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A modeling approach to determine the importance of dynamic regulation 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, with the purpose of investigating the effect of environmental and endogenous factors on the growth and water relations of the maize plant. This functional–structural plant model (FSPM) encompasses the entire soil-plant-atmosphere continuum with a sub-organ resolution. The model simulates the growth and development of an individual maize plant and the flux of water through the plant structure, from the rhizosphere to the leaf boundary layer. Leaf stomatal conductance and root radial and axial conductivities are considered as functions of local water potential. Finally, a simple carbon allocation rule is included in the model to allow the feedback effect of water deficit on plant growth. The model was successfully used to reproduce experimental plant hydraulic behavior in response to water deficit. The quantitative contribution of leaf conductance and root conductivities were assessed individually and in combination.

Our results highlight the importance of regulating hydraulic properties in FSPM as these can strongly modify the water uptake dynamics and lead to emerging water uptake behaviors. The modeling results also indicate that plant hydraulic properties can theoretically be tailored to improve plant water use in challenging environments.

1. Introduction

The flow of water in the soil-plant-atmosphere continuum is a passive process driven by water potential differences and enabled by the continuity of the liquid phase of water between the soil and the leaf mesophyl (Steudle, 2001). For a given driving force, the flow of water in the plant is set primarily, though not exclusively, by the radial conductance of the root system, the axial conductivity of the xylem and the leaf conductance.

The leaf conductance, which is largely determined by the density and aperture of the stomata, sets the maximum amount of water that can be transpired under a given environmental demand. Due to the obvious and major role of stomata, the mechanisms underlying their regulation have received much attention from the scientific community, leading to numerous experimental and modeling approaches (reviewed by Damour et al., 2010).

The root radial conductance is a complex property reflecting the composite nature of water movement from the root surface to the xylem. It both depends on irreversible processes like the deposition of hydrophobic barriers in the endodermis and exodermis (Enstone et al., 2003), and on time-varying features like the activity of water channels (Maurel et al., 2008; Javot and Maurel, 2002). The crossing of root tissues is generally considered as an important limiting step in the water uptake process (Steudle and Peterson, 1998).

The axial conductivity of the xylem vessels is also a complex property which combines the structural features of the xylem, the dynamics of cavitation events occurring when the tension in the xylem is too large (Sperry et al., 1998) and the extent of embolized vessels refilling that occurs when the tension vanishes but possibly also under tension (McCully et al., 1998; Zwieniecki and Holbrook, 2009; Holbrook and Zwieniecki, 1999). While the leaf conductance sets the amount of water extracted by the plant, the distribution of root axial conductivities and radial conductances throughout the root system (the *hydraulic architecture*) determines the sites of water uptake in the soil. This role of root hydraulic properties has often been considered as minor in comparison with root length density, but this should be reconsidered in view of recent data (Draye et al., 2010). Therefore, considering leaf, root and environmental factors simultaneously may be an important

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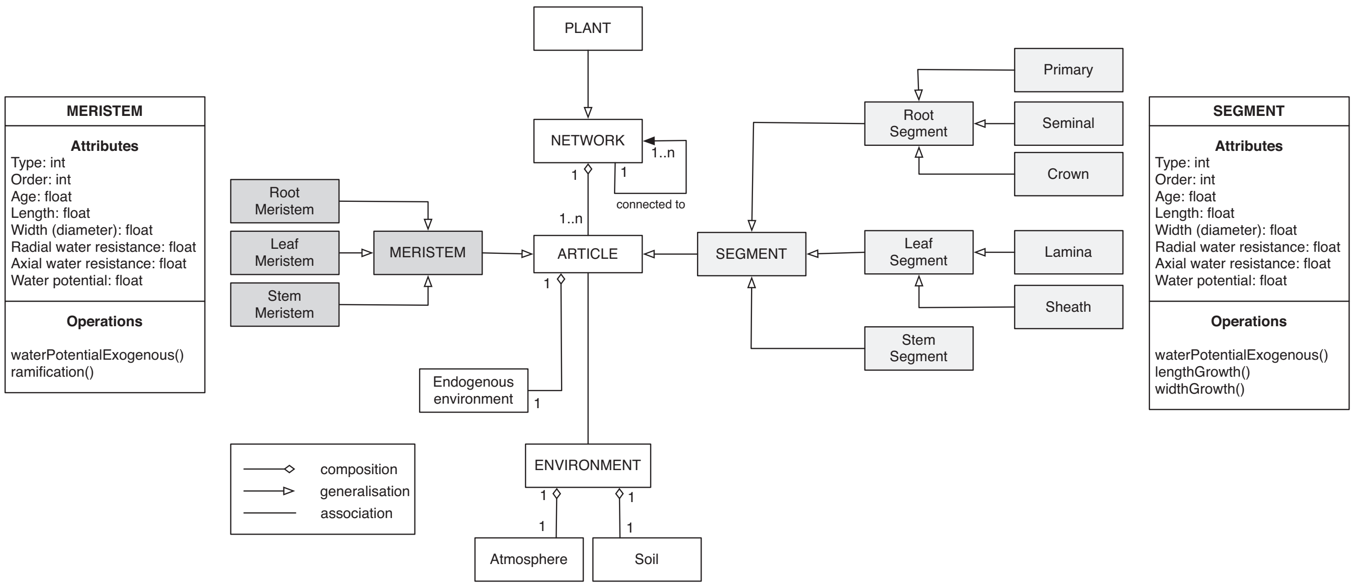

Fig. 1. PlaNet-Maize UML scheme. Light grey boxes represent the segments classes. Dark grey boxes represent the meristem classes.

contribution if we aim to tailor plants with improved resistance to water deficit.

For many years, scientists have developed computer models to simulate how biological processes, described individually or at an organ scale, integrate and scale up in the soil-plant-atmosphere system. On the root side, models evolved from architectural models reproducing the root system shape and growth (Diggle, 1988; Pagès et al., 1989; Lynch et al., 1997) to functional–structural models simulating physical, chemical or physiological processes such as nutrient acquisition (Ge et al., 2000), carbon allocation (Bidel et al., 2000) or water uptake (Somma et al., 1998; Javaux et al., 2008). A similar trend was observed for shoot models (Fournier and Andrieu, 1998). While some models address simultaneously the root and shoot systems (Drouet and Pagès, 2003; Janott et al., 2011), the vast majority focus on either part of the plant and use simplified descriptions of the other. As of today, we are not aware of any model that simulates the water dynamics of a complete plant with a detailed description of each organ.

This situation led us to develop the PlaNet-Maize model, which simulates at a sub-organ resolution the growth and architecture, the water flows and the main hydraulic regulations of a whole maize plant. The model uses simplified rules for the production and allocation of assimilates to the different organs.

2. Model description

2.1. General principles

PlaNet-Maize adheres to the principles of the metal-model PlaNet (Plant as a Network), developed by Loïc Pagès, that defines a building schema for the creation of various whole plant models. In PlaNet, the plant structure is viewed as a network of articles interconnected in a tree-like structure and localized in space. Articles are typically organs, but can be defined as smaller or larger entities. They have three fundamental behaviors: (1) they can grow and create new articles (morpho-generator), (2) they have their own metabolic activity (bio-reactor), and (3) they can transport substances from and to neighboring articles and environment (carrier). As articles are localized in space and in the network topology, these behaviors can be dependent on local environment information as well as on network-derived information.

Two types of articles are typically considered in PlaNet. The first are the segments, which make up the structure of the plant. The second are the meristems, which generate new segments and/or meristems and ensure growth and branching. These two types of articles can be sub-divided 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 during the vegetative stage (Fig. 1).

The PlaNet-Maize model uses PlaNet rules to simulate the growth and structure of a maize plant and includes modules specific to water movement and hydraulic regulatory processes. PlaNet-Maize was developed in Java and is integrated in the modeling platform CrossTalk (Draye and Pagès, 2006) that enables the coupling with environment models, the 3D visualization and the *in situ* interactive modification of the plant during a simulation (e.g. pruning). The CrossTalk platform allows users to easily modify simulation parameters such as the initial environmental condition or the simulation time-step (in hours).

2.2. Architecture module

2.2.1. Root system

The root system of PlaNet-Maize comprises four types of roots: the primary root (first embryonic root), the seminal roots (embryonic roots initiated from the scutelar node), the crown roots (shoot-born roots) and the first and second order lateral roots (Hochholdinder et al., 2004). Its implementation was inspired from previous root architecture models (Pagès et al., 2004; Drouet and Pagès, 2003) with the distinction that root axes in PlaNet-Maize originate from different types of organs (Fig. 2B). The primary and seminal roots arise from the seed while crown root meristems are initiated by the stem meristem. It follows that there is no single connection between the root system and the shoot and that preferential water flow may occur between crown roots and the leaf initiated at the same node. Root elongation rate was computed as a function of the root meristem diameter (Drouet and Pagès, 2003; Mollier and PEllerin, 1999).

2.2.2. Shoot system

The shoot architectural module of PlaNet-Maize was largely inspired from the model GRAAL where leaf and stem growth and development are determined by morphogenetic processes and are