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Root hydraulics: The forgotten side of roots in drought adaptation

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ABSTRACT

Roots have long been proposed as a major avenue of research to improve crop adaptation to water limitations. The simple assumption is that deeper and more profuse root systems could tap extra water from the soil profile and alleviate drought effects. However, after decades of research, success in breeding cultivars with improved root systems is lagging behind. Here, we attempt to analyze the possible reasons for this, and re-focus on what root traits might provide the most promising avenues for drought adaptation. We approach the root system from the angle of water extraction, using data from a lysimetric system that allows monitoring and comparing plant water use over the entire crop life cycle and yield, and analyze whether and how differences in water extraction lead to improved yield across different crops. The main message from that analysis is that water extraction during reproduction and grain filling is critical and comes from a number of traits that influence the rate at which plant use the available water before and during stress. Roots may have an effect on this, not from the traditionally thought density or depth, but rather from their hydraulic characteristics. Plants can indeed control water use by controlling leaf area development and this is a "long term" control. Plants also control water losses by controlling stomata opening under high vapor pressure deficit (VPD) conditions, in a transient manner. Both processes (leaf development and stomata opening) are mostly controlled by hydraulic processes. The role of roots in drought adaptation could be there, along with the soil, in setting an hydraulic environment that allow plants to use water in a way that allow maximizing water use for these critical stages.

1. Introduction

Agriculture production worldwide is often limited by water deficits and the case is very acute in semi-arid tropics of Asia and Africa where populations are large, dense, and depend on subsistence agriculture. Developing "drought" tolerant cultivars has then become a critical agenda to breeding programs in many crops species. Because the root system is the plant organ in charge of capturing water and nutrients, besides anchoring the plant in the ground, it is naturally seen as the most critical organ to improve crop adaptation to water stress. Here we review the research carried out on roots for drought adaptation and mostly on root depth and density (Kashiwagi et al., 2006; Silim et al., 1993; Gowda et al., 2011). Then we review the limitation to these "traditional" approaches to root architecture, discuss the relevance and limit of pursuing water extraction at depth, and address the limits to the current experimental approaches to measure root systems. Especially, we highlight the need to progress toward 3-D in situ representation of the root system (Burton et al., 2012; Mooney et al., 2012) to reach a true representation of the roots in their environment, and of their potential to capture water.

In a Section 2, we present an alternative way to approach the role of root for water stress adaptation, moving away from actual root measurements and, instead, assessing water extraction by roots as a way to harness the functionality of root systems. This recent approach consists of a lysimetric system, i.e. a set of long and large PVC tubes in which plants are grown individually and have plant spacing and soil volume available for soil exploration close to what is practiced under field conditions (Vadez et al., 2008; 2013a). In that section we present results on the genetic variation for water extraction under different types of water stress in different legumes and cereal crops. We also discuss the usually low/inexistent relationships between total water extraction and grain yield, in comparison to the positive relationships between the grain yield and the harvest index (HI) or the transpiration efficiency (TE), i.e. the other components of the Passioura equation ($Y = WU \times TE \times HI$, Passioura, 1983). By contrast, recent evidence across several species point out to the importance for crops to secure water availability at the critical stages of reproduction and grain filling (e.g. chickpea, Zaman-Allah et al., 2011b); pearl

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millet (Vadez et al., 2013a); wheat (Kirkegaard et al., 2007). Therefore this section highlights the importance of (often) small but critical water availability for reproduction and grain filling, and briefly presents the traits that make this possible. Here we mostly refer to a recent paper where these traits, mostly related to the shoot, are exhaustively reviewed (Vadez et al., 2013c). The end of this section is then a transition in which we discuss the linkage between some of these traits related to the plant water budget and the plant hydraulic characteristics. There is indeed evidence that some of the traits related to the plant water budget are ruled by hydraulic mechanisms, e.g. the control of leaf expansion (Reymond et al., 2003; Simonneau et al., 2009), or the transpiration response to high vapor pressure deficit (VPD) (Sinclair et al., 2008), and some of these are determined by differences in the root hydraulics (Parent et al., 2010). Of course, water conservative mechanisms should not be seen as "drought tolerance" mechanisms, but rather as mechanisms that alter the plant water budget and that need to be tailored to specific drought scenarios.

The last section then deals with possible root characteristics that can influence root hydraulics (Maurel et al., 2010) and eventually can alter the different traits related to the water budget. We first briefly review the existing differences in root absorption kinetics within and across species (Dardanelli et al., 1997; Collino et al., 2000; Dardanelli et al., 2004), and then the architecture of the root cylinder and how water penetrates the root (Steudle and Peterson, 1998; Steudle, 2000a). Then we review the "root development" options to alter root hydraulics, in particular the xylem vessel sizes (Richards and Passioura, 1989), but also other root characteristics like the root cortical aerenchyma or root cell size and file number, which have been approached from the angle of root carbon cost (Lynch and Brown, 2012; Burton et al., 2013; Lynch, 2013) but that could have a role on the root hydraulics. Finally we review the role of aquaporins in influencing hydraulic conductance of plant tissues, focusing here on their role in root tissues (e.g. Ehlert et al., 2009; Thompson et al., 2007).

2. "Traditional" root traits and their contribution to drought adaptation

2.1. Current views

More profuse (higher root length density, RLD) and deeper root systems are often viewed as desirable traits for drought adaptation. Using a root box method, drought tolerant cowpea cultivars were shown to have a higher root dry matter per unit of leaf area and a downward movement of roots indicating that they would invest more in deeper rooting for water capture (Matsui and Singh, 2003). In that study, the possible role of water saving traits was overlooked. In chickpea, genotypes reaching higher yield under terminal stress condition had higher RLD (Kashiwagi et al., 2006). Several other studies also show an advantage of having superior root traits for yield under stress conditions (e.g. Silim and Saxena, 1993; Price et al., 2002b; Ober et al., 2005; Sarker et al., 2005; Tuberosa et al., 2002; Gowda et al., 2011). A modeling study in wheat shows that roots are a more limiting factor than expected (Jamieson and Ewert, 1999). In particular, deep rooting has been shown to be important under water limitation and in the case of water availability at depth (e.g. Gowda et al., 2011; Henry et al., 2011; Lynch, 2013; Wasson et al., 2012). Therefore, there is an important body of evidence that RLD and root depth matter for drought adaptation.

There are also a number of studies that question the importance of root traits. For instance, in a rice mapping population between the deep rooting Azucena and a shallow rooting Bala, the effects of root traits coming from the Azucena allele on drought avoidance were smaller than expected and water conserving shoot traits from Bala appeared to be more important than the root traits (Price et al., 2002a). In the chickpea study cited above, the relationship between root traits and drought tolerance was strongly influenced by one genotype on each of the extremes and in the other trial presented in that study there was no relationship between RLD at depth and seed yield (Kashiwagi et al., 2006). In a recent study in peanut more profuse roots in the deeper soil layer was reportedly correlated to higher yield under water stress conditions and the authors concluded that a higher root length density (RLD) at depth was responsible for more water extraction (Jongrungklang et al., 2012). However, the water depletion at the 60–90 cm layer was only about 0.02 $cm^3 cm^{-3}$ in both years, which would amount to about 6 mm. Using the TE formula (Bierhuizen and Slatyer, 1965), such that TE = dry weight/transpiration = k/VPD where k is a TE (constant in Pascals) with an average VPD estimated to 1 kPa in both trials and taking a TE coefficient of 4.5 Pa for the computation, 6 mm from the 60–90 cm layer would contribute to 270 kg ha^{-1}, assuming an optimal case where the 6 mm would contribute entirely to pod yield, which is much below the range of genotypic pod yield differences in that study. Therefore, our interpretation is that there was something else than the RLD explaining pod yield differences in Jongrungklang et al. (2012). Similarly, a study on 20 chickpea lines with similar phenology, contrasting for their seed yield under terminal water stress (Krishnamurthy et al., 2010), showed no relationship between grain yield under terminal water stress and RLD (Zaman-Allah et al., 2011b) but showed a close link between water saving traits and terminal stress adaptation (Zaman-Allah et al., 2011a). In another study in peanut, no relationship was found between the pod yield under a range of intermittent stresses (from mild to severe) and RLD (Ratnakumar and Vadez, 2011). A recent study in wheat re-analyzed the implication of root system size and water capture and concluded that because of the close link between shoot growth and root growth, the development of a large root system might be better suited to environments where the crop depends on in-season rainfall like the Mediterranean environment, whereas under terminal stress conditions a vigorous root system, then linked to a vigorous shoot, would run the risk of a rapid water depletion of the soil profile and eventually a severe stress during reproduction and grain filling (Watt et al., 2005; Liao et al., 2006; Palta et al., 2011). In fact, two recent modeling studies illustrate this idea (Sinclair et al., 2010; Vadez et al., 2012) and a recent review argues that roots need to be looked at with a view to the whole plant (Comas et al., 2013), and with a view to resource availability in time and space (Lynch, 2013).

In summary, while roots are potentially important for plants under drought stress, they do not contribute to drought adaptation in all stress conditions since in many cases the degree of differences in root growth among genotypes do not explain the degrees of differences in yield. This can be interpreted in different ways: (i) root depth and/or RLD are not akin to water extraction; (ii) deep or profuse rooting would have no effect in shallow soil, in soil where there is no water at depth, or under conditions of mild water stress; (iii) root and shoot growth are closely coordinated and deeper rooting might lead to faster soil water depletion, which would be a problem for crops depending on stored soil moisture; (iv) capturing deep layer water is a one-time benefit since any rainfall/irrigation event would wet the profile from the top in progressive drought stress conditions.

2.2. Limits to deep and profuse rooting

We see several limits to seeing root depth and root length density as the main traits to ensure water supply. There is indeed a lot of controversy around the relationship between water extraction and RLD, with some studies showing a close relationship (e.g.

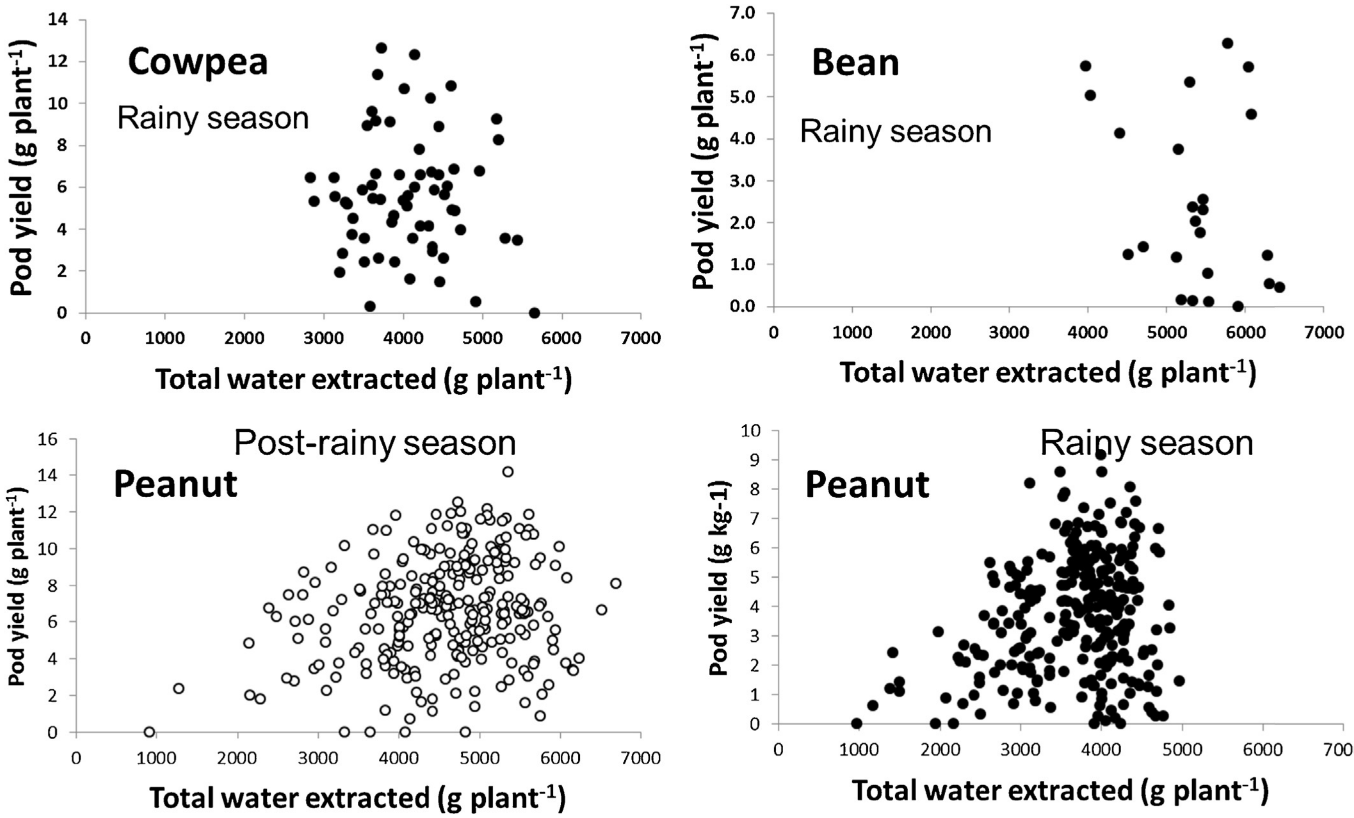

Fig. 1. Water extraction under water stress conditions in lysimeters in several legumes species and relationship to pod yield. Experiment were either carried out in the rainy or post-rainy season.

Hund et al., 2009; Vadez et al., 2013b), while others show no relationship (e.g. Hamblin and Tennant, 1987; Dardanelli et al., 1997; Amato and Ritchie, 2002; Zaman-Allah et al., 2011b; Ratnakumar and Vadez, 2011). In a range of soil for the level of compaction, large gradients of soil water content were caused by local root clustering, explained by localized compaction (Amato and Ritchie, 2002). Therefore, more profuse root growth does not necessarily relate to more water extraction because beyond their presence, roots need to have the adequate hydraulic characteristics (see last section) to allow water uptake. In addition, there are aspects of the volumetric exploration by the roots, namely the root hairs, that can significantly contribute to water extraction but that are not measured when RLD is assessed (Mackay and Barber, 1985; Segal et al., 2008; Lynch, 2013). The distribution of roots in the soil profile is also very important and genotypes with similar overall RLD could have a very different distribution in the soil profile. For instance, transgenic peanut (*rd29*::DREB1A) had similar average RLD but several events had proportionally a higher RLD at depth (Vadez et al., 2013b). Similar finding occurred in wheat (Manschadi et al., 2006).

Another limitation is in assuming that deep roots would have unlimited access to water, like a wick, while of course soil profile refilling occurs from the top. Hence, crops depending on in-season rainfall would extract most water from the top layer and little from the deep layer, except in the case of extremely sandy soil with low water retention. Also, the variation we can expect from rooting depth is limited. For instance in wheat, the root penetration rate (in cm day^{-1}) was considered a good indicator of potential rooting depth (Kirkegaard and Lilley, 2007) but showed limited variation among genotypes. In chickpea, the maximum differences in rooting depth measured under controlled conditions between the shallow- and deep-rooted germplasm were about 30 cm (Kashiwagi et al., 2005). In sorghum, the water extraction variation among diverse germplasm varied by about 3 L plant^{-1}, equivalent to 30 mm (assuming a planting density of 10 plant m^{-2}) (Vadez et al., 2011b). Therefore, a maximum “reasonable” variation within species in the amount of available water that can be gained by deep rooting is about 30 mm, equivalent to about 30 cm soil depth assuming that about 0.10 cm^3 cm^{-3} is available for plant extraction. Let’s note that these are variations among germplasm and that probably less variation exists among breeding material. Nevertheless, even smaller differences can lead to significant yield increases, *if this entire water can be extracted*. For instance in wheat, 10.5 mm of sub-soil moisture led to 0.62 t ha^{-1} of increase in seed yield of wheat in Australia (Kirkegaard et al., 2007), and this fits indeed to theoretical calculations using the TE formula (Bierhuizen and Slatyer, 1965 – see above), here assuming a season VPD average of 0.75 kPa. For chickpea cultivation in semi-arid tropical area, assuming an average VPD of 2 kPa during a typical post-rainy season and a TE coefficient of 4.5 Pa, a 30 mm of extra water from the sub-soil would lead to an increase in grain yield of 0.67 t ha^{-1}. These two examples illustrate the case of crops that are cultivated on small amount of water, and in fairly low VPD conditions in the case of wheat, and the increase in yield represents an important percentage of practiced yields (2–3 t ha^{-1}).

The proportional benefit of these extra 30 mm would be much less in longer duration crops demanding more water. For instance a crop yielding, say, 6 t ha^{-1} would need transpiration water losses in the amount of 300 mm, assuming a harvest index of 0.5, a *k* coefficient of 4 Pa, and a mean VPD of 1.0 kPa. A 30 mm increase in deep water access would represent only 10% of the total required. Therefore, deep rooting has a value in those cases where the extra water from depth represents a large portion of the entire crop water need. Moreover, the same hypothetical crop yielding 6 t ha^{-1}, but cultivated under higher VPD (say 2 kPa), would have transpiration water losses in the amount of 600 mm and an extra 30 mm would represent only 5% of that total. Therefore, an important factor determining the potential benefit of the deep water extraction is also bound to the VPD prevailing for any given crop, as it has also been concluded from a recent study (Yang et al., 2012b). For semi-arid tropical crops growing under high VPD conditions, the advantage of the deep rooting might then be limited, especially for crops with high water requirement. Last but not least, the hypothetical cases presented above assume that all of the putative 30 mm would be extracted. Therefore, the capacity to extract the available water at depth is probably more critical than having root at depth, and this may come from deep roots that have a high hydraulic conductivity (see last section).

In fact, the importance of deep water extraction would be more if its timing coincided with the time of most critical water demand, i.e. reproduction and grain filling. Recent evidence indeed shows that higher grain yield in chickpea (Zaman-Allah et al., 2011b), pearl millet (Vadez et al., 2013a), wheat (Kirkegaard et al., 2007; Manschadi et al., 2006), were related to water availability during the grain filling period. Root growth is known to stop its downwards movement around anthesis (Robertson et al., 1993), although maintenance of growth can also be found (e.g. Hafner et al., 1993) and this might be a trait worthy of screening, provided water is available at depth. To reach the same goal, time from sowing to flowering has been increased in the Australian wheat programs by combining an early sowing and the combination of vernalization and photoperiod genes (Richards, 2006). However, matching water extraction at depth and critical timing for water extraction might remain a difficult exercise because root and shoot growth are reported to be very closely related (Watt et al., 2005; Palta et al., 2011; Maurel et al., 2010; Bouteille et al., 2012) and within a given species genotypes with large shoots are also bound to have a large roots. For instance, a QTL for root dry weight in chickpea was also identified as a shoot QTL in chickpea (Chandra et al., 2004) or in pearl millet (our unpublished data). Intuitively, since root and shoot are part of a same hydraulic continuum, shoot growth would simply match root growth and access to soil water reservoir, with a risk of depleting it before reaching the critical crop stages. A modeling study in soybean has shown that increasing the rate of rooting depth would lead to faster soil depletion and yield penalties, especially in the driest quartile of the years, and there would be no benefit, but even a penalty from faster and deeper rooting (Sinclair et al., 2010). Whether there are genotypic differences in the proportion of root to leaf exchange area that might alter the rate of soil moisture depletion (for instance with a larger leaf area per unit of root absorbing area) is essentially unknown. Therefore, research on allometric growth coefficient (root exchange surface versus leaf exchange surface) would be needed, especially to assess the extent of intra-specie genetic differences, and possible effects of environmental conditions on this.

In summary, selecting for deep rooting to access water at depth could be potentially interesting. The conditions to the success of this breeding strategy are: (i) that water would be available at depth (deep soil and water available at depth); (ii) deep water extraction would have an increased benefit if it took place during the grain filling period and that might imply searching for genetic material capable of sustaining root growth during reproductive development; (iii) cropping conditions of moderate VPD in crops where this potential extra water uptake from deep rooting would represent a large proportion of the total transpirational water needs. Of course, deep and profuse rooting would also be a question of metabolic cost of growing these roots and keeping them metabolically active (Ho et al., 2005). These "root economics" issues might explain in part the G×E interactions of root traits effect.

2.3. The need for 3-D methods to capture root architecture in situ

In many of the studies on RLD so far, roots are extracted from a given soil volume and assumed to be equally distributed in that soil volume. This is an important flaw because the information on the 3-D architecture of the root system is lost during root washing. For instance, large variation in the soil water content were explained by localized root clustering influenced by different soil structure (Amato and Ritchie, 2002). Therefore, future progress on the role of roots to extract water will come with information on the 3-D architecture of root system. Root tomography is one such approach that allows to assess the 3-D architecture in situ (Mooney et al., 2012). There are also some root development model that are capable of reconstituting root system architecture in a 3-D context by measuring angles and nodes of different portions of the root system (de Dorlodot et al., 2007; Draye et al., 2010; Pages et al., 2010; Lobet et al., 2011; Trachsel et al., 2011), which gives a lot more power to interpret water extraction data, and also open to the possibility to harness the genetics of the components of this architecture (e.g. root angles, different types of roots, branching patterns, etc.) (Draye et al., 2010; Lobet et al., 2011; Trachsel et al., 2011; Lynch and Brown, 2012). For instance in sorghum, root angle QTL was found to have a positive effect on yield across a subset of population (Mace et al., 2012). Other study has shown that the root-soil contact is the main limitation for extracting deep soil water and that root hair or additional root proliferation in root pores would be potential traits (White and Kirkegaard, 2010). Therefore, the controversy about the relationship between water extraction and RLD could be somewhat clarified if a 3-D dimension of the root density was considered. There are also methods being developed using ground penetrating radar, although the current resolution may be restricted to trees (Zenone et al., 2008).

3. Roots and water capture: a shift in the approach to the functionality of root systems

3.1. Description of the lysimetric method

Morphological root assessments are difficult, prone to errors and then have low heritability, are destructive and inaccurate because they assume equal distribution of roots across the soil profile. Their relationship to water extraction is also highly questionable. Finally, they are time consuming and cannot be easily applied at a large scale, although improvements have recently been made (Trachsel et al., 2011). These experimental limitations partially explain why the great promises of improving crops for their root system has seen so far very limited practical breeding applications. To overcome these constraints, a lysimetric method has been developed to measure water extraction instead of morphological root parameters. The system uses long and large PVC columns where plants are cultivated individually, with a soil volume to explore and a plant spacing similar to the field conditions (Vadez et al., 2008, 2011a, 2013a; Ratnakumar et al., 2009; Zaman-Allah et al., 2011a). This method has been quite successful at demonstrating the importance of water extraction at critical stages (e.g. Zaman-Allah et al., 2011b; Vadez et al., 2013a). A small scale approach had been developed earlier and had seemingly not expanded further and here we present a large scale version of it with thousands of lysimeters that can cater for the size of populations or germplasm sets that breeding programs use. This system has revealed variation for the potential of genotypes to extract water from the soil profile (Vadez et al., 2011b). Probably more exciting than measuring water extraction differences, the system has demonstrated an extreme robustness to screen for TE gravimetrically (Ratnakumar and Vadez, 2011; Vadez et al., 2011b, 2013a). For instance, the range of variation for TE in a portion of the sorghum reference collection was 100% (about

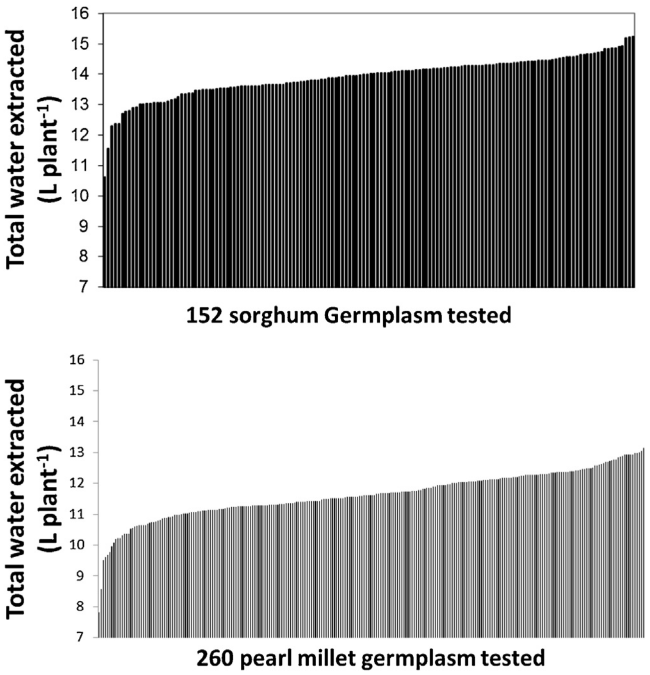

Fig. 2. Water extraction under water stress conditions in lysimeters in sorghum and pearl millet.

3–6 g kg^{-1} water transpired), whereas the range of variation for the total water extraction was only about 30% (Vadez et al., 2011b). Multi-linear regression then showed that the main yield differences beyond those explained by the harvest index were mostly driven by TE and little by the total water extraction.

3.1.1. Water extraction results in different crops

Using the lysimetric system above, we have compared the water extraction capacity in different crops. In the case of legumes, using lysimeters of 1.2 m long and 20 cm diameter, the range of variation in the total water extracted from a Vertisol was 7.4–9.2 L in a set of 20 chickpea genotypes contrasting for terminal drought yield (Zaman-Allah et al., 2011b). As a comparison, 20 rice genotypes from the OryzaSNP panel grown in these same tubes extracted between 2.5 and 4.5 L (Fig. 2b in Gowda et al., 2012), indicating the much lower water extraction capacity of rice than chickpea. Using lysimeters filled with Alfisol, the range of water extraction in 44 cowpea genotypes contrasting for their seed yield across different yield trials (Belko et al., 2014) was 3–5.5 L plant^{-1} (Fig. 1a). Using the same tubes, the range of variation in 24 bean genotypes, also contrasting for seed yield under terminal stress (S Beebe, personal communication) was 4–6.5 L plant^{-1} (Fig. 1b). The range was similar in the reference collection of peanut when measured during the rainy season (2.5–6 L plant^{-1}) (Fig. 1c), although this range fell substantially when these same materials were assessed during the rainy season (2–5 L plant^{-1}) (Fig. 1d). In any case, the most striking result from Fig. 1 is that none of the crops showed any relationship between the total water extracted and the seed yield under stress conditions (Fig. 1), and so was also the case in 20 genotypes of chickpea (Zaman-Allah et al., 2011b).

A similar set of trials was carried out in sorghum and pearl millet, using lysimeters of 2.0 m length and 25 cm diameter. In sorghum, 152 lines from the reference collection had water extraction ranging from 12 to 15 L plant^{-1} (Vadez et al., 2011b) (Fig. 2a), and from 10.5 to 15 L plant^{-1} in a set of lines introgressed with staygreen QTL (Vadez et al., 2011a). In that latter case, introgression of *Stg1* QTL increased the potential to extract water in the background of S35, i.e. a line with relatively poor water extraction capacity, but not in the background of R16, i.e. a line with good water extraction capacity, indicating the importance of the genetic background in determining the potential effect of altering a trait on yield. In the case of pearl millet, 260 germplasm entries of a set representing most of the genetic variation available in this specie, water extraction varied between 9 and 13 L plant^{-1} (Fig. 2b). As in the case of the several legume species reported in the previous paragraph, there was no relationship between the total water extraction and grain yield (Vadez et al., 2011b) for sorghum (Vadez et al., unpublished data for pearl millet).

In summary, the lysimetric system described above has allowed us over the last few years to evaluate the range of genetic variation for the capacity to extract water from a soil profile in different legume and cereal species and has revealed modest inter-specific differences, and some inter-specific differences. More exciting than the genotypic differences in water extraction capacity were the very large differences in transpiration efficiency (TE) (total biomass per unit of water used), which were measured over almost the entire crop cycle and were very robust (e.g. Vadez et al., 2011b). These assessments also showed very clearly that the total water extracted under water stress conditions was unrelated to grain yield differences, whereas several crops showed clear positive relationships between the water extraction during grain filling and grain yield (see next section). As it was recently stated, it is important to match root foraging with resource availability in time and space (Lynch, 2013) and where water is the most limiting factor, it is critical that plant manage water in a way that it keeps water available for the reproductive and grain filling stages.

3.1.2. The importance of water access at key times – link to water saving traits

Recent evidence indeed shows that higher grain yield in chickpea (Zaman-Allah et al., 2011b), pearl millet (Vadez et al., 2013a), wheat (Kirkegaard et al., 2007; Manschadi et al., 2006), were related to water availability during the grain filling period. Because there is only limited vegetative growth after anthesis, the water extraction during that period almost fully contributes to grain growth and has then very high water use efficiency in term of kg grain mm^{-1}, ranging from about 37 to 59 kg mm^{-1} in the references cited before. As we have seen above, this extra water is not contributed by a larger overall water extraction, or by water extraction from deeper roots, but by other traits affecting plant water use and being mostly shoot traits, and which contribute to making more water available for extraction during the grain filling period.

A recent review exhaustively presents the possible options plants have to control water use (Vadez et al., 2013c). A first set of traits revolves around limiting leaf conductance, either under moderate VPD conditions (e.g. Kholova et al., 2010a; Zaman-Allah et al., 2011a), or under high VPD (e.g. Kholova et al., 2010b; Belko et al., 2012). Indeed, at similar leaf area, differences in water use would be determined by the leaf conductance. A second set of traits revolves around leaf canopy size (e.g. Ratnakumar and Vadez, 2011; Vadez et al., 2011a; Zaman-Allah et al., 2011a), but also around the kinetics of leaf canopy development (Kholova et al., unpublished), simply because smaller/larger or quicker/faster canopy development sets crops water use. A third option to control water comes from differences in how transpiration responds to progressive water deficit, in which "conservative" genotypes show an early transpiration decline and then save water early on. Genetic variation has been identified for that trait (Soltani et al., 2000; Zaman-Allah et al., 2011a; Belko et al., 2012), and crop simulation modeling has shown a potential benefit in soybean (Sinclair et al., 2010), although not in chickpea (Soltani et al., 2000). In any case, except the last one involving roots in the sensing mechanism of water stress, all the others involve the shoot in the regulation of plant water use. Here it should be mentioned that these water saving traits have been linked to higher level of plant tolerance to water deficit in different semi-arid tropic crops. However, these traits should not be seen as "drought tolerance trait", but simply traits having the capacity of altering the plant water budget. Whether they can be useful depends on the crops species and the water stress scenario (Tardieu, 2012).

There are evidence that some of these traits related to the plant water budget are ruled by hydraulic mechanisms, e.g. the control of leaf expansion (Reymond et al., 2003; Simonneau et al., 2009), or the transpiration response to high vapor pressure deficit (VPD) (Sinclair et al., 2008; Ocheltree et al., 2014; Parent et al., 2010). In fact, plant responses to evaporative demand were shown to be related to both leaf and root hydraulic conductance (Ocheltree et al., 2014). For instance, it was found that differences in the root hydraulic conductivity led to differences in the rate of leaf expansion, although the transpiration stream was unchanged, and this was in turn related to differences in the level of aquaporin transcripts (Ehlert et al., 2009).

3.2. Looking at roots through the angle of their hydraulic characteristics

3.2.1. Water extraction and root hydraulics

Plant water supply is driven by the evaporative demand and regulated by the stomata. However, this supply is limited by the maximum steady-state water flux that goes through the soil-plant-atmosphere continuum and it has been argued that the roots could represent the weakest link of that continuum (Jackson et al., 2000). As we discussed in the first section, there is controversy in the relationship between RLD and water extraction, although current crop models still assume a relationship between RLD and water extraction. However the finding of different value for a 'k' coefficient ruling the relationship between water extraction and RLD gives strong evidence that water extraction in a given soil profile is not only about RLD (Dardanelli et al., 2004), even above a threshold where a model would assume all water can be extracted. Variations in the 'k' coefficient have been reported in several species including sunflower, groundnut, soybean and alfalfa (Dardanelli et al., 1997). In a study comparing old and modern semi-dwarf wheat cultivars, the RLD of older varieties was higher although they did not have higher plant water use, suggesting an increase in the root hydraulic conductivity of modern cultivars (Siddique et al., 1990). A study in 11 soils also showed that the transpiration response to progressive soil drying was independent of RLD and soil depth (Sinclair, 2005). A recent study also shows that root length density was not correlated to water extraction in peanut (Ratnakumar and Vadez, 2011). In fact, peanut genotypes had RLD ranging from 1.5 to 2.5 cm cm^{-3} while RLD values ranging from 0.2 to 0.6 cm cm^{-3} were reported in chickpea (Kashiwagi et al., 2006), indicating that peanut has apparently a poor water extraction capacity per unit of root length, implying differences in the root hydraulic conductivity of these two species and in agreement with earlier measurement of extraction coefficient (kl) in peanut (Dardanelli et al., 1997). In their early work on root length density Hamblin and Tennant (1987) also reported 5–10 larger RLD in cereals than in legumes despite having lesser leaf area differences, and they already perceived that RLD was "not necessarily the root morphological characteristic most responsible of efficiency of water uptake in drought-stressed environments".

3.2.2. Water transport in the root cylinder

It is well established that the hydrostatic pressure created by transpiration from the shoot is transmitted to the xylem vessels of the shoot and the roots, which drives water in the root cylinder toward the xylem vessels (Steudle, 1995; Tyree, 1997). A large part of that water travels across the intercellular space between cells (apoplast), although water uptake also involves specialized membrane transporters (aquaporins) (Agre et al., 1993; Chrispeels and Maurel, 1994; Tyerman et al., 2002; Javot and Maurel, 2002). Indeed, during the night when there is no transpiration, water can be taken up by roots through an osmotic gradient (Steudle, 2000b). Therefore, the current model of water uptake through the root cylinder to the xylem, the composite transport model, is such that water is taken up via two major pathways: (i) an apoplastic pathway where water travels through the apoplast of the cells in the root cortex, toward the endodermis and the xylem vessels; (ii) a pathway of symplastic water transfer where water goes through cells, traveling in the membrane continuum (endoplasmic reticulum and plasmodesmata) using membrane transporters (aquaporins) (Steudle and Peterson, 1998; Steudle, 2000b). As far as we know, there is limited knowledge on which pathway predominates for water movement across and within species. This fact matters because the hydraulic conductivity of each of these pathways differs and the respective role of either pathway might also be strongly influenced by a number of environmental factors including the evaporative demand. Several reports have shown intra- and inter-specific differences in the relative proportion of water traveling through each of these pathways (Steudle and Frensch, 1996; Yadav et al., 1996; Steudle and Peterson, 1998; Jackson et al., 2000). Intra-specific differences in the hydraulic properties of roots would affect the rate of soil water use, or could lower the root length density needed to absorb a given amount of water. The exodermis could represent a variable apoplastic barrier that plant could use to modulate their water transport characteristics (Hose et al., 2001). Under various stresses such as drought, salinity, nutrient deficiency, root aging, or environmental conditions such as temperature, humidity, or light, the resistance to water flow varies (Steudle and Henzler, 1995; Clarkson et al., 2000), and, for instance, usually increases under water deficit (Steudle, 2000b). Most of that resistance is located in the root cylinder (radial resistance), whereas xylem vessels normally offer much less resistance (axial resistance) (Steudle, 2000b). Of course, there are several root types (seminal, nodal, etc.) and each might have different properties to extract water, although nothing is known about it and this would deserve more research.

In summary, water penetrates the root cylinder through the apoplast and the symplast in route to the xylem, and there are many factors that can influence the root hydraulic conductivity. This is because roots act as variable and heterogenous rheostats, in charge of balancing water flow in the way that matches shoot water demand to the available water, also in relation to other factors that affect plant growth such as nutrient or temperature (Maurel et al., 2010).

3.2.3. Root anatomical traits

Xylem vessels size and abundance. Water flow in any given conduit is the fourth power of the radius of the conduit (Tyree and Ewers, 1991). Xylem conduits were found to be about 4 times larger in deep roots than in shallow roots and that explained the higher propensity to cavitation in deeper roots (Jackson et al., 2000). Hamblin and Tennant (1987) attributed the higher water extraction per unit of root length to large metaxylem vessels in the legumes than in the cereals. A recent review on the most promising root traits in wheat suggest that deep rooting with low radial and axial resistance to water movement would facilitate water extraction (Wasson et al., 2012). Lowland rice had fewer root xylem vessels than upland rice (Bashar, 1990). The water uptake rate was higher in lupin than in cereals and this appeared to be related to larger and more abundant metaxylem vessels in lupin (Hamblin and Tennant, 1987). Another study on lupin and wheat also showed that lupin had larger xylem vessels and then higher hydraulic conductivity (Gallardo et al., 1996). There were larger stele and xylem areas in maize landraces than in teosynthe wild ancestors (Burton et al., 2013). In wheat the evolution from wild type to cultivated types, with a concomitant increase in the ploidy level, increased the root hydraulic conductivity of plants (Zhao et al., 2005). Therefore, there are a number of evidences that show how the abundance and overall size of the xylem vessels can influence the hydraulic properties of the root system. This far, the evidence is rather at the interspecific level but we think there is a great scope to search for variant within species. In sorghum it was found that the transpiration rate was higher in lines having more metaxylem vessels per nodal roots (Salih et al., 1999). A breeding program was initiated in wheat about 20 years ago to target small xylem vessels (Richards and Passioura, 1989), which would restrict plant water hydraulic conductivity and then contribute to slower plant water use. In rice, drought tolerant Dular had smaller xylem diameter than drought susceptible IR64 under drought stress and although the reasons for this are still unclear (Henry et al., 2012), it suggests these differences alter the water supply in these contrasting lines and have a role to play in their drought adaptation differences. Hence, there is a need to carry out a systematic screening of germplasm in different species for the variation in xylem characteristics, with the aim of attempting a relationship to root hydraulic properties.

Root cortical aerenchyma (RCA). High RCA in maize contributes to drought adaptation by reducing the metabolic cost of roots in favor of deeper soil water exploration (Zhu et al., 2010; Postma and Lynch, 2011). Genetic variation for RCA was explored in maize and showed large genetic variation among a set of 583 inbred lines (Burton et al., 2013). In these studies, RCA was seen from the point of view of their metabolic cost. However, RCA could also decrease the radial water transport in the root cylinder (Lynch, 2007; Yang et al., 2012a), although in rice it was suggested that the RCA may not have been the zone of main hydraulic limitation (it was rather the endodermis), but this was related to the presence of mono-layered cortical septa going through the RCA and allowing smooth water flow through the aerenchyma (Ranathunge et al., 2003). Therefore, in situations where there is a need to limit water flow, RCA would have the double advantage of limiting the metabolic cost of roots and of reducing plant hydraulic conductivity, with possible beneficial effects on some water saving traits (see Section 2). Here also, any trait should not be seen as a “tolerance” trait and RCA has also been shown to limit root hydraulic conductance of rice in comparison to other species, as seen above in the water extraction section, to the disadvantage of rice.

Root cell size and root cell file number. Reducing the number of root cells (Lynch and Ho, 2005) or of root cell files (Burton et al., 2012) has also been seen as a way to reduce the metabolic cost of root system development. However, the possible effect of these traits on the root hydraulic characteristics has not been considered. The indirect consequence of these two traits is that the amount of intercellular air spaces would be altered. In the case of a lower number of cells, each with a larger cell volume, the amount of intercellular space would be reduced and this could restrict the apoplastic water transport, assuming the standard space between cells is unchanged. We could expect some implications for the root hydraulic conductivity. In the case of a lower number of cell files, the radial length of apoplast to be crossed by water before reaching the stele would also be reduced, and we hypothesize that it would increase the hydraulic properties of the root. As far as we know, no work has been performed to assess the possible involvement of these traits, initially targeted as metabolic cost savers, for their possible role in altering root hydraulic properties. Because the technique is now available to evaluate these anatomical traits (Burton et al., 2012), there is now a great scope to characterize these traits in different crops where evidence of water saving have been identified, with a view to their possible effects on the root hydraulic properties.

3.2.4. Aquaporins

According to the composite transport model, water flows through either the apoplast or the symplast, with a dominant apoplastic transport (Steudle, 2000b). The interpretation in that paper is that in the absence of transpiration, the water transport is osmotic in nature and has high resistance because water has to cross many membranes through specialized water transport channels (aquaporins, Agre et al., 1993). This contrasts somewhat with the view of aquaporins as “water transport facilitators” and highlights a possible role of aquaporin to alter the hydraulic properties of the roots (Tyerman et al., 2002; Maurel et al., 2009). Aquaporin are also hypothesized to play an important role in the regulation of water use, either under stress or during re-wetting after stress (Martre et al., 2002), or during the time of the day, which was evidenced by the large diurnal variation in aquaporin expression (Vandeleur et al., 2005; Beaudette et al., 2007; Henry et al., 2012). There is now much evidence that relate root hydraulic properties to aquaporin gene expression. For instance in Arabidopsis, changes in hydraulic properties were not related to changes in the root suberization but to changes in certain PIP transcript abundance (Sutka et al., 2011). In a comparison of lupin and wheat, lupin had mostly an apoplastic water transport whereas wheat was heavily dependent on symplastic water transport through aquaporin and these had a major influence on the root hydraulic conductivity (Bramley et al., 2009). In poplar, the water potential recovery under high evaporative demand was driven by an increase in the expression of aquaporins, indicating that plants had the capacity to modulate water uptake dynamically, depending on the environmental conditions (Laur and Hacke, 2013). In maize, higher aquaporin abundance of mostly PIP2 (ZmPIP2;5, ZmPIP2;6, and ZmPIP2;1/2;2) was related to increases in the water permeability of the root cortex. Therefore, upon exposure to osmotic stress, or when more of the water was forced to take the cell-to-cell pathway in the root cylinder (by inducing the formation of Casparian bands in the root cylinders), the response was of an increase in the transcript level and protein abundance of these aquaporins (Hachez et al., 2012). In tomato, root hydraulic conductivity was increased in transgenics over-producing ABA (over-expression of 9-cis-epoxycarotenoid dioxygenase, NCED) (Thompson et al., 2007). It was later found in maize transgenics that were also over-producing ABA with the same over-expression of NCED, high ABA had a positive effect on aquaporin transcript expression and protein abundance of four PIP aquaporins, and this led to major increases in the hydraulic conductivity of the root and the overall plant hydraulic conductance (Parent et al., 2009). These results in tomato and maize therefore showed that ABA had long lasting effects on the hydraulic properties of the roots and these effects were mediated through aquaporin activity. In maize roots, the inhibition of aquaporin activity by an acid load had no effect on the stomatal conductance under low evaporative demand but led to closure of the stomata under high evaporative demand, indicating a function of aquaporin-mediated water transport in case of higher transpirational demand (Ehlert et al., 2009). In our work, we compared sorghum germplasm contrasting in their transpiration response to high VPD and showed major difference in the aquaporin transcript and aquaporin protein abundance between lines, with VPD-insensitive lines showing higher transcript and protein abundance under high VPD (Aparna et al., unpublished).

In summary, there is now a lot of evidence of aquaporin playing a central role in the regulation of the root hydraulic conductivity. How this regulation occurs, especially in response to environmental cue, is still unknown. The fact that genetic variation exists in how that regulation occurs and then leads to differences in traits controlling plant water use open an exciting avenue of regulating plant water use.

4. Conclusion

Root traits, especially root length density and root depth, have long been seen as critical trait to harness in order to improve crop adaptation to water stress. While roots are indeed important for drought adaptation, having deep and profuse rooting is a necessary but not always sufficient condition to obtain "drought tolerant" lines. This is in part because root length density does not necessarily relate to more water extraction, and to the fact that having water available at critical crop stages is probably more crucial than having large water uptake overall. This appears to be the consequence of a series of traits controlling the plant water budget in a way that matches water supply and demand, namely through leaf conductance, leaf canopy, and transpiration response to soil drying. In this review, we have shown that these water controlling traits are often related to certain characteristics of the plant hydraulic conductance. It appears that certain root anatomical traits such as the xylem vessel size and abundance, root cortical aerenchyma, the number of root cells or the number of root cell files could alter these hydraulic properties. The aquaporin activity has also a major role to play in water transport and could be another way to control root hydraulic properties. The alteration of hydraulic properties by these different anatomical and biochemical traits provide the plants with the attributes to control plant water use in a way that it eventually makes water available for the critical crop stages, namely during reproduction and grain filling. Therefore, the main message is that root contribution to drought adaptation ought not to be seen from the angle of length density and depth but rather from the angle of the building blocks of its hydraulic properties and how these eventually affect critical water use traits.

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