Exploiting the functionality of root systems for dry, saline, and nutrient deficient environments in a changing climate

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Introduction

Increasing episodes of drought, lack of sufficient nutrients, exposure to toxic minerals, and soil compaction are just a few examples of the environmental constraints that the roots are exposed to during plant growth. Understanding how roots respond to these stresses is crucial for improving crop production under such conditions. Yet, investigating roots is a very difficult task and, therefore, very little is known about the precise role that the roots play in contributing to plant adaptation to hostile environments. It is assumed that while the root depth and abundance would contribute to drought tolerance, profuse rooting would enhance nutrient capture, and where the membrane transporters would exclude salts from the root cells. However, a great deal is still unknown about how these mechanisms actually operate; for example which particular characteristics of roots and root hydraulics actually contributes to water uptake in a way that confers increased tolerance, how the stress signaling from the roots affects the physiological relations in the shoot and those between the shoot and the root, how water and nutrient absorption relate to one another when both are limiting, or how roots avoid the loading of salt in xylem vessels.

In this paper, our intention is not an exhaustive review of roots, but to highlight a few research topics related to abiotic stresses - mostly drought stress, but also nutrient limitation (especially phosphorus) and salt stress - where roots and their hydraulics are at the center stage. First, we provide an update on root structure, root hydraulics, and modes of water and nutrient absorption, mainly focusing on how inter- and intra-specific variations in these aspects can modify the way roots respond to a range of abiotic stresses. We then review scattered reports across a range of crops showing the contribution of roots to stress tolerance, and then report our own assessment of the role of roots using near isogenic lines (NILs) containing a terminal drought tolerance QTLs. We next review the breeding efforts on roots, some aspects of genetics, and report recent work at ICRISAT where the DREB1A gene appears to positively affect root growth in transgenic groundnut under drought conditions. We follow by looking at the role of roots in nutrient acquisition, and how water and nutrient uptake issues need to be addressed holistically. Then, we look at roots from the angle of salinity tolerance, reviewing where roots can contribute to salt tolerance. The following part is on root functionality and we argue that further progress on roots should concentrate of measuring both volume and kinetics of water uptake rather than root morphological traits. Finally, we review how water use efficiency (WUE) and other mechanisms involved in water saving in the soil profile, can eventually allow roots to sustain water uptake. This is considered from the angle of the chemical and hydraulic signaling taking place between roots and shoots. Based on the above, we conclude by proposing research avenues to unlock our knowledge on roots, in a way that eventually allows breeding for improved root characteristics in the face of current climate uncertainty.

Roots and stress tolerance – A review of past efforts

The composite transport model - Besides the fact that roots supply water to the plant and contribute to the overall plant water balance, relatively little is known about the processes and regulations of water uptake. 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 (Tyree, 1997; Steudle, 1995). It is also clear that the hydrostatic pressure is not the only factor responsible for water uptake, which also involves specialized membrane transporters (aquaporins) (Chrispeels and Maurel,1994, Tyerman et al., 2002, Javot and Maurel, 2002). Indeed, under no transpiration, water can be taken up by roots through an osmotic gradient (Steudle, 2000a). Therefore, the current model of water uptake through the root cylinder to the xylem, the composite transport model (Steudle, 2000a), is such that water is taken up via three 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 and remains in the cytoplasm, traveling in the membrane continuum (endoplasmic reticulum and plasmodesmata); and (iii) a pathway through the vacuoles of cells (Steudle and Petersen, 1998; Steudle, 2000b) (Figure 1). It is considered that (ii) and (iii) represent the cell-to-cell pathway, as these components are difficult to separate and both are using membrane transporters (aquaporins). This pathway usually offers a large resistance to water flow in contrast to the apoplastic pathway, which predominates when transpiration demand is high (Steudle, 2000a&b).

Regulation of radial resistance and abiotic stresses - 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), and, for instance, usually increases under water deficit (Steudle, 2000a). Most of that resistance is located in the root cylinder (radial resistance), whereas xylem vessels normally offer much less resistance (axial resistance) (Steudle, 2000a). In the root cylinder, the cell-to-cell pathway is a highly regulated movement, involving the crossing of many membranes through membrane transporters (aquaporins, Tyerman et al., 2002, Javot and Maurel, 2002), which usually offers a large resistance to water flow. Therefore, the understanding of which components of the composite model (Steudle, 2001) predominate under non-stressed conditions, and how these components change under a range of abiotic stresses, are crucial in understanding how plants regulate the rate of water and nutrient supply and eventually support transpiration and growth. 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 Petersen, 1998, Steudle, 1993, Jackson et al., 2000). Intra-specific differences in the hydraulic properties of roots would affect the rate of soil water use, or would lower the root length density needed to absorb a given amount of water. The water traveling through the apoplastic pathways also lacks a “filtering” effect from the cells (the reflection coefficients of nutrients is usually small or close to zero), thereby taking along a number of nutrients such as salt (Azaizeh et al., 1992) or ABA (Hartung et al., 1998; Freundl et al., 2000) (“solvent drag”). In summary, the predominance of either one of the pathways could have a dramatic influence on the regulation of water uptake, with or without water stress. It also could have dramatic effects on the absorption of toxic salts (see below the section on salinity). Since, nutrient stress also affects the resistance provided by roots to the water flow; a nutrient deficiency would also affect the plant by influencing its water balance.

Roots as a consequence of an evolutionary strategy - Before going any further, we feel that it is important to "demystify" the importance of root for stress adaptation, in particular drought. For instance, many desert plants have been reported not to have a deep root system, whereas a deep rooting would become a more common trend in less extreme dry areas (Kummerow, 1980). In fact, the importance of any aspect of rooting pattern (depth, depth distribution, root length density, etc.) is totally relative to the distribution and amounts of water or nutrients in the soil profile. For example, an increased root depth/root volume is useful only where there is significant water available to exploit by increasing soil volume explored by roots. An increased root length density (RLD) is important only where there are significant amounts of water which is tightly bound to the soil matrix and does not readily move in response to local gradients created by root extraction – e.g. montmorillonitic clay soils. Also plant strategies for water uptake vary; some desert plants such as cacti have extensive but shallow systems to quickly capture large amounts of rainfall and nutrients from soil surface layers because they can store this for long periods, whereas others such as the creosote bush have roots to as much as 20 m, to tap water very deep in the soil profile where there is limited competition for water from other species. So, we believe that rooting aspects in most plants are evolutionary strategies to exploit environmental opportunities. We should therefore approach the roots of crops in the same way to exploit their diversity and their adaptive potential. What follows is a summary of the work on roots in ICRISAT´s mandate crops and few others, mostly focused on the adaptation to drought.

Roots in chickpea – In South Asia chickpea is mostly grown during the postrainy season in deep clay soil and depends on the residual moisture contained in the soil profile, therefore facing water deficit in the latest part of the growth cycle. In this context of terminal drought, breeding for root traits appears to be the right approach and Kashiwagi and colleagues (2006) have shown the importance of roots for seed yield under terminal drought conditions in chickpea. This work has been a major effort at ICRISAT for the past 20 years (Saxena, 1984, Johansen et al., 1997, Krishnamurthy et al., 1999) where a better adaptation of plants to terminal drought has been shown to be due to deeper rooting and higher root length density (RLD) in the deep layers. However, no work has been done to improve the nutrient uptake by chickpea plants. It has been reported that chickpea was able to allocate more roots to the deeper soil layers under conditions of stress than other legumes (Benjamin and Nielsen, 2005), or than more sensitive genotypes (Kashiwagi et al., 2006). However, this was so only when the phenology of the genotype was well suited to the test environment. For example, the chickpea genotypes K1189 and ICC898 had adequate RLD compared to ICC4958 and Annigeri in the work by Kashiwagi and colleagues (2006), but their yields were poor under terminal drought, mostly because they were longer duration varieties. As such, the putatively beneficial effect of roots on terminal drought yield was overridden by the effect of crop phenology. Also, the testing of a mapping population developed between two elite parental lines of chickpea varying for their root volume showed that the differences in RLD would not always translate in a yield increase (Serraj et al., 2004), especially in locations where the season length is higher and the evaporative demand lower such as in North India (Krishnamurthy et al., 2004), thereby, showing that parameters other than roots also played a more crucial role. Therefore, roots are only one component of the overall performance of chickpea under terminal drought conditions, and needs to be addressed together with other traits. Similar principles are very likely to prevail in other crops.

<u>Roots in groundnut</u> - Despite the paucity of studies on roots, it has been shown that roots are expected to play an important role in drought adaptation in the light textured and deep soils of the South West US (Ketring et al., 1982, 1984; Pandey et al., 1984), where a relation between root depth and pod yield has been established (Robertson et al. 1980, Boote et al., 1982). However, only a few genotypes were tested in these experiments, even though differences in the rooting depth were found (Krauss and Deacon, 1994). As for the putative role of root for nutrient uptake in nutrient poor soils, virtually no work has been made in groundnut in that respect. A few studies in the late 70's and early 80's reported root responses to water stress and indicated that the growth of roots increased upon water deficit (Allen et al., 1976), in particular rooting depth (Lenka and Misra, 1973; Narasimham et al., 1977, Ketring and Reid, 1993). Ketring and Reid (1993) found that groundnut was able to establish both a deep and laterally spreading root system fairly early during the growing cycle, providing adaptation to drought occurrence during and later in the season. By contrast, Robertson et al (1980) did not find any RLD differences at shallow soil depths between well-irrigated and water stressed conditions. Meisner and Karnok (1992), contrary to previous studies cited above, found that root growth decreased upon water deficit, though not as much in the deeper layer where

water was still available. In summary, rooting characteristics appear to vary in groundnut but the dynamics of root growth under water deficit are still unclear. To date, data are still lacking to conclude which root trait, in which soil, environment, and stress type, could contributes to drought tolerance in groundnut.

<u>Roots in pigeonpea</u> - Virtually nothing is published on roots in pigeonpea under water stress, except for a few reports from the late 70's (Narayanan and Sheldrake, 1975, 1976, Arihara et al., 1991). It is assumed that pigeonpea is deep-rooted and that confers drought tolerance because the crop is usually grown on deep soils and completes its life cycle on residual moisture. More work has been accomplished in pigeonpea in relation to its ability to absorb nutrient having low solubility such as P, thanks to the secretion of pissidyc acid (Ae et al., 1991). Recent data on the hydraulic characteristics of pigeonpea roots, in particular the ability for hydraulic lift, might be an interesting asset for both nutrient and water (Sekiya and Yano, 2002, 2004 – See related paragraph). As we will see below, the capacity for hydraulic lift may be at the price of a well-developed endodermis, which may allow excess salt to flow-in freely and cause salt stress sensitivity. In any case, pigeonpea is a legume crop where, probably a lot more work on roots is needed to fully exploit the potential and particularities of its roots. Yet, studies on pigeonpea root traits have remain largely anecdotal; how roots of pigeonpea contribute to its adaptation to dry environment, how its ability to take up low solubility nutrient would interact with water uptake under water deficit, are virtually unknown. Like chickpea, the large variations in flowering time across the pigeonpea germplasm would require a comprehensive consideration of both phenology and roots.

<u>Roots in sorghum</u> – Sorghum is considered as a drought tolerant crop whose well-known deep roots are assumed to play a key role in its drought adaptation. To the best of our knowledge, no work has targeted the roots of sorghum to enhance to nutrient absorption in low fertility environments. Although, a lot of drought-related studies have been carried out with sorghum, surprisingly very limited work has been done on the roots. Only a few reports have presented evidence of genotypic variation for root traits (Bhan et al., 1973, Mayaki et al., 1976, Jordan et al., 1979), and these studies have focused on only a few breeding lines with a limited genetic base. Genotypic variations for root traits have been found in other studies using solution culture (Blum et al., 1977), or in small pots (Abd-Ellatif et al., 1978), but the results should be

considered with caution. A more recent study showed that a drought tolerant sorghum line possessed roots at least 40 cm deeper than a drought sensitive one (Salih et al., 1999). This agrees with some of our own observations showing deeper rooting of staygreen lines under drought conditions (Vadez et al., 2005) (Figure 2). In fact, most of the drought-related work in sorghum has focused on the staygreen trait which is known to be extremely complex (Borrell and Hammer, 2000). Different hypotheses have been advanced to explain staygreen; these include the N balance between leaves and grain (Van Oosterom et al., 2006a&b, 2007), or differences in transpiration efficiency (Borrell et al., 2000). It has been shown that the staygreen characteristic of two maize hybrids would correlate with a higher N uptake during grain filling in the staygreen type (Rajcan and Toollenaar, 1999). Surprisingly, no one has hypothesized that N uptake differences could result from water uptake differences during grain filling. More work is certainly needed in this direction, since it has been shown that root growth continues well into the grain filling stage in hybrid sorghum (Bower, 1972, cited by Jordan et al, 1979).

<u>Roots in pearl millet</u> – Like sorghum, pearl millet is also a deep rooted and a drought-adapted crop. Unfortunately, few studies have explored the genetic variation for root traits and none has attempted to use these differences in breeding. Data from Chopart (1983) indicate that the rooting depth of pearl millet in deep sandy soils can reach at least 200 cm and that the root front can increase as much as 3.5 cm per day between 15 and 50 days after sowing. Bruck et al (2003) found no genotypic differences in the root depth of 5 pearl millet varieties, but found genotypic differences in the RLD, especially at depths between 50 and 175 cm, with RLD as high as 0.30 cm per cm^3 at 125 cm depth. In such case, root expansion would be both for water and nutrient capture, in the erratic rainfall and poor fertility conditions under which it is cultivated in the Sahel. At ICRISAT, we have assessed the rooting depth and RLD in long PVC tubes (2.4 m long, 16 cm diameter) in hybrids based on parental lines contrasting for terminal drought tolerance and in near isogenic lines with and without terminal drought tolerance QTLs. We found that the terminal drought tolerant lines do have a relatively more profuse rooting in the deeper layers than the sensitive lines (Vadez et al., 2005) (Figure 3). Our current hypothesis is that a slight increase in deep rooting would help sustain higher water uptake during the post anthesis period, which in turn would contribute to better grain filling, under environments in which water is available in deeper soil layers.

<u>Roots in other crops</u> - Roots have also been investigated in other crops, although with a similar limited focus and a "non-sustained approach". These include white clover (Blaikie and Mason, 1993), lentils (Silim et al., 1993a, 1993b), wheat (Gregory and Eastham, 1996), cotton (Taylor and Klepper, 1975; Quisenberry et al., 1981), oats (Carrigan and Frey, 1980), rice (Champoux et al., 1995; Yadav et al., 1997; Price et al., 1999, 2000) and maize (Jenison et al., 1981; Guingo et al., 1998; Tuberosa, 2002, 2003), or simply not investigated although terminal drought conditions would prevail (Frahm et al., 2004). For example, upland rice was considered more adapted to drought conditions than lowland rice because it has a deeper and more prolific root system (Steponkus et al, 1980). In broad bean, deep cultivation enhanced water extraction by promoting deeper root growth (Rowse and Barnes, 1979). The capacity of roots to penetrate a compacted soil layer (Bengough et al., 1997, Unger and Kaspar, 1994, Clark et al., 2003) has been given importance in wheat (Gemtos et al., 1999, 2000; Ishaq et al., 2001; Kubo et al., 2004), cotton (Coelho et al., 2000), soybean (Flowers and Lal, 1998), and rice (Ray et al., 1996). Roots have been looked at for a better phosphorus uptake in common bean (for a review, see Lynch and Brown, 2001), or specialized types of roots for P acquisition in *Lotus japonicus* (proteoid roots) (Lambers et al., 2006).

Roots for water supply and drought tolerance

<u>Usual assumptions on roots for water-limited conditions</u> - Under conditions of drought, it has long been considered (Miller, 1916, cited by Kashiwagi et al., 2006, O'Toole and Bland 1987) that an increased root depth would contribute to better drought tolerance. Under such conditions, Jordan and colleagues (1983) have shown that deeper rooting would increase crop yield under drought stress. It has been reported that an increased soil volume explored would increase crop yield under water-limited environments (Jones and Zur, 1984). Since sorghum is deeper rooted than maize, a theoretical analysis has shown that increasing the root depth of maize to that of sorghum would contribute to a yield increase in most dry years (Sinclair and Muchow, 2001). Ludlow and Muchow (1990) have reviewed 16 traits that potentially contribute to drought tolerance. The three most important traits included plant phenology, osmotic adjustment, and rooting depth. Although in these studies, the type of drought imposed was not fully described, it is understood that roots would have an essential role under terminal drought conditions, i.e., for those crops grown on residual soil

moisture after the end of the rains, and where drought stress usually occurs after flowering. Whether roots contribute during intermittent drought still needs investigation, as there is virtually no published data on the topic. In any case, there is a consensus that root should contribute to a better adaptation to dry conditions.

Current status of breeding for roots - Very limited efforts to breed for root traits have been undertaken, mostly because of the difficulties involved, the incomplete knowledge of the key parameters in the rooting characteristics that contribute to drought tolerance, and a lack of the knowledge of the range of variations available for root traits that can be used for breeding. Despite the importance given to roots in the drought scenario, few teams have undertaken breeding for root traits. Even if root QTL have been identified in certain crops such as rice (Champoux et al., 1995; Yadav et al., 1997; Price et al., 1997, 1999), no products have appeared. There is also some doubt on the contribution of root QTL to drought tolerance in rice (Price et al., 2002). In maize, where the root pulling force is well related to root length density (Merill and Rawlins, 1979; Sanguinetti et al 1998), Bolanos and colleagues (1993) have found a negative correlation between root pulling force and grain yield under drought conditions. In fact, no relation was found between the *Root-ABA1* QTL on maize bin 2.04, and grain yield (Giuliani et al., 2005). Hence, to breed for roots, not only is a lot of work needed to explore the diversity for root traits: (i) methods still need to be designed to have sufficient throughput to deal with large number of accessions and with sufficient heritability to permit breeding, (ii) there is also an important need to establish a sufficient relationship between the measurement of root traits and their impact on yield under water limited conditions.

Breeding efforts in chickpea – Some of these efforts have been made in chickpea (Serraj et al., 2004) where massive investments in labor have been made to measure roots in the field. Since field-based data is frequently associated with poor heritability that undermine the use of these traits for breeding, simpler systems have been designed for assessing variation in root traits, which consist of growing plants in 1.2 m tall and 16 cm diameter cylinders, and measuring RLD at every 15 cm depth interval at 35 days after sowing (Kashiwagi et al., 2006). Cylinder measurements show good agreement with depth and RLD determined in the field and have been used to explore the diversity for these traits in chickpea (Kashiwagi et al., 2006). Also by using this method, root depth and RLD are being phenotyped in RIL populations and

QTLs identified. In fact, a major putative QTL for RLD was identified in a population involving a profuse rooting parent ICC4958 and the contrasting Annigeri (Chandra et al., 2004).

Although it is critical for deciding breeding strategies, the available information about the genetics of root characteristics is still limited, except for some reports on heritability estimates compared to the progress on agronomical and physiological studies of root characteristics (Krishnamurthy et al., 2004; Kashiwagi et al., 2005). In chickpea, a major contribution of additive gene effects and additive × additive gene interactions on the root dry weight and root length density were reported (Kashiwagi et al., 2007). In addition, the consistent direction of the gene effects toward increasing root growth was also observed. Similar results were reported in common bean about gene components that control the expression of root dry weight and root surface area (Araujo et al., 2004). Similarly in cotton also, the gene effects of root characteristics showed that additive and additive × additive gene effects accounted for about 50% of the variation in root length in one of the two crosses tested at seedling stage (Eissa et al., 1983). Since, the root characteristics in both the legume crops including chickpea and common bean showed additive × additive epistasis, an advised selection procedure should be taken into account to exploit their interallelic interaction. This suggested that delaying selections to later generations and generating larger populations for selections could be important strategies for improving root systems of chickpea to exploit additive × additive interaction, as shown earlier (Upadhyaya and Nigam, 1998). By contrast, early-generation selection would be less effective. Further, it would be advantageous to backcross one or more times with recurrent parent before selection to enhance the probability of obtaining superior lines (Dudley, 1982). Since it is practically impossible to investigate a large population for RLD and RDW screening, marker assisted selection needs to be sought for proper screening of these characteristics.

<u>Breeding efforts in maize</u> - Breeding for root traits is on-going in maize, where QTLs for root traits have been identified (Tuberosa et al., 2002, 2003). For this, a hydroponic system has been used in which primary and seminal root growth was assessed at about 3 weeks after germination. An obvious criticism of such a system is whether root growth differences in hydroponics would result in consistent root growth differences in a soil/field environment, and whether these would eventually be reflected in differences in drought

tolerance in the field. Although, previous work has shown a relation between seminal root traits in hydroponics and root lodging in the field (Landi et al., 1998; Sanguinetti et al., 1998), weak relations have been found between seminal root traits in hydroponics and root pulling resistance in the field (Landi et al., 2001), and between seminal root traits in hydroponics and field grain yield under water stress conditions (r = 0.20) (Tuberosa et al., 2002). In fact, this work even showed a weak, significant but negative relation between primary rooting in hydroponics and the grain yield under water stress in the field (r = -0.27). Even so, a QTL on marker CSU61b in bin 1.06 appeared to have a major effect on root traits in hydroponics, co-mapping with grain yield under both well-watered and water stress conditions (Tuberosa et al., 2002). Interestingly, one of these QTLs, *Root-ABA1* on maize bin 2.04 was recently found responsible for both primary and seminal root growth and increased ABA concentration in the leaf (Giuliani et al., 2005, Landi et al., 2005). With the current advances in syntenic studies across the cereal species, more work is needed to clarify the functional role of roots in terminal drought tolerance QTL of pearl millet and staygreen QTL of sorghum, and to explore the putatively conserved genomic regions involved in rooting traits across cereal genomes.

Genetics of root systems - To promote the use of root traits in breeding programs, a better understanding of the genetics of root development is needed. In this respect, although the QTLs for root traits above may not relate well to better performance in field conditions, the work from Tuberosa and colleagues has the merit of shedding light on the genomic portions involved in early root development, an aspect that several authors indicate as important to cope with water deficit (Araki and IIjima, 1998; Jesko, 2001). This is a first step to understand the genetics of root development. In that respect, recent studies are now trying to tackle in a more systematic way how root growth is genetically controlled, which was not possible before (Hochcholdinger et al., 2004; Malamy, 2005; Kashiwagi et al., 2007). Root traits have also been targeted by genetic transformation in tomato, where an *Arabidopsis* gene related to the vacuolar H^+ pyrophosphatase (AVP1), led to an increased root growth under water deficit (Park et al., 2005), which was hypothesized to be related to a modification in the auxin fluxes. A recent study carried out at ICRISAT also shows the involvement of *DREB1A* transcription factor driven by a stress responsive promoter from the *rd29* gene of *Arabisopsis thaliana*, on the development of groundnut roots under drought stress conditions (Vadez et al., 2007). These transgenic plants of groundnut variety JL 24 were grown in 1.2 m long and 16 cm diameter cylinders under well-watered conditions for 30 days before withdrawing irrigation in half of the plants. Forty days later, upon drought treatment the root growth was dramatically found to increase in the transgenics, whereas roots remained unchanged in the non-transgenic plants (Figure 4). This resulted in a higher water uptake from the soil. This work suggests that *DREB1A* triggers native genes of groundnut that might be involved in root development, and needs further investigations.

Prospects for better exploiting the potential of root systems for drought - Overall, there have been a number of scattered studies on roots in different crops, documenting root systems and their putative contribution to drought tolerance. While these studies are of high value, they suggest a number of comments. First, a common feature in most of these studies is the very “static” manner in which the roots were assessed, i.e., destructive samplings at one or several points in time, giving virtually no information on the “dynamics” of root characteristics. From these studies, what particular root trait, or what particular aspect of root growth would contribute to a better adaptation to water deficit remain unclear. Second, the limited number of genotypes tested in each crop does not permit an exhaustive assessment of the range of variations available and the potential for breeding these traits. This drawback is mostly explained by the difficulty in studying roots, thus requiring a simplification of the methods used to evaluate a larger number of lines. Third, when testing the putative relation between differences in rooting traits and drought tolerance, genotype phenology (drought escape) was often the overriding factor explaining plant tolerance (Blum et al., 1977, Kashiwagi et al., 2006). Therefore, the exact contribution of roots to drought tolerance can only be tested once sufficient genetic variations in root traits are found within groups of genotypes sharing a similar phenology. Given these limitations and to remove the “static” approach used so far, we propose that our future approach on roots should focus on root functionality rather than morphology. We should first measure water uptake under water deficit, in a “dynamic” and precise way, in a large range of genotypes representative of the species’ diversity. Such lysimetric system is shown in Figure 5. This should carefully consider the phenology of genotypes, and determine the relation between a given pattern of kinetics/volume of water uptake and drought tolerance. Once contrasting genotypes are identified, root developmental and morphological patterns can be investigated thoroughly.

Root for water supply and nutrient uptake in poor soil fertility of the SAT

The objective of this section is not to make an exhaustive review of the contribution of roots to nutrient uptake, especially phosphorus (P). There are several reviews and reports on the root traits related to P uptake (Lynch and Brown, 2001; Sinclair and Vadez, 2002; Hinsinger et al., 2003; Gahoonia and Nielsen, 2004, Lambers et al., 2006). Instead, we will focus on how roots can contribute to the acquisition of both water and nutrients, with a focus on P, in an integrative way rather than looking at roots for nutrients and for water separately.

Root architecture needed for water and nutrient uptake - Both nutrients and water are concomitantly limiting factors in many areas of the semi-arid tropics (SAT). It is increasingly becoming clear that in these areas, poor fertility is a primary factor for poor crop performance rather than water stress (Payne et al., 1990). These authors found that the poor fertility limited root development in pearl millet that was unable to capture the water contained in the profile and water drainage occurred below the root zone. As a consequence, plants suffered from drought stress when rains receded, although water was available deeper in the profile (Payne et al., 1990). Root establishment in poor fertility soil is essential to ensure full use of available water. To acquire nutrients, the development of secondary roots is needed mostly in the soil surface layers where the nutrients usually concentrate and their absorption is made easier because of higher microbial activity such as in bean (Lynch and Brown, 2001; Lynch and Beebe, 1995; Liao et al., 2001) and wheat (Manske et al., 2000). To acquire water, in contrast, profuse rooting in the deeper soil layers would be required. It appears from a recent study that P acquisition is less in deeper-rooted plants than in shallow-rooted plants (Ge et al., 2000), thus indicating that shallow and deep rooting are rather antagonistic developments (Lynch and Brown, 2001), as suggested earlier by Chopart (1983). Yet, there is a need to identify rooting patterns that allow both nutrient acquisition and water uptake. The use of molecular markers for these two traits – water and nutrient acquisition – might be useful to break this negative linkage, at least partially, if effective QTL for these two traits can be identified.

How to maintain nutrient uptake in soils that frequently dry - In addition to the fact that , as Lynch and Brown (2001) admit, a "nutrient foraging" phenotype would have a poorer capacity for water uptake from deep in the profile, such a phenotype may also not fit in environments where the top surface is likely to be dry for long periods. Therefore, the hypothesis that a shallow rooting pattern contributes to an enhanced nutrient acquisition in nutrient deficient environment needs to be revisited when top soil drying is a common feature. Some work would also be needed to assess the volumetric soil moisture threshold where nutrient acquisition is no longer possible. The question then remains, how to ensure superior nutrient uptake in these poor nutrient environments? A shallow root system may still be valid for rainfed crops of the SAT where the top soil would be re-wetted periodically and in particular in unfertilized soils where most of the nitrogen would be present in the top surface and would need to be absorbed before being leached down the soil profile. A more profuse root system in this case might also contribute to both water and nutrient acquisition. For instance, it has been shown that pearl millet roots can expand both horizontally for over a meter and vertically in a sparse stand (Bruck et al. 2003a,b). Helping early plant establishment may be also a way to ensure that a minimum root development has occurred to take full benefit of the on-going rains. The microdosing method used in West Africa (Tabo et al., 2005) would be one more option. A more recent work shows that a minute application of P close to the root of pearl millet seedlings helps plant establishment and growth under P limited environments (Valluru et al., 2007), and pearl millet seed coating with P is also showing very similar results (unpublished results). Yet, the presence of water around the seed is a prerequisite for seedlings to take up nutrients, and the question of nutrient absorption in nutrient and water scarce environments remains unresolved. The hydraulic lift may be part of the answer.

Hydraulic lift – This is an interesting root feature that could be relevant for the absorption of nutrients in dry top soil. This phenomenon (Caldwell et al., 1991) has been reported in different crops and particularly pigeonpea (Wan et al., 2000; Sekiya and Yano, 2002) and it is related to the morphology of the root system, in particular, the presence or absence of an endodermis. Under conditions of high transpirational demand, the pressure gradient in the root (lower water potential than in the soil) is in favor of water absorption by the roots. During the night, when there is no transpiration and only a modest osmotic gradient, the soil water potential is usually lower than the potential in the roots. Unless there is a particular mechanism in place, water would normally flow back to the soil, following pressure gradients. That backflow is normally prevented by the endodermis which acts as a barrier to the flow of water from the root to the soil (Freundl et al., 2000). For deep rooted crops, the roots are in contact with wet soil and the osmotic gradient is sufficient to allow water uptake by the deepest roots. By contrast, the shallow roots are exposed to a dry soil, and the pressure gradient between roots lacking an endodermis and soils in these layers allows water to flow back to the soil. This phenomenon is called the hydraulic lift and consists of lifting water from the deep layers to the top layers. Such a feature might help take up nutrients from the rhizosphere in the top soil in environments where drying is frequent. A species like pigeonpea, in which hydraulic lift has been reported, and which is also known to perform well under low soil P (Ae et al., 1991), might be of great interest. Last but not the least, an interesting study with maize hybrids showed that the drought tolerant line was able to hydraulically lift water from the deep and wet soil layers to the shallow and dry soil layers during the night (Wan et al., 2000). The capacity for hydraulic lift is directly related to differences in the anatomy of the root cylinder (Figure 1) and likely related to the absence of an endodermis (Steudle, 2000a).

<u>Relation between nutrient deficiency and WUE</u> – To achieve a high WUE, plants need to maintain a low CO2 concentration in the stomatal chamber, which can be possible if the photosynthetic rate is high. Nutrient deficient plants (in particular N and P) can have decreased rates of photosynthesis, explaining a putatively close association between water and nutrients with regards to WUE. To account for poor fertility, sparse planting densities are commonly used which dramatically increase the evaporation component of the crop's evapotranspiration, and decreases water use overall (Payne 2000). Moreover, in nutrient depleted environments, one factor involved in the calculation of WUE (Tanner and Sinclair, 1983) can also be decreased by low fertility ("m" factor explained by Payne 2000, citing DeWit, 1958). Other evidence indicate that WUE drops in different crops cultivated under nutrient deficient conditions (Bruck et al., 2003a,b). Finally, under nutrient limited conditions, it has been shown that the hydraulic conductance of plants decreases (Clarkson et al., 2000), although no evidence of any genetic differences in this decrease have been reported. Therefore, it is clear that the nutrient and water limitations interact closely, and that the root hydraulic conductance is involved.

Root characteristics and salt stress tolerance

In this part also, the purpose is not an extensive review on salt stress tolerance, but to focus only where roots could be of importance, focusing on certain aspects that, we feel, have not received lots of attention.

How roots interact with salt stress? - Under saline conditions, roots are obviously the plant organs exposed to salt stress. There are different ways in which roots play an important role in the plant response to salt stress: (i) avoiding the entry of sodium in the root cell or favoring its exclusion in the root medium; (ii) avoiding its loading in the xylem vessels, to prevent its build up in the shoot tissues; and (iii) signaling to the shoot via hormones such as ABA. Here, we will not review exhaustively the exclusion of Na from the root cells since (i) has received much attention and reviews are available (Tester and Davenport, 2003; Munns, 2002; Munns et al., 2002). We would look at (ii) and (iii) where much less work has been done, and where again the root architecture as described initially appears to matter.

Roots for excluding Na from the plant - Sodium (Na) exclusion from the shoot is indeed the major trait considered important to confer salinity tolerance in several crops. As a consequence, a lot of the work currently focused on improving the capacity of roots to deal with Na exclusion (item (i) above), either by exploiting the natural variation for this trait, like in wheat (Munns et al., 2002, Munns and James, 2003), or in rice (Gregorio et al., 1993), or through genetic transformation where there is a plethora of reports (eg: Apse et al. 1999; Shi et al. 2003; Vinocur and Altman, 2005; Denby and Gehring, 2005; Chinnusamy et al., 2005, Mathuis, 2006 and most citations there in). In this respect, breeding is currently on-going at IRRI, where salt-exclusion QTLs have been found and are in the process of being introgressed in locally adapted lines to confer them the adaptation to salty conditions. Nevertheless, whether salt exclusion from the shoot is the key factor explaining differences in salt stress tolerance is still an issue that requires clarification since very few studies have investigated the relation between a accumulation in the shoot and salt tolerance based on yield evaluation. We recently reported no such relation in a large set of chickpea genotypes (Vadez et al., 2007). In fact, the reason for the differences in salt accumulation in the shoot in many studies, in particular those using transgenics, may be the use of hydroponic systems, which are also known to affect the structure of the root systems, since hydroponically grown plants lack an exodermis in contrast to aeroponically grown plants (Freundl et al., 2000; Hose et al., 2001) and therefore the related hydraulics. For instance, salinity appears to induce the subberization of the hypo- and endodermis (Shannon et al., 1994), or the development of the exodermis (Reinhardt and Rost, 1995). More arguments follow thereafter, to justify a closer look at how the root structure may explain a great deal of how much salt eventually reach the shoot.

Loading of salt in the root xylem and relation with the composite transport model - Much less has been done to avoid the loading of salt in plant organs and we feel that it is an important issue to consider. Here, the composite transport model of water uptake may help explain genotypic differences in the loading of salt in the xylem. As we saw earlier, plants take up water from the soil through an apoplastic or cellular pathway (Steudle, 2000b) (Figure 1). In the apoplastic flow, the reflection coefficient of the minerals is close to zero, and minerals are dragged in the water flow until the endodermis, as previously found with ABA (Hartung et al., 1998; Freundl et al., 2000), or the exodermis (Hose et al., 2001). There is reason to believe that crop genotypes having a less developed endodermis, or no/loose Casparian band, and a predominant apoplastic pathway for water uptake (such as maize) may allow salt loading into the xylem. By contrast, plants with a well developed endodermis, or favoring a cell-to-cell pathway for water uptake (like barley, Steudle 2000a), may have a more efficient system to filter salt before they reach the xylem. We believe that further work is needed to test whether contrasting materials for salt tolerance are related with putative differences in the way they take up water from the root hydraulic standpoint. Little work has been done to explore that hypothesis, although reports show that indeed a higher apoplastic water uptake was related to a higher accumulation of salt, in intravarietal selections of line IR36 with different degrees of salt accumulation (Yadav et al., 1996; Yeo et al., 1999). In another report, most salt tolerant genotypes of *Prosopis strombulifera* had an early suberization of the endodermal cells (Reinoso et al., 2004). An interesting "coincidence" is that plants displaying the hydraulic lift behavior reported above would also lack the capacity to "filter" salt through the endodermis. Pigeonpea is one such example, and it happens to be extremely sensitive to salinity compared to other crops (Srivastava et al., 2006). Therefore, an investigation of salt tolerance with regard to particular differences in the root morphology such as the presence of Casparian bands, or subberization of the cells at the level of the endodermis, may provide interesting insights. Looking into those mechanisms may also help understand why the effects of salt stress are higher under high VPD conditions, since under such conditions, the proportion of water channeled through the apoplast would be higher (Steudle, 2000a).

Root signaling under salt stress - A third area where roots are involved and where relatively little attention has been paid is related to signaling. As in the case of drought, plants respond to salt stress by producing ABA that result in stomatal closure and reduced water/salt uptake (Fricke et al., 2006). Work on sorghum and salt stress has shown that ABA was responsible in the adaptation to salt stress when plants were pre-treated with ABA (Amzallag et al., 1990), and suggest that part of the plant adaptation to salt could be mediated by differences in the root production of ABA. Also, salt stress is reported to decrease the hydraulic conductance of roots (Tyerman et al., 1989). As for drought, there seems to be both chemical and hydraulic signals involved in the response to salt stress. A better understanding of these would help prioritize the approach to increase tolerance to salt stress. In any case, these signals would contribute to a decrease in the transpiration rate. This would have two antagonistic effects: (i) a beneficial effect of decreasing the influx of salt accompanying the water flux into the root; and (ii) a limitation to the transpiration water to support carbon fixation and, therefore, a loss in biomass accumulation. We can clearly see that an optimal biomass production under salt stress would become a tradeoff between both aspects. Work is needed to determine how each of these antagonistic effects vary across genotypes reported to differ in salt tolerance. For instance, we have recently started work to measure the apparent Na concentration in the xylem and found very large differences between groundnut and pigeonpea genotypes that vary for tolerance. Yet, we have shown that the rate of transpiration drops relatively more upon salt stress in salt tolerant groundnut genotypes than in sensitive ones. By contrast, salt tolerant groundnuts compensate for more limited transpiration rate by increasing their transpiration efficiency (TE) to a relatively greater extent. Therefore, the salt-tolerant genotypes of groundnut, apparently manage to reduce their transpiration stream (and the related Na flux), but compensate the carbon fixation loss by increasing their levels of TE relatively more than salt sensitive genotypes.

Root dynamics – Toward capturing volume and kinetics of water uptake

We know little on the range of variations for root traits, their development pattern, and their contribution to drought tolerance. In most of the previous studies, knowledge has increased mostly on root morphology (Mc Cully, 1995), and traits such as RLD, depth, or weight, rather than root functions (water uptake, growth kinetics), have been measured (e.g. in Merill and Rawlins, 1979). Yet, water uptake is perhaps the most important component of a simple crop growth model defined by Passioura (1977) (Y = T x TE x HI, where Y is the yield, T is transpiration and accounts for the amount of water taken up by roots, TE is transpiration efficiency, and HI is the harvest index). So, the first requirement of roots is a high water uptake.

<u>Root length density and water uptake</u> - How much water is taken up would obviously relate somewhat to the RLD, but this link is still unclear because of the lack of data comparing the two parameters. Several authors concluded that RLD and water uptake is related (Passioura, 1983; Monteith, 1986, Lafolie et al., 1991). This view is challenged by other studies showing poor relations between water uptake and RLD across several cereals and legumes (Hamblin and Tennant, 1987; Dardanelli et al., 1997; Katayama et al., 2000, Amato and Ritchie, 2002). In fact, it appears that cereals and legumes have large differences in their specific root water uptake, because of finer roots in the cereals than in legumes. Nevertheless, the relation between RLD and water uptake remains weak even after considering cereals and legumes separately. The above authors conclude that legumes have more abundant metaxylem vessels, which decrease their axial resistance to water flow, explaining the higher rate of water intake per unit root length. However, it has also been shown that a small length of roots in deep layers where water is plentiful would be sufficient to amply supply water to the plant when the top soil is dry (Gregory et al., 1978; Sharp and Davies, 1985). This would logically offset the linear relation between water uptake and RLD. It would also dismiss the hypothesis of differences in axial resistance limiting the rate of water flow across cereal and legumes, in agreement with Steudle’s hypothesis (2000a&b). In any case, the lack of relation between water uptake and RLD agrees well with our data on groundnut (unpublished data). By contrast, we found a good relation between water uptake and RLD in *DREB1A* groundnut transgenics, where a higher water uptake of transgenic plants under water deficit was well related to higher RLD below the 40 cm depth (Vadez et al.,

2007). Hence, there are clearly some controversies over the water uptake and RLD relationship. Finally, water uptake should be the prime target as suggested previously (McIntyre et al., 1995; Dardanelli et al., 1997) and such water uptake is unlikely to be dependent on differences of axial resistance to water flow. New models have been designed to take this into account (Dardanelli et al., 2004).

Water uptake and phenology - Under drought conditions, the primary factor contributing to better yield is a suitable phenology, adjusted to the water available from rainfall or soil moisture to allow the crop to complete its life cycle (drought escape mechanism) (Serraj et al., 2004). Several studies indicate that "superior" root traits contribute to drought tolerance of genotypes provided these have a suitable phenology (Blum et al., 1977, Kashiwagi et al., 2006). Therefore, while measuring the volume of water taken up by roots is certainly an important factor, understanding the kinetics of water uptake, and how this kinetics relates to the phenological stage of a plant, are equally important issues. This view is shared by Boote et al. (1982, cited in Meisner and Ketring, 1992), who argue that sufficient amounts of water at key times during the plant cycle is more important than across the whole cycle. We hypothesize that these key stages may be the reproductive stages and the later stages of grain filling. Previous work on roots indicates that root growth can persist at very different stages and under different conditions such as drought (Chopart, 1983; Hafner, 1993; Ketring and Reid, 1993), although genotypic assessment for this is lacking. A key missing link in these studies is how the reported root growth relates to differences in water uptake, and how much the water uptake varies among genotypes over the growth cycle Therefore, our working hypothesis is that differences in root growth under drought during reproduction and the latest part of grain filling would result in differences in water uptake, in turn resulting in differences in reproduction (seed number) and better grain filling (see next two paragraphs). We therefore suggest that the genotypic differences for water uptake during these key periods would be extremely difficult to determine by measuring only the roots, especially because of the usual large experimental errors in root measurements (Figure 2 & 3).

Water uptake and plant reproduction – Plant reproductive stages is extremely sensitive to any type of stress (Boyer and Westgate, 2004). Here, we consider the reproductive stages as the sequence of events between the emergence of a flower bud to the beginning of grain filling. It is important to understand the kinetics of water supply under stress during these stages, the existence of any genotypic difference in the kinetics, how such differences finally relate to yield differences. Our recent data show that groundnut plants grown in long and large PVC cylinders and exposed to water stress during flowering had very distinct patterns of water use, where some genotypes had a "liberal" behavior and maximized transpiration during the first 10 days following withdrawal of irrigation, but ran short of water during later stages (Figure 6). Others had a "conservative" use of water, limited their transpiration quickly after withdrawing irrigation, but were able to extract water for a longer period of time. The latter genotypes also had higher ABA content, both under well-watered and under water stressed conditions (unpublished data). Although we did not test whether these differences in kinetics had any bearing on the relative yield, but the data suggests that the stress intensity suffered by plants during their reproduction, probably varied across lines in relation with the differences in the kinetics of water uptake and in ABA. More work is needed to elucidate these differences.

<u>Water uptake and grain filling</u> - Differences in water uptake during grain filling would affect photosynthesis and consequently the supply of carbohydrates to the maturing grains. For instance, a good relation between RLD in the deep layer and the HI (indicative of grain filling) was observed, especially under severe drought conditions (Kashiwagi et al., 2006). A similar phenomenon may also prevail in sorghum where the staygreen phenotype correlates with better grain filling. We consider that the maintenance of physiologically active and green leaves under terminal moisture stress possibly provided a minimum water uptake to sustain growth under these conditions, which is in agreement with a deeper rooting of staygreen genotypes under water stressed conditions (Vadez et al., 2005) (Figure 3). Such water uptake would in turn maintain photosynthetic activity and carbohydrate supply to the growing grain. We are currently testing a similar hypothesis to study the putative role of root water uptake during the grain filling in pearl millet genotypes introgressed with a terminal drought tolerance QTL that contributes to an enhanced panicle harvest index (PNHI). A better grain filling might be explained by enhanced water uptake toward the late stages of grain filling. We hypothesize that the water needed to sustain grain filling may be relatively small and due to minute differences in the root development (depth, RLD). Such differences would be difficult to capture by a physical assessment of roots, but could be measured by an assessment of

water uptake, which would "integrate" the benefit of slight RLD differences over time. Work would also be needed to determine the threshold amount of water required to sustain grain filling.

Water uptake and soil characteristic – One difficulty to assess previous work on root also relates to the large differences in soils used to investigate roots. In this review, we pay a particular attention to the hydraulics of roots, as a way to explain part of the plants response to a range of stresses. The hydraulics of roots under conditions of receding moisture is obviously closely related to the hydraulic properties of the soil, such as the soil porosity. A recent theoretical analysis concluded that the transpiration response of plants is relatively uniform across a range of soils in which transpiration decline usually occurs when about 60% of the volumetric soil water has been depleted (Sinclair, 2005). However, the soil type would influence its hydraulic properties in a way that would determine the hydraulic integrity of the soil-plant-atmosphere continuum. Here, how intention is not to review that complex issue and we rather relate to recent reviews where the hydraulic properties of the soil and of the plants are taken holistically (Taylor and Klepper, 1978; Sperry et al., 1998, 2002; Jackson et al., 2000; Passioura, 2002; Sinclair, 2005). We also argue here that the use of modeling to predict soil water extraction (e.g. Jamieson and Ewert, 1999; Dardanelli et al., 2004) may ease the understanding of the role of soil in water extraction by plants exposed to progressive drying.

The metabolic / development cost of root – Whether the metabolic and development cost of roots is "expensive" for the plant, and whether the overall carbon/nutrient balance between roots and shoots can significantly impact the economic yield are still subject to debate. For instance, Passioura (1983) hypothesized that yield could be increased by decreasing roots as they represent a high energy investment. Van der Werf (1988) calculated that the ATP cost of producing one gram of root was equivalent to the maintenance cost of that same gram for 10 days. This cost could even be higher under stress conditions since, Eissentstat (1992, 1997) estimated that root carbon cost could reach about 40% of total plant cost under phosphorus stress. This would explain the high turnover of root systems, i.e., the fact that plants shed roots to limit their metabolic cost which represents a net carbon contribution to the soil (Krauss and Deacon, 1994). Siddique and colleagues (1990) found that wheat genotypes with high HI would have lower root/shoot ratios, indicating less investment in roots. In fact, the turnover of roots can be relatively rapid, with a half life of 30-40 days in groundnut (Krauss and Deacon, 1994). Therefore, even if the root/shoot ratio at a given point in time in many species is only between 10 and 40%, a complete turnover of roots in about 40 days would bring the root/shoot ratio close to 100% over the entire life cycle. This would be a substantial part of plant carbohydrate and protein investment. While this is certainly an important characteristic for the long term sustainability of low input agro-ecosystems, in relation to the organic matter returned to the soil, it is potentially an immediate yield decreasing factor in case the development of large root systems is not needed. Yet under conditions of limited soil P or limited plant available water, this investment may be necessary to support shoot growth. Therefore, a critical need is to assess the target stress conditions under which a significant investment in root mass would contribute to a better drought adaptation. Interestingly, it has been shown in several studies that elevated CO_2 would contribute to an increased root growth (Rogers et al., 1992, 1996). Work would also be needed to investigate whether differences in the root hydraulics, i.e., conferring differences in resistance of roots to water flow, could minimize the requirement in terms of RLD to capture water.

Water saving behavior – Relation with leaf conductance to water

In the three-component yield architecture model presented above (Passioura, 1977), water uptake and water use efficiency (WUE) are called “drought avoidance” parameters, i.e., plants would “avoid” drought by either tapping into more water from the soil, or by using that water better (Serraj et al., 2004). Eventually, a higher WUE would save water in the soil profile, which would help sustain water uptake by plants. The root-related drought avoidance is closely intertwined with the WUE-related drought avoidance, although these components have been considered to be independent. Therefore, more work is needed to better understand their links and complementarities.

Can higher TE contribute to saving water in the soil profile? - It has been previously stated that there was little hope of finding differences in the intrinsic transpiration efficiency (TE, the instantaneous rate of carbon fixation divided by the instantaneous rate of transpiration, an important component of WUE in plants) in plant genotypes of a given species (Tanner and Sinclair, 1983). However, genetic variations for

TE have been found in various crops like wheat (Ehdaie et al., 1991; Condon et al., 2002, Rebetzke et al., 2002, Richards et al., 2002) cowpea (Hall et al., 1992; Ismael and Hall, 1992), bean (Elheringer et al., 1991), and groundnut (Hubick et al., 1986; Wright et al., 1994, Bindhu madava et al, 1999 Krishnamurthy et al., 2007). These differences are explained by more active mesophyll efficiency (Uday Kumar et al., 1998), or a lower stomatal conductance such as in the wheat cultivar Quarrion (Condon et al, 2002) or in transgenic groundnut (Bhatnagar Mathur et al., 2007). In a recent large screening of 440 representative groundnut germplasm and breeding lines, we found a 4-fold range of variation for TE (unpublished results), a range of variation which has not been reported before. The question remains whether a better TE contributes to water saving in the profile that can be used by roots during grain filling.

<u>A maximum rate of transpiration to save water in the soil profile</u> - Another aspect of water saving relates to the control of the overall water loss at the leaf level. Recent upstream work on the *ERECTA* gene, involved in the regulation of TE in *Arabidopsis*, shows that *ERECTA* plays a role not only on the regulation of the photosynthetic system, but also on the stomatal conductance (through stomata density) (Masles et al., 2005). We have observed before that certain species such as pearl millet in semi-arid conditions do maximize transpiration even if the vapor pressure deficit (VPD) is high (above 2.5 kPa) (Squire, 1979; Henson and Mahalakshmi, 1985). In the work reviewed by Bidinger and Hash (2004), no attention was paid to possible genetic variations in this strategy, although recent modeling data show that a maximum daily transpiration rate would indeed contribute to saving water in the soil profile and would increase TE (Sinclair et al., 2005). We recently found that a major difference among pearl millet genotypes having similar phenology but differing for terminal drought tolerance was indeed a lower rate of water loss per unit of leaf area (transpiration over a period of 1-2 days divided by leaf area) in terminal drought tolerant genotypes (unpublished data). These differences have been measured under well-watered conditions, indicating that this trait is constitutive. These results have been observed very consistently across experiments, either on whole plants taken at different stages or on detached leaves over short periods of time. This index, which reflects the leaf´s stomatal conductance over a period of time, would save water and make it available for the later stages of the crop cycle, in particular grain filling. It may not be a coincidence that the phenotype used to identify QTLs for terminal drought tolerance was the panicle

harvest index, a direct measurement of grain filling in plants. Water saving from a maximum rate of transpiration would decrease the proportion of water used before anthesis, and fits well with an old hypothesis by Passioura (1983) that a higher proportion of water loss after anthesis would contribute to better grain filling under water stress conditions, a hypothesis recently revived by Hammer and colleagues in sorghum (2007).

Sensitivity of stomata to VPD to save water in the soil profile - Pearl millet has been found to be sensitive to high VPD levels, usually above 3-4 kPa where the stomata close to avoid wasteful water loss (Squire, 1979). This is a well-known characteristic in crops growing in dry environments where stomata close when the evaporative demand is too high to be supported by the maximum water supply by the roots. However, possible genotypic variations for the sensitivity to VPD have not been studied, especially at intermediate VPD levels (2-3 kPa) where it is still assumed that genotypes would maintain their stomata fully open. Recent studies on a long known “slow-wilting” genotype of soybean (PI416937) used in breeding drought tolerant varieties indicates that the transpiration increased linearly in response to increases in VPD until about 2 kPA in all genotypes. Above these levels, transpiration rates remained essentially constant. In genotype PI416937, at least a partial stomatal closure did occur above 2.0 kPa, whereas other genotypes maintained a linear increase in transpiration up to VPD values of about 3.5 kPa (Sinclair et al., 2007). A consequence of this trait is that the leaf canopy temperature would increase under well-watered conditions, making it a fairly easy trait to measure using infrared thermometers, provided it is measured at the adequate VPD above 2 kPa. In fact, there is some indirect evidence of this “slow-wilting” trait in the canopy temperature literature. For instance, we believe that the differences in the canopy temperature between genotypes Senegal Bulk and HMP559 reported in Singh and Kanemasu (1983) are likely to be due to either differences in the sensitivity of stomata to VPD in these lines, or differences in their rate of water loss per unit leaf area. In our recent work, we have gathered evidence of such contrasting behavior in pearl millet genotypes that differ in terminal drought tolerance (unpublished). Therefore, further work is needed to assess whether this trait exists in other crops, and to use it for breeding varieties with water saving behavior.

Relation with hydraulic conductance - Signaling aspects

We have seen above that differences in how leaves would regulate their water loss would indirectly save water in the soil profile and allow roots to take up water for longer periods of time. In turn, roots are the sensors of drought or salt stresses and can relay the signal to shoots through hormones such as ABA (Davies and Zhang, 1991, Davies et al., 2000), through hydraulic signals in the case of more severe stresses (Sperry et al., 2002), or through an integration of chemical and hydraulic signals (Tardieu and Davies, 1993, Comstock, 2002). Such signaling would eventually contribute to decreasing stomatal conductance and would mechanically act on increasing the overall water use efficiency of plants (Farquhar et al., 1982, 1988, 1989, Condon et al., 2002).

Can differences in root hydraulic conductance explain a maximized transpiration rate? - The reason for differences in the rate of water loss per unit leaf area, or in the sensitivity of stomata to VPD (see above) are unclear and may involve some sort of differences in the overall plant conductivity to water. Assuming that there is no limitation in the axial conductance to water, the main "points" where conductivity can vary are at the leaf-atmosphere interface or at the root-rhizosphere interface. As far as roots are concerned, differences in the two later traits above could be explained by constitutive differences in the hydraulic conductance of roots. In fact, only hydraulic signals from the roots could explain the rapidity of the response to an increased VPD. Hence, it would be very interesting to look at the contrast for terminal drought tolerance in pearl millet from the angle of root hydraulic conductance; for example, by looking at the relative contribution of the cell-to-cell and apoplastic pathways to the root hydraulic conductance. Indirect assessment of this could be done by measuring the effect of mercuric chloride, a specific inhibitor of aquaporin on the rate of transpiration in plants (Maggio and Joly, 1995, Maurel, 1997; Maurel and Chrispel, 2001; Tyerman et al., 2002; Martre et al., 2002).

Work has also been done about 25 years ago on the contribution of small xylem vessels to high axial hydraulic resistance (Richards and Passioura, 1981a&b; Passioura, 1983). In this work, certain wheat genotypes had smaller xylem vessels that contributed to their increased WUE. In any case, it would also be interesting to compare the size of xylem vessels in pearl millet genotypes that contrast for terminal drought tolerance and rate of water loss per unit leaf area.

Root signaling to control stomata movement - The contribution of roots to the water use efficiency of transpiring organs may be through signaling. Roots are the primary organ exposed to a range of abiotic stresses and the signaling of these stresses to the shoot through ABA is well established (Zhang and Davies, 1991a&b, Stoll et al., 2000). It is hypothesized that the signaling takes two steps: (i) a first step at early stages of drought stress when ABA is transported to the shoot causing a drop in stomatal conductance and leaf expansion rate, and (ii) a second step at higher stress intensities where hydraulic signals are received by the shoot and contribute to *de novo* synthesis of ABA in the leaves, thereby accentuating the effect of ABA (Saab and Sharp, 1989). Such signaling also occurs under conditions of rapid stress imposition to avoid cavitation in the xylem vessels (Sperry et al., 2002). The ABA-related drop in stomatal conductance would contribute to an increase in TE. ABA also contributes to the development of roots (Saab et al., 1990; Sharp et al., 1994; Munns and Cramer, 1996; Spollen et al., 2000) and then to the water uptake. Hence, it would be very important to study the signaling from the roots to understand how water use efficiency is regulated in the shoots. It was interesting to note that in our work where groundnut genotypes were tested in long PVC lysimeters (Figure 4), the two genotypes showing the "conservative" behavior also had a high level of ABA in their leaves, even under well-watered conditions. We also found that pearl millet genotypes having a lower rate of water loss per unit leaf area had a higher ABA concentration in the leaves under well-watered conditions. The origin of this ABA and the role of roots in these differences require further investigation.

Conclusion

Roots play a central role in their response to many abiotic stresses, either directly or indirectly through their involvement in signaling. We have indicated in this review that many aspects of the plant response to drought, nutrient, and salt stress can be studied from the angle of the root structure and hydraulics, especially in the way a plant acquires water. In the case of drought stress, it is evident that there is a large deficit of knowledge on the contribution of roots to tolerance to water deficits, but that filling in this gap will likely require a dramatic improvement in the methods used to investigate roots. Our inclination is to focus more on measuring water uptake by roots and relatively less on understand the root structural development needed to increase water uptake. Obviously, such an approach needs to have a sufficiently high throughput to allow the assessment of large number of genotypes. Regarding the role of roots in response to nutrient stress, there is a need to look at both water and nutrient stress in a comprehensive way, as our target is the semi-arid tropic where both stresses are concomitant. It is also likely that root structure differences will partly explain differences in the salt tolerance of plants.

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Figure 1. Representation of a root cylinder and the pathways for water and nutrient movements in roots (reproduced from Steudle, 2000b, with permission from the author). The vacuolar and symplastic pathways represent together the cell-to-cell pathway and cannot be easily distinguished.

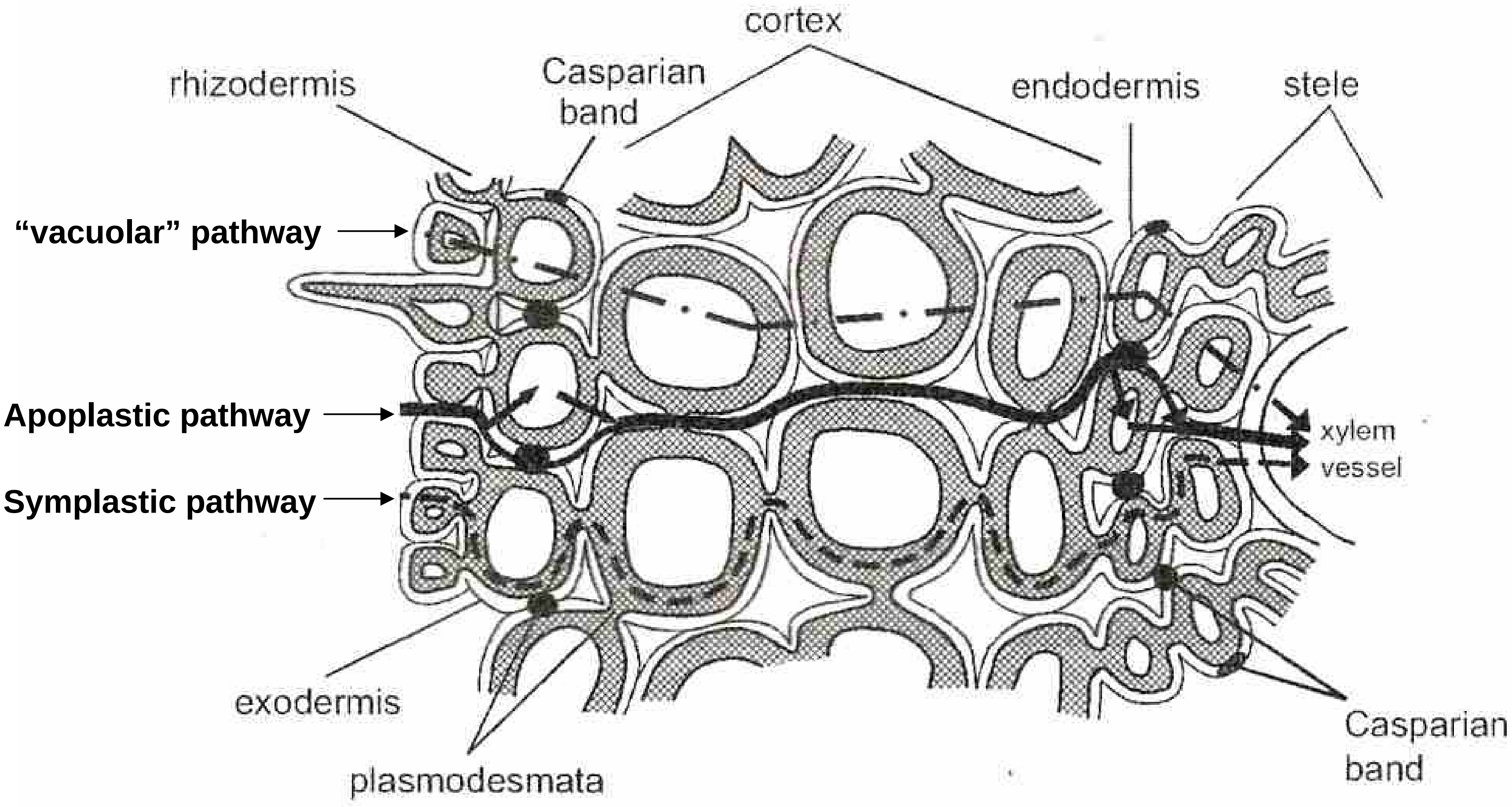

Figure 2. Root DW at different depths under drought conditions, expressed in % of the root dry weight in the 0-30 cm layer, in senescent (blue bars) and staygreen sorghum (red bars) (RSG 04012 is a re-selection from a cross between E36-1 and R16). Staygreen materials tend to root deeper than senescent ones. Experimental (SE) errors at measuring roots are usually very large.

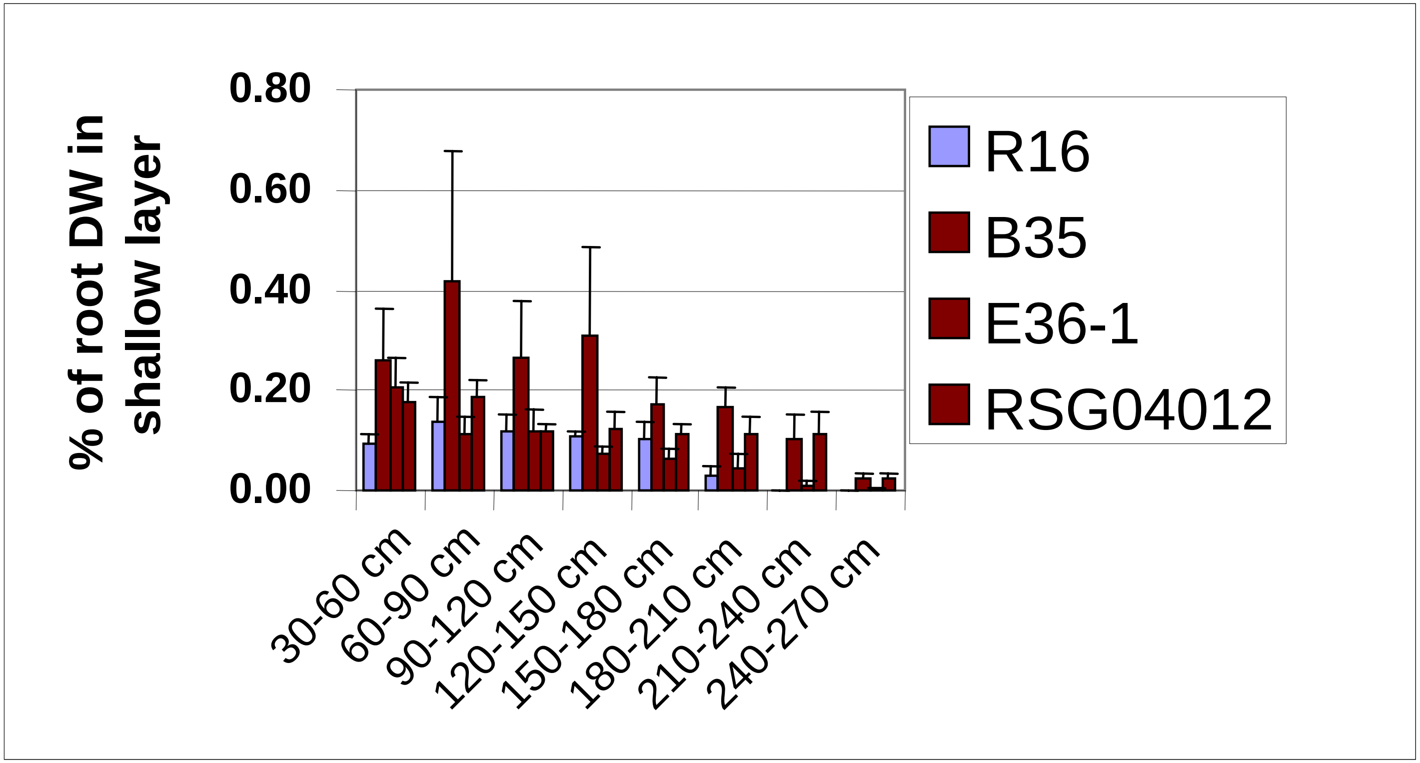

Figure 3. Root DW at different depths, expressed in % of the root dry weight in the 0-30 cm layer, in drought sensitive and tolerant pearl millet (ICMR 01029 and ICMR 01031 have H77/833-2 background and are introgressed with a terminal drought tolerance QTL from donor PRLT 2/89-33). Bars represent SE.

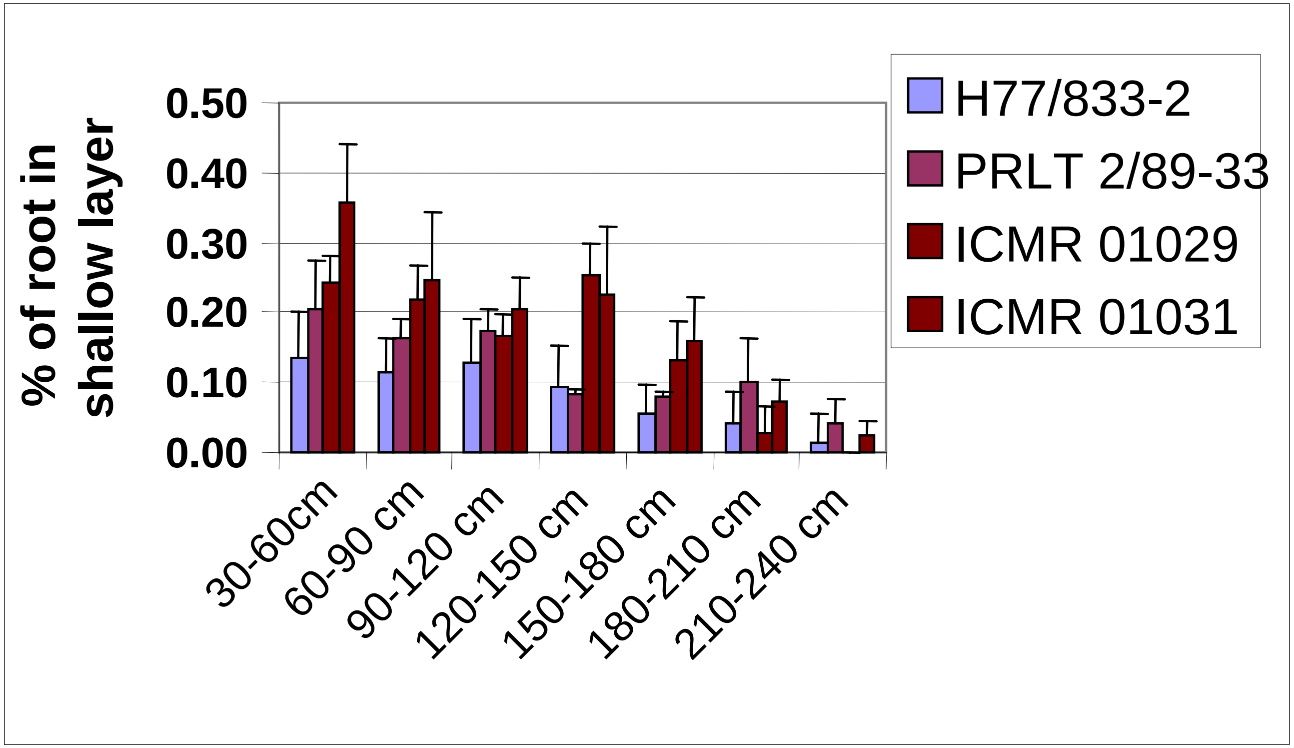

Figure 4. Root dry weight (g plant^{-1}) in 5 transgenic events and wild-type JL24 grown in PVC tubes (1.2 m long, 16-cm diameter) under well watered conditions (WW) and exposed to water stress (WS) from 30 days after sowing. Bars represent SE.

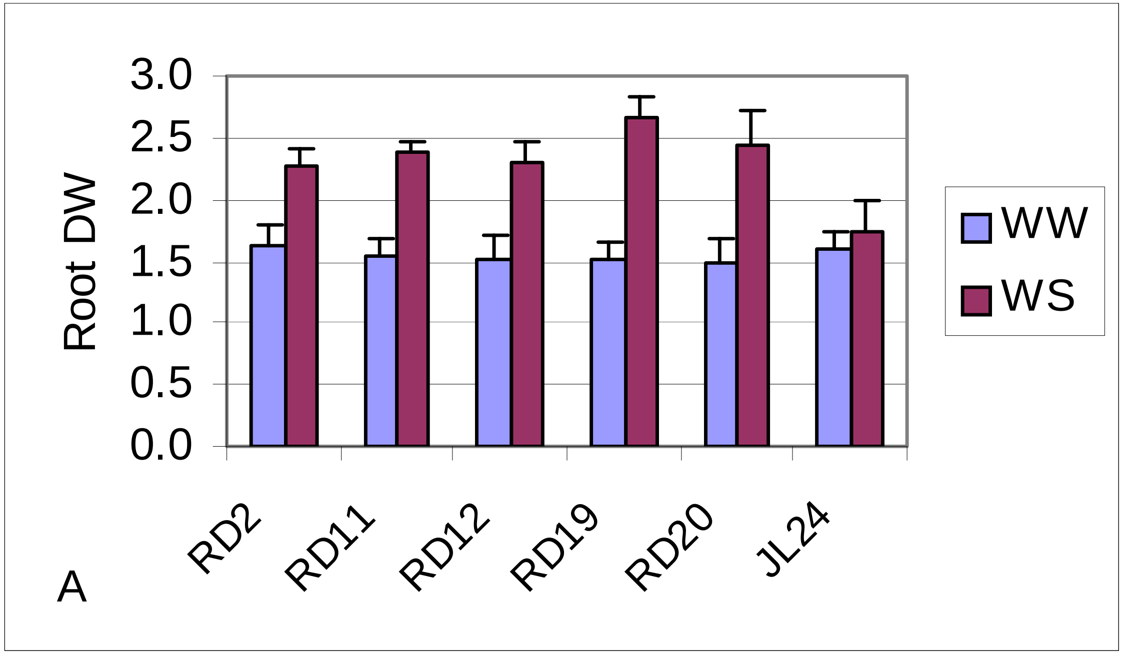

Figure 5. Lysimetric system newly used at ICRISAT to evaluate plant water uptake in PVC tubes (1.2 m long, 20-cm diameter). The length and diameter of the tubes are designed so that the soil volume available to each plant is equivalent to the soil volume available under field conditions at current sowing densities (for groundnut and chickpea). The system is used here for the evaluation of transgenics in P2 facilities. A larger system has been set up outdoors for germplasm screening.

Figure 6. Cumulated evapotranspiration (g plant^{-1}) in four groundnut cultivars in the first 10 days after being exposed to stress, or between 10 and 40 days after being exposed to stress. Plants were grown in PVC tubes (1.2 m long, 16-cm diameter) under well watered conditions until 30 days after sowing and then exposed to water stress (WS) for 40 days. Bars represent SE.