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Hydraulic conductivity of soil-grown lupine and maize unbranched roots and maize root-shoot junctions

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ABSTRACT

Improving or maintaining crop productivity under conditions of long term change of soil water availability and atmosphere demand for water is one the big challenges of this century. It requires a deep understanding of crop water acquisition properties, i.e. root system architecture and root hydraulic properties among other characteristics of the soil-plant-atmosphere continuum. A root pressure probe technique was used to measure the root hydraulic conductances of seven-week old maize and lupine plants grown in sandy soil. Unbranched root segments were excised in lateral, seminal, crown and brace roots of maize, and in lateral roots of lupine. Their total hydraulic conductance was quantified under steady-state hydrostatic gradient for progressively shorter segments. Furthermore, the axial conductance of proximal root regions removed at each step of root shortening was measured as well. Analytical solutions of the water flow equations in unbranched roots developed recently and relating root total conductance profiles to axial and radial conductivities were used to retrieve the root radial hydraulic conductivity profile along each root type, and quantify its uncertainty. Interestingly, the optimized root radial conductivities and measured axial conductances displayed significant differences across root types and species. However, the measured root total conductances did not differ significantly. As compared to measurements reported in the literature, our axial and radial conductivities concentrate in the lower range of herbaceous species hydraulic properties. In a final experiment, the hydraulic conductances of root junctions to maize stem were observed to highly depend on root type. Surprisingly maize brace root junctions were an order of magnitude more conductive than the other crown and seminal roots, suggesting potential regulation mechanism for root water uptake location and a potential role of the maize brace roots for water uptake more important than reported in the literature.

1. Introduction

Global crop production is negatively affected by drought, which is the most significant abiotic stress in agriculture (Cattivelli et al., 2008). This stress can be defined as the plant's inability to take up and transport water to the shoot at the rate required to sustain transpiration, with such inability leading to stomata closure and reduced yield (Farooq et al., 2009). The extraction of water from soil and supply to the shoot to maintain the transpiration and the carbon capture for photosynthesis is one of the major roles of the root systems (McElrone et al., 2013). Recently, it has received increasing attention as a promising target for breeding drought-tolerant crops in a climate change context (Comas et al., 2013; Hammer et al., 2009; Schoppach et al., 2014).

Both architectural and hydraulic properties of the root system determine the location and uptake rate of water (Leitner et al., 2014), and by extension its availability (Couvreur et al., 2014). These properties are captured in the concept of "hydraulic architecture" that facilitates the water uptake that is driven by the transpiration demand of the atmosphere (Doussan et al., 1998a; Lobet et al., 2014). From the

Abbreviations: L, length; T, time; P, pressure

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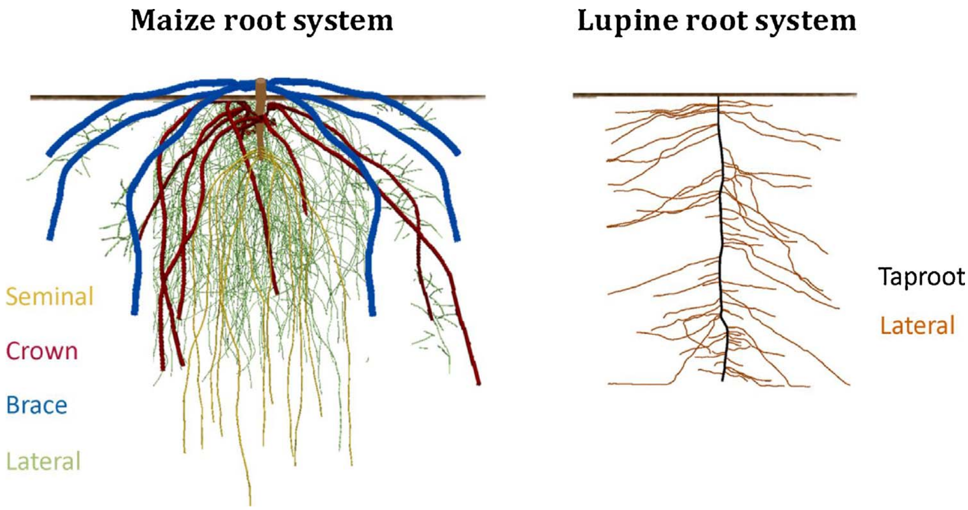

Fig. 1. Schematics of maize (left) and lupine (right) root systems, respectively simulated in CRootBox and observed in rhizotron. Root nomenclature and color code are consistent throughout the manuscript.

hydraulic perspective, the flow of water between soil-root interfaces and xylem vessels is regulated by root radial hydraulic conductivity, which depends on anatomical and physiological properties of the root cross-section (Steudle, 2000). Beyond that point, water transfer up to the shoot is controlled by root axial conductance (Passioura, 1980), which depends on the size, the abundance and the maturation level of the xylem vessels (Martre et al., 2000; Sanderson et al., 1988).

From the architectural perspective, root types and branching patterns impact soil exploration and resource capture in a dynamic way, with strategic consequences on plant fitness to its environment (Draye et al., 2010; Lynch, 2013; Lynch and Brown, 2012). In plants with adventitious root systems, such as maize, the root system consists of four different root types classified as primary, seminal, crown, and brace root (see left panel in Fig. 1, simulated in the software CRootBox (Schnepf et al., 2017)). From these main root axes, the substantial amount of lateral roots that branches out would play a critical role in water acquisition (Ahmed et al., 2016). Lupine (*Lupins Albus* L.), on the contrary, only develops a single primary "tap" root, which branches into laterals of different orders (see right panel in Fig. 1, observed in rhizotron (Zarebanadkouki et al., 2016)). How these root orders translate into different root segment hydraulic properties is still not clear from the literature (Vadez, 2014). In addition, as a result of different growth and maturation rates, these different types of roots will also have a different evolution of their radial and axial hydraulic properties along the axis as a function of their age (Vetterlein and Doussan, 2016). The resulting combination of architecture and root property distribution (called hydraulic architecture) will define the root system conductance.

Although root hydraulic properties partially control water uptake pattern in heterogeneous environments (Javaux et al., 2008; Zarebanadkouki et al., 2016) and have an important breeding potential (Schoppach et al., 2014; Vadez, 2014), their measurement remains challenging, in particular for plants growing in soil. Yet, their accurate determination would allow breeders to better understand how root hydraulics combines to architectural traits, in the determination of species and/or genotypes performances in water-limited environments (Meunier et al., 2017; Meunier et al., 2016b; Tardieu, 2012; Tardieu et al., 2015).

The objective of this study is to evaluate the variability of hydraulic properties along different root types in maize and lateral roots in lupine, as well as the conductance of junctions between the shoot and the principal roots in maize (i.e. the particular zones connecting maize main roots and the stem in the way of the sapflow towards the leaves). This will improve the understanding of the contribution of specific root types and root regions to the overall root conductivity, and their consequences on water uptake patterns.

To do so, we develop methods to characterize root hydraulic properties for different root types. A root pressure probe technique is used to measure profiles of axial and total hydraulic conductances along roots of maize and lupine plants grown in soil, as well as the conductance of root-stem junctions in maize. These measurements are combined with an inverse modeling scheme to retrieve the profile of radial hydraulic conductivity of each root type. These values are finally compared with direct and inverse measurements reported in the literature.

2. Materials and methods

2.1. Soil and plant material

Nine maize and nine lupine plants were grown in aluminium containers (size of 40 × 40 × 1 cm) filled with sandy soil (92% sand – 5% silt – 3% clay). The aluminium containers consisted in two aluminium plates of 40 × 40 cm, which were held together at the edges by aluminium bars of 1 × 1 × 1 cm. This construction enabled us to open the container from one side and carefully dig out roots from soil. Maize seeds were soaked in 10% H_2O_2 solution for 10 min and then germinated on moist filter paper for 48 h. One seedling was then planted at a depth of 1 cm into each container and the upper soil layers were covered with a 1 cm layer of quartz gravel to reduce evaporation from soil surface. The plants were grown with a daily light cycle of 14 h and 10 h of darkness, a light intensity of 500 μmol $m^{-2} s^{-1}$, day and night temperature of 24 and 19 °C, respectively and relative humidity of 60%. During the growth period, plants were irrigated every four days to keep soil at an average water content of 0.20–0.25 $cm^3 cm^{-3}$. When plants were seven-week old, the containers were opened from one side and roots were carefully washed from the soil. Unbranched segments of different root types of maize (lateral, seminal, crown, and brace roots) and lateral roots of lupine were excised and connected to a pressure probe to measure their hydraulic properties (Bramley et al., 2009; Frensch and Steudle, 1989). The methodology was applied to the different species and root types. For lupine, we only considered the lateral roots since the taproot is rapidly branched. For maize, we analysed seminal, crown, brace and lateral unbranched roots as well as the conductance of the root-shoot junction. Four to five replicates per root type were considered. The procedure of root pressure probe experiment was slow. Three to four root segments per day could be characterized. To avoid age variation among the sampled roots, the nine plants were