Genetic Manipulation of Root System Architecture to Improve Drought Adaptation in Sorghum

11

Dinesh Joshi, Vijaya Singh, Erik van Oosterom, Emma Mace, David Jordan and Graeme Hammer

Abstract

Drought is one of the most important abiotic stresses and severely affects global agricultural production. Root system architecture (RSA) is the key determinant of water acquisition under moisture stress, and therefore has utility in breeding for drought tolerance in sorghum. Various components of RSA are known to influence drought tolerance in sorghum without any negative impact on yield. The growth angle of nodal roots is an important target trait for improving drought tolerance. Genetic variation for nodal root angle has been reported in sorghum, and this has been associated with grain yield under drought stress. Rapid advances in sorghum genomics have led to the identification of various quantitative trait loci (QTL) governing RSA, but the accuracy and preciseness in identification of QTL is the major hindrance in development of drought-tolerant cultivars through genetic manipulation of root traits. Hence, the complex genetic control of RSA and the lack of a high-throughput phenotyping platform have hampered integration of selection for RSA in breeding programs. These limitations can be overcome by designing a robust phenotyping platform

D. Joshi (✉)
ICAR-Indian Grassland and Fodder Research Institute, Jhansi 284003, UP, India
e-mail: dinesh.pbl@gmail.com

V. Singh · E. van Oosterom · G. Hammer
Queensland Alliance for Agriculture and Food Innovation, The University of Queensland, St Lucia, Australia

E. Mace
Department of Agriculture and Fisheries, Hermitage Research Station, Warwick, QLD 4370, Australia

D. Jordan
Queensland Alliance for Agriculture and Food Innovation, The University of Queensland, Hermitage Research Station, Warwick, QLD 4370, Australia

that can maximize heritability and repeatability of RSA. Inclusion of the extensive phenotyping information with the recently developed genomic resources of sorghum will lead to mining of alleles that govern RSA and tailor a cultivar harboring genes for RSA that improve sorghum production under drought stress. This chapter provides an overview of the latest developments in RSA research in sorghum and gives direction to future breeding strategies to enhance the genetic gain for root traits.

1   Introduction

Drought is one of the most important abiotic stresses that can severely affect crop production by preventing plants from expressing their full yield potential (Mitra 2001). Moisture stress alone causes 70 % of agricultural yield loss across the globe (Jha et al. 2014). Worldwide, sorghum [*Sorghum bicolor* (L.) Moench] is the fifth most important cereal crop after wheat, rice, maize, and barley. Sorghum is predominantly cultivated in dryland areas of the world due to its good adaptation to moisture-limited environments. World sorghum production has had a slight increase from 60–65 metric tons over the past decade (Mutava et al. 2012), in spite of reduction in area to the tune of 154,000 ha year^{-1} (Rakshit et al. 2014). However, predictions of increased frequency of drought as a result of accelerated climate change (IPCC 2012) may adversely affect its yield potential in the semi-arid tropics, imposing a threat to the food security in these regions. Therefore, genetic improvement of sorghum is necessary for drought adaptation in variable climatic conditions and this has been the major focus of sorghum breeding programs around the world.

Because of the unpredictable nature of the timing and intensity of occurrence of drought stress, breeding for drought tolerance has always been a challenging task for sorghum. Past efforts to improve drought tolerance in sorghum were largely focused on genetic and physiological aspects of aboveground plant parameters, namely stay-green (Rosenow et al. 1983; Tuinstra et al. 1996; Sanchez et al. 2002; Vadez et al. 2011; Jordan et al. 2012; Borrell et al. 2014),

photosynthetic parameters (Tingting et al. 2010; Li et al. 2011), canopy temperature and leaf rolling (Blum et al. 1989; Mutava et al. 2012), and osmotic adjustment (Girma 1989; Girma and Krieg 1992; Patil and Ravikumar 2011). However, very few efforts have been made to improve the root system architecture (RSA), which is the key determinant of the ability of a plant to access water and nutrients to support shoot growth in moisture stress conditions. Studying the root system is complex, tedious, and expensive compared with aboveground components.

RSA refers to the spatial and temporal configuration of roots in the soil and is used to describe the shape and structure of root systems (de Dorlodot et al. 2007). In cereals, RSA is of fundamental importance to soil exploration and belowground resource acquisition, which ultimately determines the yield potential of cultivars in drought-prone environments. Simulation studies on maize suggested that manipulation of RSA and associated soil water capture are the main reasons for increasing yield trend of the US corn belt (Hammer et al. 2009). Likewise, studies on wheat demonstrated that selection for narrow root angle and higher number of seminal roots could significantly improve the water capture mechanism in dryland cropping regions (Asseng and Turner 2007; Manschadi et al. 2008; Lilley and Kirkegaard. 2011). Taking into account the ample genetic variability in root traits in different crops (e.g., rice, Kato et al. 2006; wheat, Manschadi et al. 2008; Nakhforoosh et al. 2015; sorghum, Singh et al. 2011), it can be expected that genetic manipulation of RSA is a feasible agronomic option to improve drought adaptation of sorghum. With the aid of high-throughput root

phenotyping platforms and advanced genotyping tools, genes related to root morphological characteristics and physiological functions can be identified or cloned, which will present an opportunity for further improvement of crop productivity in moisture-limited environments.

Sorghum, by virtue of its adaptation to moisture-limited environments, is known to possess a vertically oriented, uniformly distributed, and deep root system, but very little is known about the role of various RSA component traits in plant adaptation to harsh environments. Nodal roots are particularly important in sorghum as they have a major influence on development of RSA as the plant matures (Blum et al. 1977; Singh et al. 2012). However, genetic control and physiological aspects related to water and nutrient transport via RSA and the nodal root system are barely explored. One reason for the scarcity of data on sorghum root characteristics is the unavailability of a high-throughput phenotyping platform for robust root screening that can be applied on a large scale. Nonetheless, screening techniques for rooting depth, root angle, and distribution have been developed for other cereals (Oyanagi et al. 1993; Bengough et al. 2004; Hargreaves et al. 2009) and combined with the advancement in genotyping tools, this has led to the identification of a number of quantitative trait loci (QTLs) and candidate genes related to root morphological characteristics and physiological functions for those crops. This has opened an opportunity for further improvement of crop productivity in moisture-limited environments through root system modifications. None of these techniques has been applied or tested at the scale of a breeding program, in particular in sorghum. Research at University of Queensland, Australia on the morphology and genetics of sorghum root systems identified genotypic variation in nodal root angle that can inform breeding priorities in selection for RSA (Singh et al. 2010, 2012).

This chapter provides a review of RSA research in sorghum. First, we provide an overview of recent developments in root phenotyping platforms that can thoroughly investigate the structural and functional aspects of RSA.

Second, we provide an overview of cereal root structure with particular reference to sorghum influencing drought tolerance and impact of moisture stress on RSA. Additionally, we provide a critical appraisal of existing genetic variation for root traits and their genetic control. Finally, the prospects of deploying root traits to improve drought tolerance through molecular breeding approaches are discussed.

2 High-Throughput Phenotyping Platforms for Screening Root Architecture

Recent availability of multiallelic resources such as backcross (BC)-nested association mapping (NAM) population (Jordan et al. 2011), which offer power to dissect complex quantitative traits along with advances in genomic resources including development of the consensus genetic map (Mace et al. 2009) and availability of resequencing data (Mace et al. 2013) in sorghum have the potential to provide a thorough insight on genetic control of RSA. Despite rapid advances in sorghum genomics, the scarcity of low-cost and high-throughput phenotyping platforms for screening RSA parameters remains a major obstacle to elucidate the underlying genetic control and to incorporate such traits in breeding programs through marker-assisted selection (MAS). A detailed list of various phenotyping methods utilized for studying the genetic and physiological basis of root traits in cereals is presented in Table 1. Currently, the most widely used methods for RSA phenotyping are those that are carried out in controlled conditions using hydroponics, gel chambers, soil, and other artificial substrates (Clark et al. 2011, 2013; Planchamp et al. 2013). Supported with novel 2D and 3D imaging platforms, these methods allow measurement of root traits with high resolution, precision, and accuracy (van Weele et al. 2003; Bengough et al. 2004; Basu et al. 2007; Clark et al. 2011). These methods have proven their utility in characterization of embryonic seminal roots in cereals (Hund et al. 2009; Planchamp et al. 2013; Richards et al.

2015). However, these methods are of little importance for sorghum as seminal roots do not constitute the major proportion of the mature root system and the postembryonic nodal roots dominate the RSA of mature plants. Furthermore, late appearance of nodal roots (sixth leaf stage, nearly 3 weeks after planting) and the larger size of the root and shoot system at this stage impose restrictions on utilizing these methods for phenotyping nodal roots mainly for genetic mapping studies. Despite their major importance, only few methods are available for phenotyping of nodal roots. The split pot system in wheat (Volkmar 1997) and paper pouch method in maize (Hochholdinger et al. 2004a) were developed to differentiate primary seminal roots from nodal roots. Rostamza et al. (2013) utilized the split pot system adopted from Volkmar et al. (1997) to investigate the effect of varying water supply on nodal roots of sorghum. However, these methods are not suitable for large-scale phenotyping of nodal roots. Singh et al. (2010) proposed a root chamber-based method to screen nodal root angle in sorghum precisely. The root chamber method is a greenhouse-based high-throughput phenotyping platform designed to study nodal roots in sorghum. The phenotyping platform includes specially built root observation chambers (60 cm × 40 cm × 3 mm) filled with soil. These chambers support the growth of sorghum plants up to the sixth leaf stage and the transparent Perspex sheets on both sides enable viewing and capturing images of nodal roots. This phenotypic platform has proven its utility in quantifying the genetic variation for nodal root angle across a diverse range of inbred lines and a biparental mapping population (Singh et al. 2011; Mace et al. 2012). Le Marié et al. (2014) proposed a paper based on nondestructive, high-throughput phenotypic method called "rhizoslides" in maize. The advantage of rhizoslides over previously developed paper-based methods is that they allow characterization of nodal roots in cereals by physically separating them from embryonic seminal roots through different layers of rhizoslide sandwich construction. Both root chambers and rhizoslides were designed

primarily to phenotype nodal roots at the seedling stage, which makes them unsuitable to phenotype RSA at the adult plant stage. As an alternative, Traschel et al. (2011) proposed a field-based method "shovelomics", which visually scores post-embryonic root architectural traits at the flowering stage. In shovelomics, roots were excavated by standard shovels, which are capable of removing a soil cylinder of 40 cm diameter and 25 cm depth. After excavation roots were thoroughly washed in water containing a mild detergent to remove soil. The washed roots were visually scored for root angles using a 1 (shallow root angles, 10°) to 9 (steep root angles, 90°) scale. In addition to visual scoring, root angles were measured by placing washed roots on a phenotyping board fitted with a large protractor. Significant correlations between measured and visually scored trait values for growth angles of crown and brace roots confirmed accuracy and reliability of the method. The shovelomics approach has been utilized to quantify visually the excavated structure of the root crown in 218 recombinant inbred lines (RILs) of maize (Traschel et al. 2011). However, manual scoring of RSA traits is prone to error and imposes limitations on both the number of traits measured and number of genotypes screened. Recently, a high-throughput imaging system, which facilitates estimation of root traits based on digital images taken under field conditions was proposed to overcome the problems associated with manual scoring of the shovelomics approach (Bucksch et al. 2014).

Inaccurate phenotyping due to the lack of high-throughput root phenotyping platforms often leads to imprecise QTL identification. Therefore, immediate attention needs to be placed towards developing high-throughput phenotyping methods because it may be the only way to derive valid conclusions. However, each phenotyping method has its own limitations. For instance, extracting the intact roots and avoiding damage to finer components of RSA such as root tip and root hairs is the major problem of field-based screening methods. The currently used controlled environment

Table 1 List of various phenotyping methods used for characterization of RSA in cereals

Phenotyping method	Screened root traits	Stage for phenotyping	Crop	Reference
Clear pot method	Seminal root number (SRN), seminal root angle (SRA)	5 DAS (SRA) 11 DAS (SRN)	Wheat	Richard et al. (2015)
Gellan gum growth method	Median and maximum number of roots, average root radius, specific root length, total surface area, total root length, depth, volume, length distribution, maximum horizontal width, and width-to-depth ratio	14 DAS	Rice	Iyer-Pascuzzi et al. (2010)
Gel observation chamber method	Root length, elongation rate, longest root, deepest root, SRN, and SRA	9 DAS	Barley, wheat	Bengough et al. (2004), Manschandi et al. (2008)
Growth pouch method	Axile and lateral root growth, SRA, SRN	3–7 DAS (axile and lateral root growth 20 DAS (SRN and SRA)	Maize, wheat	Hund et al. (2009), Richard et al. (2015)
Hydroponics	Root thickness, dry root weight, root volume, RLD, primary root growth, total root growth	4 DAS	Rice, maize	Clark et al. (2013)
Rhizoslides	Embryonic and post-embryonic root traits	20 DAS	Maize	Le Marie et al. (2014)
Root box method	Number of roots, root length, root thickness, dry root weight	56 DAS	Rice	Kono et al. (1987), Price et al. (2002)
Root chamber method	Nodal root angle	21 DAS	Sorghum	Singh et al. (2010)
Root Trak method (X-ray computed tomography)	Maximum root system depth and maximum root system width	21 DAS (maize) 10 DAS (wheat)	Maize, wheat	Mairhofer et al. (2012)
Soil coring method	Rooting depth, root penetration rate, density, deeper rooting length, and root distribution	At maturity	Wheat	Wasson et al. (2014)
Shovelomics	Number of brace root whorls, brace root number, brace root angle, brace root branching, crown root number, crown root angle, crown root branching	At flowering	Maize	Trachsel et al. (2011)
Wax layer method/fabric cover method	Root penetration ability	24 DAS	Rice	Yu et al. (1995), Price et al. (2000)

phenotyping methods are also not an effective solution, because RSA is influenced by various soil parameters that cannot be reproduced in artificial growth systems. Mathematical simulation of RSA with models, which are better equipped to integrate the complex biological, physical, and chemical factors affecting roots in soil, can be utilized as an alternative approach for root phenotyping. Simulation packages, such as *SimRoot* have been specifically designed to study RSA and are capable of integrating soil heterogeneity and plasticity of root responses to soil factors into one mathematical framework (Lynch et al. 1997).

3 Root System Architecture in Cereals

3.1 RSA of Sorghum

Root system development of sorghum passes through the same sequence of events as that of the shoot. The hypocotyl or mesocotyl that emerges from the seed develops into leaves, stems, and reproductive organs and branches of the shoot. Likewise, for the root system, the radicle or primary root emerges first followed by the emergence of secondary roots, nodal roots, and lateral root branches. The structural and functional aspects of root and shoot are quite different, but the growth and development of these two systems are interdependent (Gregory 1983; Klepper et al. 1984).

In general, the RSA of cereals is complex and comprises several root types at various developmental phases. It is primarily composed of embryonic seminal and post-embryonic shoot-born nodal roots (Esau 1977; O' Toole and Bland 1987; Gregory 2006). In other cereals including maize, wheat, and rice, secondary seminal roots emerge about four days after germination, bearing first- and second-order lateral branches (Feldman 1994). Sorghum, however, is characterized by a sole primary seminal root (Singh et al. 2010) that originates as a radicle in the embryo and becomes visible only two or three days after germination. The post-embryonic shoot-born roots emerge from consecutive underground and aboveground nodes of the stem and are called nodal and brace roots, respectively (Hochholdinger et al. 2004a; Singh et al. 2010). Considerable variation has been reported in the timing of emergence of nodal roots in cereals. For example, the nodal root in maize emerges approximately 7 days after germination (second leaf stage), whereas in sorghum it appears approximately 21 days after germination (fifth to sixth leaf stage; Feldman 1994; Singh et al. 2010). Successive flushes of nodal roots emerge from successive stem internodes at a rate that is similar to leaves, such that the total number of nodal roots increases as the shoot grows (Klepper et al. 1984). By contrast, brace roots emerge

much later, approximately 7 weeks after germination (Hochholdinger et al. 2004b).

The root system of sorghum grows around 2–3 cm per day (Dardanelli et al. 1997; Whish et al. 2005; Singh et al. 2010) and its maximum size is reached around anthesis (Gregory 2006). However, some roots survive for only a few days and remain short, whereas others may continue to grow for weeks and grow much longer. Contradictory reports on the functional life of various root types create complications in attempting to understand the development of the root system. For instance, some researchers reported that seminal roots can persist and remain functional throughout the life cycle of the plant (Kiesselbach 1949; Kausch 1967; Kozinka 1977; McCully and Canny 1988; Gregory 2006), whereas others have observed that the primary and other seminal roots die after the development of nodal roots (Lawson and Hanway 1977; O' Toole and Bland 1987; Feldman 1994). In sorghum, the seminal root system generally constitutes only 1–14 % of the mass of the entire root system (Singh 2010). Routley et al. (2003) reported that sorghum nodal roots may grow to depths of 2 m by the initiation of flowering, and can efficiently extract water to a distance of 1.6 m from the plant. Generally, growth of nodal roots ceases after flowering. However, in some of the stay-green sorghum genotypes active growth of nodal roots has been reported up to the grain-filling phase (Robertson et al. 1993).

Anatomical organization of roots has not been well studied in sorghum. It has been observed that sorghum genotypes with large xylem vessel diameter in both seminal and nodal roots were better adapted to drought-prone environments (Amelework et al. 2015). Hochholdinger et al. (2004b) provide a comparative overview of root anatomy of cereals and *Arabidopsis*. Generally, the cereal roots comprise 8–15 layers of root cortical cells and one endodermal cell layer, whereas the *Arabidopsis* roots comprise a single endodermal and cortical layer. In cereals, the quiescent center (QC), a central region of the root tip, consists of 800–2000 cells whereas the *Arabidopsis* QC contains only four cells (Jiang et al. 2003). Lateral roots in cereals originate

from pericycle and endodermis cells, whereas in *Arabidopsis* lateral roots originate only from pericycle cells (Fahn 1990; Beeckman et al. 2001). Vascular cambium, which replaces the dead or old xylem vessels with new ones, is absent in cereal roots, yet is an integral part of dicotyledonous roots. Vascular segmentation offers flexibility over the lack of cambia by forming "safety zones" in cereal roots, which protect them from cavitation and embolism at the root–shoot junction during moisture or freezing stress (Luxova 1986). Functional xylem anatomy reveals that the development of vascular segmentation in the root–shoot junction varies among cereal species. For example, cereal species, namely, rye, wheat, and barley, which develop several seminal roots, exhibit a high degree of vascular segmentation that results in formation of safety zones at the root–shoot junction. On the other hand, sorghum, which typically develops a single primary seminal root, contains unsafe vessels and exhibits a smaller degree of vascular segmentation (Luxova 1989; Aloni and Griffith 1991). Appearance of nodal roots in later stages of plant development provides some flexibility over the lack of vascular cambia in sorghum.

3.2 Genetic Variation for RSA in Sorghum

To a large extent, success of any crop improvement program depends on existing genetic variability in crop germplasm. Keeping this in view, studies were conducted to investigate the extent of genetic variation for root traits in sorghum. For instance, Damodar et al. (1978) observed significant genetic variation for vertical distribution of roots for 11 sorghum genotypes evaluated in moisture-limited environments. Wright et al. (1983) reported greater root length density for drought-tolerant sorghum cultivar E-57 especially below 80 cm, compared with a drought-susceptible sorghum cultivar, TX-671. As a result, the tolerant genotype extracted more water from below 80 cm after the booting stage. Similarly, Irwin et al. (1985) identified two

distinct phenotypic classes for root angle in a set of 11 hybrids in sorghum, which included a horizontally oriented and a more vertically oriented nodal root system. However, their study did not relate the structural difference to function. Observation of distinct classes for root orientation among genotypes provides ample scope for its improvement through breeding. Likewise, Singh et al. (2011) observed a wide range of nodal root angle (14°–50°) in a set of 44 inbred lines and 30 hybrids. In addition to nodal root angle, they observed significant genetic variation for root length, root diameter, and root dry weight among the inbreds and hybrids. Interestingly, they observed a weak association between nodal root angle and plant size (root weight, shoot weight, and leaf area). The weak association indicates that nodal root angle and plant size are governed by different mechanisms for drought adaptation to water-limited environments. Mace et al. (2012) also observed a wide range of genetic variation for nodal root angle (14.6°–32.3°) in a set of 141 recombinant inbred lines of sorghum derived from a cross between inbred lines B923296 (narrow root angle, 18.3°) and SC170-6-8 (wide root angle, 32.3°).

In any crop species, landraces offer a great genetic potential for both biotic and abiotic stress tolerance due to their adaptation to wide agroecological niches and they are not subjected to selection over a long period of time. Sorghum landraces by virtue of their wide adaptation to moisture- and nutrient-limited environments offer great scope for genetic manipulation of RSA. Keeping this in view, Ali et al. (2009) investigated the genotypic variation for root traits in local landraces of Pakistani origin and observed considerable genetic variation for dry root weight, which is an important determinant of drought tolerance in sorghum.

Although a vast genetic variation for many drought-adaptive traits has been reported in sorghum, surprisingly very limited work has been done on the RSA. The above-mentioned reports have presented sufficient evidence of genotypic variation for root traits; however, these studies have focused on a limited set of genotypes with a narrow genetic base. Thus an exhaustive search

of potential donors to root traits is the foremost step in genetic manipulation of RSA to enhance drought adaptation of sorghum. Given the context, a list of the genotypes identified as a potential source for root traits contributing to drought tolerance in sorghum is presented in Table 2. These sources can be utilized as potent sources for introgressing the quantitative trait loci governing superior root traits to drought-susceptible genotypes.

3.3 Impact of Moisture Stress on RSA of Sorghum

Soil water content strongly influences root morphology, root anatomy, and the overall pattern by which different components of RSA contribute to water transport (Salih et al. 1999). Various authors have studied the impact of moisture stress on the sorghum root system. Nivedita et al. (1992) reported that a gravimetric moisture content of less than 19 % and bulk density of 1.65 g cm^{-3} were detrimental to germination as well as seedling emergence in sorghum and pearl millet under moisture stress. Passioura (1982)

reported that extreme moisture stress imposes a negative effect on RSA by impeding growth and development of nodal roots, which often results in complete crop failure. A contrasting distribution profile of nodal roots under varying soil water regimes has been observed in sorghum. For instance, watering of the top soil around the plant crown can lead to the formation of new nodal roots, whereas the extension rate of existing nodal roots is inhibited (1984). This type of growth pattern ultimately results in a horizontally distributed and shallow RSA. In contrast, a marked reduction in the number of new nodal roots and an increase in the extension rate of existing roots were observed when growing conditions changed from wetter to drier (Jordan et al. 1979), resulting in a more vertically oriented RSA with more uniform root distribution at deep soil layers. Likewise, Pardales and Kono (1990) observed that seminal and nodal roots responded differently to rewatering of stressed sorghum plants, with a significant increase in both the number and length of nodal roots, but no response of seminal roots to rewatering. Rostamaza et al. (2013) performed a comparative analysis of the response of sorghum and pearl

Table 2 Sources of superior root traits contributing drought tolerance in sorghum

RSA component	Source	Reference
Narrow nodal root angle	R993396, B923296, SC56-14E, BTx642, R931945-2-2, ATx642 × RQL36	Singh et al. (2011)
Wide nodal root angle	SC999, SC170-6-8, BTx623, ISI2611C, ATx623 × RTx7000	Singh et al. (2011)
Vertically oriented RSA	Aispuri	Damodar et al. (1978)
Extensive lateral root development	IS 9673, IS 9183, B 36-1, and IS 9357	Bhan et al. (1973)
Root length density	FJS-1, FJS-11, FJSS-17, SSM1611, IS16101, SSM249	Ali et al. (2009), Chopart et al. (2008)
Root weight	AS2752, AS5057, AS4289, MS7819, IS5379, AS8038, AS6616, K3, MS7837, ISI2611C, B923296	Vinodhana and Ganesamurthy (2010), Singh et al. (2011)
Root thickness	QL 36, SPV 570, SC636-6,	Singh et al. (2011), Rajkumar et al. (2013)
Higher number of brace roots	Sansui	Li et al. (2014)
Higher number of primary and secondary roots	IS 1183, IS 1137	Bhan et al. (1973)

millet nodal roots to varying moisture regimes. The investigation revealed that differences between two species were associated with root branching and nodal root length which influenced the water uptake pattern. Faster root branching rate and increased nodal root length were the key factors for more plastic response of pearl millet than sorghum to moisture stress.

Root elongation rate (RER) is one component of RSA that is strongly affected by a variety of soil factors: water and nutrient availability (Dunbabin et al. 2000), soil temperature (Diggle 1988; Pages and Jordan 1989), and soil bulk density (Clausnitzer and Hopmans 1994). In general, low soil water content inhibits RER (Salim et al. 1965) and leads to thinner roots (Sharp et al. 1988) and poor lateral branching (Stasovski and Peterson 1991). Changes in growth angle of roots have also been observed with varying moisture regime in cereals (Oyanagi et al. 1993). Soil water content along with several other factors therefore can play an important role in modifying root architecture and functioning for plant survival and growth in given environments.

3.4   Key Components of RSA Influencing Drought Tolerance in Sorghum

Various components of RSA in terms of their number, length, diameter, weight, volume, density, surface area, and elongation rate determine the capacity of sorghum genotypes to survive and grow in drought-prone environments. Sorghum genotypes adapted to moisture-limited environments are often characterized by a deep and vigorous root system (Blum et al. 1997). Bibi et al. (2012) assessed the genetic potential of different sorghum accessions to drought tolerance at the seedling stage and reported that root length was the highest contributor towards drought tolerance. Many studies have identified dry root weight and root length density (RLD) as reliable and easiest root components to determine the drought tolerance in sorghum (Nour et al. 1978; Matsuura et al. 1996; Ali et al. 2009).

A study by Robertson et al. (1993) in sorghum indicated a low RLD threshold of 0.2 cm cm^{-3} above which any increase in RLD would not increase water extraction. However, Cherif-Ari et al. (1990) reported a RLD threshold from 0.29 and 0.86 cm cm^{-3} for sorghum genotypes subjected to moisture stress. Thresholds for sorghum are generally below those found for maize, for which values of around 0.5–0.6 cm cm^{-3} (van Oosterom et al. 2016) and 1.70–2.56 cm cm^{-3} (Aina and Fapohunda 1986) have been reported. Blum and Arkin (1984) observed higher total cumulative root length and RLD for the late as compared to early maturing sorghum genotype under moisture stress. RLD beyond the threshold can indicate excessive dry mass allocation to roots at the expense of reproductive organs, which can negatively affect drought adaptation (van Oosterom et al. 2016).

Apart from these components, spatial distribution of roots and rooting depth are the critical factors for determining the drought-tolerance potential and survival of plants in drought-prone environments. The importance of spatial distribution of roots and rooting depth for crop productivity arises from the fact that soil resources are haphazardly distributed in time and space and are subjected to localized depletion in stress environments (Robinson 1994). This is especially important in crops such as sorghum, as they are frequently grown in moisture-limited environments. Root growth angle is an important determinant of RSA that strongly influences the spatial distribution and rooting depth in sorghum. In fact, the root angle spread at an early growth stage can serve as a useful predictor of the distribution and root biomass at the adult stage (Singh 2010) and may serve as a good reference point for comparison to other environmental conditions. Studies have demonstrated that the vertical distribution pattern of roots as a consequence of narrow root angle enhances the rooting depth, which is important if water availability in the upper soil layers becomes insufficient in terminal drought-stress environments (Manschandi et al. 2008; Hammer et al. 2009; Uga et al. 2011). On the other hand, wide root angle, which results in more horizontally distributed and shallow

RSA, is more relevant in skip-row-management systems in water-limited environments (McLean et al. 2003; Whish et al. 2005).

In sorghum, Singh et al. (2012) carried out a thorough investigation to study the effect of nodal root angle on the water extraction pattern of mature sorghum plants. Four inbred lines with contrasting nodal root angle, SC170-6-8, SC636-6, B923296, and R931945-2-2, at the seedling stage were grown up to flowering in large rhizotrons. The root systems of B923296 (narrow angle) and SC170-6-8 (wide angle) showed clear differences in vertical and horizontal distribution of roots at flowering. B923296 had more roots visible against the glass surface of the rhizotrons than SC170-6-8 at 100 cm depth immediately below the plant, whereas SC170-6-8 had more roots visible than B923296 at 80 cm depth, 120 cm away from the plant. These findings suggest that nodal root angle at the seedling stage can affect the spatial distribution of roots of mature plants. Genotypes with narrow root angle potentially increase root distribution at depth, which is important if water availability in the upper soil layers becomes insufficient to enable the crop to complete its life cycle. On the other hand, a genotype with wider root angle but shallower root system may be able to exploit small events of in-season rainfall from the upper soil layer.

The role of xylem vessel diameter has been clearly demonstrated in influencing drought tolerance in cereals. For instance, xylem vessel diameter has been used as an effective selection criterion in spring wheat breeding programs in Australia (Richards and Passioura 1989) and rice breeding programs in Asia (Yambao et al. 1992; Sibounheuang et al. 2006; Abd Allah et al. 2010), where the goal is to improve water acquisition from drying soils. In sorghum, Bawazir and Idle (1989) reported significant genetic variation for xylem vessel conductivity in seminal and nodal roots of nine genotypes in response to moisture stress. Genotypic differences in drought tolerance between sorghum cultivars "Tabat" (susceptible) and "Gadambalia" (tolerant) have been associated with anatomical components of RSA (Salih et al. 1999). As compared to drought-susceptible cultivar Tabat, the RSA of drought-tolerant cultivar Gadambalia was characterized by its ability to produce a smaller number of late metaxylem vessels and presence of sclerenchyma sheath around the vascular system, which reduced the axial water flow during moisture stress. Anatomical traits, root cortical aerenchyma (RCA), cortical cell file number (CCFN), and cortical cell size (CCS), were reported to reduce the metabolic cost of root growth in maize under moisture and nutrient-limited environments (Lynch 2015). Zhu et al. (2010) compared maize recombinant inbred lines (RILs) differing for RCA formation under moisture stress in the field and soil mesocosms in greenhouse. In field conditions, lines with high RCA had high RLD and produced 30 % more shoot biomass at flowering compared with the lines with low RCA. On average, high RCA lines yielded eight times more than low RCA lines. In mesocosms, high RCA lines were characterized by less seminal root respiration, deeper rooting, and greater shoot biomass compared with low RCA lines. These findings suggested that RCA deserves consideration as an important component of RSA to improve drought tolerance in cereal breeding programs. Therefore, there is an urgent need to explore the genetic basis and functional aspects of root anatomical traits in sorghum. Identification of genomic regions governing root anatomical traits would greatly facilitate their use in sorghum breeding programs.

4 Genetic Control of RSA in Sorghum

4.1 Gene Action and Heritability

Prior information on genetic control, prevailing gene action, and estimates of heritability is mandatory for designing a suitable breeding strategy for genetic improvement of any trait. However, information on gene action and heritability of sorghum root traits is very limited. Jordan et al. (1979) showed that root characters, root length, mass, and volume, were

polygenically controlled. Vinodhana and Gane-samurthy (2010) reported higher estimates of phenotypic and genotypic coefficient of variation coupled with high broad sense heritability and expected genetic gain for root volume in sorghum. Likewise, high heritability estimates and genetic advance for other traits, namely, root length, number of roots per plant, root fresh weight, root dry weight, and root-to-shoot ratio in sorghum have been reported (Thudi 2004; Ali et al. 2009; Rajkumar et al. 2013). Such high estimates for root traits in sorghum indicate that they are more likely to be controlled by additive gene action and selection will be effective for these traits to improve drought tolerance in sorghum breeding programs. Singh et al. (2011) assessed the inheritance pattern of nodal root angle and dry root weight in a set of 44 inbred lines and 30 hybrids. It was observed that both traits were polygenically controlled and exhibited moderate heritability. Although the heritability of nodal root angle was moderate, its genetic architecture was not simple, as illustrated by the significant specific combining ability (SCA) effects and the high contribution of male and female interactions to the heritability.

Drought tolerance in plants is often associated with the capacity of the roots to absorb available nutrients under moisture-limited environments (Amelework et al. 2015). For instance, Shang-guan et al. (2005) reported that hydraulic conductivity of seminal and nodal roots in sorghum was strongly influenced by phosphorus availability under water deficiency. Keeping this in view, efforts were carried out to find the gene action underlying root length, root dry weight, and root/shoot dry weight under low phosphorus availability using the F_2 segregating generation derived from the cross between "B69" and "Numbu" in sorghum (Trikoesoemaningtyas et al. 2015). The investigation elucidated that additive gene action is involved in genetic control of root length, root dry weight, and root/shoot dry weight. In addition to this, high heritability and moderate genotypic coefficient of variation (GCV) indicated that root length and root dry weight can be used as selection criteria in low-P condition at the seedling stage.

In general, high to moderate heritability estimates were reported for the majority of root traits in sorghum. However, heritability estimates were thus far mainly calculated based on replications within homogeneous experimental conditions under a controlled environment (laboratory/greenhouse). A decreasing trend in heritabilities under low nitrogen condition have been observed for root traits such as root angle and branching density in maize due to the pronounced effect of soil heterogeneity (Cai et al. 2012; Colombi et al. 2015). Therefore, it remains to be elucidated whether heritabilities of root traits stay high in sorghum, when compared across years and soil environments.

4.2   Quantitative Trait Loci (QTLs) Governing RSA

A number of QTLs governing various root traits in cereals have been identified, which can be introgressed into drought-susceptible cultivars through marker-assisted selection (MAS). Among the cereal species, rice has been thoroughly investigated for QTLs controlling RSA and some of them explained up to 50 % of phenotypic variability for root traits (Price et al. 1997, 2000, 2002; Uga et al. 2011). Although various QTLs governing yield and yield components, stay-green, flowering, and maturity under moisture stress have been mapped on 10 linkage groups of sorghum (Sanchez et al. 2002; Borrell et al. 2006), information on QTLs governing RSA is still in its infancy in sorghum. A detailed description of various QTLs governing sorghum RSA is presented in Table 3. Mace et al. (2012) for the first time carried out a comprehensive genetic mapping study to dissect the genetic control of RSA in sorghum. They identified four major QTLs governing nodal root angle and three QTLs controlling root dry weight (Table 3) in a recombinant inbred line (RIL) population derived from a cross between two inbred sorghum lines with contrasting root angle   (B923296/SC170-6-8).   Interestingly, BLAST analysis revealed that three of the four nodal root angle QTLs were homologous to

Table 3 Details of different QTLs identified for various root traits in sorghum

Root trait	Mapping population	Markers	Identified QTLs	Linkage group	Phenotypic variation (%)	Reference
Root angle	B923296 × SC170-6-8	377 DArT markers	qRA1_5, qRA2_5, qRA1_8, qRA1_10	LG 5, 8 and 10	58.16	Mace et al. (2012)
Dry root weight	B923296 × SC170-6-8	–	qRDW1_2, qRDW1_5, qRDW1_8	LG 2, 5 and 8	32.08	Mace et al. (2012)
	E36-1 × SPV570	938 markers (270 nongenic nuclear SSRs, 530 EST-SSRs and 138 SNPs)	qRD4	LG 4	9.21	Rajkumar et al. (2013)
Fresh root weight	E36-1 × SPV570	–	qRF4	LG 4	9.21	Rajkumar et al. (2013)
Root length	E36-1 × SPV570	–	qRL4	LG 4	8.33	Rajkumar et al. (2013)
Root volume	E36-1 × SPV570	–	qRV1, qRV4	LG 1 and 4	27.05	Rajkumar et al. (2013)
Number of roots/plant	E36-1 × SPV570	–	qRN1	LG 1	17.87	Rajkumar et al. (2013)
Root/shoot ratio	E36-1 × SPV570	–	qRS10, qRS10.1	LG 10	16.03	Rajkumar et al. (2013)
Number of brace roots	Sansui × Jiliang 2	326 SSR markers	qRT6, qRT7	LG 6 and 7	59.5	Li et al. (2014)

previously identified root angle QTLs in rice and maize. The locations of the QTLs identified in the investigation were also projected onto a sorghum consensus map (Mace et al. 2009). Importantly, all four nodal root angle QTLs identified in this study were colocated with previously identified QTLs for stay-green. The colocation of the QTLs indicated the putative genetic association between nodal root angle and the stay-green drought response in sorghum. Furthermore, a putative association between three QTLs governing nodal root angle and grain yield was identified through single marker analysis conducted on yield data recorded in a subset of the mapping population grown in hybrid combination with three different tester lines.

Similarly, Rajkumar et al. (2013) reported colocalization of QTL for root volume with QTL for root fresh weight and root dry weight on chromosome number 4 of sorghum. The colocalization of QTLs for root traits in sorghum can assist in their introgression in drought-susceptible cultivars through MAS utilizing the same linked markers. Further association analysis revealed that root-related QTLs identified were quite distinct from the QTLs governing yield component traits identified in the same population. However, a nonsignificant but positive association was observed between root traits and seed yield/plant. It is thus possible to combine grain yield and desirable root traits to enhance productivity under moisture stress.

Root architecture is the key factor in determining the phosphorus uptake of the cereals in harsh environmental conditions (Doumbia et al. 1993, 1998). In rice, a major QTL, *phosphorus uptake 1* (*Pup1*) was mapped on the long arm of chromosome 12 (Heuer et al. 2009). High-resolution mapping of *Pup1* locus identified a gene designated *phosphorus-starvation tolerance 1* (*OsPSTOL1*), which is known to increase P uptake through enhancement of early root growth and development under low-P conditions (Gamuyao et al. 2012). Hydraulic conductivity of seminal and nodal roots in sorghum is known to be strongly influenced by phosphorus availability under water deficiency (Shangguan et al. 2005). Hufnagel et al. (2014) investigated the role of *SbPSTOL1*, an homologous gene of the rice *OsPSTOL1* in sorghum on plant performance under low-P conditions. Two association mapping panels—sorghum association panel subset (SAPst) and West African association panel (WAP)—were rigorously phenotyped for P uptake and root morphology in hydroponics, and grain yield under low-P conditions in Brazil and Mali. The investigation elucidated *SbPSTOL1* alleles involved in reducing root diameter under low-P condition in hydroponics and increased root surface area in low-P soil. Furthermore, the role of *SbPSTOL1* was validated through linkage mapping in a large RIL population derived from the sorghum parents with contrasting root morphology. Interestingly, *SbPSTOL1* alleles were colocalized with QTL governing root length, root diameter, and root surface area under low-P conditions in sorghum.

4.3   Marker-Assisted Selection (MAS) for RSA

Genetic studies confirmed that the RSA of sorghum is a complex character, which is controlled not only by major-effect QTLs but also by plenty of minor QTLs exerting smaller effects on the root phenotype. Additionally, the presence of genotype × environment interactions also hampers the progress of RSA improvement using a conventional breeding approach. Therefore, several molecular breeding schemes have been developed recently that have enabled the detailed dissection of the complex root traits. Among various molecular breeding schemes, thus far marker-assisted backcrossing (MABC) in rice (Steele et al. 2006) and advanced backcross QTL (AB-QTL) analysis in barley (Naz et al. 2014) are the methods utilized for incorporation of desirable root traits in different genetic background in cereals. The best evidence of successful utilization of a molecular breeding scheme to pyramid various root traits to improve crop drought tolerance is the development of a highly drought-tolerant cultivar "Birsa Vikas Dhan 111," which is developed by introgressing quantitative trait loci governing deeper rooting length through MABC in rice (Steel et al. 2013). To the best of our knowledge, to date there is no report on marker-assisted introgression of QTLs governing superior root characters to drought-susceptible genotypes in sorghum. The major reason for this is the lack of high-throughput phenotyping platforms for accurate and efficient screening of root traits in large breeding populations (Francia et al. 2005). In addition to this, imprecise QTL identification, inconsistency in validation of QTLs detected in controlled and field conditions, their unstable expression across the populations and environments, and unfavorable epistatic interaction have adversely affected the breeding programs entailing manipulation of RSA through MAS. For these reasons, there have been very few reports on the use of MAS for improvement of RSA in cereal breeding programs and there is no report on marker-assisted introgression of QTLs governing superior root characters to drought-susceptible genotypes in sorghum. A holistic molecular breeding approach combined with rigorous controlled and field-based phenotyping of root traits for genetic manipulation of RSA in sorghum has been proposed (Fig. 1) in this chapter. The approach is followed after the development of high-throughput phenotyping and genotyping methods. The best germplasm sources for an effective screening of root traits are multiparental breeding populations, core and mini-core collections, and diversity
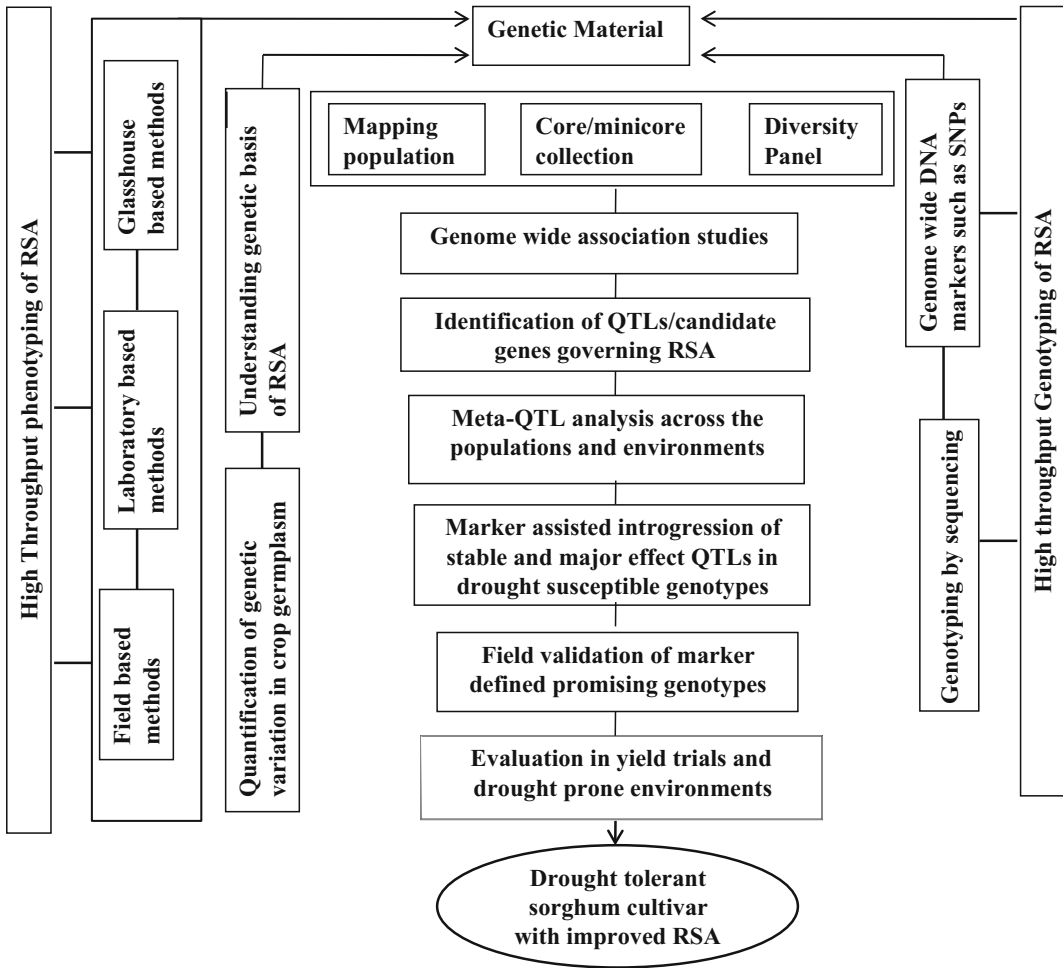
Fig. 1 Overview of molecular breeding approach to manipulate the root system architecture (RSA) in sorghum

panels. This approach combines QTL mapping and genomewide association studies (GWAS) with MAS. Last, this approach involves multilocation field testing of the marker-defined promising genotypes to assess their performance for the ultimate breeding target (grain yield).

5 Summary and Outlook

Genetic manipulation of RSA holds great promise to enhance productivity of sorghum under water deficit. The majority of the RSA components discussed in this chapter have shown genetic variation among crop genotypes, and

thus could be integrated in breeding programs. However, quantification of genetic variation and genetic control of root traits is at its beginning stage. Therefore, an exhaustive characterization of diverse germplasm sources, namely core collections, diversity panels, multiparental breeding populations, and landraces, is required for identification of appropriate donors for superior root traits. In addition to the mainstream gene pool, wild species can serve as potential donors for the root traits due to their ability to colonize a wide range of moisture and soil regimes and to withstand harsh and nutrient-limited environments. Potential donors for root traits have been observed in wild species of barley (Grando and

Ceccarelli 1995), rice (Liu et al. 2004), and wheat (Reynold et al. 2007; Placido et al. 2013). However, wild sorghum species are still unexplored for root traits. Utility of RSA components such as nodal root angle, dry root weight, and RLD is fairly well established to influence drought tolerance in sorghum. In addition to this, traits such as nodal root angle at the early seedling stage have been suggested as proxy traits to determine drought tolerance of adult sorghum plants. However, a challenging obstacle to the deployment of these RSA components in sorghum breeding is the difficulty in evaluating root phenotypes of a large number of breeding lines or multiparental mapping populations. Therefore, efforts should be directed towards development of robust root screening platforms that are capable of (i) expressing high heritability for the measured component trait, (ii) minimizing the G × E interaction, (iii) screening the root trait at the early seedling stage to shorten the selection cycle and speed up genetic improvement, and (iv) finally, establishing the genetic correlation between the root trait phenotyped on the platform and ultimate breeding objective.

QTLs have been identified for traits related to root morphology, which has resulted in a great magnitude of knowledge and better understanding of the genetic control of RSA in sorghum. However, the root anatomy of sorghum is very poorly understood at present. Therefore, immediate attention needs to be paid towards identification of genomic regions governing root anatomical phenes, which will greatly facilitate their use in breeding programs. Meta–QTL analysis followed by cloning of QTLs, which are stable across populations and environments, will provide a driving force in molecular breeding for RSA because a cloned QTL can offer a reliable marker for MABC. However, the impact of a cloned QTL or candidate gene underlying the QTL region on plant productivity needs to be tested in a given environment. Furthermore, transformation of the knowledge acquired from genomics-oriented approaches into a drought-tolerant high-yielding cultivar with improved RSA is the most daunting challenge faced by breeders.

Efforts should also be directed towards understanding the physiological mechanisms that control functional aspects of RSA and its impact on crop performance in the field. Understanding the physiological mechanism and signaling behavior of roots in response to stress and subsequent physiological alterations in shoots will certainly assist plant breeding efforts towards RSA improvement in sorghum. Indeed, a multidisciplinary approach is required to integrate growing omics techniques with plant physiology, agronomy, and breeding to improve productivity of sorghum under drought through genetic manipulation of RSA.

References

Abd Allah AA, Shimaa AB, Zayed BA, Gohary AAE (2010) The role of root system traits in the drought tolerance of rice (*Oryza sativa* L.). Int J Agric Biol Sci 1:83–87

Aina PO, Fapohunda HO (1986) Root distribution and water uptake patterns of maize cultivars field-grown under different irrigation. Plant Soil 94:257–265

Ali MA, Niaz S, Abbas A, Sabir W, Jabran K (2009) Genetic diversity and assessment of drought tolerant sorghum landraces based on morph-physiological traits at different growth stages. Plant Omics 2:214–227

Aloni R, Griffith M (1991) Functional xylem anatomy in root-shoot junctions of six cereal species. Planta 184:123–129

Amelework B, Shimelis H, Tongoona P, Laing M (2015) Physiological mechanisms of drought tolerance in sorghum, genetic basis and breeding methods: a review. Afr J Agric Res 10:3029–3040

Asseng S, Turner NC (2007) Modelling genotype x environment management interactions to improve yield, water use efficiency and grain protein in wheat. In: Spiertz JHJ, Struik PC, Van Laar HH (eds) Scale and complexity in plant systems research: gene–plant–crop relations, vol 21. Wageningen UR Frontis Series, Netherlands, pp 93–103

Basu P, Pal A, Lynch JP, Brown KM (2007) A novel image anlaysis technique for kinematic study of growth and curvature. Plant Physiol 145:305–316

Bawazir AA, Idle DB (1989) Drought resistance and root morphology in sorghum. Plant Soil 119:217–221

Beeckman T, Burssens S, Inze D (2001) The peri-cell-cycle in Arabidopsis. J Exp Bot 52:403–411

Bengough AG, Gordon DC, Al-Menaie H, Ellis RP, Allan D, Keith R, Thomas WB, Forster BP (2004) Gel observation chamber for rapid screening of root traits in cereal seedlings. Plant Soil 262:63–70

Bhan U, Singh HG, Singh A (1973) Note on root development as an index of drought resistance in sorghum (Sorghum bicolor (L.) Moench). Indian J Agric Sci 43:828–830

Bibi A, Sadaqat HA, Tahir MH, Akram HM (2012) Screening of sorghum (Sorghum bicolor Var Moench) for drought tolerance at seedling stage in polyethylene glycol. J Anim Plant Sci 22:671–678

Blum A, Arkin GF (1984) Sorghum root growth and water-use as affected by water supply and growth duration. Field Crops Res 9:131–142

Blum A, Ritchie JT (1984) Effect of soil surface water content on sorghum root distribution in the soil. Field Crops Res 8:169–176

Blum A, Arkin GF, Jordan WR (1977) Sorghum root morphogenesis and growth. I. Effect of maturity genes. Crop Sci 17:149–153

Blum A, Golan G, Golan G (1989) Agronomic and physiological assessments genotypic variation for drought resistance in sorghum. Aust J Agric Res 40:49–61

Blum A, Golan G, Mayer J, Sinmena B (1997) The effect of dwarfing genes on sorghum grain filling from remobilized stem reserves under stress. Field Crops Res 52:43–54

Borrell A, Jordan D, Mullet J, Henzell B, Hammer G (2006) Drought adaptation in sorghum. In: Ribaut JM (ed) Drought Adaptation in Cereals. The Haworth Press, Binghamton, pp 335–378

Borrell AK, Mullet JE, George-Jaeggli B, van Oosterom EJ, Hammer GL, Klein PE, Jordan DR (2014) Drought adaptation of stay-green cereals associated with canopy development, leaf anatomy, root growth and water uptake. J Expt Bot 65:6251–6263

Bucksch A, Burridge J, York LM, Das A, Nord E, Weitz JS, Lynch JP (2014) Image-based high-throughput field phenotyping of crop roots. Plant Physiol 166:470–486

Cai H, Chen F, Mi G et al (2012) Mapping QTLs for root system architecture of maize (Zea mays L.) in the field at different developmental stages. Theor Appl Genet 125:1313–1324

Cherif-Ari O, Housley TL, Ejeta G (1990) Sorghum root length density and the potential for avoiding Striga parasitia. Plant Soil 121:67–72

Chopart JL, Sine B, Dao A, Muller B (2008) Root orientation of four sorghum cultivars: application to estimate root length density from root counts in soil profiles. Plant Root 2:67–75

Clark RT, MacCurdy RB, Jung JK, Shaff JE, McCouch SR, Aneshansley DJ, Kochian LV (2011) Three-dimensional root phenotyping with a novel imaging and software platform. Plant Physiol 156:455–465

Clark RT, Famoso AN, Zhao K, Shaff JE, Craft EJ, Bustamante CD, Mccouch SR, Aneshansley DJ, Kochian LV (2013) High-throughput two-dimensional root system phenotyping platform facilitates genetic analysis of root growth and development. Plant Cell Environ 36:454–466

Clausnitzer V, Hopmans JW (1994) Simultaneous modelling of transient three-dimensional root growth and soil water flow. Plant Soil 164:299–314

Colombi T, Kirchgessner N, Le Marie CA, York LM, Lynch JP, Hund A (2015) Next generation shovelomics: set up a tent and REST. Plant Soil 388:1–20

Damodar R, Rao JVS, Rao NGP (1978) Genetic analysis of some exotic x Indian crosses in sorghum: Genotypic differences for root activity. Indian J Genet 38:421–430

Dardanelli JL, Bachmeier A, Sereno R, Gil R (1997) Rooting depth and soil water extraction patterns of different crops in a silty loam and Haptustoll. Field Crops Res 54:29–38

de Dorlodot S, Forster B, Pages L, Price AH, Tuberosa R, Draye X (2007) Root system architecture: opportunities and constraints for genetic improvement of crops. Trends Plant Sci 12:474–481

Diggle AJ (1988) ROOTMAP-a model in three dimensional coordiantes of the growth and structure of fibrous root system. Plant Soil 105:169–178

Doumbia MD, Hossner LR, Onken B (1993) Variable sorghum growth in acid soils of sub humid West Africa. Arid Soil Res Rehabil 7:335–346

Doumbia MD, Hossner LR, Onken AB (1998) Sorghum growth in acid soils of West Africa: variations in soil chemical properties. Arid Soil Res Rehabil 12:179–190

Dunbabin V, Diggle AJ, Rengel Z, van Hungten R (2000) Modelling the interactions between water and nutrient uptake and root growth. Plant Soil 239:19–38

Esau K (1977) Anatomy of seed plants, 2nd edn. Wiley, New York

Fahn A (1990) Plant anatomy, 4th edn. Pergamon press, Oxford

Feldman L (1994) The maize root. In: Freeling M, Walbot V (eds) The maize handbook. Springer, New York, pp 29–37

Francia E, Tacconi G, Crosatti C, Barabaschi D, Bulgarelli, D, Dall'Aglio E et al (2005) Marker assisted selection in crop plants. Plant Cell Tiss Org Cult 82:317–342

Gamuyao R, Chin JH, Pariasca-Tanaka J, Pesaresi P, Catausan S, Dalid C, Slamet-Loedin I, Tecson-Mendoza EM, Wissuwa M, Heuer S (2012) The protein kinase Pstol1 from traditional rice confers tolerance of phosphorus deficiency. Nature 488:535–539

Girma S (1989) Osmotic adjustment: A drought tolerance mechanism in sorghum. Sci Eng 50:4570–4573

Girma SF, Krieg DR (1992) Osmotic adjustment in sorghum. I. Mechanisms of diurnal osmotic potential changes. Plant Physiol 99:577–582

Grando S, Ceccarelli S (1995) Seminal root morphology and coleoptile length in wild (*Hordeum vulgare* ssp. *spontaneum*) and cultivated (*Hordeum vulgare* ssp. *vulgare*) barley. Euphytica 86:73–80

Gregory PJ (1983) Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.). III. Root development. J Expt Bot 34:744–756

Gregory PJ (2006) Plant roots. Growth, Activity and Interaction with Soils. Blackwell Publishing, Oxford

Hammer GL, Dong ZS, McLean G, Doherty A, Messina C, Schussler J, Zinselmeier C, Paszkiewicz S, Cooper M (2009) Can changes in canopy and/or root system architecture explain historical maize yield trends in the U.S. Corn Belt? Crop Sci 49:299–312

Hargreaves CE, Gregory PJ, Bengough AG (2009) Measuring root traits in Barley (*Hordeum vulgare* ssp. *vulgare* and ssp. *spontaneum*) seedlings using gel chambers, soil sacs and X-ray microtomogrphy. Plant Soil 316:285–297

Heuer S, Lu X, Chin JH, Tanaka JP, Kanamori H, Matsumoto T, De Leon T, Ulat VJ, Ismail AM, Yano M et al (2009) Comparative sequence analyses of the major quantitative trait locus *phosphorus uptake 1 (Pup1)* reveal a complex genetic structure. Plant Biotechnol J 7:456–471

Hochholdinger F, Katrin W, Sauer M, Dembonsky D (2004a) Genetic dissection of root formation in maize reveals root-type specific development programmes. Ann Bot 93:359–368

Hochholdinger F, Park WJ, Sauer M, Woll K (2004b) From weeds to crops: genetic analysis of root development in cereals. Trends Plant Sci 9:42–48

Hufnagel B, de Sousa SM, Assis L, Guimaraes CT, Leiser W, Azevedo GC, Negri B, Larson BG, Shaff JE, Pastina MM, Barros BA, Weltzien E, Rattunde HFW, Viana JH, Clark RT, Falcão A, Gazaffi R, Garcia AAF, Schaffert RE, Kochian LV, Magalhaes JV (2014) Duplicate and conquer: multiple homologs of PHOSPHORUS-STARVATION TOLERANCE1 enhance phosphorus acquisition and sorghum performance on low-phosphorus soils. Plant Physiol 166:659–677

Hund A, Trachsel S, Stamp P (2009) Growth of axile and lateral roots of maize: I development of a phenotyping platform. Plant Soil 325:335–349

IPCC (2012) Summary for policymakers. In: Field CB, Barros V, Stocker TF, Qin D, Dokken DJ, Ebi KL, Mastrandrea MD, Mach KJ, Plattner GK, Allen SK, Tignor M, Midgley PM (eds) Managing the risks of extreme events and disasters to advance climate change adaptation. A special report of working groups I and II of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, UK, and New York, NY, USA, pp 3–21

Irwin RL, Johnson WC, Elkins CB (1985) Highlights of agricultural Res. 32. No. 1, Albama Agricultural Experiment Station, Auburn University, Albama, USA

Iyer-Pascuzzi AS, Symonova O, Mileyko Y, Hao Y, Belcher H, Harer J, Weitz JS, Benfey PN (2010) Imaging and analysis platform for automatic phenotyping and trait ranking of plant root systems. Plant Physiol 152:1148–1157

Jha UC, Chaturvedi SK, Bohra A, Basu PS, Khan MS, Barh D (2014) Abiotic stresses, constraints and improvement strategies in chickpea. Plant Breed 133:163–178

Jiang K, Meng YL, Feldman LJ (2003) Quiescent center formation in maize roots is associated with an auxin-regulated oxidizing environment. Development 130:1429–1438

Jordan WR, Miller FR, Morris DE (1979) Genetic variation in root and shoot growth of sorghum in hydroponics. Crop Sci 19–23

Jordan DR, Mace ES, Cruickshank AW, Hunt CH, Henzell RG (2011) Exploring and exploiting genetic variation from unadapted sorghum germplasm in a breeding program. Crop Sci 51:1444–1457

Jordan DR, Hunt CH, Cruickshank AW, Borrell AK, Henzell RG (2012) The relationship between the stay-green trait and grain yield in elite sorghum hybrids grown in a range of environments. Crop Sci 52:1153–1161

Kato Y, Abe J, Kamoshita A, Yamagishi J (2006) Genotypic variation in root growth angle in rice (*Oryza sativa* L.) and its association with deep root development in upland fields with different water regimes. Plant Soil 287:117–129

Kausch W (1967) Lebensdauer der Primarwurzel von Monokotyledons. Naturwissenschaften 54:475

Kiesselbach T (1949) The structure and reproduction of corn. Nebrasca Agric Expt Station Res Bullet 161:3–96

Klepper B, Belford RK, Rickman RW (1984) Root and shoot development in winter wheat. Agron J 76:117–122

Kono Y, Yamauchi A, Nonoyama T, Tatsumi J, Kawamura N (1987) A revised experimental system of root-soil interaction for laboratory work. Environ Contor Biol 25:141–151

Kozinka V (1977) Primary seminal root, a permanent part of the root system of *Zea mays* L. Biologia Bratislava 32:779–786

Lawson WE, Hanway JJ (1977) Corn production. In: sprague G (ed) Corn and corn improvement. American Society of Agronomy Publishers, Madison, WI, USA, pp 625–669

Le Marié C, Kirchgessner N, Marschall D, Walter A, Hund A (2014) Rhizoslides: paper-based growth system for non-destructive, high-throughput phenotyping of root development by means of image analysis. Plant Methods 10:13. doi:10.1186/1746-4811-10-13

Li W, Zhang S, Shan L, Egrinya EA (2011) Changes in root characteristics, gas exchange and water use efficiency following water stress and rehydration of Alfalfa and Sorghum. Aust J Crop Sci 5:1521–1532

Li R, Han Y, Lv P, Du R, Liu G (2014) Molecular mapping of the brace root traits in sorghum (*Sorghum bicolor* L. Moench). Breed Sci 64:193–198

Lilley JM, Kirkegaard JA (2011) Benefits of increased soil exploration by wheat roots. Field Crops Res 122:118–130

Liu L, Lafitte R, Guan D (2004) Wild *Oryza* species as potential sources of drought-adaptive traits. Euphytica 138:149–161

Luxova M (1986) The hydraulic safety zone at the base of barley roots. Planta 169:465–470

Luxova M (1989) The vascular system in the roots of barley and its hydraulic aspects. In: Loughman BC, Gasparikova O, Kolek J (eds) Structural and functional aspects of transport in roots. Kluwer Academic Publications, London, pp 15–20

Lynch JP (2015) Root phenes that reduce the metabolic costs of soil exploration: Opportunities for 21st century agriculture. Plant Cell Environ 38:1775–1784

Lynch JP, Nielsen KL, Davis RD, Jablokow AG (1997) SimRoot: modelling and visualization of root systems. Plant Soil 188:139–151

Mace ES, Rami JF, Klein RR, Kilian A, Wenzl P, Xia L, Halloran K, Jordan DL (2009) A consensus map of sorghum that integrates multiple component maps and high-throughput Diversity Array Technology (DArT) marker. BMC Plant Biol 9:1–14

Mace ES, Singh V, Oosterom EJ, Hammer GL, Hunt CH, Jordan DR (2012) QTL for nodal root angle in sorghum (*Sorghum bicolor* L. Moench) co-locate with QTL for traits associated with drought adaptation. Theor Appl Genet 124:97–109

Mace ES, Tai S, Gilding EK, Li Y, Prentis PJ, Bian L, Campbell BC, Hu W, Innes DJ, Han X, Cruickshank A, Dai C, Frère C, Zhang H, Hunt CH, Wang X, Shatte T, Wang M, Su Z, Li J, Lin X, Godwin ID, Jordan DR, Jl Wang (2013) Whole genome sequencing reveals untapped genetic potential in Africa's indigenous cereal crop sorghum. Nat Commun 4:2320

Mairhofer S, Zappala S, Tracy SR et al (2012) RooTrak: automated recovery of three-dimensional plant root architecture in soil from X-ray microcomputed tomography images using visual tracking. Plant Physiol 158:561–569

Manschadi AM, Hammer GL, Christopher JT, deVoil P (2008) Genotypic variation in seedling root architectural traits and implications for drought adaptation in wheat (*Triticum aestivum* L). Plant Soil 303:115–129

Matsuura A, Inanaga S, Sugimoto Y (1996) Mechanism of interspecific differences among four graminaceous crops in growth response to soil drying. Jpn J Crop Sci 65:352–360

McCully ME, Canny MJ (1988) Pathways and processes of water and nutrients movements in roots. Plant Soil 111:159–170

McLean G, Whish J, Routley R, Broad I, Hammer GL (2003) The effect of row configuration on yield reliability in grain sorghum: II. Modelling the effects of row configuration. In: Proceedings of the 11th Australian Agron conference Geelong, VIC, Australia, 2–6 Feb 2003. http://www.regional.org.au/au/asa/2003/c/9/mclean.htm. Accessed 29 June 2016. The Regional Institute, Gosford, NSW, Australia

Mitra J (2001) Genetics and genetic improvement of drought resistance in crop plants. Curr Sci 80:758–763

Mutava RN (2012) Evaluation of sorghum genotypes for variation in canopy temperature and drought tolerance. PhD Thesis, Kansas State University, Manhattan, Kansas, USA, 163 p

Nakhforoosh A, Grausgruber H, Kaul HP, Bodner G (2015) Dissection of drought response of modern and underutilized wheat varieties according to Passioura's yield-water framework. Front Plant Sci 6:570

Naz AA, Arifuzzaman M, Muzammil S, Pillen K, Leon J (2014) Wild barley introgression lines reveal novel QTL alleles for root and related shoot traits in the cultivated barley (*Hordeum vulgare* L.). BMC Genet 15:107

Nivedita M (1992) Effect of Moisture Status and Bulk Density on Germination and Emergence of Pearl Millet, Sorghum and Groundnut on an Alfisol. MSc Thesis. Andhra Pradesh Agricultural University Hyderabad, India, pp 144

Nour AM, Weibel DE, Tood GW (1978) Evaluation of root characteristics in grain sorghum. Agron J 70:217–218

O' Toole JC, Bland WL (1987) Genotypic variation in crop plant root system. Adv Agron 41:91–145

Oyanagi A, Nakamoto T, Morita S (1993) The gravitropic response of roots and the shaping of the root system in cereal plants. Environ Exp Bot 33:141–158

Pages L, Jordan MO (1989) A simulation model of the three-dimensional architecture of the maize root system. Plant Soil 119:147–154

Pardales JR Jr, Kono Y (1990) Development of sorghum root system under increasing drought stress. Jpn J Crop Sci 59:752–761

Passioura JB (1982) The role of root system characteristics in the drought resistance of crop plants. In: Holmes JC, Taho WM (eds) Drought resistance in crops with emphasis on rice. International Rice Research Institute, Los Baños, Manila, Philippines, pp 71–82

Patil BS, Ravikumar RL (2011) Osmotic adjustment in pollen grains: a measure of drought adaptation in sorghum? Curr Sci 100:377–382

Placido DF, Campbell MT, Folsom JJ, Cui X, Kruger GR, Baenziger PS, Walia H (2013) Introgression of novel traits from a wild Wheat relative improves drought adaptation in wheat. Plant Physiol 161:1806–1819

Planchamp C, Balmer D, Hund A, Mauch-Mani B (2013) A soil-free root observation system for the study of root-microorganism interactions in maize. Plant Soil 367:605–614

Price AH, Tomos AD, Virk DS (1997) Genetic dissection of root growth in rice (*Oryza sativa* L) 1: a hydroponic screen. Theor Appl Genet 95:132–142

Price AH, Steele KA, Moore BJ, Barraclough PB, Clark LJ (2000) A combined RFLP and AFLP linkage map of upland rice used to identify QTLs for root-penetration ability. Theor Appl Genet 100:49–56

Price AH, Steele KA, Gorham J, Bridges JM, Moore BJ, Evans JL, Richardson P, Jones RGW (2002) Upland rice grown in soil-filled chambers and exposed to contrasting water-deficit regimes: I. Root distribution, water use and plant water status. Field Crops Res 76:11–24

Rajkumar Fakrudin B, Kavil SP, Girma Y, Arun SS, Dadakhalandar D, Gurusiddesh BH, Patil AM et al (2013) Molecular mapping of genomic regions harbouring QTLs for root and yield traits in sorghum (*Sorghum bicolor* L. Moench). Physiol Mol Biol Plants 19:409–419

Rakshit S, Hariprasanna K, Gomashe S, Ganapathy KN, Das IK, Ramana OV, Dhandapani A, Patil JV (2014) Changes in area, yield gains, and yield stability of sorghum in major sorghum-producing countries, 1970 to 2009. Crop Sci 54(4):1571–1584

Reynolds M, Dreccer F, Trethowan R (2007) Drought-adaptive traits derived from wheat wild relatives and landraces. J Exp Bot 58:177–186

Richard CAI, Lee TH, Susan F, Raeleen J, Karine, C Christopher JT (2015) High-throughput phenotyping of seminal root traits in wheat. Plant Methods 11:13

Richards RA, Passioura JB (1989) A breeding program to reduce the diameter of the major xylem vessel in the seminal roots of wheat and its effect on grain yield in rain-fed environments. Aust J Agric Res 40:943–950

Robertson MJ, Fukai S, Ludlow MM, Hammer GL (1993) Water extraction by grain sorghum in a sub-humid environment. II. Extraction in relation to root growth. Field Crop Res 33:99–112

Robinson D (1994) The responses of plants to no-uniform supplies of nutrients. New Phytol 127:635–674

Rosenow DT, Quisenberry JE, Wendt CW, Clark LE (1983) Drought tolerant sorghum and cotton germplasm. Agric Water Manag 7:207–222

Rostamza M, Richards RA, Watt M (2013) Response of millet and sorghum to a varying water supply around the primary and nodal roots. Ann Bot 112:439–446

Routley R, Broad I, McLean G, Whish J, Hammer G (2003) The effect of row configuration on yield reliability in grain sorghum: I. Yield, water use efficiency and soil water extraction. In: Proceeding of the 11th Australian agronomy conference, Geelong, Australia, 2–6 Feb 2003. www.regional.org.au/au/asa/2003/c/9/routley.htm. Accessed 29 June 2016. The Regional Institute, Gosford, NSW, Australia

Salih AA, Ali IA, Lux A, Luxova M, Cohen Y, Sugimoto Y, Inanga S (1999) Rooting, water uptake, and xylem structure adaptation to drought of two sorghum cultivars. Crop Sci 39:168–173

Salim MH, Todd GW, Schlehuber AM (1965) Root development of wheat, oats and barley under conditions of soil moisture stress. Agron J 57:603–607

Sanchez AC, Subudhi PK, Rosenow DT, Nguyen HT (2002) Mapping QTLs associated with drought resistance in sorghum (*Sorghum bicolor* (L) Moench). Plant Mol Biol 48:713–726

Shangguan ZP, Lei TW, Shao MA, Xue QW (2005) Effect of phosphorous nutrient on the hydraulic conductivity of sorghum (*Sorghum vulgare*) seedling roots under water deficiency. J Integr Plant Biol 47:421–427

Sharp R, Silk W, Hsiao T (1988) Growth of the maize primary root at low water potentials. I. Spatial distribution of expansive growth. Plant Physiol 87:50–57

Sibounheuang V, Basnayake J, Fukai S (2006) Genotypic consistency in the expression of leaf water potential in rice (*Oryza sativa* L.). Field Crops Res 97:142–154

Singh V (2010) Genotypic variability in structure and function of sorghum root systems. PhD Thesis, University of Queensland, Australia, 112 p

Singh V, van Oosterom EJ, Jordan DR, Messina CD, Cooper M, Hammer GL (2010) Morphological and architectural development of root systems in sorghum and maize. Plant Soil 333:287–299

Singh V, van Oosterom EJ, Jordan DR, Hunt CH, Hammer GL (2011) Genetic variability and control of nodal root angle in sorghum. Crop Sci 51:2011–2020

Singh V, van Oosterom EJ, Jordan R, Hammer GL (2012) Genetic control of root angle in sorghum and its implication in water extraction. Eur J Agron 42:3–10

Stasovski E, Peterson CA (1991) The effects of drought and subsequent rehydration on the structure and vitality of *Zea mays* seedling roots. Can J Bot 69:1170–1178

Steele KA, Price AH, Shashidhar HE, Witcombe JR (2006) Marker-assisted selection to introgress rice QTLs controlling root traits into an Indian upland rice variety. Theor Appl Genet 112:208–221

Steele KA, Price AH, Witcombe JR, Shrestha R, Singh BN, Gibbons JM, Virk DS (2013) QTLs associated with root traits increase yield in upland rice when transferred through marker-assisted selection. Theor Appl Genet 126:101–108

Thudi M (2004) Molecular profiling and phenotyping of root and shoot traits in selected Rabi Sorghum (*Sorghum bicolor* (L.) Moench) genotypes. MSc Thesis, University of Agricultural Science, Dharwad, Karnataka, India

Tingting X, Peixi S, Lishan S (2010) Photosynthetic characteristic and water use efficiency of sweet

sorghum under different watering regimes. Pak J Bot 42:3981–3994

Trachsel S, Kaeppler SM, Brown KM, Lynch JP (2011) Shovelomics: high-throughput phenotyping of maize (*Zea mays* L.) root architecture in the field. Plant Soil 341:75–87

Trikoesoemaningtyas YS, Didy S, Ardi EWS, Satya N (2015) Estimation of genetic parameters and gene actions of sorghum (*Sorghum bicolor* (L.) Moench) tolerance to low P condition. Int J Agron Agric Res 7:38–46

Tuinstra MR, Grote EM, Goldsborough PB, Ejeta G (1996) Identification of quantitative trait loci associated with preflowering drought tolerance in sorghum. Crop Sci 36:1337–1344

Uga Y, Okuno K, Yano M (2011) Dro1, a major QTL involved in deep rooting of rice under upland field conditions. J Exp Bot 62:2485–2494

Vadez V, Deshpande SP, Kholova J, Hammer GL, Borrell AK, Talwar HS, Hash CT (2011) Stay-green quantitative trait loci's effects on water extraction, transpiration efficiency and seed yield depend on recipient parent background. Funct Plant Biol 38:553–566

van Oosterom EJ, Yang Z, Zhang F, Deifel KS, Cooper M, Messina CD, Hammer GL (2016) Genotypic contrast in root system efficiency in maize: potential link to drought adaptation. Funct Plant Biol (in press)

van Weele d, Jiang HS, Palaniappan KK, Ivanov VB, Palaniappan K, Baskin TI (2003) A new algorithm for computational image analysis of deformable motion at high spatial and temporal resolution applied to root

growth. Roughly uniform elongation in the meristem and also, after an abrupt acceleration, in the elongation zone. Plant Physiol 132:1138–1148

Vinodhana NK, Ganesamurthy K (2010) Evaluation of morpho-physiological characters in sorghum (*Sorghum bicolor* (L.) Moench) genotypes under post-flowering drought stress. Elec J Plant Breed 1:585–589

Volkmar KM (1997) Water stressed nodal roots of wheat: effects on leaf growth. Aust J Plant Physiol 24:49–56

Wasson AP, Rebetzke GJ, Kirkegaard JA, Christopher J, Richards RA, Watt M (2014) Soil coring at multiple field environments can directly quantify variation in deep root traits to select wheat genotypes for breeding. J Exp Bot 63:3485–3498

Whish J, Butler G, M C, Cawthray S, Broad I, Carberry P, Hammer GL, McLean G, Routley R, Yeates S (2005) Modelling the effects of row configuration on sorghum in north-eastern Australia. Aust J Agric Res 56:11–23

Wright G, Smith R, MccWilliam J (1983) Differences between two grain Sorghum genotype in adaptation to drought stress. 1. Crop growth and yield responses. Aust J Agric Res 34:615–626

Yambao EB, Ingram KT, Real JG (1992) Root xylem influence on the water relations and drought resistance of rice. J Exp Bot 43:925–932

Yu LX, Ray JD, O Toole JC, Nguyen HT (1995) Use of wax–petrolatum layers for screening rice root penetration. Crop Sci 35:684–687

Zhu JM, Brown KM, Lynch JP (2010) Root cortical aerenchyma improves the drought tolerance of maize (*Zea mays* L.). Plant Cell Environ 33:740–749