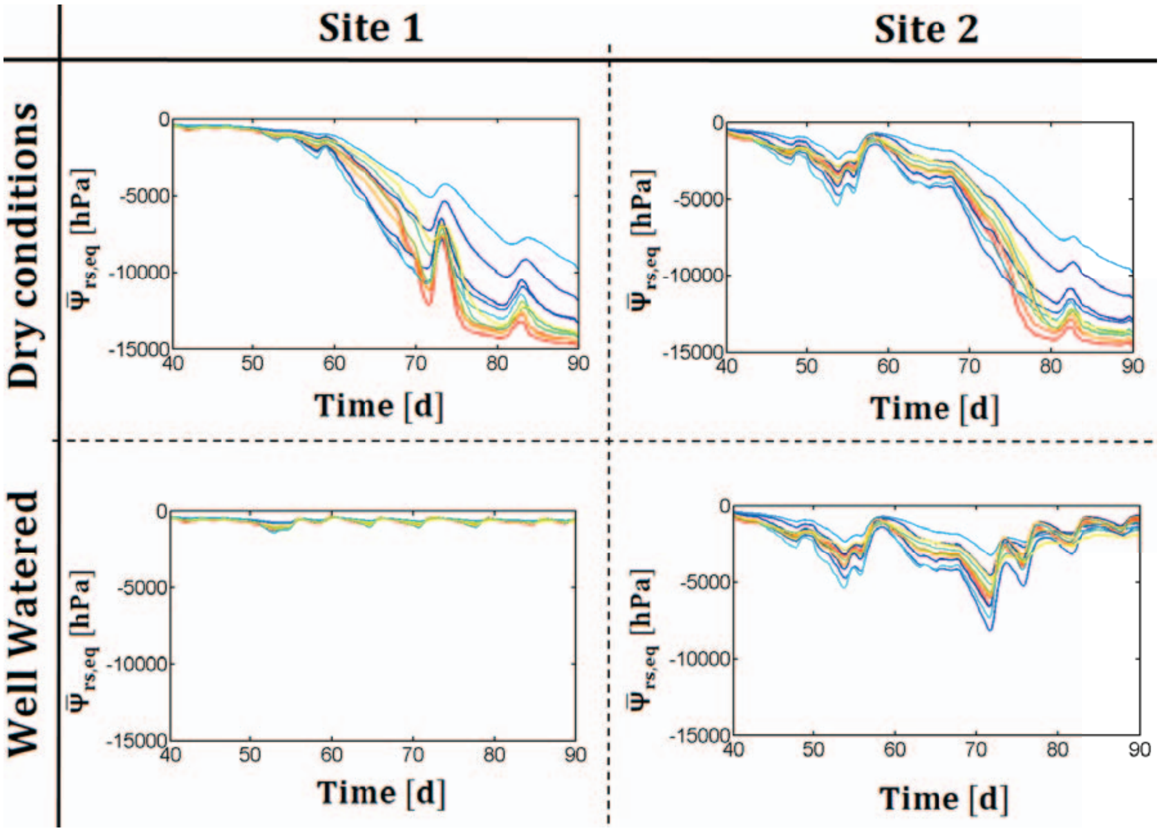


**Fig.6. Mean equivalent root-soil interface potential of the last day:** as calculated by (9) with $\Delta t = 1d$ for the eleven selected cultivars (the colors correspond to Figures 1 and 2) in dry (top panels) and wet (bottom panels) conditions for the two simulated sites (corresponding columns).

uptake. This is due to both root growth and development of the root system that make the root water uptake sites deeper in the soil (see Fig.1) and to the water content decrease in the topsoil layers because of the root water uptake. Some inversions may be easily highlighted when irrigations and/or rains increase the water content of the topsoil. These inversions are more manifest for dry conditions and for the root systems with high conductances. Interestingly the ranking of the cultivars regarding mean uptake depth under well-watered conditions follows their $z_{SUF}$ (see top panel of Fig1.) as the soil water potential under such conditions is almost homogeneous (see Fig.3, bottom line). On the opposite, under dry conditions ranking changes: the red cultivar takes up the water the deepest. This is because for water spender cultivars, the water content distribution is highly heterogeneous in dry conditions (as it can be also seen from Fig. 3, top-left panel) and their high conductance allows them to take up more water where it is available, which increases the contribution of the compensatory water uptake (see (2) with increasing root system conductance).

Fig. 6 represents the day-averaged equivalent soil-root potential felt by the plant calculated using (9) between days 40 and 90. Huge differences clearly exist between sites and treatments. First we observe low (in absolute value) felt potential in the intermediary period of day 40 to 60. This is moment when the demand is met for all cultivars and conditions. The water available in the soil is enough in any case to successfully fulfil the potential transpiration. After this time and especially in the 20 last days of simulation scenarios diverge. In well-watered conditions this potential remains low, especially for the loamy soil (site 1). The soil water potential varies more in the second site due to the hydraulic properties of the sandy soil layers but thanks to the irrigation the equivalent potential never decreases beyond -1MPa. Interestingly in the second site and for wet conditions the red cultivar senses the lowest potential (in absolute value) even though it has emptied his water storage the most by transpiring the most. This is due to his large conductance and its high normalized depth of uptake where the maximal water content is located. In dry scenarios, the potential progressively increases (in absolute value) and reaches very high values for all cultivars (-1.4 MPa), especially the water spenders. The water savers because they have economized part of the water volume contained in the soil experience less extreme potentials.

Fig. 7 illustrates the z-profiles of the water content for each scenario and each single root system after 80 days of simulations. Obviously the water content is much higher in well-watered conditions than in water-limited conditions. As stated before the water content in wet conditions is generally higher in the topsoil layers thanks to the rains and/or irrigation while the opposite is observed in dry scenarios. Interestingly the water content profiles are really similar between cultivars for each single scenario with only differences of few percent making them probably hard to discriminate if measured in the fields. The biggest differences appear in the topsoil layers of the wet soils with almost 10% of volumetric water content.

## V. Discussion

First it must be pointed out that with a very simple notion of species (set of common architectural and hydraulic rules) and cultivars (variability of traits), this model enables generating different comportments in terms of both water uptake location and volume. In the simulation study presented above, the selected eleven cultivars offer a range of behaviors. Their performance varies between environments (water demand, soil hydraulic properties) and treatments (irrigation volume and timing) highlighting the genotypes x environment x management interactions. This model makes clear than no perfect ideotypes exist that perform ideally in any situation. On the contrary quantitative traits that make cultivars more adapted to their location and farming practices exist and can be selected for. We showed that the macroscopic parameters of Couvreur et al. seem to well explain their behavior.

The model is physically-based and describes the main processes of the water flow at the plant scale in three dimensions but remains relatively fast: most of the scenarios presented here ran in less than 12 hours CPU time for 90 days of simulation. Taking advantage of computer clusters makes possible its use for testing specific root traits or root cultivar performance in a really large set of changing environments. It makes this model also suitable to optimize management practices (sowing date, irrigation volume and time) on the long-term.

The cultivars generated in these simulations are virtual. In next studies however, specific root traits characterizing cultivars will be implemented and tested in order to compare the measured *vs* simulated field performances. Combining yield observations and local water content measurements or plant transpiration would also allow us to validate the model.

In this study we assume that all cultivars had the same above-ground properties (stomatal behavior, canopy development). In further studies these properties will be included in the analysis and different stomatal regulation strategies will be implemented to represent a larger range of plant behavior [17]. Similarly, further studies will focus on analytic relation between local traits and the macroscopic parameters. Such relations would allow breeders to develop

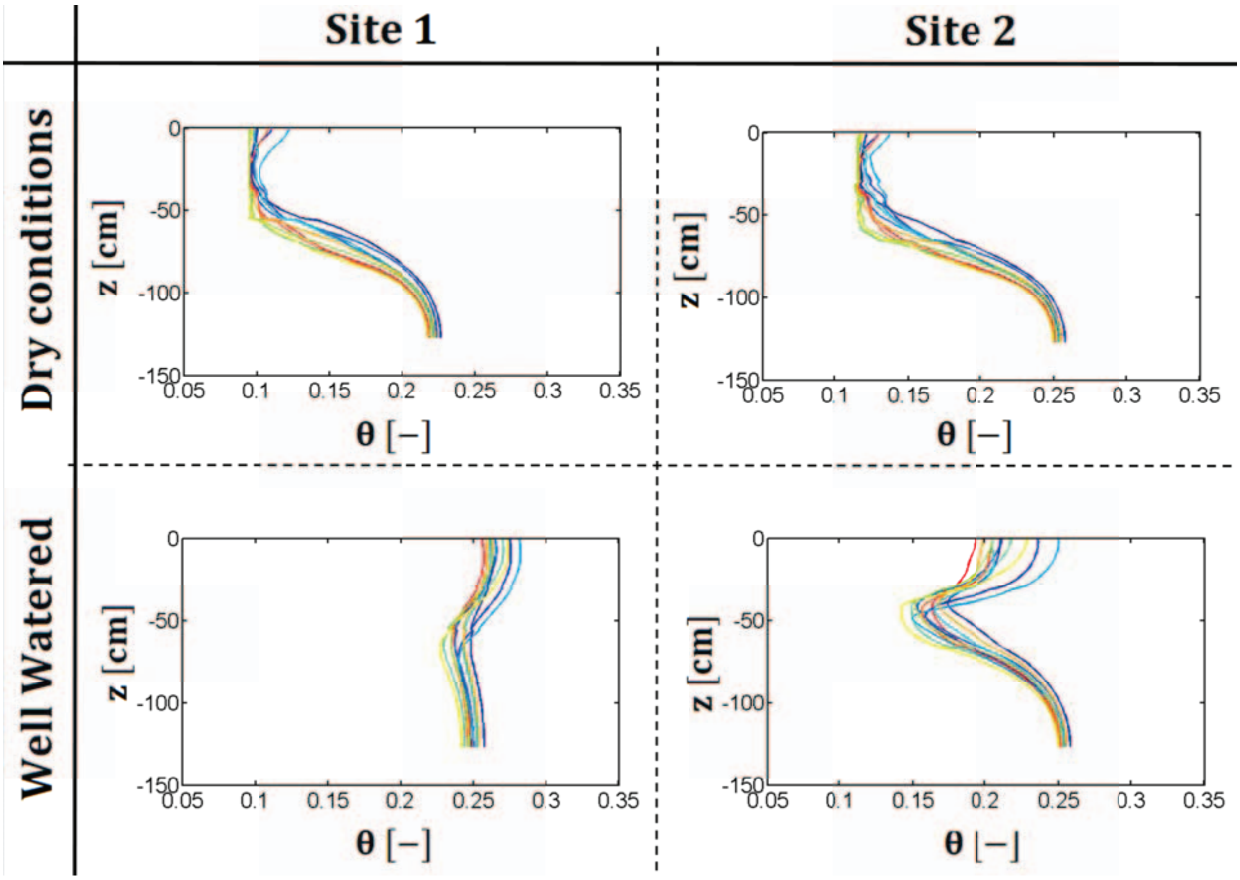


**Fig.7. Water content profiles:** for all the considered cultivars (the colors correspond to Figures 1 and 2) in dry (top panels) and wet (bottom panels) conditions and for the two environments (corresponding columns).

quantitative ideotypes and physiologist to quantify traits beneficial for the plant in specific conditions and to link local traits and field performance through such a kind of simulation study. Even without considering between root traits different water strategies appear. In the future we could also link given root parameters.

Impact of water stress on growth and other plant regulation mechanisms were not accounted for in this study and constitute probably the biggest model limitation. However they can be easily implemented in the model if expressed under quantitative relation between experienced stress (leaf water potential) and local elongation growth rate for example.

## VI. Conclusion

We presented a new model able to optimize the water acquisition over full crop growth and development cycles. This model simulates the water flow in the soil-plant-atmosphere continuum through solving the Richards equation in 3D with a physically-based sink term. In a simulation study using this modeling approach we illustrate its potentiality for quantitative breeding by linking local root traits and field performances through simulation over the full crop season. Different strategies - water saving and water spending - appear and no ideal strategy exist but we were able to pick the best cultivar for water uptake in each specific management and environment interaction situation.

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## Appendix A

**Tab.1. Summary of the cultvars parameters:** parameters variable between cultivar with their definition, their reference value (and unit) in the litterature and the chosen variability. All the other growth or hydraulic parameters come from the litterature (see especially [5] for the architectural parameters and [12] for the hydraulic parameters)

| | Definition | Reference value | Range | Unit |
|---|---|---|---|---|
| **Root growth parameters** | | | | |
| **I. Primary roots** | | | | |
| • $d_{inter}$ | Distance between two successive laterals | 0.2 | 0.1-0.4 | cm |
| • $l_{max}$ | Maximal root length | 125 | 75-200 | cm |
| | | | | |
| **II. Secondary roots** | | | | |
| • $v_0$ | Initial elongation rate | 0.8 | 0.2-1.4 | cm $d^{-1}$ |
| • $l_{max}$ | Maximal root length | 8 | 2-10 | cm |
| • r | Root radius | 0.05 | 0.025-0.075 | cm |
| | | | | |
| **Root hydraulic parameters** | | | | |
| **I. Primary roots** | | | | |
| • $age_I$ | Transition age I (early protoxylem) | 5 | 4-6 | days |
| • $age_{II}$ | Transition age II (early metaxylem) | 10 | 8-12 | days |
| • $age_{III}$ | Transition age III (late metaxylem) | 20 | 15-25 | days |
| • $k_{xI}$ | Intrinsic axial conductance I | 0.00173 | 0.000173-0.0173 | $cm^4$ $hPa^{-1}$ $d^{-1}$ |
| • $k_{xII}$ | Intrinsic axial conductance II | 0.295 | 0.0295-2.95 | $cm^4$ $hPa^{-1}$ $d^{-1}$ |
| • $k_{xIII}$ | Intrinsic axial conductance III | 4.32 | 0.432-43.2 | $cm^4$ $hPa^{-1}$ $d^{-1}$ |
| | | | | |
| **II. Secondary roots** | | | | |
| • $age_I$ | Transition age I | 5 | 4-6 | days |
| • $age_{II}$ | Transition age II | 13 | 11-15 | days |
| • $k_{xI}$ | Intrinsic axial conductance I | 0.0000864 | 0-0.000864 | $cm^4$ $hPa^{-1}$ $d^{-1}$ |
| • $k_{xII}$ | Intrinsic axial conductance II | 0.00173 | 0.000173-0.0000173 | $cm^4$ $hPa^{-1}$ $d^{-1}$ |
| • $k_{rI}$ | Radial conductivity I | 0.000181 | 0.0000181-0.00181 | cm $hPa^{-1}$ $d^{-1}$ |
| • $k_{rII}$ | Radial conductivity II | 0.0000173 | 0.00000173-0.000173 | cm $hPa^{-1}$ $d^{-1}$ |
| | | | | |
| **Root leaf behavior** | | | | |
| • $\Psi_{lim}$ | Minimal collar potential | -15000 | | hPa |