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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 × TE × 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.