Soil water uptake and water flow through root systems.

Guillaume Lobet[1], Charles Hachez[2], François Chaumont[2], Mathieu Javaux[1,3] and Xavier Draye[1]

[1] Université catholique de Louvain, Earth and Life Institute, Belgium

[2] Université catholique de Louvain, Institut des Sciences de la Vie, Belgium

[3] Forschungszentrum Juelich GmbH, Agrosphere IBG-3, Germany

Glossary

SPAC	Soil-Plant-Atmosphere Continuum
L_{pr}	Root system conductivity
K_x	Root axial conductivity
K_r	Root radial conductance
L_{pcell}	Cell conductivity
L_p	Plant conductivity
K_{sat}	Soil saturated conductivity
ABA	Abscissic Acid

Introduction

Water is by far the ressource that plants absorb in largest amounts from their environment. However, only a tiny fraction of the water taken up is used for the production of new assimilates. The largest part is lost to the atmosphere as stomata open to allow diffusion of carbon dioxyde into leaves. For maize alone, this expensive bargain represents annually ca. $3x10^{14}$ litres of water worldwide, about twice the volume of the Dead Sea (FAO 2012). Although transpiration is needed to prevent excessive heating of sunlit leaves and to ensure long-distance transport of nutrients from the bulk soil to plant organs, the contrasting transpiration efficiencies of C3 and C4 species is an indication that actual crop water use often exceeds theoretical requirements. However, the fact that breeding for reduced crop water use has often led to negative results (Blum 2005) stresses that a more detailed consideration of the dynamics of water fluxes in the soil-plant-atmosphere system will be needed in the future (Gregory *et al.* 2005).

In a transpiring plant, the diffusion of vapor to the atmosphere through stomata leads to the evaporation of water from the mesophyl cell walls and the displacement of the water-air interface to narrower intersticial spaces between wall fibrils. This increases capillary forces at the wall surface and the tension at the leaf-side of the soil-plant hydraulic continuum. In the absence of any resistance to water flow along the continuum, this tension would lead to an immediate displacement of water from the soil and maintain the system in its original state. However, water movement is impeded by several features of both the soil matrix and plant structures, which complicates water entry in the plant and decrease the water potential in the whole continuum (fig. 1A). The master control played by stomata, which operates where the water potential gradient is the largest, is therefore subordinated to the ability of the downstream continuum to cope with the transpirational demand. If the impedance between the bulk soil and the stomata gets so large that the plant water potential decreases to damaging levels, the plant will have no other solution than

closing stomata.

Biologists often use the analogy with the Ohm's law to express the dependency between water potential, water flux and hydraulic resistance (van den Honert 1948). At the whole plant scale, the electrical analogy is expressed as $E = (\psi_{atm} - \psi_{soil}) * L_p$,where E is the total water flow, ψ_{atm} is the water potential of the atmosphere and L_P and ψ_{soil} are aggregated values of the plant hydraulic conductivity and soil water potential. As will be explained throughout this chapter, the complex hydraulic architecture of the soil-plant system and the values of all resistances impeding water movement contribute, for a given transpiration rate, to determine the water potential, flow and conductivity at every location in the system. It is their integration at a higher scale which sets the spatial distribution and amount of water E flowing through the plant, referred to as « uptake ».

Excellent reviews of root water uptake have been published already (Jackson *et al.* 2000, Javot *et al.* 2002, Draye *et al.* 2010, Maurel *et al.* 2010, Aroca *et al.* 2011). This chapter focuses on the mechanisms or principles which impede (and, thereby, control) water flow on its way from the bulk soil to the shoot of transpiring plants, and on novel ways to analyse how water uptake patterns emerge from the integration of several hydraulic controls in the soil-plant system. The scenario of root pressure-driven flow is deliberately left aside as it does not contribute to the massive absorption of water discussed above.

Water moves in a complex system

Despite a general agreement on the driving forces of water flow in the soil-plant-atmosphere continuum, on the possible routes taken by water and on the local mechanisms which control (impede) its flow, it remains difficult to predict quantitatively the contribution of specific mechanisms to the regulation of root water uptake. We believe that this is largely due to the composite pathway and the spatially distributed and temporally variable nature of the hydraulic controls.

Insert here figure 1

Before entering the root, water flows in the bulk soil towards the soil-root interface. Its movement follows ψ_{soil} gradient and is impeded by friction against the solid phase. Because soils are comprised of an ensemble of pores of different sizes, their hydraulic conductivity decreases non-linearly with water content (fig. 1B), viz. with water getting restricted to narrower pores. As mentioned above, transpiration decreases the water potential around the roots, which, in a homogeneous domain, is susceptible to cause an important drop of the soil conductivity, leading to a redistribution of the sites of water uptake. In the corresponding electrical analogy, the soil domain would comprise spatially distributed capacity and resistivity that are physically linked to the soil water potential.

When entering the root, water flows into a structure comprised of several layers of differentiated cells. As stated in the composite transport model {Steudle :1998tt}, water crosses the successive layers using pressure-driven apoplastic (cell wall and intercellular spaces) and symplastic (plasmodesmata) pathways or osmotically-driven transcellular pathways (water channels). As water flows preferably in routes of low resistance, the contribution of the three pathways is ultimately controlled by the geometry, cell wall properties and membrane permeability of each layer (Steudle *et al.* 1998, Steudle 2000) (fig. 1C). The

most obvious controlling features are the number of cell layers laid down by the meristem (organ level), the irreversible deposition of hydrophobic barriers in the apoplast (tissue level; see chapter 5 from Meyer and Peterson, Enstone and Peterson (Enstone *et al.* 2003, Ranathunge *et al.* 2011)) and the dynamically regulated activity of water channels (cell level, (Maurel *et al.* 1993, Javot *et al.* 2002, Chaumont *et al.* 2005)). The electrical analogy could be used to integrate cell, tissue and organ level effects on the control of the radial flow. It would comprise resistances to flow between the different compartments (cell walls, intercellular space and cytoplasm), connected in agreement to the radial anatomy and subjected to a difference of water potential between the root surface and the xylem lumen.

Once in the xylem, water flows over long distances through the network of vessels (fig. 1D). Because xylem conductivity is by several order of magnitude higher than that of radial tissues, it is often assumed that the xylem route imposes a neglegible impedance to water flow in the soil-plant-atmosphere continuum (Steudle *et al.* 1998). However, this route is by large the longest one taken by water within the plant. In a maize plant, for example, water runs for several meters in the xylem, against few millimeters from the root surface to the xylem and from the xylem to the mesophyl cells, viz. a difference of three orders of magnitude. There is also abundant evidence that the xylem route can be the limiting piece of the system as the likelihood of cavitation increases with path length (Peirce 1936, Tyree *et al.* 1989, Sperry *et al.* 2002). Frictional drag and cavitation, the major limitations to water flow in the xylem, obey to very different laws, with friction being predicted by Poiseuille's law while cavitation is, at best, only predicted by probability functions. As previously, an electrical analogy could be used to work out the detailed flow of water through the network of xylem conduits. Here, however, in addition to using resistances where friction is operating, on/off switches with partially stochastic behaviors would be needed at the level of each xylem vessel.

The obvious need to integrate different types and scales of control at the sub-organ level also applies at the whole plant level. Indeed, water flows simultaneously from many different places in the bulk soil and

enters the plant through many different roots, and none of those trajectories are hydraulically equivalent. Even for plants growing in uniform hydroponic systems, water uptake is unlikely to be uniform over the root surface. The structure and geometry of the soil/root system place therefore additional constraints on water flow and uptake. It is certainly at this level that the electrical analogy has been most used (Doussan, Pagès, and Vercambre 1998), probably due to the simplicity of the circuit, comprising a simple tree of nodes connected by axial resistances and linked to their local environment by radial resistances (fig. 1E).

Looking at the whole array of conductivities of the media or structures in which water is flowing, some appear to be variable on long time scales while others are highly dynamic; some appear to vary following simple physical laws, while others follow intrinsic or responsive regulatory pathways. In the next section, we review our understanding of the phenomenons responsible for the variation of these conductivities, considering successively those which operate in the soil, in the radial path, in the xylem network and at the system level.

Water flow control in the soil matrix

Soil hydraulic properties that affect water flow to roots

In soils, water follows passively the water hydraulic gradient to move from the soil to the root surface. Accordingly, the soil water potential gradients and the soil hydraulic conductivity will at a given time control the supply of water to the plant. As discussed below, these hydraulic properties of the soil compartment display highly dynamic behavior, which is most likely to imprint the patterns of water availability and uptake. A crucial feature of soils is their ability to store water, which is due to their porous structure. However, the amount of energy needed to extract water from the soil increases as the soil water content decreases, because capillary and surface-binding forces reduce the free energy of water

retained in pores (matric potential). At equilibrium, the matric potential is bound to the volumetric soil water content by a water retention (or release) curve, which is principally determined by the medium pore size distribution and the wetting properties of the pore surfaces. Water retention curves also display hysteresis according to the wetting or drying cycle of the soil.

A second crucial feature of soils is their ability to transmit water when subjected to a hydraulic gradient. The soil hydraulic conductivity is inversely related to friction and is therefore affected by fluid properties (viscosity and density) and soil structure, i.e., the size, shape, tortuosity and connectivity of the pore network filled with water. Even in fully saturated conditions, the conductivity value (K_{sat}) may vary by several orders of magnitude between fine- and coarse-textured soils. At the field scale, values of the saturated conductivity in certain horizons exhibit a coefficient of variation up to 900%, mainly impacted by structural features like macropores (Mallants *et al.* 1997). When the soil desaturates, the hydraulic conductivity decreases dramatically because flow paths become increasingly tortuous and drag forces between the fluid and the solid phases increase. This steep curve induces ratios between saturated and unsaturated conductivity values at 1.5 MPa ranging between 10^6 (for a clay) and 10^{21} (for a sand). The hydraulic conductivity curve characterizes this dependency of hydraulic conductivity on soil moisture.

Soil water dynamics in the presence of roots

The Richards equation (Richards 1931) is usually used to model soil water flow, taking into account the non-linear water release and hydraulic conductivity behaviors of soils. At the root scale, considering a radial geometry, the solution of this equation close to the root surface indicates that, under constant uptake, the soil matrix potential decreases non-linearly towards the root surface, which results in a higher resistance to water flow compared to the bulk soil(Gardner 1965). In conditions of high transpiration rate and medium to dry soil moisture, the decreased soil conductivity near the root surface may limit root water uptake, despite the presence of sufficient water in the bulk soil (Schröder *et al.* 2009).

The redistribution of soil water can also affect root water uptake. At night, as long as the plant hydraulic conductivity is large enough and no capillary or hydrophobic barrier developed during the previous days, soil hydraulic potential tends to even out, restoring the water content around roots and in depleted zones. As mentioned above, the intensity of this lateral and vertical redistribution depends on soil hydraulic properties and on the soil and plant hydraulic status. At the field scale, it also depend on soil hydraulic properties that are shaped by natural (e.g. soil horizons due to pedogenesis) and antropic processes (e.g. soil tillage), but also by soil topography (through runoff) and row / inter-row patterns

Hydraulic properties in the rhizosphere

The rhizosphere is the soil zone that surrounds and is affected by roots. Its boundaries are diffuse and its spatial extent ranges from sub-µm to supra-cm scales, depending on the process of interest (Darrah 1993, Hinsinger *et al.* 2005). In the rhizosphere, soil hydraulic properties can be profoundly modified by the presence and activity of roots and microorganisms. The combination of structural, chemical and biological effects is relatively complex and not well understood. In addition, the hydraulic properties of the rhizosphere are difficult to measure with conventional techniques. It follows that different and sometimes contradicting results were obtained about the impact of rhizosphere processes on soil hydraulic properties (Moradi *et al.* 2012).

Root growth causes compaction of the surrounding soil in front of the root apex (Dexter 1987). This increases the bulk density (Guidi *et al.* 1985) and reorganizes the soil pore distribution and continuity. While Whalley *et al.* (2004) suggested that this would generate a decrease of the infiltration, Aravena *et al.* (2011) modelled instead that this could increase the soil conductivity by raising soil water connectivity.

Exudates from roots and microbial and fungal communities also affect the hydraulic properties of the rhizosphere. Mucilage principally contains polysaccharides that retain a high water content at low water

potentials (Watt *et al.* 1994, McCully *et al.* 1997, Read *et al.* 1999). They contains lipids that can act as surfactants and reduce the surface tension of soil solution (Read *et al.* 2003). Other hydrophobic compounds increase the soil water repellency as compared to bulk soil (Hallett *et al.* 2003), potentially generating a slower rate of infiltration in drier soils (Czarnes *et al.* 2000). Carminati *et al.* (2011) combined the observations of a higher water holding capacity and unsaturated conductivity into a simple model and proposed that water availability to plants would be increased under unsaturated conditions.

Finally, the shrinking of roots and soil under dry periods may alter the geometry of the root-soil contact and generate an air gap at the soil-root interface (Veen *et al.* 1992, Carminati *et al.* 2009). When this occurs, the transfer of water between soil and root is dramatically decreased locally.

The soil, constitutive part of the SPAC

Because the water supply from the bulk soil to the root surface depends on soil properties that are shaped by prior water uptake, the non-linear water retention and hydraulic conductivity behaviors of the soil, combined with the array of rhizosphere processes are likely to generate complex patterns of water uptake at the whole plant scale.

As soil has long been considered as a continuous medium, the analogy with the electrical circuit has never been used in soil physics. Unlike plants, the whole soil domain can be approached with a unique equation, such as Richard's equation, that can be solved numerically.

The complexity of the soil compartment has been largely neglected in the past and water uptake has been assumed to be mostly determined by root length density. This simplified view is supported by several reports showing, by experiments or calculations, that under wet conditions, the soil conductivity is much higher than the root radial conductivity (Gardner *et al.* 1962, Newman 1969a, 1969b, Arya, Blake, and Farrell 1975, Arya, Farrell, and Blake 1975, Passioura 1980). However, under low moisture conditions

that are often encountered, the soil conductivity may become limiting for water uptake (Draye *et al.* 2010). Interestingly, this suggests that our current understanding of water capture largely ignores many aspects of its dynamics.

Regulation and control of radial water flow

Radial water movement

In response to hydraulic gradients, water molecules entering the root have to flow through the complex anatomical structure of roots, as described by the composite transport model (Steudle *et al.* 1998). Depending on the tissue anatomy, developmental stages and environmental conditions, water will use a combination of paths that offers the lowest hydraulic resistance to its passage. It was generally assumed that under transpiring conditions, when hydrostatic water gradients are dominant, the apoplastic path would be dominant (Steudle *et al.* 1998). This simplified view has been recently challenged by recent reports that water flowing via the cell-to-cell path could account for almost the whole radial root water transport even under transpiring conditions (Bramley *et al.* 2009, Knipfer *et al.* 2010, 2011). In addition, the relative contribution of cell-to-cell and apoplastic paths to the total hydraulic conductivity depends on the species and even on the ecotype(Bramley *et al.* 2009, Sutka *et al.* 2011). Nowadays, the common view is states that there is no purely apoplastic nor pure cell-to-cell root water movement but rather a combination of both due to the local variations of water potentials, cell wall and cell membrane hydraulic resistances

Modification of anatomical structures

The conductivity of the root apoplasm is primarily determined by the overall structure of the cortex viz. the number of cell layers, wall thickness and cell size. This basic organisation can be further modified by highly selective cell death and dissolution in the cortex leading to the formation of large air cavities

(aerenchyma) within the root cortical cylinder. This results in a reduction of root conductivity (L_{pr}) which is at least partly due to a drastic reduction of the cumulated membrane surface and of the aquaporin-mediated radial transport of water (Fan *et al.* 2007, Yang *et al.* 2012).

The hydraulic conductivity of the apoplasm is locally disrupted by the deposition of lignin and suberin compounds within the cell wall matrix, which occlude wall pores otherwise filled with water (reviewed in chapter 5 of this book and in Schreiber and Franke (1999)). The endodermis is a major apoplastic barrier which develops with a very regular maturation pattern in most angiosperm species and (Perumalla *et al.* 1986).It, contributes to the prevention of water loss (cutting-off apoplastic by-passes), the maintenance of root pressure (Peterson *et al.* 1993) and the protection against pathogen and detrimental environmental conditions (Hose *et al.* 2001, Enstone *et al.* 2003, Thomas *et al.* 2007).

The exodermis (defined as an hypodermis with Casparian bands) fulfils similar functions (with the exception of root pressure maintenance). However, the extent, composition and rate at which exodermal apoplastic barriers develop strongly depend on environmental cues such as drought, anoxia, salinity, heavy metals or nutrient stresses (Hose *et al.* 2001, Enstone *et al.* 2003, 2005). The cultivation of maize seedlings in aeroponic conditions induces the formation of an exodermis in primary roots (Zimmermann *et al.* 2000, Hachez *et al.* 2006, 2012), leading to a reduction of L_{pr} by a factor 1.5 to 3.6 compared to hydroponic culture. Furthermore, water deficit is known to promote or intensify the development of root apoplastic barriers (both endodermis and exodermis) that tend to develop closer to the tip (Perumalla *et al.* 1986, Hose *et al.* 2001, Karahara *et al.* 2004, Enstone *et al.* 2005, Vandeleur *et al.* 2009).

Regulation by water channels

For a given size and anatomy, plants have the ability to rapidly alter their L_{pr} in a span of a few minutes to a few hours (Moshelion *et al.* 2002, Javot *et al.* 2003, Lopez *et al.* 2003, Cochard, Venisse, Barigah,

Brunel, *et al.* 2007, Hachez *et al.* 2012). This fine regulation is under metabolic control and may be accounted for by changes in cell membrane permeability triggered by the expression and specific activation of water channel proteins known as aquaporins (Maurel *et al.* 2001, Cochard, Venisse, Barigah, Brunel, *et al.* 2007, Maurel *et al.* 2008). Angiosperm species possess the highest multiplicity of aquaporin isoforms of all kingdoms of life with 33, 35, 36, 55 and 71 homologs in rice, Arabidopsis, maize, poplar and cotton, respectively falling into 4 to 5 phylogenetic subfamilies (Chaumont *et al.* 2001, Johanson *et al.* 2001, Sakurai *et al.* 2005, Gupta *et al.* 2009, Park *et al.* 2010). Plant aquaporins are found in all subcellular compartments forming or derived from the secretory pathway (Maurel *et al.* 2008) as well as in some organelles such as chloroplasts (Maurel *et al.* 2008, Uehlein *et al.* 2008). Among aquaporin subfamilies, Plasma Membrane Intrinsic Proteins (PIPs) mostly localize in the plasma membrane where they mediate and control the bulk of the cell membrane water movement, as supported by numerous pharmacological and reverse genetics evidences (Martre *et al.* 2002, Siefritz *et al.* 2002, Tournaire-Roux *et al.* 2003, Hachez *et al.* 2006).

In roots, contribution of aquaporins to total root water flow ranges from 20 up to 80 % (Maurel *et al.* 2001, Javot *et al.* 2003) as assessed by the use of aquaporin inhibitors (such as silver (as AgNO3 or silver sulfadiazine), gold (as HAuCl4), mercurial compounds (Tyerman *et al.* 1999, Niemietz *et al.* 2002, Bramley *et al.* 2009), acid load (Tournaire-Roux *et al.* 2003), hydrogen peroxide (Ye *et al.* 2006)) or reverse genetics approaches (reviewed in Hachez *et al.* (2006)). Reverse genetics has turned particularly useful to characterize the role of specific isoforms, although this approach presents clear limitations due to the multigenic nature of aquaporin subfamilies and compensation effects by close homologs of the gene whose expression has been altered (reviewed in Hachez *et al.* (2006)).

In plants, silencing of PIP isoforms (by RNAi or knockout mutants) generally results in a lowered hydraulic conductivity of root cell plasma membrane (denoted as L_{pcell}) (Kaldenhoff *et al.* 1998, Martre *et al.* 2002, Siefritz *et al.* 2002, Javot *et al.* 2003). In Arabidopsis, transgenic lines where expression of

several PIP isoforms had been knocked out compensated for a 3- to 5-fold decrease in L_{pcell} by increasing the root/leaf dry mass ratio, so that the overall L_{pr} tends to remain the same (Kaldenhoff *et al.* 1998, Martre *et al.* 2002). However, an increase of the root/shoot mass ratio is not a general trend as different plant species use different ways to cope with such reduction in L_{pcell} (reviewed in Hachez *et al.* (2006)).

Root water flow is generally higher during the day than at night in order to meet the high evaporative demand inherent to the evapotranspiration process. One of the plants short-term resources to increase their root system conductance is to decrease the cell-to-cell water resistance, which is achieved through a tight control of aquaporin expression and/or activity. Diurnal expression of aquaporin transcripts and/or proteins has been reported in a wide variety of plant species like *Zea mays* (Lopez *et al.* 2003, Hachez *et al.* 2012), *Samanea saman* (Moshelion *et al.* 2002), *Lotus japonicus*, walnut tree (Cochard, Venisse, Barigah, Brunel, *et al.* 2007), *Helianthus annuus* , *Vitis vinifera* or rice (Sakurai-Ishikawa *et al.* 2011) where aquaporin levels and activity are usually higher during the day than at night, although exceptions to this trend exist for some specific isoforms. The overall higher aquaporin expression and activity observed during the day facilitates the water movement via the cell-to-cell path by significantly increasing the L_{pcell} compared to night-time values (Hachez *et al.* 2012).

L_{pcell} also tends to increase from the root surface towards the endodermis and this further supports the importance of the cell-to-cell path in mediating radial root water flow (Bramley *et al.* 2009). This increase in conductance of the cell-to-cell path could serve as a compensatory mechanism to the decreasing apoplastic space available as water radially progresses towards the stele.

Regulation of aquaporin expression and activity is of prime importance as it allows a fast adaptation of the cell membrane hydraulics to the cell ever changing surrounding environment. Multiple levels of regulation have been unraveled and novel mechanisms are still to be discovered (the reader can refer to thorough reviews by Chaumont *et al.* (Chaumont *et al.* 2005, Maurel *et al.* 2010)).

Expression of aquaporins is under a tight transcriptional control from a variety of environmental or hormonal cues of biotic or abiotic origin. Such transcriptional control allows the plant to cope with adverse or changing environmental conditions impacting soil water availability, evapotranspiration rate or plant water uptake ability (Maathuis *et al.* 2003, Alexandersson *et al.* 2005). Long-term abiotic stresses such as drought, cold and salinity usually induce a marked drop in L_{pr}, mostly achieved through down-regulation of aquaporin expression and activity although some upregulated isoforms have been identified (Jang *et al.* 2004, Alexandersson *et al.* 2005).

Whereas concomittent downregulation of L_{pr} and L_{pcell} is usually expected upon stress, this is actually not always the case and both parameters can actually vary independently (Vandeleur *et al.* 2009, Sutka *et al.* 2011, Hachez *et al.* 2012). In response to stress, L_{pcell} may even increase (as a result of an increase in aquaporin expression and activity) while L_{pr} may decrease or remain unchanged (Vandeleur *et al.* 2009, Hachez *et al.* 2012). One plausible hypothesis for such discrepancies between L_{pcell} and L_{pr} behaviours would be that the increase in cortex cell conductivity is insufficient to compensate the drop in L_{pr} due to the presence of other control points acting as bottlenecks to water flow, most likely at locations where membranes need to be crossed (as discussed in Hachez *et al.* (2012), see below).

Once synthesized, PIP protein amounts in the plasma membrane are modulated by regulation of their subcellular localization. Constitutive cycling of PIPs between the plasma membrane and endomembrane compartments has been demonstrated (Li *et al.* 2011, Luu *et al.* 2011). Modulation of the cycling turnover presents a way to fastly modulate PIP abundance at the plasma membrane in response to stress (Boursiac *et al.* 2008, Li *et al.* 2011). In addition to that, PIP subcellular localization can also be regulated by specific physical interaction between different isoforms (Zelazny *et al.* 2007).

The aperture or closure of the aquaporin pore (gating) is also controlled by cytosolic calcium or pH, both

of which triggering conformational changes occluding the pore (Tournaire-Roux *et al.* 2003, Törnroth-Horsefield *et al.* 2006, Boursiac *et al.* 2008). Other factors possibly affecting the gating behavior involve methylation, acetylation, phosphorylation, heteromerization, pressure pulses, solute gradients and temperature (for review, see Chaumont *et al.* (2005) and Maurel *et al.* (2010)).

Finaly, hormonal signals also control aquaporin expression and L_{pr}. Abscisic acid (ABA), a well-known stress hormone, has long-lasting effects on plant water status (Nagel *et al.* 1994, Thompson *et al.* 2007, Parent *et al.* 2009). Root hydraulic properties indeed respond to application of exogenous ABA, the most common effect being an increase in L_{pr} (Zhang *et al.* 1995, Aroca *et al.* 2006, Mahdieh *et al.* 2009, Ruiz-Lozano *et al.* 2009). As inferred from a study on transgenic maize lines deregulated in ABA biosynthesis, this increase of L_{pr} occurs via the up-regulation of aquaporin activity. However ABA can actually trigger either an up- or a down-regulation of aquaporin expression/activity, depending on time, dose (exogenously applied or not) or species (Hose *et al.* 2000, Martinez-Ballesta *et al.* 2003, Parent *et al.* 2009), reviewed in Maurel *et al.* (2010).

Interplay between root anatomy and aquaporin activity

Not surpisingly, the changes in root anatomy described earlier may be accompanied by a concomitant adjustment of aquaporin expression/activity. Expression of root aquaporins has been detected in the vicinity of apoplastic barriers where they presumably facilitate a transmembrane flow of water (Hachez *et al.* 2006, Vandeleur *et al.* 2009, Hachez *et al.* 2012). Such phenomenon has been recently reported in maize where a correlation between exodermis suberization and PIP protein localization could be drawn (Hachez *et al.* 2012). Plants which were grown under aeroponic conditions and which developed a hypodermis with Casparian bands, effectively forcing more water along a membranous uptake path, showed increased levels of some PIP isoforms in the vicinity of the apoplastic barrier when compared to roots lacking such suberized exodermis. However, such correlation between suberization pattern and root

hydraulic properties could not be observed in Arabidopsis (Sutka *et al.* 2011).

Interestingly ABA has been shown to induce suberin biosynthesis in *Arabidopsis* roots and the genes involved in this process were up-regulated by this hormone in *Agrobacterium*-induced tumors developing a suberization of their cell walls (Duan *et al.* 2005, Efetova *et al.* 2007). These observations suggest that root suberization might be induced by ABA, whose role in regulating aquaporin expression level and activity has been demonstrated as discussed in the previous section. The interplay between ABA endogenous levels, extent of root suberization and aquaporin expression and activity clearly deserves further characterization.

Root radial water conductivity is therefore controlled by several processes acting either on the long term (developmentally-driven or in response to lasting adverse environmental conditions) or on the short term (e.g. in response to diurnal variation to transpiration demand). The interplay between both type of processes and their relative contributions seem to be highly dependent on the plant species and the growing conditions. Alltogether, this multilevel regulation of root water conductivity could confer a high plasticity and adaptation potential to root water uptake.

Control of the axial water flow

Cavitation onset

As stated earlier, most of the plant water movement takes place in the interconnected network of xylem vessels. The hydraulic continuity of this vascular network can be locally disrupted, as xylem vessels under tension are threatened by the nucleation of small gas bubbles whose rapid expansion (embolism) leads to cavitation. Because the conductivity of embolized vessels drops to zero, the movement of water is

forced through the remaining adjacent and non-cavitated vessels (Peirce 1936, Sperry, Donnelly, and Tyree 1988a, Tyree *et al.* 1989). As a result, the flow rate and friction in the remaining vessels increases and, by virtue of the Ohm's analogy, the water potential downstream of the cavitation site decreases. This might increase the likelihood of cavitation in the system in a feed-forward way, unless the remaining vessels are less prone to cavitation. As long as the tension in the xylem is maintained (or increases, due to a lesser availability of water in the soil) an increasing number of vessels will likely get more prone to embolization, as shown on figure 1D. The relation between xylem tension and the proportion of embolized vessels describes a plant susceptibility to cavitation.

The susceptibility to cavitation has been shown to have various effects on the plant water status, ranging from changes in leaf conductivity (Johnson *et al.* 2012) and stomatal conductance (Cochard 2002, Zufferey *et al.* 2011) to lowering plant yield (Cochard, Casella, and Mencuccini 2007). It remains controversial whether the axial water movement is the weak link of the hydraulic flow in the SPAC. It is indeed often assumed that in crop plants the limiting factor is the radial component (Steudle *et al.* 1998). More experiments are therefore required to clarify the functional importance of cavitation events.

Cavitation avoidance

Although xylem cavitation is essentially a passive phenomenon, plants use two strategies to keep some level of control. The first strategy embraces all plant features that influence its susceptibility to cavitation. The existence of a control at this level is demonstrated by the variability of the susceptibility to cavitation between plant species (Sperry *et al.* 1997, Pockman *et al.* 2000), cultivars (Cochard, Casella, and Mencuccini 2007, Li *et al.* 2009) and even organs (Hacke *et al.* 1996, Sperry *et al.* 1997, Hacke *et al.* 2000).

In several instances, differences in cavitation susceptibility have been linked to differences in xylem wall

(and pits) structure in both angiosperms (Herbette *et al.* 2010, Christman *et al.* 2012) and gymnosperms (Hacke *et al.* 2009, Delzon *et al.* 2010). Such structural features are thought to influence gas leakage from an embolized vessel and the formation of nucleation sites in functional adjacent vessels (Tyree *et al.* 1989, Jarbeau *et al.* 1995, Delzon *et al.* 2010). A recent hypothesis states that the total surface of the pit membrane is positively correlated with the susceptibility to cavitation (Christman *et al.* 2012). In addition, cavitation can weaken xylem vessels and render them more prone to further cavitation, a phenomenon that does not occur to the same extent in all plant species (Hacke *et al.* 2001, Stiller *et al.* 2002).

Other options to restrict cavitation susceptibility are to avoid excessive increase in xylem tension. The surface ratio between the roots and the leaves appears to be a key factor controlling the maintenance of a low tension. For example, an undersized root system (relative to the leaf evaporative surface) would lead to an increase in xylem tension and a greater susceptibility to cavitation (Sperry *et al.* 1998, Hacke *et al.* 2000, Sperry *et al.* 2002). Similarly, isohydric stomatal behaviors preventing the variation of the plant water potential (Tardieu *et al.* 1998) are also likely to reduce the risk of cavitation.

Cavitation recovery

The second strategy consists in the restoration of the lost hydraulic conductivity through the refilling of embolized vessels. The osmotically-driven pressure build-up that can occur at very low transpiration flow (viz. during the night or winter) is the first mechanism supporting this strategy. Provided the xylem pressure rises above a threshold value which depends on the xylem diameter (Yang *et al.* 1992), the gas present in the embolized vessel may dissolve into the water that is pushed into the vessels until they are refilled (Sperry *et al.* 1987, Sperry, Donnelly, and Tyree 1988b, 1988a, Sperry *et al.* 1994). The extent and frequency of pressure-driven refilling vary widely between species.

Recently, xylem refilling under tension (i.e. while the plant is transpiring), has been observed in several species and environmental conditions (McCully *et al.* 1998, McCully 1999, Zufferey *et al.* 2011). This discovery caused lively debates within the scientific community but it seems now accepted that "novel refilling" (Hac*ke et al.* 2003) does indeed occur. Nonetheless, the mechanisms remain unclear and several theories coexist (Holbrook *et al.* 1999, Clearwater *et al.* 2005). Figure 2 illustrates the conceptual framework proposed by Zwieniecky and Holbrook (2009) to «provoke discussion, organize existing information and provide a useful guidelines for future studies of xylem refilling under tension». In this framework, active transport of solutes from neighboring parenchyma cells to the embolized vessels generates an osmotic flow of water into the vessel forming high osmotic droplets at the wall surface. The expression of specific aquaporin isoforms appears to be involved in this osmotic flow (Secchi *et al.* 2010, Secchi and Zwieniecki 2011, Secchi, Gilbert, and Zwieniecki 2011). The partially hydrophobic xylem walls prevent water from the embolized vessel to leak to the neighboring vessel under tension, while small gas-filled channels in the vessel wall enable the exit of gas trapped in the embolized vessel. Finally, additional supply of water in vapor phase from the neighboring vessel is proposed as a novel pathway for refilling.

The hydraulic conductivity of the network of xylem vessels appears therefore as a complex and dynamic variable in the soil-plant continuum. Its complexity lays in the very different nature of the many components that contribute to its regulation. The active solute transport and the multiple paths for water entry and gas exit during refilling deserve more attention as these processes are extremely important in controlling plant long distance water movement.

Root architecture

Root system architecture and the potential for water uptake

Root systems are structured and ever changing populations of roots of different types (Eshel *et al.* 1996). Much of their structure arise from growth and branching processes, the latter being responsible for their tree-like topological structure. The mechanisms that lead to the formation of a meristem or a new branch are under strong genetic control (Péret *et al.* 2009). However, growth and branching respond to global and local environmental cues, including soil water potential (Pregitzer *et al.* 1993, Hodge 2004, Zhu *et al.* 2005), which provides an additional control of water flow. There are indeed several ways by which root architecture influences the ability of root systems to take up water.

Firstly, the tree-like topological structure of root systems impacts how water tension generated in the shoot organs propagates simultaneously to thousands individual roots, which influences their hydraulic conductivities (see sections above) and the local driving force for water uptake.

Secondly, roots belong to a hierarchy of root types whose features (e.g. diameter, axial conductance or growth rate are often assumed to decrease with the root order) affect their impedance to radial and axial water flow. As root architecture is developping, the total root size increases, but the relative proportions of the different root types change as well, leading to a complex evolution of the root systems hydraulic properties.

Thirdly, roots comprise a succession of segments of increasing age from the tip to the base. As roots segments get older, the deposition of apoplastic barriers decreases their radial conductivity, while the maturation of xylem vessels increases their axial conductivity (Steudle *et al.* 1989, Doussan, Vercambre, and Pagès 1998, Hachez *et al.* 2006). Young segments located behind the elongation zone appear to be sites of peak absorption while older segments are thought to be mainly conductive pipes for the water

absorbed by more distal segments and branches (Boyer 1995). One has to note, however, that the relation between segment age and segment position is not absolute and depends on root growth rate (Lecompte *et al.* 2001).

The coupling of root architecture with the hydraulic features of root segments has been referred to as the "hydraulic architecture" of a root system (Doussan, Pagès, and Vercambre 1998). It has been shown that radial and axial water flows in individual segments can be obtained simultaneously for all segments of a root system using the Ohm's analogy, which turns into a system of multiple linear equations whose structure is set by the hydraulic architecture of the root system (Landsberg *et al.* 1978, Doussan, Pagès, and Vercambre 1998). This findeing led to a family of models that formalise the strong relationship between root architecture, hydraulic properties and water uptake capacity of root systems (Doussan *et al.* 2006, Javaux *et al.* 2008).

Root placement and the availability of water

Beyond size and topology, root architecture also embraces the three-dimensional localization of root segments in the soil. Root placement is at the core of the water flow dynamics from the soil to the plant because soil moisture is usually not uniform and varies in space and time under the influence of the environment and of the root system itself (Draye *et al.* 2010).

The most recognised contribution of root system architecture to water uptake is certainly to determine the root system ability to explore layers containing water reserves during critical phenological phases. In a crop stand, where strong horizontal competition with neighbouring plants is occuring, it is generally assumed that a deeper root system gives access to more water (King *et al.* 2003), although the optimal exploration strategy should also depend on the scenario of climate, soil water and plant water use over the whole season. Indeed, multiple studies have hightlighted the link between rooting depth and drought

resistance in a panel of species such as vegetables (Johnson *et al.* 2000), cereals (Shen *et al.* 2001, Steele *et al.* 2007, Bernier *et al.* 2009, Henry *et al.* 2011, Wasson *et al.* 2012), trees (Nagarajah *et al.* 1981, Pinheiro *et al.* 2005), grasses (Marcum *et al.* 1995, Hammer *et al.* 2009) or legumes (Kashiwagi *et al.* 2006).

Several traits contribute to rooting depth, including root insertion angles and gravitropism (Hammer *et al.* 2009), timing of axial roots emission and penetration ability of hard subsoil (Lynch *et al.* 2012). Recent work has also shown that an increased proportion of root cortical aerenchyma leads to a substantial decrease in root maintenance respiration (Zhu *et al.* 2010), which is thought to account for more than 50% of the global assimilate consumption (Nielsen *et al.* 1998). By decreasing the maintenance cost, an increased allocation of assimilates to primary root growth can be achieved, leading to deeper rooting and improved resistance to water deficit under both control and drought conditions. Traits influencing root depth appear to be under the control of multiples genes (Johnson *et al.* 2000, Shen *et al.* 2001, de Dorlodot *et al.* 2007, Steele *et al.* 2007, Bernier *et al.* 2009), indicating some potential for improvement.

A less recognised contribution of root system architecture to water uptake relates to the ability of root systems to shape soil moisture gradients in a way that optimizes water flow from the bulk soil to the root. During the growing season, evaporation and drainage create pronounced vertical water potential gradients that are modified by the spatial patterns of root water uptake in a way that orients water flows to the depleted areas close to roots. However, parts of the root system that are surrounded by zones with high root length densities (RLD) can fail to attract water from the bulk soil if they are unable to decrease the soil water potential below that of the surrounding zone. In this context, the gravitropic behavior of crown roots in cereals may contribute to keep vertical “low-RLD channels” between crown roots, in which capillary rise occurs and supplies water to the upper layers. Finally, the maintenance of root system extention also contributes to place young segments in new soil regions and ensure strong soil-root water potential gradients near the most conductive root segments.

Integration of water flow in the soil-plant domain

Contrasting with the extent of ongoing research on the controls operating in the successive compartments of the soil-plant continuum, our understanding of the hydraulic behavior at the whole plant (or crop) scale is much less advanced. The complexity of the whole system raised numerous discussions about the main resistance to water flow in the soil-plant domain. Analyses of the plant hydraulic conductance in soils coupled with simplistic or inaccurate assumptions led to apparently contradictory conclusions on the main resistance (in the cortex, the xylem, or the rhizosphere). Several authors found that under wet conditions, soil conductivity is much higher than root radial conductivity, and vice-versa (Gardner *et al.* 1962, Newman 1969b, Arya, Farrell, and Blake 1975, Passioura 1980). Recently, a comparison of root and soil conductances suggested that there is an important range of soil moisture where both of them can locally limit water uptake (fig. 3, Draye *et al.* 2010). Therefore, understanding how these controls cooperate (e.g. additive, feedback of feedforward actions) has become pivotal for predicting the patterns of water uptake and the evolution of soil moisture.

Insert here figure 3

The major perspective in the area of root water uptake is therefore to bridge the gap between local controls or regulatory mechanisms and water flow within the soil-plant domain. For this to happen, we need to build a systems view integrating the regulation of the driving force, the hydraulics of the soil-plant domain at different scales and the additional regulation layer provided by shoot-root signalling. Hopefully, novel tools are being developped that will move research into this direction. This section introduces some of these tools and illustrate with few examples how such integration can help elaborating and validating new hypotheses.

Novel techniques supporting integration

The practical difficulties to capture the water dynamics of the whole system that are largely responsible for the low pace of progress at the system scale are now being addressed with novel experimental approaches that support the integration of root architecture with 2- or 3-D soil water content. Neutron tomography (Carminati *et al.* 2010, Esser *et al.* 2010) and nuclear magnetic resonances (Jahnke *et al.* 2009, Borisjuk *et al.* 2012) but also X-ray computer tomography (Mairhofer *et al.* 2012) and light transmission imaging enable to vizualise root growth and the impact of water uptake on the soil properties and soil moisture distribution. Coupled with tracer experiments and detailed measurements of the plant water potential and xylem fluxes, these techniques are expected to help analysing how plant and soil resistances are distributed, evolve and affect water flow.

In parallel to experimental techniques, novel integrated modeling approaches have been recently proposed. These rely on the coupling of a 3D physical model of water flow in the soil with a bio-physical model of plant water flow based on the root hydraulic architecture (Javaux *et al.* 2011). The R-SWMS model (Javaux *et al.* 2008) performs this coupling using Richard's equation for the soil compartment (see above), and defining the sink term for each soil voxel (typically having a volume lower than 1 cm^3) based on the solution of Doussan's equations for the root segments present in the voxel. The latter equations are solved using, for each segment, the local values of the soil water potential that satisfy Richard's equations. An iterative numerical algorithm is used to find the 3D water flows in the whole soil-plant domain that satisfy both models. Using this type of model, it is possible to consider the different controls that have been discussed above. For example, the radial conductivity can be set to evolve with root order and segment age (Doussan, Vercambre, and Pagès 1998) or the axial conductivity can decrease with xylem water potential using a susceptibility function (Li *et al.* 2009).

Need for integration in plant physiology studies

The appeal of deciphering cellular mechanisms underlying local conductivities should not take the attention away from the fact that their effect on the local water flow is largely dependent on the hydraulic state of the whole system. For example, the effect of aquaporin activity on the radial conductivity of deep roots is likely to be marginal under well watered conditions in the upper layers, while it would make a strong contribution to water uptake when water has been depleted from the upper layers. Understanding the regulation of local controls may thus require consideration of other parts of the system.

Recent experiments on ABA signalling during root zone drying indicated that the response of root xylem ABA concentration to decreasing soil water potential varied with the texture of the soil substrate (fig. 4A, Dodd *et al.* 2010). The mechanisms responsible for this substrate dependance were not clearly understood. Interestingly, independent simulation experiments with the R-SWMS model indicated that the concentration of a stress factor (called « ABA analog ») in the xylem sap would follow very similar trends and substrate dependency (fig. 4B, Draye *et al.* 2010). The explanation proposed in the modelling study relied on the hydraulic specificities of soil substrates (see above). In particular, the conductivity of the sand substrate (semi-dashed lines) is likely to drop before that of the clay loam substrate (dashed lines) in the vicinity of the roots, leading to a local water deficit experience (and ABA production) at higher soil water potential in the sand substrate. Although this hypothesis remains to be tested, this example indicates that an integration of the soil and plant hydraulic may provide new hypotheses in plant physiology experiments.

Insert here figure 4

Integration helps understanding water uptake patterns

When soil moisture content is heterogeneously distributed and relatively low, a small part of the root

system located in a wetter zone may acquire a large part of the soil water, essentially because water uptake is driven by the local water potential difference between soil and root. In this situation, water is not extracted proportionally to RLD and it is said that a lack of uptake in certain root zones is compensated by increased uptake in wetter zone (Jarvis 2010). Similar deviations from the proportionality of uptake to RLD are expected to occur when the xylem conductivity is reduced (Draye *et al.* 2010).

Compensation is a passive process resulting from the relative distributions of soil and plant water potential and arising intrinsically from the physical laws underlying water flow in the SPAC (as seen is previous sections). However, compensation is also determined indirectly by root placement and hydraulic architecture. It follows that differences between water extraction patterns of different genotypes that result from compensation and can be explained by pure physical laws should not require complex biological explanations (see examples in Draye *et al*. (2010)). Using an integrated approach, it becomes possible to extract the part of the variation that can be accounted for by simple compensation, and to isolate the part of variation for which a specific biological explanation is needed.

Integration to find where and when control are effective

As mentionned above, the radial flow of water is unlikely to be uniform over the entire root system surface, nor is the axial flow through all root segments. It follows that the many controls or regulatory processes that have been discussed in this chapter are unlikely to operate equally at all locations within the soil-plant domain. Depending on the objective, this heterogeneity may or may not be relevant. The case of xylem cavitation, which impedes the rate of water uptake under dry soil conditions and high evaporative demand is one example where this heterogeneity matters. The hydraulic effect of xylem embolism has mostly been analyzed using the susceptibility to cavitation curves that quantify the loss of axial conductance, usually at the shoot or whole plant level. However, because the soil-plant system is not hydraulically uniform, cavitation may be more important in some parts of the system than in other, and

this is likely to be reflected in the patterns of water uptake and in the evolution of soil water potential.

To illustrate the benefits of integration, xylem cavitation was implemented in the R-SWMS model using a Weibull function that simulates the loss of xylem conductivity in response to the xylem water potential (Li *et al.* 2009). Simulations with maize and with a day-night sinusoidal transpiration demand in a globally wet soil reproduced the expected decrease of transpiration (fig. 5). Interestingly, the simulations indicated that cavitation occurred preferentially in the distal part of deep crown roots (no shown), which was not an intuitive result. Obviously, additional experiments are needed to verify if this prediction matches the reality or if our understanding of soil-plant hydraulics (as formalised in the model) needs further refinement. Nevertheless, if the prediction turned to be experimentally validated, failure to account for this assymetric occurrence of cavitation would lead to inaccurate predictions on the spatial distribution of water uptake.

Insert here figure 5

Future outlooks

The last decade has seen an increasing awareness that soil and plant hydraulics (and not only root length density) plays an important quantitative role in water capture, especially in drought-prone environments (de Dorlodot *et al.* 2007, Lynch 2007, Bernier *et al.* 2009). This shift of emphasis was made possible thanks to the accumulation of new data on the molecular and cellular processes controlling water flow in the plant and to the development of novel tools allowing the integration of water flow in all compartments and at different scales.

The major perspective in the area of root water uptake is therefore to capitalize on this evolution to bridge the gap between local controls or regulatory mechanisms and water flow within the soil-plant domain. For this to happen, we need to build a systems view integrating the regulation of the driving force, the

hydraulics of the soil-plant domain at different scales and the additional regulation layer provided by shoot-root signalling. In particular, there is a need for plant biologists and soil hydrologists to develop together their understanding of water flow in the soil-plant system.

In this context, developping a holistic view of the mechanisms controlling the distribution of water uptake (spatial and temporal) will be crucial for our understanding of plant water use and soil water availability, mainly because water uptake sets the limits to future water availability. Being able to separate between the contributions of the many controls to water flow during the crop cycle will be especially important in predicting the water availability to plants with promising traits.

Functional Structural Plant Models are likely to play a pivotal role in future research, especially because they offer a unique mathematical framework to integrate, in a quantitative way, molecular, physiological, biophysical and hydrological data relating to important aspects of plant water use as phenology, assimilation, growth and long-distance signalling (Godin *et al.* 2005). The relevance of models considering the flow of water to individual rootlets of a complete root system has long been questioned in soil physics, primarily because the precise geometry of the root system is impossible to capture (Molz *et al.* 1970, King *et al.* 2003). As exploration tools, however, such models have a great potential since they enable visual, intuitive and quantitative appreciation of the hydraulic behaviour of root systems in their soil environment.

References

Alexandersson, E., Fraysse, L., Sjovall-Larsen, S., *et al.*, 2005. Whole gene family expression and drought stress regulation of aquaporins. *Plant Molecular Biology*, 59 (3), 469–484.

Aravena, J.E., Berli, M., Ghezzehei, T.A., and Tyler, S.W., 2011. Effects of Root-Induced Compaction on Rhizosphere Hydraulic Properties - X-ray Microtomography Imaging and Numerical Simulations. *Environmental Science & Technology*, 45 (2), 425–431.

Aroca, R., Ferrante, A., Vernieri, P., and Chrispeels, M.J., 2006. Drought, Abscisic Acid and Transpiration Rate Effects on the Regulation of PIP Aquaporin Gene Expression and Abundance in Phaseolus vulgaris Plants. *Annals of Botany*, 98 (6), 1301–1310.

Aroca, R., Porcel, R., and Ruiz-Lozano, J.M., 2011. Regulation of root water uptake under abiotic stress conditions. *Journal of Experimental Botany*, 63 (1), 43–57.

Arya, L., Blake, G., and Farrell, D., 1975. Field Study of Soil-Water Depletion Patterns in Presence of Growing Soybean Roots .2. Effect of Plant-Growth on Soil-Water Pressure and Water-Loss Patterns. *Soil Science Society of America Journal*, 39 (3), 430–436.

Arya, L., Farrell, D., and Blake, G., 1975. Field Study of Soil-Water Depletion Patterns in Presence of Growing Soybean Roots .1. Determination of Hydraulic Properties of Soil. *Soil Science Society of America Journal*, 39 (3), 424–430.

Bernier, J., Serraj, R., Kumar, A., *et al.*, 2009. The large-effect drought-resistance QTL qtl12.1 increases water uptake in upland rice. *Field Crops Research*, 110 (2), 139–146.

Blum, A., 2005. Drought resistance, water-use efficiency, and yield potential—are they compatible, dissonant, or mutually exclusive? *Australian Journal of Agricultural Research*, 56 (11), 1159–1168.

Borisjuk, L. and Rolletschek, H., 2012. Surveying the plant's world by magnetic resonance imaging - Borisjuk - 2012 - The Plant Journal - Wiley Online Library. *The Plant Journal*.

Boursiac, Y., Boudet, J., Postaire, O., *et al.*, 2008. Stimulus-induced downregulation of root water transport involves reactive oxygen species-activated cell signalling and plasma membrane intrinsic protein internalization. *The Plant Journal*, 56 (2), 207–218.

Boyer, J.S., 1995. *Measuring the water status of plants and soils*. Academic Press.

Bramley, H., Turner, N., Turner, D., and Tyerman, S.D., 2009. Roles of Morphology, Anatomy, and Aquaporins in Determining Contrasting Hydraulic Behavior of Roots. *Plant Physiology*, 150 (1), 348–364.

Carminati, A., Moradi, A.B., Vetteriein, D., *et al.*, 2010. Dynamics of soil water content in the rhizosphere. *Plant and Soil*, 332 (1-2), 163–176.

Carminati, A., Schneider, C.L., Moradi, A.B., *et al.*, 2011. How the Rhizosphere May Favor Water Availability to Roots. *Vadose Zone Journal*, 10 (3), 988–998.

Carminati, A., Vetterlein, D., Weller, U., Vogel, H.-J., and Oswald, S.E., 2009. When Roots Lose Contact. *Vadose Zone Journal*, 8 (3), 805–809.

Chaumont, F., Barrieu, F., Wojcik, E., Chrispeels, M., and Jung, R., 2001. Aquaporins constitute a large and highly divergent protein family in maize. *Plant Physiology*, 125, 1206–1215.

Chaumont, F., Moshelion, M., and Daniels, M.J., 2005. Regulation of plant aquaporin activity. *Biology of the Cell*, 97, 749–764.

Christman, M.A., Sperry, J.S., and Smith, D.D., 2012. Rare pits, large vessels and extreme vulnerability to cavitation in a ring-porous tree species. *New Phytologist*, 193, 713–720.

Clearwater, M.J. and Goldstein, G., 2005. Embolism Repair and Long Distance Water Transport. *In*: N.M. Holbrook and M.A. Zwieniecki, eds. *Vascular Transport in Plants*. London: Elsevier Academic Press, 375–399.

Cochard, H., 2002. Xylem embolism and drought-induced stomatal closure in maize. *Planta*, 215 (3), 466–471.

Cochard, H., Casella, E., and Mencuccini, M., 2007. Xylem vulnerability to cavitation varies among poplar and willow clones and correlates with yield. *Tree Physiology*, 27 (12), 1761–1767.

Cochard, H., Venisse, J.-S., Barigah, T.S., Brunel, N., *et al.*, 2007. Putative role of aquaporins in variable hydraulic conductance of leaves in response to light. *Plant Physiology*, 143 (1), 122–133.

Czarnes, S., Hallett, P.D., Bengough, A.G., and Young, I.M., 2000. Root- and microbial-derived

mucilages affect soil structure and water transport. *European Journal of Soil Science*, 51 (3), 435–443.

Darrah, P.R., 1993. The rhizosphere and plant nutrition: a quantitative approach. *Plant and Soil*, 155-156 (1), 1–20.

de Dorlodot, S., Forster, B., Pagès, L., *et al.*, 2007. Root system architecture: opportunities and constraints for genetic improvement of crops. *TRENDS in Plant Science*, 12 (10), 474–481.

Delzon, S., Douthe, C., Sala, A., and Cochard, H., 2010. Mechanism of water-stress induced cavitation in conifers: bordered pit structure and function support the hypothesis of seal capillary-seeding. *Plant, Cell and Environment*, 33 (12), 2101–2111.

Dexter, A., 1987. Compression of Soil Around Roots. *Plant and Soil*, 97 (3), 401–406.

Dodd, I.C., Egea, G., Watts, C.W., and Whalley, W.R., 2010. Root water potential integrates discrete soil physical properties to influence ABA signalling during partial rootzone drying. *Journal of Experimental Botany*, 61 (13), 3543–3551.

Doussan, C., Pagès, L., and Vercambre, G., 1998. Modelling of the hydraulic architecture of root systems: An integrated approach to water absorption - Model description. *Annals of Botany*, 81, 213–223.

Doussan, C., Pierret, A., Garrigues, E., and Pagès, L., 2006. Water Uptake by Plant Roots: II – Modelling of Water Transfer in the Soil Root-system with Explicit Account of Flow within the Root System – Comparison with Experiments. *Plant and Soil*, 283 (1-2), 99–117.

Doussan, C., Vercambre, G., and Pagès, L., 1998. Modelling of the hydraulic architecture of root systems: and integrated approach to water absorption - Distribution of axial and radial conductances in maize. *Annals of Botany*, 81, 225–232.

Draye, X., Kim, Y., Lobet, G., and Javaux, M., 2010. Model-assisted integration of physiological and environmental constraints affecting the dynamic and spatial patterns of root water uptake from soils. *Journal of Experimental Botany*, 61 (8), 2145–2155.

Duan, H. and Schuler, M.A., 2005. Differential expression and evolution of the Arabidopsis CYP86A subfamily. *Plant Physiology*, 137 (3), 1067–1081.

Efetova, M., Zeier, J., Riederer, M., *et al.*, 2007. A Central Role of Abscisic Acid in Drought Stress Protection of Agrobacterium-Induced Tumors on Arabidopsis. *Plant Physiology*, 145 (3), 853–862.

Enstone, D.E. and Peterson, C.A., 2005. Suberin lamella development in maize seedling roots grown in aerated and stagnant conditions. *Plant, Cell and Environment*, 28, 444–455.

Enstone, D.E., Peterson, C.A., and Ma, F., 2003. Root Endodermis and Exodermis: Structure, Function, and Responses to the Environment. *Journal of Plant Growth Regulation*, 21 (4), 335–351.

Eshel, A. and Waisel, Y., 1996. Mutliform and multifunction of various constituents of one root system. *In*: Y. Waisel, A. Eshel, and U. Kafkafi, eds. *Plant Roots: The Hidden Half*. Marcel Dekker, Inc.

Esser, H.G., Carminati, A., Vontobel, P., Lehmann, E.H., and Oswald, S.E., 2010. Neutron radiography and tomography of water distribution in the root zone. *Journal of Plant Nutrition and Soil Science*, 173 (5), 757–764.

Fan, M., Bai, R., Zhao, X., and Zhang, J., 2007. Aerenchyma Formed Under Phosphorus Deficiency Contributes to the Reduced Root Hydraulic Conductivity in Maize Roots. *Journal of Integrative Plant Biology*, 49 (5), 598–604.

FAO, ed., 2012. *FAO STAT*. Available from: http://faostat.fao.org/ [AccessedApr. 2012].

Gardner, W. and Ehlig, C., 1962. Some Observations on Movement of Water to Plant Roots. *Agronomy Journal*, 54 (5), 453–456.

Gardner, W.R., 1965. Dynamic Aspects of Soil-Water Availability to Plants. *Annual Review of Plant Physiology*, 16, 323–342.

Godin, C. and Sinoquet, H., 2005. Functional-structural plant modelling. *New Phytologist*, 166, 705–708.

Gregory, P.J., Ingram, J.S.I., and Brklacich, M., 2005. Climate change and food security. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360 (1463), 2139–2148.

Guidi, G., Poggio, G., and Petruzzelli, G., 1985. The Porosity of Soil Aggregates from Bulk Soil and from Soil Adhering to Roots. *Plant and Soil*, 87 (2), 311–314.

Gupta, A.B. and Sankararamakrishnan, R., 2009. Genome-wide analysis of major intrinsic proteins in the tree plant Populus trichocarpa: characterization of XIP subfamily of aquaporins from evolutionary perspective. *BMC Plant Biology*, 9, 134.

Hachez, C., Moshelion, M., Zelazny, E., Cavez, D., and Chaumont, F., 2006. Localization and quantification of plasma membrane aquaporin expression in maize primary root: a clue to understanding their role as cellular plumbers. *Plant Molecular Biology*, 62, 305–323.

Hachez, C., Veselov, D., Ye, Q., *et al.*, 2012. Short-term control of maize cell and root water permeability through plasma membrane aquaporin isoforms. *Plant, Cell and Environment*, 35, 185–198.

Hacke, U.G. and Jansen, S., 2009. Embolism resistance of three boreal conifer species varies with pit structure. *New Phytologist*, 182, 675–686.

Hacke, U.G. and Sauter, J.J., 1996. Drought-Induced Xylem Dysfunction in Petioles, Branches, and Roots of Populus balsamifera L. and Alnus glutinosa (L.) Gaertn. *Plant Physiology*, 111 (2), 413–417.

Hacke, U.G. and Sperry, J.S., 2003. Limits to xylem refilling under negative pressure in Laurus nobilis and Acer negundo. *Plant, Cell and Environment*, 26, 303–311.

Hacke, U.G., Sperry, J.S., Ewers, B.E., *et al.*, 2000. Influence of soil porosity on water use in Pinus taeda. *Oecologia*, 124 (4), 495–505.

Hacke, U.G., Stiller, V., Sperry, J.S., Pittermann, J.J., and McCulloh, K.A., 2001. Cavitation fatigue. Embolism and refilling cycles can weaken the cavitation resistance of xylem. *Plant Physiology*, 125 (2), 779–786.

Hallett, P.D., Gordon, D.C., and Bengough, A.G., 2003. Plant influence on rhizosphere hydraulic properties: direct measurements using a miniaturized infiltrometer. *New Phytologist*, 157 (3), 597–603.

Hammer, G., Dong, Z., Mclean, G., *et al.*, 2009. Can Changes in Canopy and/or Root System Architecture Explain Historical Maize Yield Trends in the U.S. Corn Belt? *Crop Science*, 49 (1), 299–312.

Henry, A., Gowda, V.R.P., Torres, R.O., McNally, K.L., and Serraj, R., 2011. Variation in root system architecture and drought response in rice (Oryza sativa): Phenotyping of the OryzaSNP panel in rainfed lowland fields. *Field Crops Research*, 120 (2), 205–214.

Herbette, S. and Cochard, H., 2010. Calcium Is a Major Determinant of Xylem Vulnerability to Cavitation [online]. *Plant Physiology*. Available from: http://www.plantphysiol.org/content/153/4/1932 [Accessed15 Apr. 2012].

Hinsinger, P., Gobran, G.R., Gregory, P.J., and Wenzel, W.W., 2005. Rhizosphere geometry and heterogeneity arising from root-mediated physical and chemical processes. *New Phytologist*, 168 (2), 293–303.

Hodge, A., 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytologist*, 162 (1), 9–24.

Holbrook, N.M. and Zwieniecki, M., 1999. Embolism Repair and Xylem Tension: Do We Need a Miracle? *Plant Physiology*, 120, 7–10.

Hose, E., Clarkson, D., Steudle, E., Schreiber, L., and Hartung, W., 2001. The exodermis: a variable apoplastic barrier. *Journal of Experimental Botany*, 52 (365), 2245–2264.

Hose, E., Steudle, E., and Hartung, W., 2000. Abscisic acid and hydraulic conductivity of maize roots: a study using cell- and root-pressure probes. *Planta*, 211 (6), 874–882.

Jackson, R.B., Sperry, J.S., and Dawson, T.E., 2000. Root water uptake and transport: using physiological processes in global predictions. *TRENDS in Plant Science*, 5 (11), 482–488.

Jahnke, S., Menzel, M.I., van Dusschoten, D., *et al.*, 2009. Combined MRI-PET dissects dynamic changes in plant structures and functions. *The Plant Journal*, 59 (4), 634–644.

Jang, J.Y., Kim, D.G., Kim, Y.O., Kim, J.S., and Kang, H., 2004. An expression analysis of a gene family encoding plasma membrane aquaporins in response to abiotic stresses in Arabidopsis thaliana. *Plant Molecular Biology*, 54 (5), 713–725.

Jarbeau, J.A., Ewers, F.W., and Davis, S.D., 1995. The mechanism of water-stress-induced embolism in two species of chaparral shrubs. *Plant, Cell and Environment*, 18 (2), 189–196.

Jarvis, N., 2010. Comment on “Macroscopic Root Water Uptake Distribution Using a Matric

Flux Potential Approach." *Vadose Zone Journal*, 9 (2), 499.

Javaux, M., Draye, X., Doussan, C., Vanderborght, J., and Vereecken, H., 2011. Root Water Uptake: Toward 3-D Functional Approaches. *In*: J. Gliński, J. Horabik, and J. Lipiec, eds. *Encyclopedia of Agrophysics*. Springer Netherlands, 717–722.

Javaux, M., Schroeder, T., Vanderborght, J., and Vereecken, H., 2008. Use of a three-dimensional detailed modeling approach for predicting root water uptake. *Vadose Zone Journal*, 7 (3), 1079–1088.

Javot, H. and Maurel, C., 2002. The role of aquaporins in root water uptake. *Annals of Botany*, 90 (3), 301–313.

Javot, H., Lauvergeat, V., Santoni, V., *et al.*, 2003. Role of a Single Aquaporin Isoform in Root Water Uptake. *Plant Cell*, 15 (2), 509–522.

Johanson, U., Karlsson, M., Johansson, I., *et al.*, 2001. The complete set of genes encoding major intrinsic proteins in Arabidopsis provides a framework for a new nomenclature for major intrinsic proteins in plants. *Plant Physiology*, 126 (4), 1358–1369.

Johnson, D.M., McCulloh, K.A., Woodruff, D.R., and Meinzer, F.C., 2012. Evidence for xylem embolism as a primary factor in dehydration-induced declines in leaf hydraulic conductance. *Plant, Cell and Environment*, 35, 760–769.

Johnson, W., Jackson, L., and Ochoa, O., 2000. Lettuce, a shallow-rooted crop, and Lactuca serriola, its wild progenitor, differ at QTL determining root architecture and deep soil water exploitation. *TAG Theoretical and Applied Genetics*, 101, 1066–1073.

Kaldenhoff, R., Grote, K., Zhu, J.J., and Zimmermann, U., 1998. Significance of plasmalemma aquaporins for water-transport in Arabidopsis thaliana. *Plant Journal*, 14 (1), 121–128.

Karahara, I., Ikeda, A., Kondo, T., and Uetake, Y., 2004. Development of the Casparian strip in primary roots of maize under salt stress. *Planta*, 219 (1), 41–47.

Kashiwagi, J., Krishnamurthy, L., Crouch, J.H., and Serraj, R., 2006. Variability of root length density and its contributions to seed yield in chickpea (Cicer arietinum L.) under terminal drought stress. *Field Crops Research*, 95, 171–181.

King, J., Gay, A., Sylverster-Bradley, R., *et al.*, 2003. Modelling Cereal Root Systems for Water and Nitrogen Capture: Towards an Economic Optimum. *Annals of Botany*, 91 (3), 383–390.

Knipfer, T. and Fricke, W., 2010. Root pressure and a solute reflection coefficient close to unity exclude a purely apoplastic pathway of radial water transport in barley (Hordeum vulgare). *New Phytologist*, 187, 159–170.

Knipfer, T., Besse, M., Verdeil, J.-L., and Fricke, W., 2011. Aquaporin-facilitated water uptake in barley (Hordeum vulgare L.) roots. *Journal of Experimental Botany*, 62 (12), 4115–4126.

Landsberg, J. and Fowkes, N., 1978. Water movement through plant roots. *Annals of Botany*, 42, 493–508.

Lecompte, F., Ozier-Lafontaine, H., and Pagès, L., 2001. The relationships between static and dynamic variables in the description of root growth. Consequences for field interpretation of rooting variability. *Plant and Soil*, 236 (1), 19–31.

Li, X., Wang, X., Yang, Y., *et al.*, 2011. Single-Molecule Analysis of PIP2;1 Dynamics and Partitioning Reveals Multiple Modes of Arabidopsis Plasma Membrane Aquaporin Regulation. *Plant Cell*, 23, 3780–3797.

Li, Y., Sperry, J.S., and Shao, M., 2009. Hydraulic conductance and vulnerability to cavitation in corn (Zea mays L.) hybrids of differing drought resistance. *Environmental and Experimental Botany*, 66 (2), 341–346.

Lopez, F., Bousser, A., Sissoëff, I., *et al.*, 2003. Diurnal Regulation of Water Transport and Aquaporin Gene Expression in Maize Roots: Contribution of PIP2 Proteins. *Plant and Cell Physiology*, 44 (12), 1384–1395.

Luu, D.T., Martiniere, A., Sorieul, M., Runions, J., and Maurel, C., 2011. Fluorescence recovery after photobleaching reveals high cycling dynamics of plasma membrane aquaporins in Arabidopsis roots under salt stress. *Plant Journal*, 69, 894–905.

Lynch, J.P., 2007. Roots of the second green revolution. *Australian Journal of Botany*, 55 (5), 493–512.

Lynch, J.P. and Brown, K.M., 2012. New roots for agriculture: exploiting the root phenome. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367 (1595), 1598–1604.

Maathuis, F.J., Filatov, V., Herzyk, P., *et al.*, 2003. Transcriptome analysis of root transporters reveals participation of multiple gene families in the response to cation stress. *Plant Journal*, 35 (6), 675–692.

Mahdieh, M. and Mostajeran, A., 2009. Abscisic acid regulates root hydraulic conductance via aquaporin expression modulation in Nicotiana tabacum. *Journal of Plant Physiology*, 166 (18), 1993–2003.

Mairhofer, S., Zappala, S., Tracy, S.R., *et al.*, 2012. RooTrak: Automated Recovery of Three-Dimensional Plant Root Architecture in Soil from X-Ray Microcomputed Tomography Images Using Visual Tracking. *Plant Physiology*, 158, 561–569.

Mallants, D., Mohanty, B.P., Vervoort, A., and Feyen, J., 1997. Spatial analysis of saturated hydraulic conductivity in a soil with macropores. *Soil Technology*, 10 (2), 115–131.

Marcum, K.B., Morton, S., Engelke, M., and White, R., 1995. Rooting characteristics and associated drought resistance of zoysiagrasses. *Agronomy Journal*, 87 (3), 534–538.

Martinez-Ballesta, M.C., Aparicio, F., Pallas, V., Martinez, V., and Carvajal, M., 2003. Influence of saline stress on root hydraulic conductance and PIP expression in Arabidopsis. *Journal of Plant Physiology*, 160 (6), 689–697.

Martre, P., Morillon, R., Barrieu, F., *et al.*, 2002. Plasma membrane aquaporins play a significant role during recovery from water deficit. *Plant Physiology*, 130, 2101–2110.

Maurel, C. and Chrispeels, M.J., 2001. Aquaporins. A Molecular Entry into Plant Water Relations. *Plant Physiology*, 125 (1), 135–138.

Maurel, C., Reizer, J., Schroeder, J., and Chrispeels, M., 1993. The vacuolar membrane protein gamma-TIP creates water specific channels in Xenopus oocytes. *EMBO Journal*, 12 (6), 2241–2247.

Maurel, C., Simonneau, T., and Sutka, M., 2010. The significance of roots as hydraulic rheostats. *Journal of Experimental Botany*, 61 (12), 3191–3198.

Maurel, C., Verdoucq, L., Luu, D., and Santoni, V., 2008. Plant aquaporins: membrane channels with multiple integrated functions. *Annual Review of Plant Biology*.

McCully, M., 1999. Root Xylem Embolisms and Refilling. Relation to Water Potentials of Soil, Roots, and Leaves, and Osmotic Potentials of Root Xylem Sap. *Plant Physiology*, 199, 1001–1008.

McCully, M.E. and Boyer, J.S., 1997. The expansion of maize root-cap mucilage during hydration .3. Changes in water potential and water content. *Physiologia Plantarum*, 99 (1), 169–177.

McCully, M.E., Huang, C.X., and Ling, L.E.C., 1998. Daily embolism and refilling of xylem vessels in the roots of field-grown maize. *New Phytologist*, 138 (2), 327–342.

Molz, F. and Remson, I., 1970. Extraction term models of soil moisture use by transpiring plants. *Water Resources Research*, 6 (5), 1346.

Moradi, A.B., Carminati, A., Lamparter, A., *et al.*, 2012. Is the Rhizosphere Temporarily Water Repellent? *Vadose Zone Journal*.

Moshelion, M., Becker, D., Biela, A., *et al.*, 2002. Plasma membrane aquaporins in the motor cells of Samanea saman: diurnal and circadian regulation. *Plant Cell*, 14 (3), 727–739.

Nagarajah, S. and Ratnasuriya, G.B., 1981. Clonal variability in root growth and drought resistance in tea (Camellia sinensis). *Plant and Soil*, 60 (1), 153–155.

Nagel, O.W., Konings, H., and Lambers, H., 1994. Growth rate, plant development and water relations of the ABA- deficient tomato mutant sitiens. *Physiologia Plantarum*, 92 (1), 102–108.

Newman, E., 1969a. Resistance to Water Flow in Soil and Plant. II. a Review of Experimental Evidence on Rhizosphere Resistance. *Journal of Applied Ecology*, 6 (2), 261–272.

Newman, E.I., 1969b. Resistance to Water Flow in Soil and Plant. I. Soil Resistance in Relation to Amounts of Root - Theoretical Estimates. *Journal of Applied Ecology*, 6 (1), 1–12.

Nielsen, K., Bouma, T., Lynch, J., and Eissenstat, D.M., 1998. Effects of phosphorus availability and vesicular–arbuscular mycorrhizas on the carbon budget of common bean (Phaseolus vulgaris). *New Phytologist*, 139, 647–656.

Niemietz, C.M. and Tyerman, S.D., 2002. New potent inhibitors of aquaporins: silver and gold

compounds inhibit aquaporins of plant and human origin. *FEBS Letters*, 531 (3), 443–447.

Parent, B., Hachez, C., Redondo, E., *et al.*, 2009. Drought and Abscisic Acid Effects on Aquaporin Content Translate into Changes in Hydraulic Conductivity and Leaf Growth Rate: A Trans-Scale Approach. *Plant Physiology*, 149 (4), 2000–2012.

Park, W., Scheffler, B., and Bauer, P., 2010. Identification of the family of aquaporin genes and their expression in upland cotton (Gossypium hirsutum L.). *BMC Plant Biology*, 10 (1), 142.

Passioura, J.B., 1980. The Transport of Water from Soil to Shoot in Wheat Seedlings. *Journal of Experimental Botany*, 31 (120), 333–345.

Peirce, G.J., 1936. The State of Water in Ducts and Tracheids. *Plant Physiology*, 11, 623–628.

Perumalla, C.J. and Peterson, C.A., 1986. Deposition of Casparian bands and suberin lamellae in the exodermis and endodermis of young corn and onion roots. *Canadian Journal of Botany*, (38), 1872–1878.

Peterson, C.A., Murrmann, M., and Steudle, E., 1993. Location of the major barriers to water and ion movement in young roots of Zea mays L. *Planta*, 190, 127–136.

Péret, B., de Rybel, B., Casimiro, I., *et al.*, 2009. Arabidopsis lateral root development: an emerging story. *TRENDS in Plant Science*, 14 (7), 399–408.

Pinheiro, H.A., DaMatta, F., Chaves, A.R.M., Loureiro, M.E., and Ducatti, C., 2005. Drought Tolerance is Associated with Rooting Depth and Stomatal Control of Water Use in Clones of Coffea canephora. *Annals of Botany*, 96 (1), 101–108.

Pockman, W.T. and Sperry, J.S., 2000. Vulnerability to xylem cavitation and the distribution of Sonoran Desert vegetation. *American Journal of Botany*, 87 (9), 1287–1299.

Pregitzer, K.S., Hendrick, R.L., and Fogel, R., 1993. The demography of fine roots in response to patches of water and nitrogen. *New Phytologist*, 125, 575–580.

Ranathunge, K., Schreiber, L., and Franke, R., 2011. Suberin research in the genomics era—New interest for an old polymer. *Plant Science*, 180 (3), 399–413.

Read, D.B., Bengough, A.G., Gregory, P.J., *et al.*, 2003. Plant roots release phospholipid

surfactants that modify the physical and chemical properties of soil. *New Phytologist*, 157 (2), 315–326.

Read, D.B., Gregory, P.J., and Bell, A.E., 1999. Physical properties of axenic maize root mucilage. *Plant and Soil*, 211 (1), 87–91.

Richards, L.A., 1931. Capillary conduction of liquids through porous mediums. *Physics-a Journal of General and Applied Physics*, 1 (1), 318–333.

Ruiz-Lozano, J.M., Alguacii, M.D.M., Barzana, G., Vemieri, P., and Aroca, R., 2009. Exogenous ABA accentuates the differences in root hydraulic properties between mycorrhizal and non mycorrhizal maize plants through regulation of PIP aquaporins. *Plant Molecular Biology*, 70 (5), 565–579.

Sakurai, J., Ishikawa, F., Yamaguchi, T., Uemura, M., and Maeshima, M., 2005. Identification of 33 rice aquaporin genes and analysis of their expression and function. *Plant and Cell Physiology*, 46 (9), 1568–1577.

Sakurai-Ishikawa, J., Murai-Hatano, M., Hayashi, H., *et al.*, 2011. Transpiration from shoots triggers diurnal changes in root aquaporin expression. *Plant, Cell and Environment*, 34, 1150–1163.

Schreiber, L., Hartmann, K., Skrabs, M., and Zeier, J., 1999. Apoplastic barriers in roots: chemical composition of endodermal and hypodermal cell walls. *Journal of Experimental Botany*, 50 (337), 1267–1280.

Schröder, T., Javaux, M., Vanderborght, J., Körfgen, B., and Vereecken, H., 2009. Implementation of a Microscopic Soil–Root Hydraulic Conductivity Drop Function in a Three-Dimensional Soil–Root Architecture Water Transfer Model. *Vadose Zone Journal*, 8 (3), 783–792.

Secchi, F. and Zwieniecki, M.A., 2010. Patterns of PIP gene expression in Populus trichocarpa during recovery from xylem embolism suggest a major role for the PIP1 aquaporin subfamily as moderators of refilling process. *Plant, Cell and Environment*, 33 (8), 1285–1297.

Secchi, F. and Zwieniecki, M.A., 2011. Sensing embolism in xylem vessels: the role of sucrose as a trigger for refilling. *Plant, Cell and Environment*, 34 (3), 514–524.

Secchi, F., Gilbert, M.E., and Zwieniecki, M.A., 2011. Transcriptome Response to Embolism Formation in Stems of Populus trichocarpa Provides Insight into Signaling and the Biology of Refilling. *Plant Physiology*, 157 (3), 1419–1429.

Shen, L., Courtois, B., McNally, K.L., Robin, S., and Li, Z., 2001. Evaluation of near-isogenic lines of rice introgressed with QTLs for root depth through marker-aided selection. *TAG Theoretical and Applied Genetics*, 103 (1), 75–83.

Siefritz, F., Tyree, M.T., Lovisolo, C., and Schubert, A., 2002. PIP1 Plasma Membrane Aquaporins in Tobacco. *The Plant Cell Online*, 14, 869–876.

Sperry, J.S. and Ikeda, T., 1997. Xylem cavitation in roots and stems of Douglas-fir and white fir. *Tree Physiology*, 17 (4), 275–280.

Sperry, J.S. and Saliendra, N.Z., 1994. Intra- and inter-plant variation in xylem cavitation in Betula occidentalis. *Plant, Cell and Environment*, 17 (11), 1233–1241.

Sperry, J.S., Adler, F.R., Campbell, G.S., and Comstock, J.P., 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant, Cell and Environment*, 21, 347–359.

Sperry, J.S., Donnelly, J.R., and Tyree, M.T., 1988a. Seasonal Occurrence of Xylem Embolism in Sugar Maple (Acer saccharum). *American Journal of Botany*, 75 (8), 1212–1218.

Sperry, J.S., Donnelly, J.R., and Tyree, M.T., 1988b. A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell and Environment*, 11 (1), 35–40.

Sperry, J.S., Holbrook, N.M., Zimmermann, M.H., and Tyree, M.T., 1987. Spring Filling of Xylem Vessels in Wild Grapevine. *Plant Physiology*, 83, 414–417.

Sperry, J.S., Stiller, V., and Hacke, U.G., 2002. Soil Water Uptake and Water transport Through Root Systems. *In*: Y. Waisel, A. Eshel, and U. Kafkafi, eds. *Plant Roots: the Hidden Half*. New York: Marcel Dekker, Inc, 663–681.

Steele, K., Virk, D., Kumar, R., Prasad, S., and Witcombe, J., 2007. Field evaluation of upland rice lines selected for QTLs controlling root traits. *Field Crops Research*, 101 (2), 180–186.

Steudle, E., 2000. Water uptake by plant roots: an integration of views. *Plant and Soil*, 226 (1),

45–56.

Steudle, E. and Frensch, J., 1989. Osmotic responses of maize roots. *Planta*, 177, 281–295.

Steudle, E. and Peterson, C.A., 1998. How does water get through roots? *Journal of Experimental Botany*, 49 (332), 775–788.

Stiller, V. and Sperry, J.S., 2002. Cavitation fatigue and its reversal in sunflower (Helianthus annuus L.). *Journal of Experimental Botany*, 53 (371), 1155–1161.

Sutka, M., Li, G., Boudet, J., *et al.*, 2011. Natural variation of root hydraulics in Arabidopsis grown in normal and salt-stressed conditions. *Plant Physiology*, 155, 1264–1276.

Tardieu, F. and Simonneau, T., 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. *Journal of Experimental Botany*, 49 (Special Issue), 419–432.

Thomas, R., Fang, X., Ranathunge, K., *et al.*, 2007. Soybean Root Suberin: Anatomical Distribution, Chemical Composition, and Relationship to Partial Resistance to Phytophthora sojae. *Plant Physiology*, 144 (1), 299–311.

Thompson, A., Andrews, J., Mulholland, B., *et al.*, 2007. Overproduction of Abscisic Acid in Tomato Increases Transpiration Efficiency and Root Hydraulic Conductivity and Influences Leaf Expansion. *Plant Physiology*, 143 (4), 1905.

Tournaire-Roux, C., Sutka, M., Javot, H., *et al.*, 2003. Cytosolic pH regulates root water transport during anoxic stress through gating of aquaporins. *Nature*, 425 (6956), 393–397.

Törnroth-Horsefield, S., Wang, Y., Hedfalk, K., *et al.*, 2006. Structural mechanism of plant aquaporin gating. *Nature*, 439 (9), 689–694.

Tyerman, S.D., Bohnert, H.J., Maurel, C., Steudle, E., and Smith, J.A.C., 1999. Plant aquaporins: their molecular biology, biophysics and significance for plant water relations. *Journal of Experimental Botany*, 50, 1055–1071.

Tyree, M.T. and Sperry, J.S., 1989. Vulnerability of Xylem to Cavitation and Embolism. *Annual Review of Plant Physiology and Plant Molecular Biology*, 40 (1), 19–36.

Uehlein, N., Otto, B., Hanson, D.T., *et al.*, 2008. Function of Nicotiana tabacum aquaporins as chloroplast gas pores challenges the concept of membrane CO2 permeability. *The Plant Cell*, 20 (3), 648–657.

van den Honert, T.H., 1948. Water transport in plants as a catenary process. *Discussions of the Faraday Society*, 3 (0), 146–153.

Vandeleur, R.K., Mayo, G., Shelden, M.C., *et al.*, 2009. The role of plasma membrane intrinsic protein aquaporins in water transport through roots: diurnal and drought stress responses reveal different strategies between isohydric and anisohydric cultivars of grapevine. *Plant Physiology*, 149 (1), 445–460.

Veen, B.W., Van Noordwijk, M., De Willigen, P., Boone, F., and Kooistra, M., 1992. Root-Soil Contact of Maize, as Measured by a Thin-Section Technique. *Plant and Soil*, 139 (1), 131–138.

Wasson, A.P., Richards, R.A., Chatrath, R., *et al.*, 2012. Traits and selection strategies to improve root systems and water uptake in water-limited wheat crops. *Journal of Experimental Botany*, 63 (9), 3485–3498.

Watt, M., McCully, M., and Canny, M., 1994. Formation and Stabilization of Rhizosheaths of Zea-Mays L. *Plant Physiology*, 106 (1), 179–186.

Whalley, W.R., Riseley, B., Leeds- Harrison, P.B., *et al.*, 2004. Structural differences between bulk and rhizosphere soil. *European Journal of Soil Science*, 56 (3), 353–360.

Yang, S. and Tyree, M.T., 1992. A theoretical model of hydraulic conductivity recovery from embolism with comparison to experimental data on Acer saccharum. *Plant, Cell and Environment*, 15 (6), 633–643.

Yang, X., Li, Y., Ren, B., *et al.*, 2012. Drought-Induced Root Aerenchyma Formation Restricts Water Uptake in Rice Seedlings Supplied with Nitrate. *Plant and Cell Physiology*, 53 (3), 495–504.

Ye, Q. and Steudle, E., 2006. Oxidative gating of water channels (aquaporins) in corn roots. *Plant, Cell and Environment*, 29 (4), 459–470.

Zelazny, E., Borst, J.W., Muylaert, M., *et al.*, 2007. FRET imaging in living maize cells reveals that plasma membrane aquaporins interact to regulate their subcellular localization.

Proceedings of the National Academy of Sciences of the United States of America, 104 (30), 12359–12364.

Zhang, J. and Zhang, X., 1995. Exudation rate and hydraulic conductivity of maize roots are enhanced by soil drying and abscisic acid treatment. *New Phytologist*, 131, 329–336.

Zhu, J., Brown, K.M., and Lynch, J.P., 2010. Root cortical aerenchyma improves the drought tolerance of maize (Zea mays L.). *Plant, Cell and Environment*, 33, 740–749.

Zhu, J., Kaeppler, S.M., and Lynch, J.P., 2005. Mapping of QTLs for lateral root branching and length in maize (Zea mays L.) under differential phosphorus supply. *TAG Theoretical and Applied Genetics*, 111 (4), 688–695.

Zimmermann, H.M., Hartmann, K., Schreiber, L., and Steudle, E., 2000. Chemical composition of apoplastic transport barriers in relation to radial hydraulic conductivity of corn roots (Zea mays L.). *Planta*, 210 (2), 302–11.

Zufferey, V., Cochard, H., Améglio, T., Spring, J.L., and Viret, O., 2011. Diurnal cycles of embolism formation and repair in petioles of grapevine (Vitis vinifera cv. Chasselas). *Journal of Experimental Botany*, 62 (11), 3885–3894.

Zwieniecki, M.A. and Holbrook, N.M., 2009. Confronting Maxwell's demon: biophysics of xylem embolism repair. *TRENDS in Plant Science*, 14 (10), 530–534.

Figures

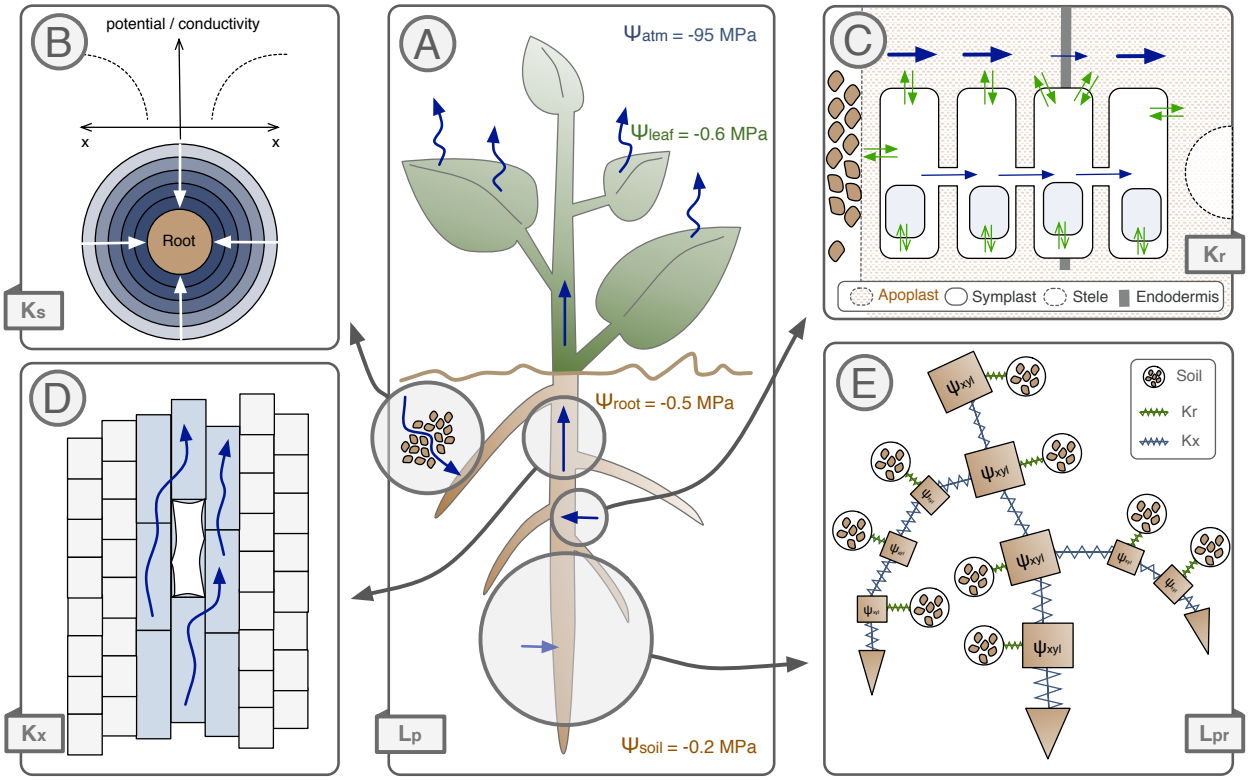


Figure 1: Water flow in the soil-plant-atmosphere continuum (SPAC). **A.** Cohesion tension mechanism. The water flows along the SPAC following the gradient of water potential between the different compartiments. **B.** Water movement in the soil. The water flows in the soil following local gradient of matricial forces. Close to the root surface, the radial nature of the water flow induces a strong water potential gradient. **C.** Radial movement of water in the root. Water entering the roots has to traverse several cell layers using a combination of symplastic, cell to cell and apoplastic pathway. Blue arrows represent pressure-driven convection while green arrows represent osmotically-driven flow. **D.** Axial movement of water in the root. Water moves in xylem vessers following water potential gradients between roots and leaves. The path can be interrupted locally at embolized vessels (cavitation). **E.** Importance of the architecture as an integrative element of the system. The analogy between the root system hydraulic architecture and an electric network makes it possible to predict the sites of water uptake across the root system.

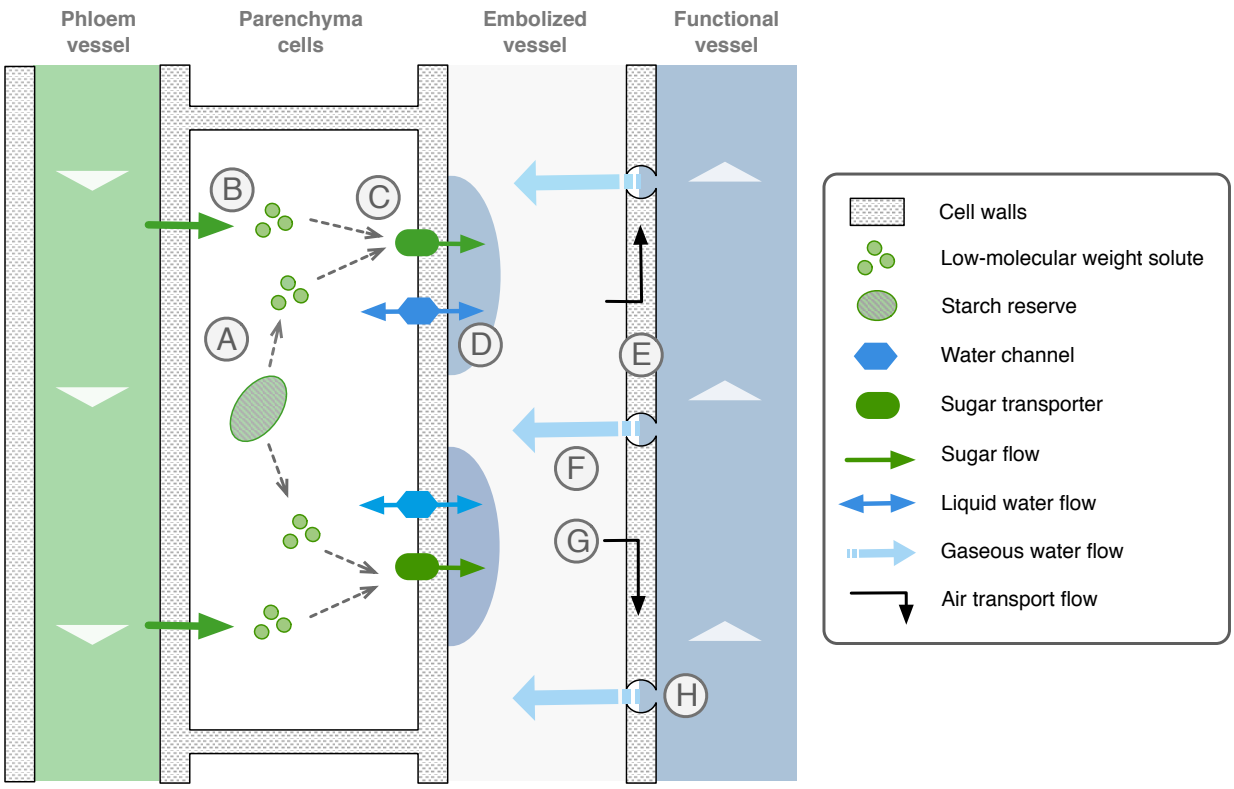


Figure 2: Scenario for xylem refilling under tension. Starch (**A**) and phloem (**B**) serves as sources of low-molecular weight solutes that are actively transported into the embolized vessel (**C**). The accumulation of solutes results in water movement from xylem parenchyma cells by osmosis, forming droplets with high osmotic activity on internal vessel walls (**D**). The partially non-wettable walls of xylem conduits prevent these droplets from being removed by suction from still-functional vessels (**E**). Condensation of water vapor provides a second pathway by which water refills cavitated conduits, allowing adjacent conduits to provide water for refilling (**F**). As the high osmotic droplets grow inside the vessel, the embolus is removed by forcing gas into solution and by pushing gas through small pores through the vessel walls to intercellular spaces (**G**). The flared opening of the bordered pit chamber acts like a check valve until the lumen is filled, thus preventing contact with the highly wettable bordered pit membranes (**H**). Reconnection occurs once the pressure in the lumen exceeds that of the entry threshold into the bordered pit chambers. A hydrophobic layer within pit membranes might provide the needed simultaneity among multiple bordered pits. (Figure reproduced following Zwieniecky and Holbrook 2009, with permission from Elsevier)

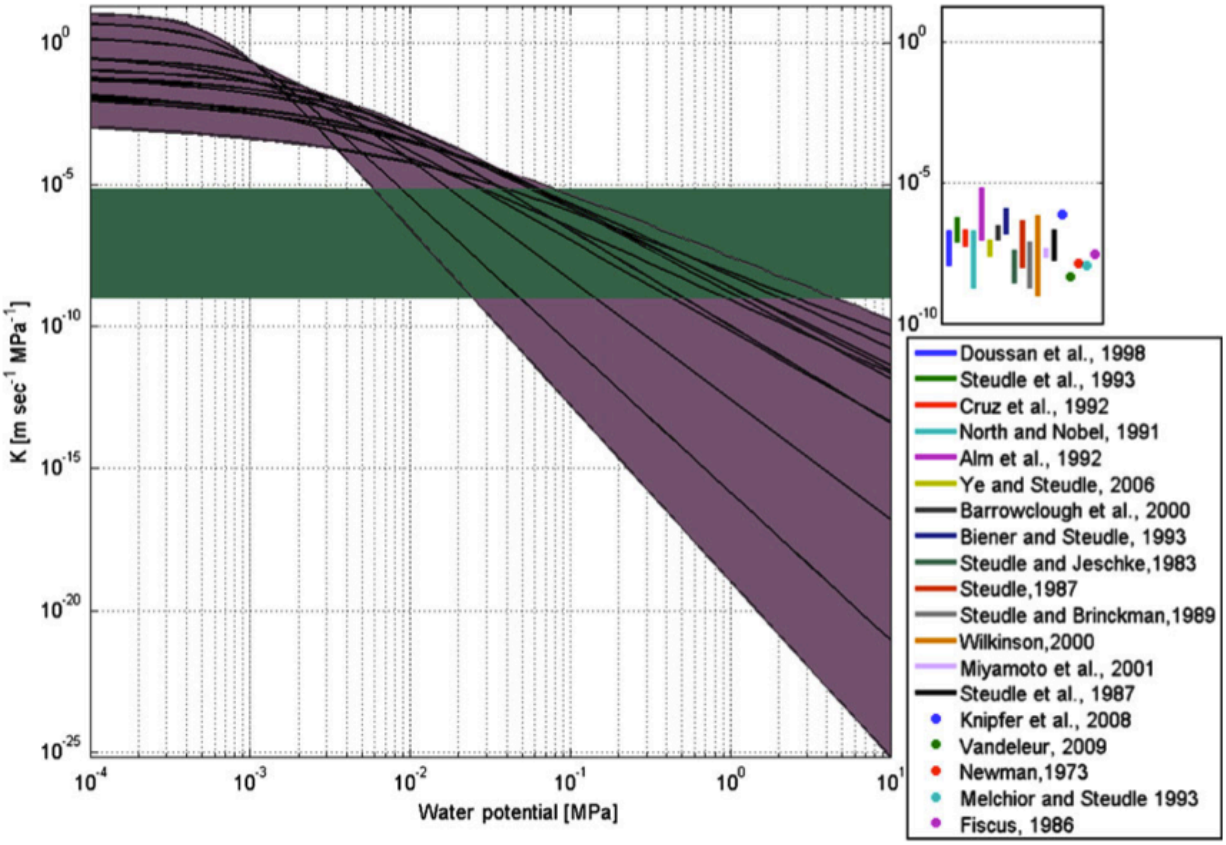


Figure 3 : Envelopes of typical soil conductivity curves (blue area) and apparent root conductivity values (green area) redrawn from the literature. The upper right plot represents root conductivity values from 19 studies .(Figure reproduced following Draye *et al.* (2010), with permission from Oxford University Press)

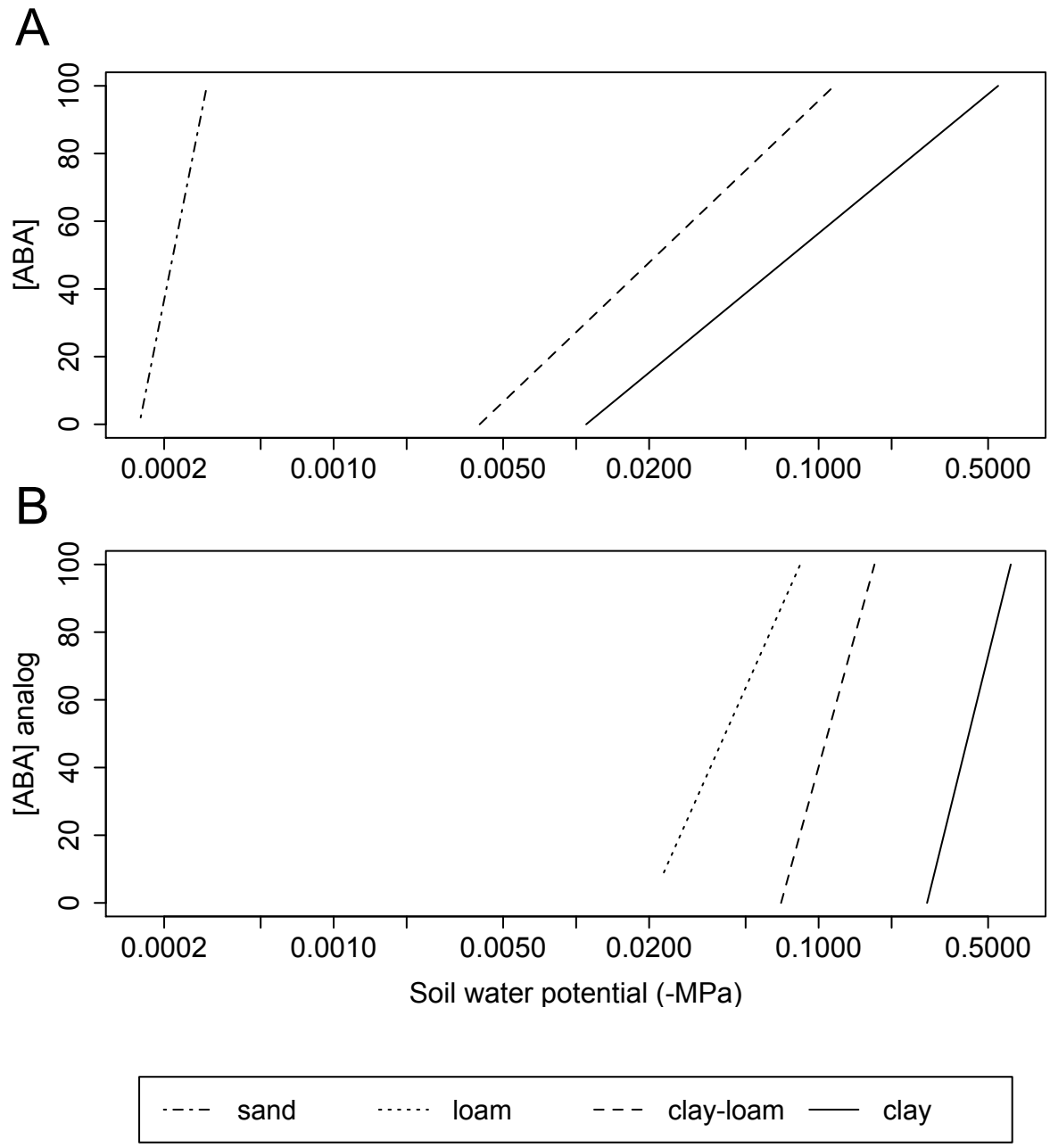


Figure 4: Evolution of xylem concentration of ABA (A, experimental) and a hypothetical stress factor (B, simulation) with decreasing soil water potential. Re-drawn from Dodd *et al.* (2010) (**A**) and Draye *et al*. (2010) (**B**)

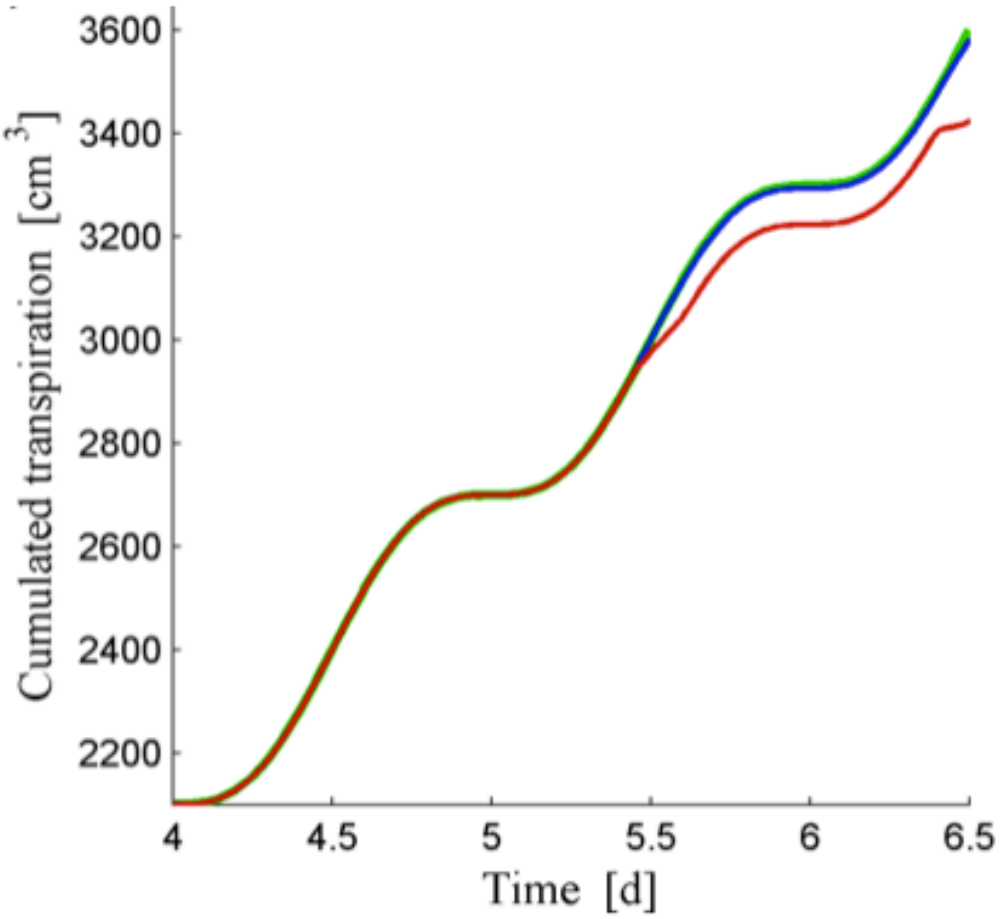


Figure 5: Cumulated transpiration rate for a plant with (blue line) and without (red line) cavitation of the xylem vessels, as compared to potential transpiration (green line).