

A modeling approach to determine the contribution of plant hydraulic conductivities on the water uptake dynamics in the soil-plant-atmosphere system

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Abstract—We present here a new model, PlaNet-Maize, which encompasses the entire soil-plant-atmosphere continuum with a resolution down to individual plant organ segments. The model simulates the growth and development of an individual maize plant, including water uptake dynamics and regulation. We successfully used the model to simulate the influence of root system size on the water status of individual plant organs. Moreover, the model was used to assess the contribution of different regulatory processes acting on the hydraulic radial conductivities and axial conductances.

Index Terms—maize, water uptake dynamics, functional-structural plant model

I. INTRODUCTION

The flux of water in the soil-plant-atmosphere continuum is a passive process enabled by water potential differences and by the presence of a continuous water column from the soil and the atmosphere [1]. In the plant, the water movement is impeded by several conductances: the root radial conductivity, the xylem axial conductance and the leaf radial conductivity. While the leaf radial conductivity, mainly regulated by the aperture of the stomata, has the largest potential impact on the total amount of water extracted by the plant, the spatial distribution of the root axial conductances and radial conductivities throughout the root system (the “hydraulic architecture”) influences the uptake sites in the soil [2]. These factors must be considered simultaneously if we aim to tailor plants with improved resistance to water deficit.

For many years, scientists have been using computer models to help understand and decrypt biological processes in the soil-plant-atmosphere system. As an example, root models evolved from simple architectural models reproducing the root system shape and growth [3]–[6] to complex functional-structural models simulating physical, chemical or physiological processes such as nutrient acquisition [7], carbon allocation [8] or water uptake [9]–[11]. The authors are not aware of any model that explicitly simulates the whole plant structure along with water relations and physiological regulatory mechanisms.

We present here a new model, PlaNet-Maize, which encompasses the entire soil-plant-atmosphere continuum with a resolution down to individual plant segments. The model simulates the growth and development of an individual maize plant, including the regulation and dynamics of water uptake.

II. MODEL DESCRIPTION

A. General principles

PlaNet-Maize belongs the modeling project PlaNet (Plant as a Network) developed in Loïc Pagès’ team. At the core of the PlaNet project lays a meta-model that serves as a building structure for the creation of various whole plant models. The PlaNet structure is currently used by several projects with various research objectives: cost/benefit analysis of nodulation in pea, effect of N nutrition on tomato or response of fruit trees to pruning.

In PlaNet, the plant structure is viewed as a network of segments, or articles, interconnected in a tree-like structure. Each article has three fundamental behaviours: morpho-generator (it can grow and create new organs), bio-reactor (it has its own metabolic activity, influenced by its direct endogenous and exogenous environments) and carrier (it can transport substances from and to neighboring articles). Two types of articles are implemented in PlaNet: the segments, which provide the structure of the plant, and the meristems, which generate new segments and / or meristems, hence ensuring growth and branching. These two types of articles can be sub-grouped based on their botanical nature: stem, leaf or root. These six types of articles are sufficient to simulate the growth and development of a whole plant (fig. 1).

The PlaNet-Maize implementation simulates the growth and structure of a maize plant with a fairly good realism. The initial model was enriched with modules specific to water movement and water-related physiological processes. PlaNet-Maize was developed in Java and is integrated in the modelling platform CrossTalk [12] which enables, among

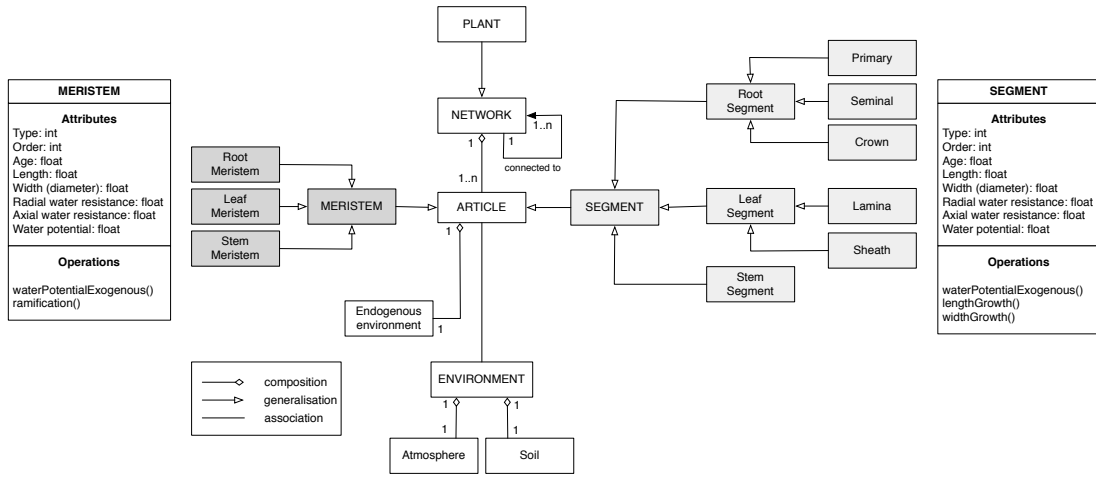


Fig. 1. UML diagram of PlaNet-Maize.

other features, the coupling with a soil model, the 3D visualisation and *in situ* the interactive modification of the plant (e.g. pruning).

B. Maize architecture

The root system in PlaNet-Maize is articulated around four root types: the primary root (first embryonic root), the seminal roots (roots initiated from the scutellar node), the crown roots (shoot-born roots) and the first and second order lateral roots [13]. Its implementation was greatly inspired by previous root models [14], [15]. However, unlike previous models, root axes in PlaNet-Maize can grow from different types of organs (fig. 2).

The shoot architectural module of PlaNet-Maize is widely inspired from the model GRAAL where leaf and stem growth and development are determined by morphogenetic processes and are a function of thermal time [15].

C. Water fluxes

Water fluxes in the whole soil-plant-atmosphere system are solved after [16] using a representation of the plant as an electrical network. In Doussan's method, classical flux equations [17] are laid down for every article and assembled as a linear equations system that is solved at the root system level. In PlaNet-Maize, we generalised this formulation in order to scale it to the whole plant level, including roots, stem and leaves as a unique interconnected system. Following this, the radial water fluxes can be described using the equation

$$J_r(z) = L_r[\psi_s(z) - \psi_x(z)]S \quad (1)$$

where $J_r(z)$ is the radial flux [$m^3 s^{-1}$], $\psi_x(z)$ and $\psi_s(z)$ are respectively the water potential of the plant article and of the soil, L_r is root radial conductivity [$m.s^{-1}.MPa^{-1}$] and S is the article surface. On the other hand, axial water fluxes are described as follow:

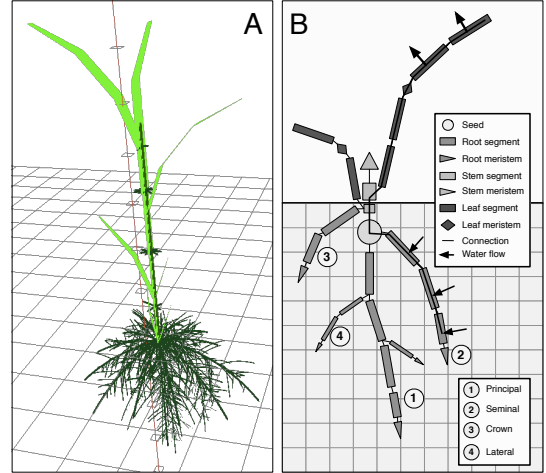


Fig. 2. A. PlaNet-Maize visual output in CrossTalk. B. Schematic representation of the node structure in PlaNet-Maize

$$J_h(z) = -K_h \frac{d\psi_x(z)}{dz} \quad (2)$$

where $J_h(z)$ is the axial flux [$m^3 s^{-1}$], $-K_h$ is the xylem conductance [$m^4 s^{-1} MPa^{-1}$], $d\psi_x(z)$ is the xylem water potential difference between two neighbour articles and dz is the distance between these articles. The Kirchhoff law is applied to every article to warrant that the sum of *in* fluxes equals that of *out* fluxes:

$$\sum_{k_{in}}^k I_{k_{in}} = \sum_{k_{out}}^k I_{k_{out}} \quad (3)$$

where $I_{k_{in}}$ is the inflow and $I_{k_{out}}$ is the outflow from the articles. The combination of these three equations has been successfully used to simulate the water transfers in the soil-plant system in different models [10], [16]. In these

models, at each time step, the equations are computed for every article and assembled as linear equations system to be solve at the root system level. In PlaNet-Maize, we generalised this formulation in order to apply it at the plant level (roots, stem and leaves).

a) Root: Root hydraulic properties described by [18] were used in PlaNet-Maize. Axial and radial properties are expressed as a function of the root developmental stage (in terms of age or distance to the apex) and type (axes or laterals). These values have been used successfully in previous models [10], [16].

b) Stem: The radial conductivity of the stem is set to zero, assuming that the stem neither loses nor uptakes water (it is only a transporter). The axial conductance of the stem is calculated according to the Hagen-Poiseuille law and considering the xylem radius to be 1.7% of the stem radius [19].

c) Leaves: Leaf and root radial hydraulic conductivity values from the literature do not use the same units (e.g. root radial conductivity [$\text{m.s}^{-1}.\text{MPa}^{-1}$] and leaf radial conductivity [$\text{m}^3\text{m}^{-2}\text{s}^{-1}$]). Moreover, unlike experimental measurements that are often based on the difference in relative humidity between the stomatal cavity and the atmosphere, the resolution of water fluxes in PlaNet-Maize relies on water potential differences between the xylem and the atmosphere. Therefore, using the flux equation

$$L_r = \frac{\Delta\Psi S}{J_{out}} \quad (4)$$

where $\Delta\Psi$ is the water potential difference between the atmosphere and the leaf, S is the leaf area and J_{out} the radial water flux, we computed that a maximal leaf radial conductivity of $3.10^9\text{m.s}^{-1}.\text{MPa}^{-1}$ would be compatible with available experimental data (data not shown). Diurnal variation in the leaf radial conductivity is then influenced by environmental conditions (light, vapor pressure deficit and temperature) following Jarvis equations [20].

D. Hydraulic regulation in plant articles

In order to investigate the regulatory dynamics of the hydraulic status of the plant, three major regulatory processes acting on radial and axial properties and on different plant organs, were added to the model: modification of the root radial conductivity (aquaporin regulation, see [21], [22]), modification of leaf radial conductivity (stomata regulation, see [23]) and modification of axial conductance in all organs (cavitation, see [19], [24]). The general equation of these curves is

$$f(x) = A + \frac{K - A}{(1 + Qe^{-B(x-M)})^{1/v}} \quad (5)$$

where A is the lower asymptote, K is the upper asymptote, B is the growth rate, $v > 0$ affects near which asymptote

maximum growth occurs, Q depends on the value $f(0)$, M is the time of maximum growth if $Q=v$ and x is the water potential. Cavitation was implemented using the Weibull function

$$f(x) = 1 - e^{-\left(-\frac{x}{b}\right)^c} \quad (6)$$

where b and c are curve parameters and x is the water potential. Following the work of [24], we implemented different curves for the different plant organs (stem > first order roots > second order roots). Figure 3 presents the different regulation curves.

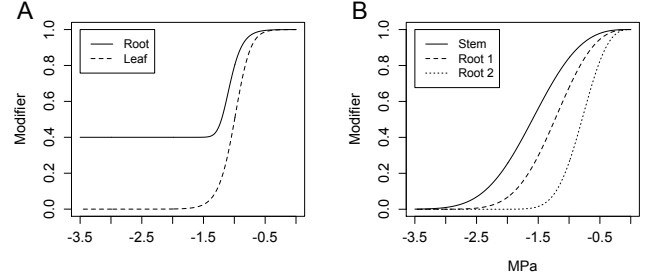


Fig. 3. Conductivity modifiers for root/leaf radial conductivities (A) and axial conductance (B) as a function of the plant water potential.

E. Soil

The soil in PlaNet-Maize is implemented as a 3D grid of voxels with a mesh size arbitrarily defined by the user. Soil water depletion is simulated by removing the uptake flux of every root article from its enclosing voxel. The relationship between the soil water content and the soil water potential (θ -h curve) is defined using a Mualen-Van Genuchten equation [25]. A basic horizontal redistribution of water in the bulk soil is ensured by the application of a mean operator on every soil element and its neighbours.

III. RESULTS

A. Conditions for simulations

The aim of the simulations presented here was to investigate to what extent a maize plant is able to control its water uptake behaviour (hence its water status) by modifying architectural and/or hydraulic traits. The first section highlights the effect of the root system size (e.g. the number of seminal roots) for given hydraulic parameters and transpiration demand. In the second section, conductivity modifiers were enabled in order to assess their quantitative importance.

In all simulations, initial soil and atmosphere water potential were respectively -0.01 and -95 MPa. The soil used in the simulations was a sandy soil, discretized using a mesh of 1cm (data not shown). Environmental conditions (temperature, light and VPD) were set according to a summer day in the greenhouse in Louvain-la-Neuve (Belgium). The time step for the plant development was 1h while that of the

water flux resolution was 15 minutes. Data export started from the 50th hour and the simulations were stopped at 300 hour.

B. Effect of the root system size on the plant water status

In the first round of simulations, the effect of the number of seminal roots emerging from the seed was studied. The hydraulic parameters and the shoot system size were kept constant. Simulations were run with 0, 2 or 4 seminal roots.

Figure 4A shows a clear difference in the root-to-shoot surface ratio (RSSR), which reflects the fact that only the root system size was changed between simulations. These changes in the RSSR induced large difference in the plant inner water potential (Ψ) (fig. 4B), leading to non-sustainable Ψ values for the plant (below the Permanent Wilting Point or -1.5 MPa). Figure 4C indicates that the RSSR is directly linked to the plant water potential and that a minimum threshold exists for RSSR in a given plant / environment scenario.

C. Effect of changing hydraulic properties on the plant water status

In order to show the interplay between local hydraulic conductance variations and the endogenous water potential, four simulations were run, using the proposed regulatory mechanisms individually or coupled. The root system was voluntarily undersized (2 seminal roots) in order to create an non-sustainable situation for the plant (according to the figure 4). The aim of these simulations was to test whether the regulatory processes implemented in the model enable the virtual plant to reach an equilibrium in terms of endogenous water potential values.

Allowing plant articles to locally adjust their hydraulic properties (both L_r and K_h (need to define them ?)) to local water potential values led to global changes at the system scale. The regulation of L_r in the roots or the leaves had opposite effects on the root system water potential. Indeed, allowing the leaves to reduce their L_r decreased the tension in the plant articles while decreasing L_r in the roots directly increased it (fig. 5A). The modifications in K_h did not seem to have a noticeable effect on the system. Interestingly, the combination of the three processes seems able to maintain the plant in a wide range of endogenous water potential values even with a small root system.

Figure 5B reveals the effect of varying hydraulic regulation on the root uptake profiles. Changes in the leaf L_r have large effects compared to root L_r or axial conductivities. Reducing the leaf L_r reduces the transpiration of the plant and therefore the uptake rates at the root level. This reduction is more important if the three processes are combined. This is probably due to the combination of the opposite effects of the root and leaf L_r regulations on the water potential. As

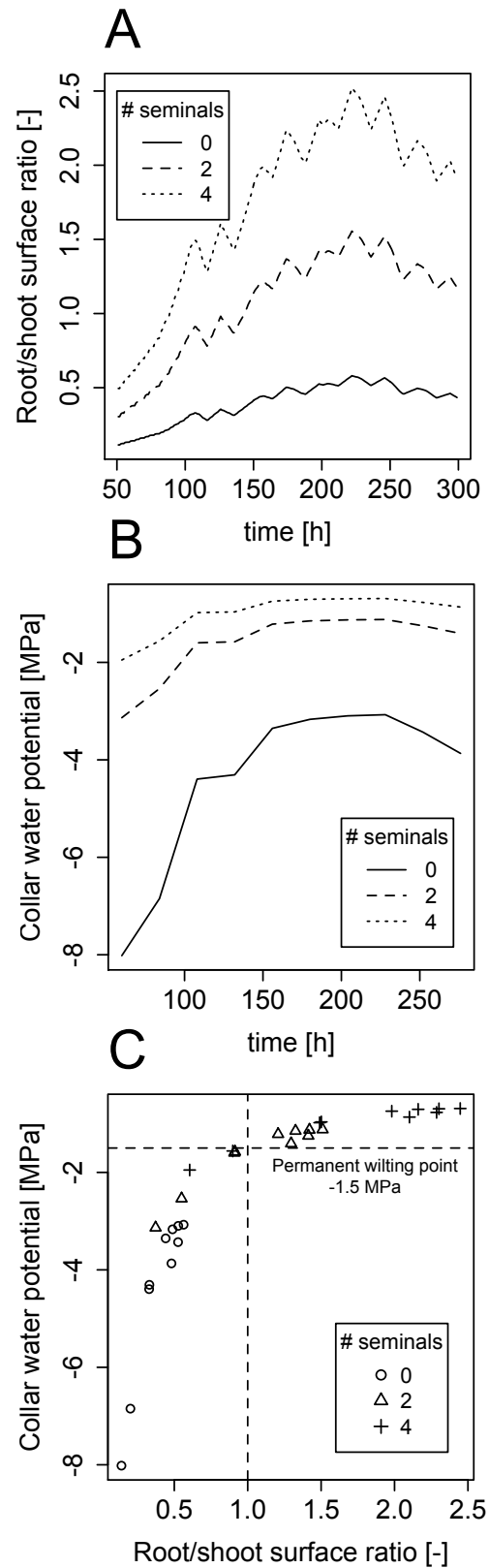


Fig. 4. **A.** Root-to-shoot surface ratio evolution for simulations with 0, 2 or 4 seminal roots. **B.** Collar water potential evolution for the three simulations. **C.** Relationship between the root-to-shoot surface ratio and the collar water potential.

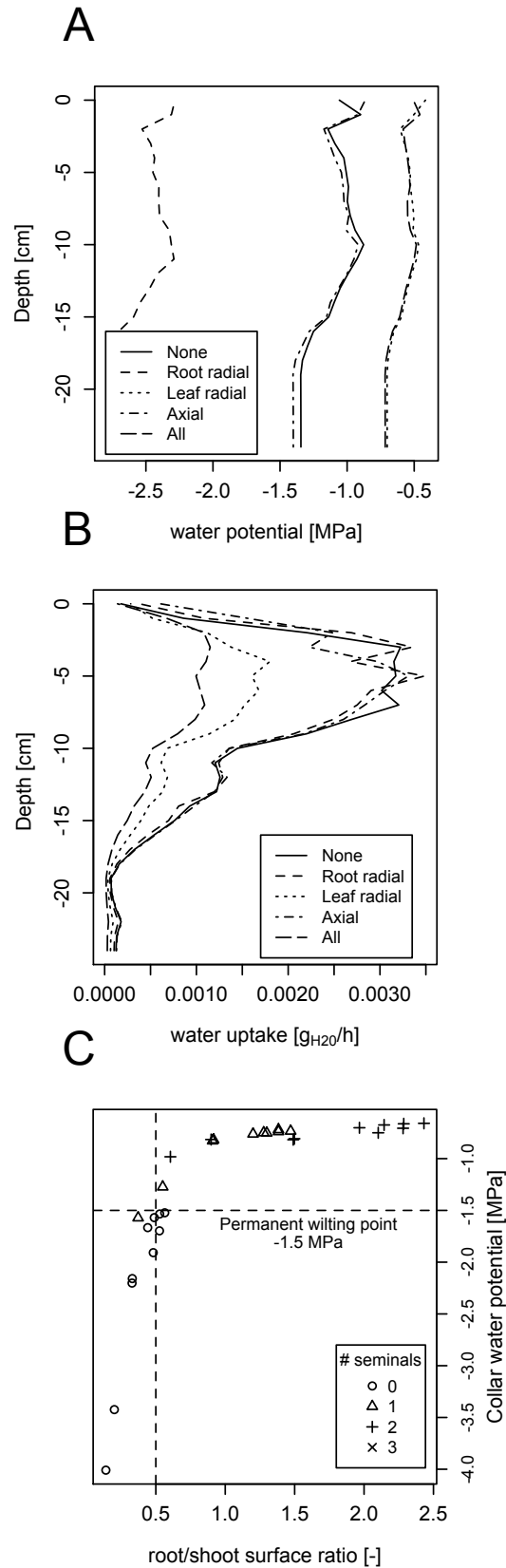


Fig. 5. **A.** Influence of regulatory processes on the root system water potential profile. **B.** Influence of the regulation processes on the root system water uptake profile. **C.** Relationship between the root-to-shoot surface ration the collar water potential.

the water potential decreases, the root Lr tends to decrease as well, forcing the leaf Lr to decrease to lower values.

Finally, figure 5C shows that the combination of Lr and Kh regulatory processes ensures a better homeostasy of the plant water status over a range of root system sizes. Indeed, compared to the figure 4C, a wider range of root system size seems to be sustainable for the plant in terms of water potential.

D. Model validation

PlaNet-Maize architectural and water flux models were validated against experimental data independent of the one used to calibrate the model. Figures ??A and ??B show that the architectural model produce realistic root and shoot development while the figure ??C show that the simulated water flux, integrated at the plant level, reflects the data obtained experimentally.

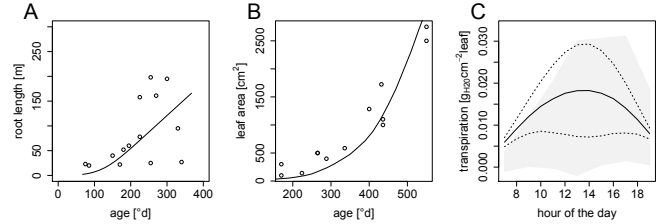


Fig. 6. Comparison between experimental and simulated data. **A.** Comparison between experimental (circles) and simulated (line) root length values. **B.** Comparison between experimental (circles) and simulated (line) shoot area values. **C.** Comparison between experimental (grey area) and simulated (lines) transpiration values. Plain line represents the mean simulated transpiration value while the dashed lines represent the standard deviation range.

IV. CONCLUSION

We used PlaNet-Maize to simulate water transport in the soil-plant-atmosphere continuum. This first version of the model was able to reproduce the effect of root architecture and hydraulic properties on the water relations in the plant as previously shown in former models [2], [11]. In addition, by implementing simple regulatory processes acting on the local values of Lr and Kh, we found that the virtual plant was able to tightly control its water status. As expected, in our model, the regulation of the leaf Lr (aka stomatal regulation) seems to be the most effective way for the plant to keep its water potential in a sustainable range by reducing its water loss. Acting on the root Lr (aka aquaporin regulation) also has an important effect on the plant water status but in the opposite way. Indeed, a reduction in the root Lr has a direct negative effect on the plant water potential. Fortunately, combining the leaf and root Lr regulation helps keeping the plant in the correct water potential range, by reducing the transpiration even more. It is worth noting that all simulations were run

using parameter values from the literature.

The model presented here is currently being improved with the implementation of carbon transport and carbon-related growth functions. These processes are indeed needed to investigate the effect of transpiration reduction on the overall plant growth and subsequent water use.

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