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Update

Core Ideas

- The threshold soil water potential for water uptake depends on stomatal control.
- Whole-plant transpiration increases hydraulic conductance in roots and shoots.
- It decreases the rhizosphere hydraulic conductance, resulting in feedback loops.
- Root system ideotypes for water uptake are not always associated with the best yields.
- Models integrating controls in shoots and roots are needed to optimize root traits.

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Root Water Uptake and Ideotypes of the Root System: Whole-Plant Controls Matter

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Simulations of plant water uptake in soil science are based on the interplay between soil and root properties, with an imposed flux or water potential at the stem base. The dialogue between roots and shoots is important in water uptake. The threshold soil water potential for water uptake represents the soil water potential at which stomatal control stops transpiration over 24 h. Measurements show that it has a large variability among species and cultivars. Isohydric plants prevent low leaf water potentials via stomatal control, so their threshold soil water potential is high. Anisohydric plants allow low leaf water potentials, resulting in lower thresholds. These behaviors have a genetic control and can be simulated via whole-plant models. In studied species, the hydraulic conductance in roots and shoots depends on the whole-plant transpiration rate. In particular, there is a "dialogue" between the daily alternations in the transpiration rate and the circadian oscillations in root hydraulic conductance that affect the hydraulic conductance of the rhizosphere, with appreciable consequences on water uptake. Root traits such as length, branching, or depth interact with shoot traits such as leaf area or stomatal control, thereby generating feedbacks. As a consequence, optimum root systems for water uptake at a given time are not always those associated with the best yields. Models that take these whole-plant results into account bring an extra level of complication but are probably indispensable whenever the aim is to optimize root traits in view of improved drought tolerance.

Abbreviations: ABA, abscisic acid; PIP, plasma membrane intrinsic protein; PRD, partial root drying.

The root system is the first actor for plant water uptake through its spatial architecture and the distribution of hydraulic conductance along root axes and branching orders. As a consequence, most models of water uptake are based on a dialogue between soil and root hydraulic properties, with an imposed flux or water potential at the base of the stem considered as the boundary of the system (Gardner, 1960; Nimah and Hanks, 1973; Feddes et al., 1976). This has resulted in models that couple soil water depletion and root water uptake (Doussan et al., 2006; Javaux et al., 2008; Schneider et al., 2010). The rationale for imposing boundary conditions at the stem base is that the water flux though the plant is primarily controlled by stomatal conductance. Indeed, the latter is several orders of magnitudes lower than any hydraulic conductance in the soil or in the plant even when stomata are fully opened. This can be visualized in plants that have defective stomatal control and wilt even under well-watered conditions (Borel et al., 2001; Dodd et al., 2009). Furthermore, root hydraulic conductance has no effect on transpiration when it is manipulated via chemical compounds (Ehlert et al., 2009).

However, transpiration is controlled via feedbacks involving both roots and shoots, namely chemical and/or hydraulic messages in the short term and soil water depletion in the longer term (Fig. 1; Tardieu and Parent, 2017). Stomatal control involves leaf water status but also, in many species, chemical compounds that originate from roots (Brodribb and McAdam, 2011; Dodd, 2013; Tardieu, 2016; Visentin et al., 2016), in interaction with the microclimatic conditions sensed by leaves (Pantin et al., 2013b). The hydraulic conductance of plants is also affected by transpiration, thereby generating a feedback loop (Vandeleur et al., 2014).

In the longer term, the development of leaf area affects plant water uptake, so faster leaf growth can initially increase transpiration. This effect can be reversed later in the cycle because of soil water depletion (Tardieu and Parent, 2017). The dialogue between roots and shoots is therefore essential for simulating plant water uptake.

Hence, it is timely to review recent progress in root–shoot interactions and how they may interfere with the modeling of root water uptake. We have considered three questions: (i) to what extent does the minimum soil water potential for water uptake depend on whole-plant controls, in particular stomatal conductance, (ii) what is the extent of interactions between the hydraulic conductance in the roots, in the shoot, and in the soil, and (iii) can the concept of "optimum root system" be discussed without an explicit reference to the time course of transpiration, itself depending on leaf area and stomatal conductance?

Lower Limit for Water Uptake Linked to Stomatal Control

The "Permanent Wilting Point" Reflects the Soil Water Potential Causing Complete Stomatal Closure over Twenty-Four Hours

Most models of water uptake consider a threshold of soil water potential below which water uptake cannot occur. For instance, the Feddes stress model (Feddes et al., 1978) has a threshold soil water potential that is a function of plant species and root system architecture but independent of transpiration rate. Other models also use a limiting soil water potential (de Jong van Lier et al., 2008) or define a limiting leaf water potential (Cowan, 1965; Nimah and Hanks, 1973; Schneider et al., 2010), which causes a null flow when the soil and leaf potentials equalize. The first experiments that identified this limit involved the wilting of plants subjected to alternations of soil drying and rehydration (Gardner and Ehlig, 1963). A permanent wilting point was considered to be reached when wilted plants could not recover. This concept has long been used in agronomy to estimate the lower limit of the "plant-available water" in soils (Veihmeyer and Hendrickson, 1927), despite the warning, by Gardner and Nieman (1964), that "while the percentage at 15 bars [–1.5 MPa] may continue to serve a useful purpose in many practical situations, it is increasingly clear that the permanent wilting point does not represent the absolute lower limit of available water. Indeed, no single limit for all plant processes can be defined in any precise way." Therefore, a more dynamic definition of the lower limit of soil water potential is still needed that can be used in models of water flow in plants.

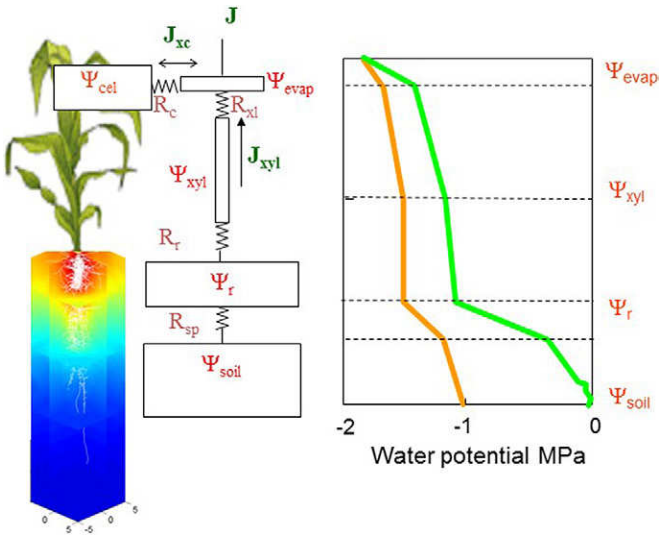

Fig. 1. Model of water transfer in the plant. The plant is represented by four compartments, each at a water potential (Ψ_r, roots; Ψ_{xyl}, xylem; Ψ_{evap}, sites of evaporation; Ψ_{cel}, leaf cells), separated by resistances R_{sp} between the soil and roots, R_r between the soil–root interface and the xylem, and R_{xl} from the xylem to the evaporation sites. Leaf cells tend to equilibrate with evaporation sites and act as a capacitance that can either take up water on rehydration or release water to the xylem on dehydration. Plants under well-watered conditions (green) or in water deficit (orange) can have similar leaf water potential via stomatal control (isohydric species). Even in this case, the xylem water potential (which controls leaf growth) is still higher in well-watered plants than in plants under drought conditions because of the steeper gradient of water potential in well-watered plants caused by higher water flux.

Water uptake can occur when the leaf water potential is lower than the highest water potential of part of the root system, thereby establishing a gradient for water flux (Fig. 1). Evolution has constrained this system in such a way that the leaf water potential stays in a narrow range (typically −0.05 to −3 MPa, Tardieu and Simonneau, 1998) in spite of rapid fluctuations in the soil water potential and evaporative demand, thereby allowing metabolism to occur under acceptable conditions in leaves and avoiding xylem cavitation. This is achieved via stomatal control, which (from an evolutionary point of view) must reduce transpiration whenever the water flow from root systems cannot match the evaporative demand. This overriding rule of stomatal control is reached via different mechanisms depending on the species, in particular with hydraulic messages and a range of chemical messages that differ among species (e.g., abscisic acid [ABA], cytokinins, sap pH, and strigolactones) (Tardieu, 2016). The degree to which these mechanisms interact and differ among species and/or environmental scenarios is still debated, with several models existing in the literature that successfully mimic observed time courses. However, the overriding rule that stomata are controlled in such a way to keep the leaf water potential below a threshold can be sufficient for many modeling applications.

Under moderate water deficits, stomata close in afternoons (this can happen even under well-watered conditions under high evaporative demand). They close increasingly early in the day as the soil water reserve is depleting, so stomatal closure in early morning occurs only at very low soil water potential (Tardieu et al., 1992). Hence, the soil water potential value that stops water uptake can be interpreted as the potential that triggers stomatal closure and transpiration arrest even in the early morning. By *soil water potential*, we mean here a resulting water potential that integrates the spatial variability at the soil–root interface (Couvreur

et al., 2014a, 2014b), as it can be measured via pre-dawn leaf water potential (assuming equilibrium) or can be modeled as proposed by Couvreur et al. (2012).

Genetic Differences in Stomatal Control Affect the Lower Limit

A key question is whether this control appreciably differs among species and genotypes. It can be addressed by considering the minimum leaf water potential observed experimentally or by considering the genetic variability of the response of physiological variables such as stomatal control or leaf growth to variations of soil water potential.

- The minimum value of measured leaf water potential differs greatly among species. Some species strictly limit leaf water potential to values higher than e.g., −1.8 MPa (maize [*Zea mays* L.], apple [*Malus pumila* Mill.], and poplar [*Populus* spp.], Fig. 2). In these species, termed *isohydric* (Tardieu and Simonneau, 1998), the somewhat counterintuitive result can be observed that plants subjected to either wet or dry soil show similar leaf water potentials under high evaporative demand (Fig. 2). Other species, termed *anisohydric* (Tardieu and Simonneau, 1998), such as sunflower (*Helianthus annuus* L.) or oak (*Quercus* spp.) frequently show leaf water potentials lower than −0.3 MPa during the day (Fig. 3). Iso- and anisohydric behaviors, initially thought to be defined at the species level (Tardieu and Simonneau, 1998), in fact show a continuum (Klein, 2014; Huber et al., 2015) even within a given species (Coupel-Ledru et al., 2014). Both phenotypic and genetic analyses have led to two, nonexclusive, physiological interpretations of iso- and anisohydric behaviors. The first interpretation involves the respective roles of chemical vs. hydraulic messages in stomatal control (Tardieu et al., 2010; Tardieu and Simonneau, 1998). In isohydric plants, transpiration is increasingly limited by stomatal control when the leaf water potential decreases, thereby keeping the latter in a narrow range in situations combining low soil water potential and high evaporative demand. In anisohydric plants, stomatal control is less stringent and is essentially independent of the leaf water potential, thereby allowing the leaf water potential to decrease to low values. This can be modeled via an equation in which stomatal conductance primarily depends on a root message such as ABA, with a sensitivity that depends on the leaf water potential. Variations in this sensitivity from zero to high values can mimic the range of iso- to anisohydric behaviors (Tardieu and Simonneau, 1998; Tardieu et al., 2015; Huber et al., 2015). The architecture of hydraulic resistance in the xylem and in the leaf can also cause contrasting degrees of isohydricity (Pantin et al., 2013b; Tardieu et al., 2015).

- An appreciable genetic variability of isohydricity exists within a species. Recently, it has been shown that cultivars of grapevine (*Vitis vinifera* L.) display different degree of isohydricity, resulting in large differences in minimum leaf water potential (Coupel-Ledru et al., 2014). Because authors performed this analysis in a mapping population, they identified genomic regions associated with minimum leaf water potential. The

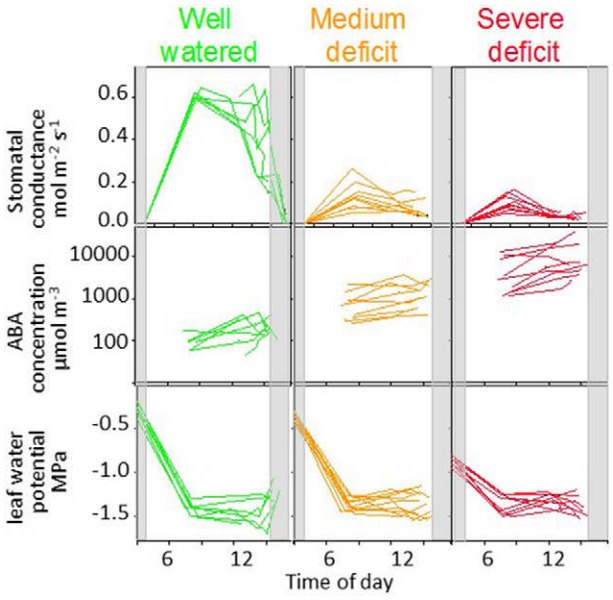

Fig. 2. Measured stomatal conductance, leaf water potential, and concentration of the stress hormone abscisic acid (ABA) in the case of poplar, a typical isohydric behavior. The three levels of soil water deficit can be visualized in the bottom row via pre-dawn values of leaf water potential. Stomatal conductance (top row) dramatically decreases and the concentration of ABA increases with soil water deficit (middle row). However, daytime leaf water potential is similar in the three treatments (bottom row). Each line represents one plant followed throughout the time of day; gray rectangles are night periods. (Redrawn from Tardieu and Simonneau, 1998).

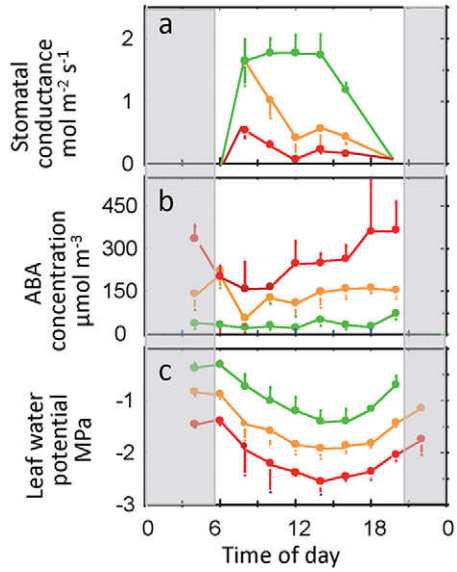

Fig. 3. Measured stomatal conductance, leaf water potential, and concentration of the stress hormone abscisic acid (ABA) in the case of sunflower, a typical anisohydric behavior. The three levels of soil water deficit (well-watered conditions, green; moderate water deficit, orange; and severe water deficits, red) can be visualized in the bottom panel via pre-dawn values of leaf water potential. In contrast with the isohydric behavior in Fig. 2, stomatal conductance (top) and leaf water potential (bottom) decrease simultaneously with soil water deficit, which increases the concentration of ABA (middle). Gray rectangles represent night periods. (Redrawn from Tardieu and Simonneau, 1998).

response of stomatal conductance to evaporative demand has been analyzed in wheat by Schoppach et al. (2016) with, again, a large genetic variation and an organized genetic architecture. In maize, the water potential that stops shoot growth was identified in 400 lines of tropical or European origins. Some genotypes continue growth at leaf water potentials as low as −1.5 MPa, whereas others stop at −0.8 MPa, again with genomic regions controlling threshold potentials (Welcker et al., 2011).

Partial Root Drying Affects Leaf Water Potential and Soil Water Uptake

Stomata tend to close, at least in some experimental systems, when part of the root system is exposed to dry soil even if another part is in contact with wet soil and can therefore potentially take up soil water at a high flux (Davies et al., 2002). In this case, leaf water potential is indistinguishable in leaves of well-watered plants and in those subject to partial root drying (PRD), whereas stomatal conductance is largely affected, e.g., by 60% in apple or 30% in tomato (*Solanum lycopersicum* L.) (Davies et al., 2002). Abscisic acid may be part of a root message as evidenced in split root systems (Davies and Zhang, 1991), but other compounds are involved. The flux at the stem boundary is lower in PRD systems than what could be expected if only soil water availability and evaporative demand were taken into account. It is noteworthy that alternate irrigation, resulting in PRD, has been successfully used to limit transpiration in commercial fields of grapevine and tomato (Davies et al., 2002).

Simulations indicate that, in soils with initially uniform soil water content, the hydraulic architecture of the root system leads to a heterogeneous distribution of root water uptake and that the resulting heterogeneity of the soil water potential accentuates that of root water uptake (Draye et al., 2010). These simulations therefore suggest that PRD, as a primary consequence of the soil–plant hydraulic architecture, is a very common phenomenon in the field. Hence, they somewhat cast doubt on the extent of stomatal closure in the case of PRD, which would cause stomatal closure when upper soil layers become dry. Such early stomatal closure is not observed in most field situations (Tardieu et al., 1992).

A Partial Conclusion

The very nature of the lower limit of the soil water potential that is used in models of water transport is largely influenced by stomatal control, with both genetic and environmental contributions. It may therefore be useful to use and develop models that consider the interplays between shoot and root to simulate the amount of water extraction, with explicit stomatal control taking into account both leaf and root roles in different species, genotypes, and management systems. A good example of such a model is the one developed by Huber et al. (2014), where ABA production and transport, stomatal conductance, and root system architecture are explicitly modeled and coupled. Such effects would account for the variation of the lower limit of water extraction, between −1.5 to −3.5 MPa depending on species or genotype, and for the effect of irrigation practices such as PRD. However, the amount of soil water reserve in the range −1.5 to −3.5 MPa largely depends on soil type so it may or may not be important to take detailed aspects of stomatal control into account when simulating water uptake, depending on the objectives of the study and on the soil types that are considered.

Physiological Control of Hydraulic Conductance on the Water Pathway from Soil to Stomata

Relative Contributions of Hydraulic Conductance in the Soil vs. in the Plant

Most models of water transfer have adopted a dynamic approach involving hydraulic conductance in the pathway from "bulk soil" to leaves. The relative contributions of conductance in the soil and in plants have been reviewed by Draye et al. (2010). Briefly, while under wet soils (soil water potential above −0.01 MPa) root radial conductivity is experimentally much lower than soil conductivity, the opposite occurs in dry soils (soil water potential below −1 MPa). In between, a gray zone exists, where rhizosphere and roots can potentially control the uptake as a function of the soil water potential at the soil–root interface.

In addition to conductivities of soil and plant tissues, the overall conductance for water transport depends on the path length of water in both soil and tissues. Many calculations of soil water uptake are based on a regular distribution in the soil (Roose and Fowler, 2004; de Jong van Lier et al., 2008), thereby underestimating distances by several orders of magnitude compared with more realistic systems (Tardieu, 1988). Finally, the contact surface area at the soil–root interface can be particularly difficult to estimate, especially in dry soils when root shrinking may occur, leading to important errors in the soil–root conductance (Carminati and Vetterlein, 2012).

In any case, hydraulic conductance in the soil and in the plant interfere with each other. It is therefore worth considering the physiological controls of hydraulic conductivity in roots and plants, their potential contribution to water uptake, and the consequence of their potential genetic variability.

Physiological Control of Hydraulic Conductance from Roots to Stomata

The hydraulic conductance of plant tissues is affected by environmental conditions, in particular in roots, leaves (Chaumont and Tyerman, 2014; Cochard et al., 2007; Maurel, 1997), and stomata (Grondin et al., 2015). In most species, measured root hydraulic conductance increases with increasing light or transpiration rate, when the flux through roots increases. This behavior is mediated by the regulation of the activity of plasma membrane intrinsic proteins (PIPs) (Cochard et al., 2007; Vandeleur et al., 2014). Conversely, the hydraulic conductivity in the rhizosphere most often decreases by several orders of magnitude when the plant water demand increases, due to local soil water depletion around roots during the day even in wet (but unsaturated) soil

(Bruckler et al., 1991; Schroeder et al., 2009; Lobet et al., 2014). Root shrinking under high evaporative demand might also decrease root–soil contact and generate air gaps that can decrease the effective conductance between soil and root (Huck et al., 1970; Faiz and Weatherley, 1982). Mucilage production may reduce this effect by increasing the water holding capacity of the rhizosphere and by ensuring a higher hydraulic conductivity and possibly a better contact between root and rhizosphere (Carminati et al., 2011; Carminati and Vetterlein, 2012; Schwartz et al., 2016). Evaporative demand might therefore have opposite effects on soil and plant conductance, a situation that potentially generates feedback loops and dynamic behavior (see below).

Water deficit and salt stress usually decrease the root hydraulic conductance (North et al., 2004; Vandeleur et al., 2009), yet the plant hormone ABA, which is overproduced under water deficit, increases the root hydraulic conductance via the expression of PIP aquaporins (Kaldenhoff et al., 1996; Parent et al., 2009; Shinozaki et al., 1998; Thompson et al., 2007). This, again, generates feedback loops. The link between root conductance and ABA production has been confirmed in transformed plants that over- or underproduce ABA, resulting in sixfold differences in root hydraulic conductivity between lines that over- or underproduce ABA (Parent et al., 2009). However, ABA may act in opposite directions on the hydraulic conductance in roots and leaves by decreasing the hydraulic conductance from the xylem to veins in *Arabidopsis thaliana* (Pantin et al., 2013a).

Other environmental factors affect tissue hydraulic conductance, in particular tissue temperature via water viscosity (Cochard et al., 2000) and plant nutrient status (Clarkson, 2000; Trifilo et al., 2014). In addition, the leaf hydraulic conductance tends to decrease with leaf age (Locke and Ort, 2014). The hydraulic conductance of tissues from roots to stomata therefore exhibits complex behaviors that can be taken explicitly into account but also be accounted for via emergent properties that avoid the complexity presented above (Tardieu and Parent, 2017).

A "Dialogue" between Circadian Oscillations of Hydraulic Conductance in the Root and Rhizosphere

The root hydraulic conductance follows a circadian rhythm, experimentally observed under continuous light in *Arabidopsis thaliana* (Takase et al., 2011) and in maize (Caldeira et al., 2014), with a period of 24 h. A counterintuitive result is that this circadian control leads to the highest root hydraulic conductance in the night and early morning when plant demand is lowest (an effect superimposed on the intrinsic effect of light and transpiration, see above). Root hydraulic conductance decreases in the afternoon when plants need the highest water uptake to counteract evaporative demand. Still more counterintuitive is that the observed amplitude of these oscillations increases if the plant has been subjected to water deficit or high evaporative demand in previous days, indicating a "memory effect" (Caldeira et al., 2014). This is an apparently absurd strategy in which plant hydraulic conductance is reduced at times of the day when plants need the highest water uptake, with the lowest conductance being observed when plants are exposed to water deficit or high evaporative demand (Fig. 4).

Simulations help understand the above experimental results. They suggest that circadian oscillations of root hydraulic conductance may contribute to acclimation to water stress by increasing root water uptake over 24 h (Caldeira et al., 2014). Indeed, a high water uptake during the afternoon has detrimental consequences on water uptake for 24 h by almost irreversibly decreasing the hydraulic conductivity of the rhizosphere (Draye et al., 2010; Lobet et al., 2014). When subjected to high water demand, roots tend to deplete the few millimeters of soil around them, thereby decreasing the soil hydraulic

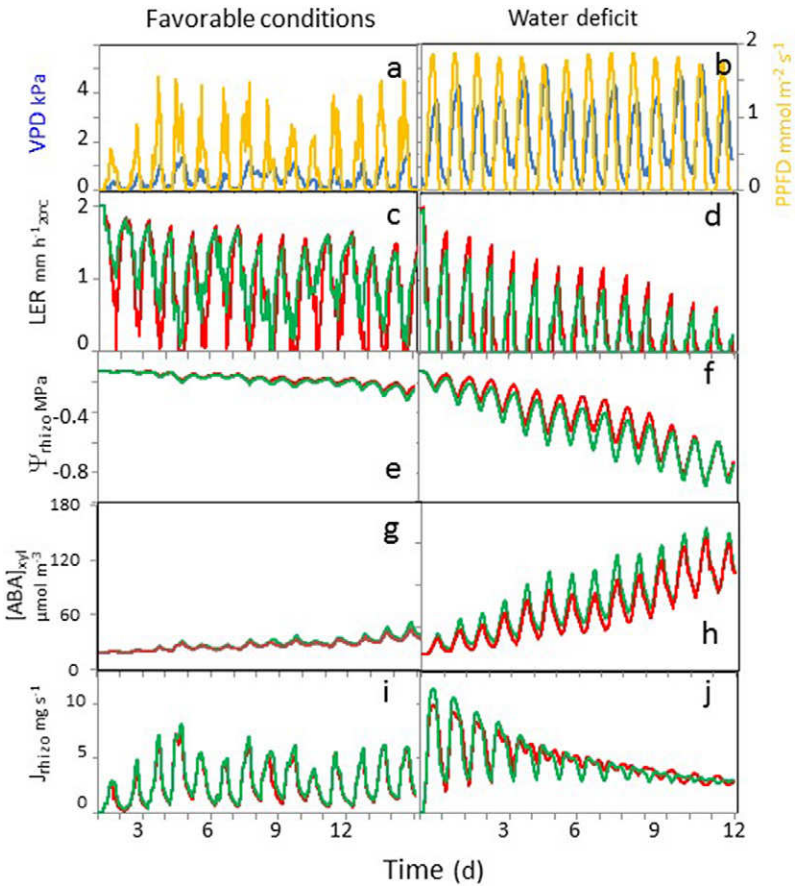

Fig. 4. Comparative advantages of high or low oscillation amplitudes of root hydraulic conductance under low (left) and high (right) evaporative demand (see [a] photosynthetic photon flux density, PPFD, and [b] vapor pressure deficit, VPD). In each scenario, red and green lines represent simulations with high and low amplitudes, respectively, of circadian oscillations of water potential: (c,d) simulated leaf elongation rate (LER) of maize; (e,f) water potential of the rhizosphere (Ψ_{rhizo}); (g,h) concentration of abscisic acid in the xylem sap ($[ABA]_{xyl}$); (i,j) water flux from the bulk soil to the rhizosphere (j_{rhizo}). (Redrawn from Caldeira et al., 2014.)

conductivity of the rhizosphere. This in turn causes more severe soil water depletion around roots and a further decrease of soil hydraulic conductivity of the rhizosphere. This impact might be reinforced by hydrophobicity in the rhizosphere induced by dehydrated mucilage (Ahmed et al., 2016; Zarebanadkouki et al., 2015) and air gaps between soil and roots (Carminati et al., 2013). This positive feedback (or autocatalytic process) can become almost irreversible after some days (see, for instance, Meunier et al., 2017), until the whole soil is heavily rewatered. Hence, restricting root hydraulic conductance in the afternoon has a transitory negative effect on the plant water status, but it increases root water uptake for 24 h by avoiding an excessive dehydration of the rhizosphere. Simulations performed with the model of Tardieu et al. (2015) compared high and low circadian oscillations of root hydraulic conductivity in two climates with high and low evaporative demand (Fig. 4). It was observed that, under high evaporative demand, high oscillations (i.e., lower root hydraulic conductance during the afternoon) have a favorable effect on the simulated soil water potential in the rhizosphere, on simulated leaf growth, and on the level of plant water stress as estimated by the simulated concentration of ABA in the xylem sap (Fig. 4d–4h). This positive effect is due to an increase in nighttime water flux from the bulk soil to roots (Fig. 4j). It is negligible under low evaporative demand (Fig. 4i), so keeping high root hydraulic conductance during the afternoon is preferable for leaf growth in this case (Fig. 4c).

These results raise the possibility that water-stress-dependent circadian oscillations of root hydraulic conductance confer competitive advantage to plants able to anticipate daily environmental variations and to synchronize growth with them. High oscillations of root hydraulic conductance, observed experimentally under water stress only, result in the maintenance of a higher water potential and hydraulic conductance in the rhizosphere. They have a trade-off under well-watered conditions, which is avoided because well-watered plants have lower oscillations of root hydraulic conductance. The "memory" effect of water deficit therefore allows the best oscillation strategy to be used, with a climatically driven control of root hydraulic conductance that improves plant performance under both stressful and optimal conditions.

A Partial Conclusion on the Effects of Root and Shoot Hydraulic Conductance on Overall Root Water Extraction

Most root water uptake models implicitly assume that the plant or root conductance is a constant, or that it only evolves with root system size and root length density, and often consider the shoot transpiration as a boundary condition. The above discussion suggests the need for models that integrate soil–root–shoot dialogues for better estimation of soil water flow and constraints on transpiration.

The debate on the respective roles of hydraulic conductance in soil, roots, and shoots has long been limited to a comparison of their orders of magnitudes. This is still useful for intuitive reasoning but, in a dynamic approach, conductance that is "in series" should be considered as a whole. The short half times of changes in transpiration rate and hydraulic conductance on environmental cues lead one to reason in terms of feedbacks rather than simple comparisons. In the example of the dialogue between the conductance of roots and rhizosphere, the control of root hydraulic conductance has a major effect on the overall water flow, although root conductance is higher than soil conductance in the system presented in Fig. 4.

The Context-Dependent Effect of Root System Architecture and Hydraulic Properties on "Drought Tolerance"

Increasing soil exploration by the root system is widely considered to be a positive feature for improving drought tolerance (de Dorlodot et al., 2007). Indeed, genomic regions controlling root system architecture under controlled conditions can also affect yield in fields under drought (Landi et al., 2010; Tuberosa et al., 2002). In fields with deep soil and/or the presence of a water table, an increased root length in deep layers improves access to water and the plant water status (Leitner et al., 2014), depending on the soil hydraulic properties. In particular, reduced crown root numbers (Gao and Lynch, 2016), changes in root cortical anatomy (Zhu et al., 2010; Chimungu et al., 2014a, 2014b), and reduced lateral root density (Zhan et al., 2015) result in a yield increase under dry conditions, possibly through their favorable effects on deep rooting. The positive correlation between low canopy temperature and yield among genotypes subjected to water deficit has also been interpreted as the effect of a deep root system, which improves water uptake and transpiration, thereby lowering canopy temperature and increasing yield (Pinto and Reynolds, 2015; Sukumaran et al., 2015).

Some Counter Examples

Several breeding programs for drought tolerance have resulted in a decrease in root biomass and length with cycles of selection (Bolaños et al., 1993; Bruce et al., 2002; Campos et al., 2004). For instance, Bolaños et al. (1993) performed eight cycles of selection of tropical maize genotypes under dry conditions. After each cycle, they selected lines that displayed the best performance under drought. At the end of the process, they studied the best lines and compared them with those at the beginning of the process. Lines improved for drought tolerance had a lower root biomass and length than those considered in the first selection cycle. This is discussed below.

Maize hybrids have been developed that restrict transpiration during the vegetative phase, so flowering time and grain filling occur with more favorable soil water status than with hybrids displaying high transpiration during the vegetative phase (Messina et al., 2015). Simulations show that this trait is favorable in the driest areas of the United States, and can be unfavorable under milder conditions (Messina et al., 2015). It is not known whether this can be attributed to root system characteristics or to stomatal control, but it shows that maximum water uptake, favored by

an efficient root system, is not necessarily a favorable trait in the driest scenarios. In the same line, saving water for later stages of the crop cycle has been obtained by reducing the xylem hydraulic conductance of wheat (*Triticum aestivum* L.) cultivars with, again, a favorable effect on yield under the driest conditions (Richards and Passioura, 1989). Simulations (Leitner et al., 2014) also showed that a change in lateral root radial conductivity may have more impact on uptake than deeper roots or longer laterals. A similar positive effect of water saving via a less efficient root system was observed by Lilley and Kirkegaard (2016) across longer timescales. Considering a wheat cropping system for several years, they found that an extensive root system is most often detrimental in shallow soils and frequently so in deeper soils (1.6–2.5 m). The reason was that extensive root systems cause water depletion in dry layers, thereby limiting water availability to the subsequent crop. It is noteworthy that such a mechanism does not occur when the soil water reserve is replenished during winter, a common situation in temperate climates.

No Unique Root System Ideotype: The Trade-Off between the Effects of Transpiration and Soil Water Depletion Depends on Environmental Scenarios

A common feature of the counter examples presented above is that the soil water reserve needs to be managed throughout the crop cycle, or even longer timescales in the case of multiyear cropping systems under dry conditions. In this case, rapid water uptake is favorable in the short term but may cause a loss of yield if this results in excessive soil water depletion at key stages of the crop cycle. A "benefit–risk" approach must be adopted, therefore, for long time series for identifying optimum ideotypes of root systems in a series of environmental scenarios.

In a recent study (Tardieu and Parent, 2017), the sensitivity of maize yield to variations in the rate of progress of rooting depth was analyzed via simulations in 55 European sites for 35 yr using the crop model APSIM (Hammer et al., 2010). Rooting depth and its rate of progression originated from in situ root mapping (Tardieu, 1988; Tardieu and Manichon, 1987), with a considered genetic variability of ±10%. This genetic variability had an effect on simulated yield that ranged from moderately negative to positive, from −400 to 1300 kg ha^{-1}, with a median value close to 0 (Fig. 5). The effect of the root growth rate on simulated yield was negligible in shallow soils of 0.5-m depth. Appreciable effects were observed only in fields with soils deeper than 1.5 m, with a large variability among fields. Increases in yield by more than 1 Mg ha^{-1} were observed only in the case of moderate water deficit in this category of soils. At intermediate soil depths of 1 to 1.25 m, changes in yield associated with the root growth rate ranged from −0.45 to 0.7 Mg ha^{-1}, depending on conditions.

Surprisingly, the effect of the root elongation rate on yield also depended on air temperature, regardless of evaporative demand,

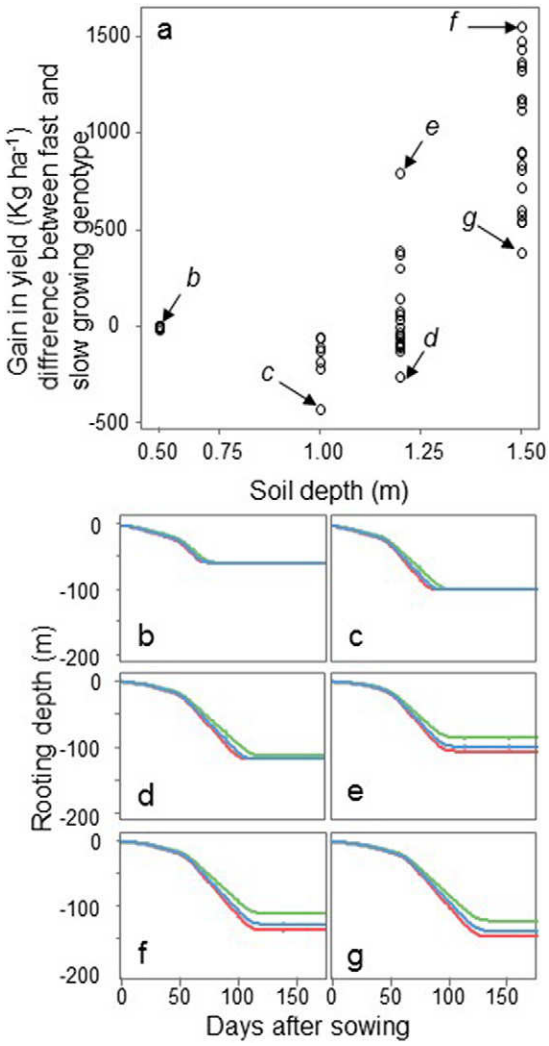

Fig. 5. Effect on yield of the rate of progression of rooting depth in different environmental scenarios. Three virtual genotypes with contrasting rates are compared at 55 sites for 35 yr: (a) difference in yield among the genotypes with maximum and minimum root growth rates averaged across 35 yr (letters near symbols refer to one field whose rooting depth is presented with the same letter in (b–g); and (b–g) mean time courses of rooting depth simulated for 35 yr in six fields for three genotypes with the slowest (green, 20 mm d^{-1}), intermediate (blue, 22.5 mm d^{-1}) or highest (red 25 mm d^{-1}) rates. Each field has a different soil depth. (Redrawn from Tardieu and Parent, 2017).

via its effect on the flowering time, when root systems usually stop expanding. In deep soils, an effect of the root growth rate on the simulated final rooting depth occurred only in the case of early flowering under high air temperatures. Under cooler air temperatures, flowering time occurred later so all genotypes had the time to reach the maximum rooting depth allowed by the considered soil.

The Carbon vs. Water Trade-Off

Root systems have a considerable metabolic cost of respiration (Rachmilevitch et al., 2006). Another trade-off therefore exists between the carbon cost of the root system, which occurs at the expense of the growth of other organs, and the probability of higher water uptake under high evaporative demand. This

trade-off further limits the interest of developing large root systems when they are not necessary (e.g., in shallow soils). Van Oosterom et al. (2016) introduced the concept of root system efficiency, i.e., transpiration per unit leaf area and per unit root mass, as a measure of this trade-off. A significant genetic variability in root system efficiency was observed, and this positive trait was associated with a reduced dry mass allocation to roots. The carbon cost can be lowered via anatomical differences (Chimungu et al., 2015; Gao and Lynch, 2016; Lynch, 2015), but the trade-off "carbon for water" still needs to be carefully considered when identifying root system ideotypes. The production of root mucilage, which can help plants sustain water extraction, is another aspect of this tradeoff because it probably represents a non-negligible carbon use (Carminati et al., 2016).

A Partial Conclusion: Ideotypes of Root Systems Differ among Environmental Scenarios

Overall, this discussion shows that there is no direct correspondence between improved soil water uptake and "drought tolerance" defined as improved yield under water deficit. Improving the root system results in spectacular effects in species that have intrinsically weak root systems and/or in soils whose depth largely exceeds the rooting depth reached at flowering time. This has been the case in rice (*Oryza sativa* L.), which has been essentially selected under water-logged conditions and is now increasingly grown under aerobic conditions. Conversely, the effect of having a deep root system with rapid development can have either positive or negative consequences on yield depending on environmental scenarios, because of early soil water depletion and/or of the carbon cost of root systems. This conclusion by no means underestimates the importance of a genetic analysis of root system characteristics. As for other traits such as stomatal conductance or shoot growth, the existing genetic variability for root traits will allow fine-tuning new cultivars for most common environmental scenarios, but no ideotype will serve for all of those. For instance, roots growing vertically and at low metabolic cost ("steep, cheap, and deep") (Lynch, 2013) are an interesting ideotype, but the above simulation shows that its interest for crop performance needs to be contextualized.

Concluding Remarks

Current models of water uptake usually share the hypothesis of a lower limit of soil water potential for water uptake, based, for example, on the concept of a permanent wilting point. We have discussed the nature of the lower limit of soil water potential and shown that it is largely influenced by stomatal control, with both genetic and environmental aspects. Current models of water uptake also assume that the plant or the root conductance is a constant or that it only changes with root system size or root length density and often consider the shoot transpiration as a boundary condition. Our review has pointed out several improvements of root water uptake models that are prerequisite for better estimation of soil water flow and plant transpiration: (i) consider the interplays between shoot and root, (ii) consider the explicit effects of species, genotype, and management system on stomatal control, (iii) consider values of root conductance that integrate soil–root–shoot dialogues via fluxes of carbon, water, and hormones. While doing so, it is also essential to contextualize the value of any individual trait that is thought to contribute to root water uptake and, ultimately, to yield under water deficit. Whether they are root- or shoot-related, traits can at best allow fine-tuning new cultivars for given environmental scenarios, but it seems increasingly clear that no single ideotype will serve a large array of environmental scenarios.

We are aware that the above considerations complicate the modeling of water uptake. Indeed, current models of water uptake have been successful in the simulation of most field situations. Reciprocally, crop models such as APSIM (Hammer et al., 2010) largely ignore complications in soil science and rely on soil water availability only. We have recently discussed the fact that simple rules such as "water uptake decreases with decreasing soil water reserve" are often sufficient to simulate simple situations (Tardieu and Parent, 2017). They are based on overriding principles dictated by evolution because any plant that does not follow these principles would have been deselected. However, it is important to appreciate that these rules do not represent the mechanisms at work in the control of transpiration. Hence, simplistic rules can be sufficient in many situations but can also be severely misleading, for example, for designing a root system ideotype for a climatic scenario.

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