

Root System Architecture and its Reaction in Cereals under Water Stressed Environment

Habtamu Demelash Tamir*

Department of Agricultural Research, Assosa Agricultural Research Center, Assosa, Ethiopia

*Corresponding author: Habtamu Demelash Tamir, Department of Agricultural Research (EIAR), Assosa Agricultural Research Center, Assosa, Ethiopia, Tel: +251 9915941324; E-mail: habtedeme@gmail.com

Received date: 05-11-2020, Accepted date: 19-11-2020, Published date: 26-11-2020

Copyright: © 2020 Tamir HD. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Abstract

Globally Climate change has increased the occurrence of extreme weather patterns these days, causing significant reductions in crop production, and hence threatening food security. Plant root traits is of great agronomic importance because it is a key determinant for plant anchoring and mechanical support, propagation, storage, and water and nutrient uptake, and as the major interface between the plant and various abiotic factors. A current challenge for crop improvement is the limited ability to phenotype and select for desirable root characteristics due to their underground location. Evaluating the association root architectural traits under water deficit will provide the basis for breeding new germplasm with suitable root traits for the efficient acquisition of soil resources and adaptation to drought. We summarize root architectural traits relevant to crop cereal productivity, analysis root phenotyping approaches and describe their advantages, limitations and practical value for cereal breeding programs. In this review, I encapsulate current progress in the genetic diversity in cereal crops, Quantitative Trait Loci (QTLs) associated with RSA, and the importance and applications of recent discoveries associated with the beneficial root traits towards better RSA for enhanced drought tolerance and yield.

Keywords: Root phenotyping; Drought tolerance; Quantitative trait loci

Introduction

Climate change has aggravated the occurrence of extreme weather patterns including an erratic distribution of precipitation, which can cause drought stress and adversely affect crop production [1]. For instance, by 2050, water shortages are expected to affect 67% of the world's population [2]. Hatfield et al. reported that Estimates crop yields would decline 30%-82% by the end of the 21st century under the current climate change, despite increasing concentrations of CO₂ that could benefit photosynthesis [3].

Drought tolerance character is most important and crucial for crop productivity under drought agro ecological area, which can be able cope up in different of ways, including drought avoidance or desiccation prevention, potentially in blending, through matching crop water use with water availability, and rescue of growth following rewetting [4].

Geneticists and breeders are in position to make strides in breeding plants for better yields under drought conditions and they have been tried to focus on the root system of the plant. Plant root is the major organ for water and nutrient acquisition, and also the first organ that primarily senses the water deficit in soil. As such, the root system is becoming an important breeding target for crop improvement [5]. Predominately Crops plants drought tolerance mechanism's was found to be highly associated with root characteristics such as root volume, root length, root number and root dry weight the root a crucial

determining factor of the ability of a plant to access water to in maintain crop production under water limiting conditions [6].

Past efforts have been in germplasm improvement program for water-limited environments have been accomplished by focusing on specific traits for particular crops and drought conditions, which appear more clearly when viewed through a framework that dissects the benchmark of water limited yield potential into independent components [7]. The goal of this review is to provide an overview all of which can serve as a resource for plant breeders, geneticists and other researchers interested in understanding the genetic variation RSA traits of cereals and integrated selection basis in water stress tolerance for practical crop improvement.

General Effect of Drought on Plant Growth and Development

Water plays a key role in the growth plants through the process of transpiration, surface cooling and carbon assimilation and drought imposes an adverse effect on plant growth and development and the effect is manifold in nature. Water deficit in plants affected the production of food of plants by worrying photosynthesis due to decreased CO₂ diffusion to the chloroplast, since the opening of stomata become closed to preserve available water in the plant system [8]. Reduced photosynthesis can also be worsened by heat stress aggravated by water deficit [9]. Due to decreased water in the plant system the chloroplast found in the mesophyll affected photosynthetic outputs due to reduced light interception [10].

Besides, reproduction of plants was also high affected by high temperature due to heat damage on pollen grain and

that consequence sterility [11]. Drought stress also prompt plants to accumulate metabolites such as proline that plays important role as protein precursors in plant metabolism and development. Proline accumulated in the plant cell serves as an excellent osmolyte, as a metal chelator, an anti-oxidative defense molecule, and a signaling molecule [12]. It is known to impart stress tolerance by maintaining cell turgor or osmotic balance, preventing electrolyte leakage by stabilizing membranes and proteins such as RUBISCO (Ribulose 1,5-bisphosphate carboxylase), mitochondrial electron transport complex II, and controlling Reactive Oxygen Species (ROS) concentrations in plants [12-14].

Root system development in cereals

The root system of monocotyledonous cereals (wheat, maize, sorghum, rice) is composed of up of seminal and adventitious (nodal) roots [15]. The primary seminal root originates as a radical in the embryo are formed in the early stage and first emerges at germination, embryonic roots penetrate the soil deeply and have numerous lateral roots. Adventitious (nodal) roots were emerges during late development, plants produce a smaller number of thicker and less branched adventitious roots that grow beneath the soil but that do not penetrate the deeper layers [16].

A specific spatial and temporal pattern of the root growth of monocots poses a challenge for high or moderate-throughput root phenotyping. The complex root systems of monocotyledonous plants require special efforts in order to maintain the equilibrium between the analysis throughput and imaging resolution. As the throughput of a screening method increases, it causes a reduction in the accuracy and precision of the measurements [17].

Root system growth and spatial configuration soil in relation to water use

Plant root traits such as, root thickness and rooting depth are important to extract water from depth [18]. A positive association between root elongation rate and root diameter has been reported for maize and barley (*Hordeum vulgare* L.) [19]. Hackett et al. reported morphological development of seminal, nodal, and lateral roots a key root traits which influences the overall development of root systems, their architecture and spatial distribution are critical for determining plant survival, water and nutrient acquisition, and competitive fitness of a particular plant species [20].

The significance of root system architecture for plant productivity arises from the fact that many the nature of soil resources are unevenly distributed in space and time and are often subject to localized depletion [21]. Especially, the capacity of roots to access available soil water throughout the life cycle is critical to crop adaptation in water-limited environments. This is exclusively essential in species such as sorghum and maize, as they are frequently grown in water-limited dry land environments.

The spatial distribution of roots governs the capacity of a plant to exploit the complex and heterogeneous nature soil resources [22]. For example, in wheat spatial configuration of root system architectural traits could contribute to improved grain yield,

drought tolerance and resistance to nutrient deficiencies [23,24]. In this context, deeper rooting can increase post anthesis water uptake at depth in a drying soil, whereas a shallow branching root system could increase lateral water uptake.

Although the spatial distribution of the root system is dynamic in nature, due to heterogeneous distribution of soil resources, root architecture is important in drought adaptation depending on the growing environment [25]. For example, deeper roots would be suited to an environment with an extended period of dry conditions, where plants rely on extraction of available water at depth. Richards et al. also identified genotypic differences among wheat varieties for rooting pattern with drought tolerant varieties having a greater proportion of roots at depth.

Root System Architecture Phenotyping Methods for Cereal Crops

RSA phenotyping in the laboratory

Phenotyping of root system architecture in the field grown plants offers accurate representation of root growth in an agriculturally importance context. Nevertheless soil obscures root system visualization in situ, and roots can form extensive networks in the soil, which prevents their easy extraction for observation for nutrient and water. Due to this limitation harmonizing laboratory and green house methods have been developed to overcome these gaps. There is a good evident that crops have a better advantage of expression their genetic potential of root system architecture when they can be grown in mesocosms such as soil or sand filled pots or PVC tubes [26]. While mesocosms may more closely reproduce field conditions compared to other laboratory methods, the challenge of visualizing the root system remains.

Due to complexity of, the soil that used visualization should be dispensed with altogether by growing plants in liquid culture, growing roots along surfaces of agar or paper or growing plants in clear gel media in transparent containers [27-29]. Non-soil techniques allow for easy and non-destructive visualization of RSA as well as precise control of the root growth environment, but may not recapitulate the three-dimensional nature of RSA in soil [30]. All these methods limited to analyze relatively the root system directly at different stage of the crops. Among the non-soil methods, root growth into transparent gel media has the advantage that it provide a solid matrix, which allows roots to grow in three dimensions (Figure 1) [28].

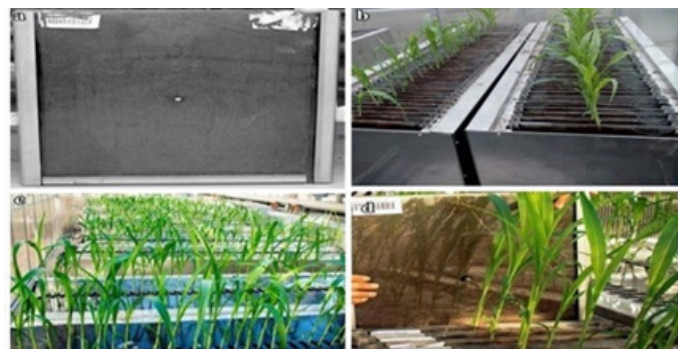


Figure 1: High throughput root phenotyping platform.

RSA phenotyping in the field

However RSA phenotyping methods provide controlled environments, allow increased throughput, and require fewer resources, they may not accurately reflect RSA under field conditions. Hence, high throughput RSA phenotyping in the field is needed to accompany and confirm laboratory studies. Earlier studies has confirmed RSA in the field by extraction of soil around the root system, or digging of the crops from the sown land and separation of roots from the soil stratum and manual root system [31,32].Excavation methods are still important for characterizing and confirmation root system architecture simultaneously both under laboratory and field condition. For example, 'shovelomics' utilizes visual assessment of excavated root crowns to assess different RSA parameters [33]. This approach proved to be relatively quick for characterizing ten RSA traits in three recombinant inbred line populations of maize [33].

Genetic Variation of Root Traits and Quantitative Trait Loci under Water Deficit in Cereal Crops

Sorghum

Sorghum is a major dryland cereal crop in areas with low and unpredictable rainfall, but opportunities to improve root related drought adaptive traits have been limited. Various mechanisms of drought adaptation have been reported for sorghum genotypes, including greater root length density, greater water extraction from depth, number of nodal roots, vertically oriented roots, and thickness of nodal roots. O'toole J et al. observed that more vertical distribution of roots was related to better performance during drought years for 11 sorghum genotypes [34]. Wright et al. reported drought tolerant E-57 sorghum cultivar had greater root length density, especially below 80 cm, yet used less water prior to booting than susceptible sorghum cultivar, TX-671, due to differences in timing of leaf area development [35]. As a consequence, the tolerant genotype extracted more water from below 80 cm after the booting stage.

Singh et al. reported genetic variation of root system was observed for sorghum both sorghum inbred lines and hybrids. The nodal root angle of inbred lines varied from about 15° to 50° Genotypes R993396 (14.4°) and B923296 (20.6°) had the narrowest root angles, whereas SC999 (50.0°), BTx623 (44.0°), and SC170-6-8 (35.7°) had the widest angles [36]. Large

variability was found in nodal root angle for hybrids, with ATx642/QL36 (14.3°) confirming the narrowest root angle and BTx623/RTx7000 (42.8°) the widest. Diversified in root angle and spatial configuration of major root axes are likely to determine the amount of horizontal and vertical foraging of the soil for nutrients and water and this considerable variations is also likely to play great role to specific adaptation soil and management systems (Figure 2) [37].

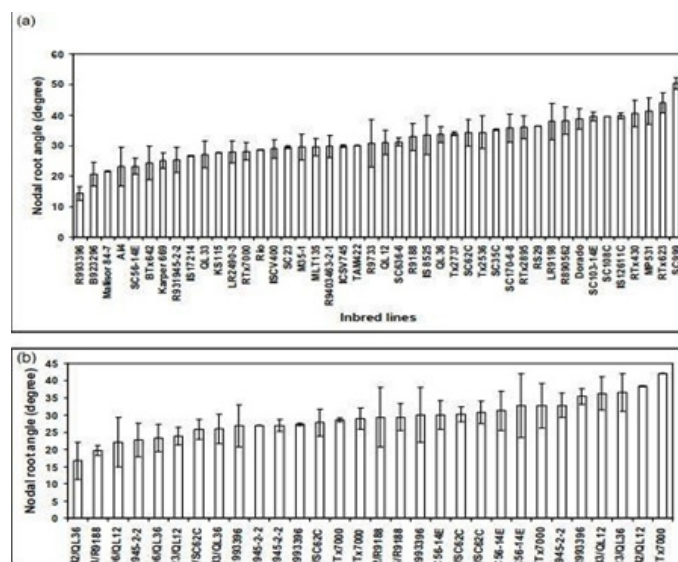


Figure 2: Encompassing nodal root angle for (a) 44 sorghum inbred lines, and (b) 30 sorghum hybrids. The vertical bar indicates the relevant standard error.

Sorghum [*Sorghum bicolor* (L.) Moench] makes an excellent model plant to study the genetic basis of plant water uptake and utilization [38]. Recently due to the availability of whole genome sequence of sorghum strategies were focus on the application of molecular marker for sorghum improvement program [39]. Studies were confirmed that Significant genomic regions were identified using SMA on the subset of 88 sorghum genotypes. Marker regression identified 5 significant genomic regions for root angle on SBI-01, SBI-04, SBI-08 and SBI-09; four significant genomic region on for root dry mass on SBI-01, SBI03, SBI-04 and SBI-08 and also SBI-08 was in common for these traits (Table 1) [40].

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	[40]
Dry root weight	B923296 SC170-6-8	-	qRDW1_2, qRDW1_5, qRDW1_8	LG 2, 5 and 8	32.08	[40]

-	E36-1 SPV570	938 markers (270 nongenic nuclear SSRs, 530 EST-SSRs and 138 SNPs)	qRD4	LG 4	9.21	[41]
Fresh root weight	E36-1 SPV570	-	qRF4	LG 4	9.21	[41]
Root length	E36-1 SPV570	-	qRL4	LG 4	8.33	[41]
Root volume	E36-1 SPV570	-	qRV1, qRV4	LG 1 and 4	27.05	[41]
Number of roots/plant	E36-1 SPV570	-	qRN1	LG 1	17.87	[41]
Root/shoot ratio	E36-1 SPV570	-	qRS10, qRS10.1	LG 10	16.03	[41]
Number of brace roots	Sansui Jiliang 2	326 SSR markers	qRT6, qRT7	LG 6 and 7	59.5	[42]

Table 1: Details of different QTLs identified for various root traits in sorghum.

Maize

The root system of maize consists of roots that are formed during embryogenesis and roots that are formed during postembryonic development. Embryogenic roots comprise primary and seminal roots, and post embryogenic roots include shoot-borne crown and brace roots and lateral roots [42-43]. In maize, the importance of a good root system has been recognized since the beginning of modern breeding [44]. A number of experiments have shown significant genetic variation for root characteristics and architecture in maize [45]. Despite this, little progress has so far been achieved in the utilization of root traits as selection criteria to indirectly improve yield in maize and other crops [44].

Kumar et al. study conducted on genotypic variation for root architecture traits in seedlings of maize (*Zea mays* L.) inbred lines among 74 maize inbred lines revealed there was significant

genetic variation on the root traits of which is important roles in plant establishment, in supplying water and nutrients during early growth stages [46]. In maize, seminal roots play important roles in plant establishment, in supplying water and nutrients during early growth stages but their role declines in the adult plants with the development of the shoot-borne roots, i.e., nodal roots which penetrate much deeper in the soil and play important role in scavenging of both mobile and immobile soil resources [47,48].

Furthermore Ali et al. suggested all the higher-yielding hybrids were found to have steeper root angles for both seminal and nodal roots while all the lower-yielding hybrids were found to have shallower root angles, and these phenomena again substantiate a possible association between root growth angles and yield performance under water-limited environments (Figure 3) [49].

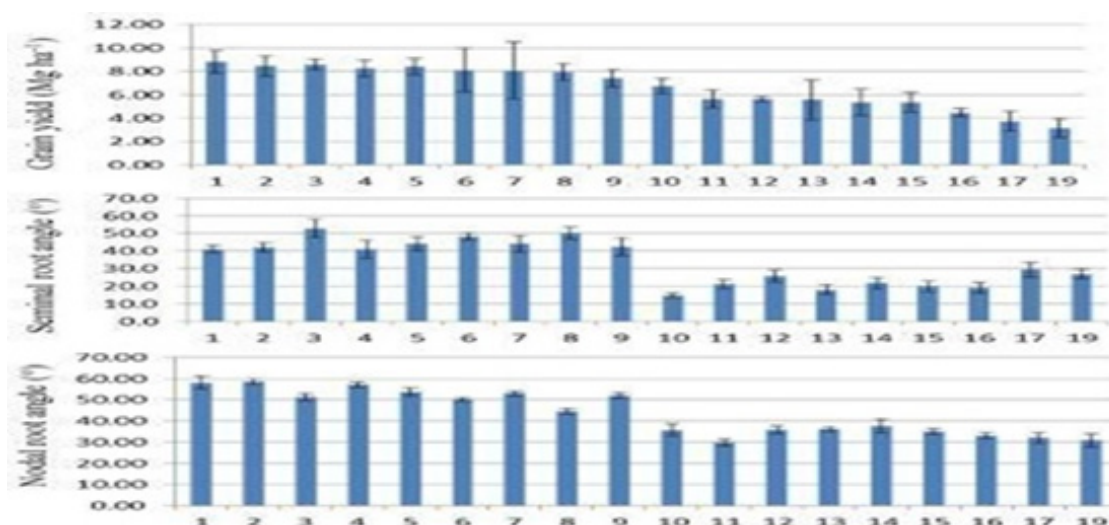


Figure 3: Eighteen hybrids showing similar variation pattern for grain yield in water-stressed field and for root angles of both seminal and nodal roots. Higher-yielding genotypes (1-9) have relatively greater (steeper) root angles while lower-yielding genotypes (10-19) have smaller shallow root angle.

The first QTLs for root traits in maize were reported by Lebreton et al., who evaluated 81 F₂ plants derived from the cross between Polj 17 and F-2, two lines widely different in abscisic acid (ABA) concentration in the leaf and for some root traits [50]. Tuberosa et al. Studied QTLs for root traits in hydroponics were shown using 171 F₃ families derived from the cross between Lo964 and Lo1016, two lines differing for root traits investigated In total, 11, seven, nine and 10 QTLs with an LOD>2.5 were found to influence primary root length (R1L), primary root diameter (R1D), primary root weight (R1W) and the weight of the adventitious seminal roots (R2W), respectively [51,52].

Other similar studies Ribaut et al. also confirmed that with in the same root traits that was conducted in hydroponics by the population Lo964 × Lo1016 were also measured in 120 RILs of the mapping population developed at CIMMYT from the

cross Ac7729 × Ac7643/TZSRW which were previously tested as F₃ families under drought conditions for yield and other agronomic traits [53]. Among the 16 bins which carried a QTL for root traits in hydroponics [54].

Tuberosa et al. observed four mapping populations have been investigated to locate QTLs for root traits under controlled conditions and/or in the field [55]. A comparative analysis of the QTL results was carried out based on the availability of molecular markers common to the investigated populations and the UMC maize reference map. There were numerous chromosome regions affected root traits in two or even three populations. Grain yield under well-watered and/or drought-stressed conditions were found among these chromosome regions (Figure 4). The most important QTL effects were detected on chromosome bins 1.03, 1.06, 1.08, 2.03, 2.04, 7.02, 8.06 and 10.04 (Table 2) [56].

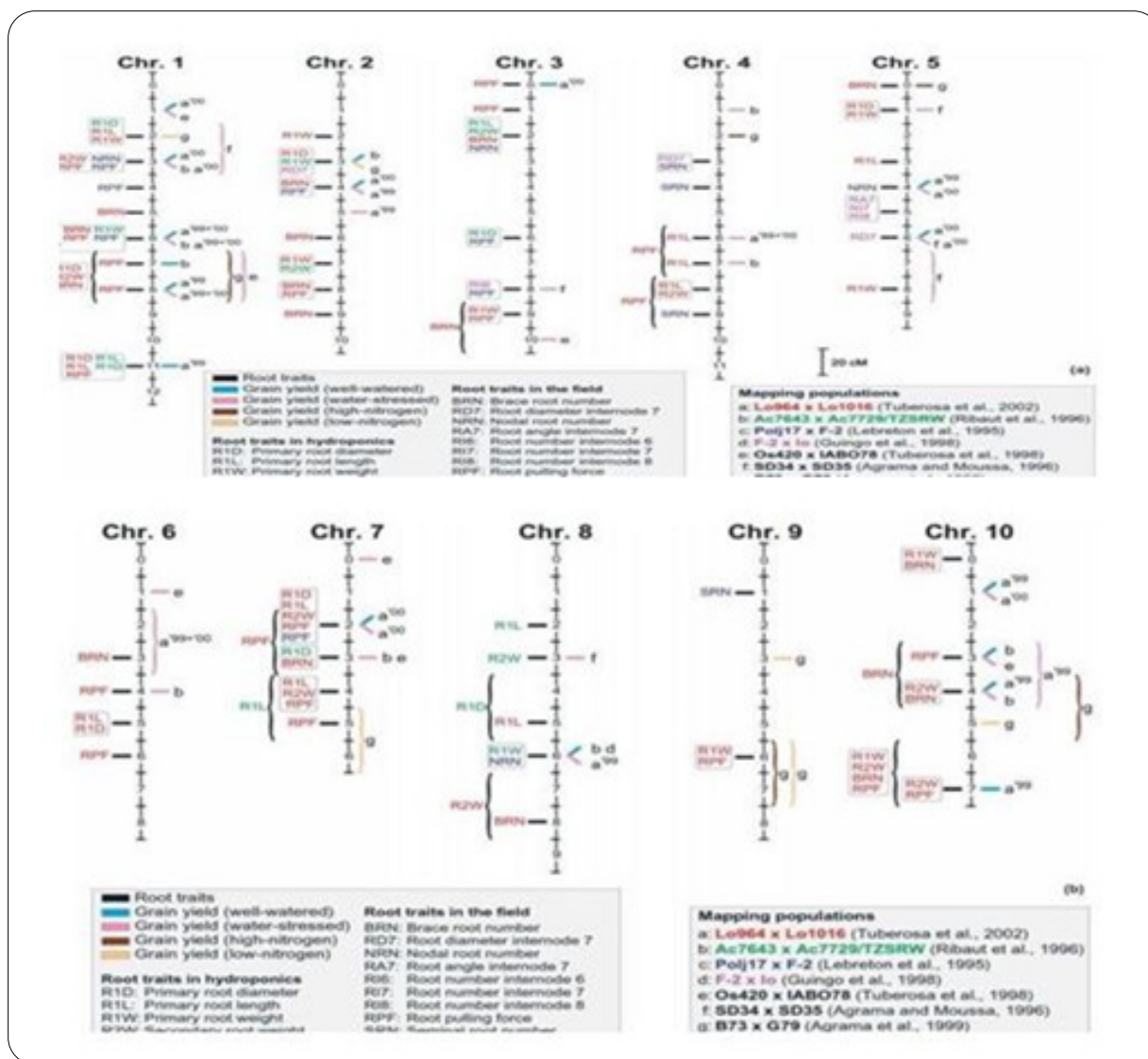


Figure 4: Bin allocation on the maize map (1a: chromosomes 1-5; 1b: chromosomes 6-10) of the QTLs identified in seven maize populations (a-g) evaluated for root traits (acronyms to the left of the chromosomes) and/or for grain yield (letters to the right of the chromosomes).

Cross Name ^a	Map dens. (cM)	Cross Type ^b	Media and treatment ^c	Stage d ^d	Traits ^e	QTLs per trait ^f	Pop. Size	Map. Method ^g	Reference
Poly17×F2	14.8	F2	Pot	R6	RPF, NoCrAx, NoSeAx	5	81	IM	[50]
Io×F2h	12.1	F5:6 RIL	Field	R1-2	NoCr5Ax, NoCr6Ax, NoCr7Ax	1	100	IM	[56]
F271×F288	20.3	F7 RIL	Field	R6	NoCr5Ax, NoCr6Ax, NoCr7Ax	2.3	135	CIM	[47]
Lo964× Lo1016	9.8	F2:3	Hydroponics	V2	DWSe, LPrAx	10.5	171	CIM	[51]
		F2:4	Pot	R2	RPF	10	118	CIM	
		F2:4	Pot	V1	LPrAx, LSeAx, LPrLat,	4.8	168	CIM	
B73×Mo17	8.9	RIL	Pot, phosphorus/ Mycorrhiza	6wks	VolRt	1	167	CIM	-

Note: a Contributing parent is underlined.

b Recombinant inbred line (RIL), inbred line (IL).

c Growth media under controlled conditions (greenhouse or growth chamber): hydroponics, solid media in pots (pot).

d Vegetative stages (V_x) with x indicating the number of fully developed leaves, reproductive stages (R1, silking; R2, blister; R6, physiological maturity and silage stage).

e RPF, root pulling force; RCT, root capacitance, for other abbreviations.

f Average number of QTLs per trait g Mapping methods were interval mapping (IM), composite interval mapping (CIM), inclusive composite interval mapping (ICIM), analysis of variance (ANOVA).

Table 2: Summary table of QTL studies reporting traits related to root length in Maize.

Rice

Rice, a monocot and a member of the Poaceae (or) Gramineae family, adapted in a wide range of environments and cropping systems have been adapted for deep-water, rain-fed lowland, upland, and irrigated conditions [57]. Rice has a well-characterized fibrous root system of monocots and exhibits seminal, nodal, and lateral roots which have been subjected to substantial morphometric, anatomical, and genetic studies [58]. Nevertheless of the climate change the nature ecosystem rice production challenged by drought so breeding efforts look towards understanding the role of roots for improving nutrient and water acquisition and increasing grain yield [59].

Studies on genetic variation for root traits in rice have been ongoing for decades. Nicou et al. reported significant genetic variation for root traits among both upland and lowland cultivars of Asia, Africa, and South America [60]. Asian lowland varieties had finer and more highly branched roots, whereas African and South American cultivars had larger diameter and less branched roots. Yoshida et al. also reported genetic variation in root depth, with a tendency for upland rice cultivars to have deeper roots than lowland rice cultivars [61].

Ingram et al. studied cultivars belonging to different types of rice for root studies and found tropical japonica types to have larger root systems than indica types [62]. In another study, Lafitte et al. investigated the genotypic variation for root traits in different types of rice and reported that indica rice types had fine, highly branched superficial roots with narrow xylem vessels and low root to shoot ratio, whereas japonica types had coarse roots with wider vessels, less branched long roots, and a large root to shoot ratio [63]. Positive associations between root length and grain yield have been documented in rice [64].

The most studied root traits in all QTL mapping studies are maximum root depth, root diameter, and root to shoot ratio. Courtois et al. identified root thickness, depth, and root mass are allied with stable QTL that are expressed in multiple environments [65]. In a meta-QTL analysis, Courtois et al. observed 119 root QTL in rice from 24 studies [65]. Many of these QTL, primarily for maximum root length, were associated with “hot spots” on chromosomes 1 and 9, which contained QTL detected in multiple populations and environments (Figures 5 and 6).



Figure 5: QTL and meta-QTLs for maximum root length on chromosome 1.

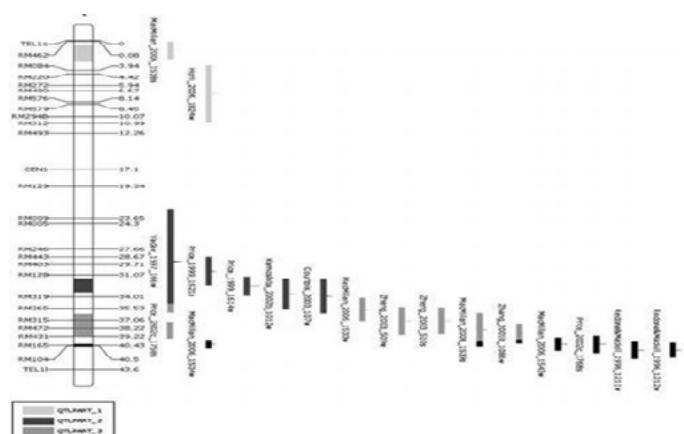


Figure 6: QTL and meta-QTLs for maximum root length on chromosome 9.

Wheat

Wheat (*Triticum aestivum* L.) is the most important cereal crop in the world, more than half of world's population relies on wheat as its major food staple [66]. Two root types are distinguished in wheat the seminal roots (also called primary roots), which develop at the scutellar and epiblast nodes of the embryonic hypocotyl of the germinating caryopsis; adventitious roots, which subsequently emerge from the coleoptilar nodes at the base of the apical culm and tillers [66]. These two categories of roots function in a complementary manner, and thus the root system must be considered as a whole.

Genotypic variation for the degree of horizontal versus vertical orientation of roots has been identified in wheat [67]. This can be associated with adaptation to cultural practices and/or drought resistance, as genotypic differences in root architecture can result in spatial and temporal differences in water extraction patterns, which in turn can affect grain yield under drought stress. In wheat, a genotype with narrow nodal root angle at the seedling stage tended to extract more water at depth than one with wider root angle, which extracted more water laterally [23].

The genetic basis of variation for RSA traits were investigated using a population of 176 Recombinant Inbred Lines (RILs) derived from the cross between two Italian elite durum wheat. N wheat, a more vertical (narrow) angle of the seminal roots and a higher number of seminal roots in seedlings has been linked to a more compact root system with more roots at depth [23]. Therefore, seminal root traits are considered useful proxy traits for desirable root-system architecture within a breeding context particularly for drought adaptation [68].

This reveals the existence of genetic variation in root system architecture across various crop species and thus in the ability to access available soil water and nutrients at critical growth stages [69]. Selection for root system architecture has been the focus of breeding programs in crops such as cowpea and rice, as there is a correlation between root system size and resistance to water stresses [18,47].

In wheat, a large number of QTL each with minor effect on components for root-system architecture have been reported, with some 31 QTL identified on chromosomes 2A, 2D, 3A, 3B, 4D, 5A, 5B, and 6A [70,71]. More specifically for root angle, four QTL have been identified on chromosomes 2A, 3D, 6A, and 6B with two suggestive QTL on 5D and 6B, and for root number two QTL have been detected on 4A and 6A with four suggestive QTL position on 1B, 3A, 3B and 4A [71].

Pearl millet

Pearl millet [*Pennisetum glaucum* (L.) is the sixth most important cereal grain in the world. It accounts for 6% of the total cereal production in Africa, and 14% in West Africa alone [72]. It is an important cereal in arid and semi-arid regions where it contributes to food security and is expected to have an increased importance in the future adaptation of agriculture to climate change in sub-Saharan Africa [72].

Passot et al. had shown the structure and dynamics of pearl millet root system has not been described and very little is known about root architecture during the early phase of pearl millet development [73]. Root phenotyping of different pearl millet 16 inbred lines revealed a high variability for two root traits within the panel, consistent with an earlier study. Here, this study showed that this variability was also visible *in vitro* at a very early stage of growth (6 DAG). This finding together with the high heritability of the primary root length could be exploited to identify the genetic determinants of primary root growth, a potentially beneficial root trait for pearl millet early establishment [73].

For instance, screening of natural variability of the primary root length have been done at the cellular level in *Arabidopsis thaliana* and led to the identification of a root meristem regulator gene. Besides, it will be interesting to exploit the large diversity we observed for primary root growth to test the adaptive value of this character for early drought stress tolerance. Most important and a major QTL for terminal drought tolerance has been identified and validated on pearl millet linkage group 2 (LG 2) using segregating populations derived from two independent crosses (H 77/833 23PRLT 2/89-33 and ICMB 8413863B) [74].

Barely

(FAO) showed barley is the fourth largest cereal grain produced (in metric tonnes) worldwide is an essential raw material for malting and beer production [72]. Robinson et al. evaluated a high degree of diversity for seminal root traits was observed in the panel of 30 barley genotypes and the DH population Seminal root angle ranged between 13.5° and 82.2° with a mean of 49.4° and SD of 16.6° and Seminal root numbers varied from 3.6 to 6.9 roots with a mean of 5.5 and SD of 0.7 [75]. Seminal root angle and seminal root number were not significantly correlated ($R^2=0.004$) (Figures 7 and 8).

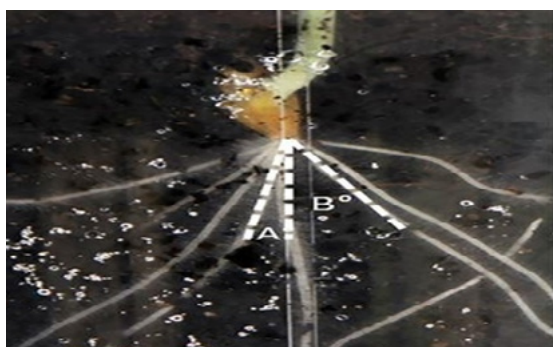


Figure 7: Illustration of seminal root angle measurement of the first pair of seminal roots. Angle A and Angle B make up the seminal root measurement, where angle A is measured from the vertical root to the first seminal root and angle B is measured from the vertical root to the second seminal root. Angle A and angle B are combined to give the seminal root angle for the first pair of seminal roots.

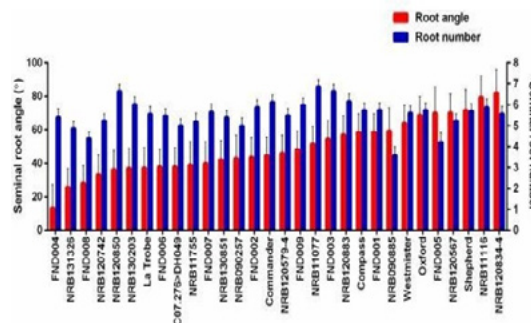


Figure 8: Seminal root angle and root number for the panel of 30 barley genotypes characterized. Seminal root angle (degrees) is displayed on the left y-axis, represented by red columns, and root number is displayed on the right y-axis, represented by blue columns. Best linear unbiased estimators are displayed for each genotype along with standard errors. Genotypes are arranged in ascending order of seminal root angle (left to right).

Franckowiak et al. reported composite interval mapping identified a total of seven QTL for seminal root traits in the ND24260 × Flagship DH population: two QTL for root angle (RAQ1-2) and five QTL for root number (RNQ1-5 [76]. The two QTL mapped to 5HL (RAQ2 and RNQ4) aligned with the same four DArT markers in the region, spanning 3.5 cm. Thus, RAQ2/RNQ4 appeared to be the same QTL influencing both traits. The effect associated with the ND24260 allele donating wide root angle and high root number in this region accounted for 9.6% of the phenotypic variation for root angle and 6.8% for root number (Table 3).

QTL	Linkage group	peak marker †	Position peak market	-log10(P)‡	Confidence interval§	Flanking markers at peak	Source ¶	Variation explained #
RAQ1	3H	bPb-8021	226.9	3.8	7.6	bPb-0049, bPb-2420	Flagship	3.8
RAQ2	5H-2	bPb-1217	235.9	8.1	16.2	bPb-5053, bPb-2689	ND24260	9.6
RNQ1	1H-1	bPb-8983	120.8	6.1	12.2	bPb-5877, bPb-7949	ND24260	5.8
RNQ2	3H	bPb-9273	79.6	9.6	19.2	bPb-0285, bPb-4645	Flagship	10.1
RNQ3	4H	bPb-6101	171.1	3.6	7.2	bPb-2677, bPb-5743	Flagship	3.2
RNQ4	5H-2	bPb-1217	235.9	7	14	bPb-5053, bPb-2689	ND24260	6.8
RNQ5	6H-1	bPb-0696	117	4.6	9.2	bPb-3184, bPb-6721	Flagship	4.1

Note: † Peak position of QTL region on genetic linkage map of the ND24260 × Flagship DH population.
 ‡ -log 10(P) score for QTL peak position derived from composite interval mapping, where a QTL significance threshold.
 § Confidence interval of QTL calculated by the two logarithm of odds drop method.
 ¶ Parental allele source for wide root angle and high root number for each QTL derived from composite interval mapping.
 # Percentage of phenotypic variation for root angle or root number explained by the QTL.

Table 3: Quantitative trait loci (QTL) for seminal root traits in the ND24260 × ‘Flagship’ doubled-haploid (DH) population in Barely.

Conclusion

The sustainability of crop production and food security is being threatened by the increasing unpredictability and severity of drought stress due to global climate changes. Incorporation of these adapted natural genetic variations into breeding programs can enrich the current genetic diversity of stress tolerance and improve yield under stress. Screening germplasm for stress tolerance traits has provided donor resources with potential to improve yield under stress conditions. Identification of the genomic regions underlying these natural genetic variations and transferring the favorable alleles into elite germplasm with the assistance of genomic technologies will speed up the genetic improvement of stress tolerance in cereal. Several QTLs associated with RSA were identified. There continue to be promising prospects for increasing communication between plant eco physiologists, geneticists, and breeders to have the potential to improve plant productivity under drought environment.

References

1. Lesk C, Rowhani P, Ramankutty N (2016) Influence of extreme weather disasters on global crop production. *Nature* 529: 84-87.
2. Ceccarelli S, Grando S, Baum M, Udupa SM (2004) Breeding for drought resistance in a changing climate. *Challen Strateg Dryland Agric* 32: 167-190.
3. Hatfield JL, Boote KJ, Kimball B, Ziska L, Izaurralde RC, et al. (2011) Climate impacts on agriculture: implications for crop production. *Agron J* 103: 351-370.
4. Passioura J (2012) Phenotyping for drought tolerance in grain crops: When is it useful to breeders? *Funct Plant Biol* 39: 851-859.
5. Collins NC, Tardieu F, Tuberosa R (2008) Quantitative trait loci and crop performance under abiotic stress: where do we stand? *Plant physiol* 147: 469-486.
6. Shinde M, Awari V, Patil V, Gadakh S, Nirmal S, et al. (2017) Root traits and its correlation with grain yield of rabi sorghum genotypes in phule root box structure under receding soil moisture condition. *Int J Curr Microbiol App Sci* 6: 977- 981.
7. Passioura J, Angus J (2010) Improving productivity of crops in water-limited environments. *Adv Agron* 106: 37-75.
8. Pinheiro C, Chaves M (2011) Photosynthesis and drought: Can we make metabolic connections from available data? *J Exper Bot* 62: 869-882.
9. Crafts-Brandner SJ, Salvucci ME (2002) Sensitivity of photosynthesis in a C4 plant, maize, to heat stress. *Plant physiol* 129: 1773-1780.
10. Fletcher AL, Moot DJ, Stone PJ (2008) Radiation use efficiency and leaf photosynthesis of sweet corn in response to phosphorus in a cool temperate environment. *European J Agron* 29: 88-93.
11. Bitu C, Gerats T (2013) Plant tolerance to high temperature in a changing environment: Scientific fundamentals and production of heat stress-tolerant crops. *Front Plant Sci* 4:273.
12. Hayat S, Hayat Q, Alyemeni MN, Wani AS, Pichtel J, et al. (2012) Role of proline under changing environments: A review. *Plant Signal Behav* 7: 1456-1466.
13. Hamilton EW, Heckathorn SA (2001) Mitochondrial adaptations to NaCl. Complex I is protected by anti-oxidants and small heat shock proteins, whereas complex II is protected by proline and betaine. *Plant physiol* 126: 1266-1274.
14. Hare PD, Cress WA, Van Staden J (1998) Dissecting the roles of osmolyte accumulation during stress. *Plant Cell Environ* 21: 535-553.
15. Gregory PJ, Bengough AG, Grinev D, Schmidt S, Thomas WBT, et al. (2009) Root phenomics of crops: Opportunities and challenges. *Funct Plant Biol* 36: 922-929.
16. Coudert Y, Perin C, Courtois B, Khong NG, Gantet P (2010) Genetic control of root development in rice, the model cereal. *Trends Plant Sci* 15: 219-226.
17. Cobb JN, DeClerck G, Greenberg A, Clark R, McCouch S (2013) Next-generation phenotyping: requirements and strategies for enhancing our understanding of genotype-phenotype relationships and its relevance to crop improvement. *Theor Appli Gene* 126: 867-887.
18. Price AH, Steele K, Moore B, Jones R (2002) Upland rice grown in soil-filled chambers and exposed to contrasting water-deficit regimes: II. Mapping quantitative trait loci for root morphology and distribution. *Field Crop Res* 76: 25-43.
19. Cahn M, Zobel R, Bouldin D (1989) Relationship between root elongation rate and diameter and duration of growth of lateral roots of maize. *Plant Soil* 119: 271-279.
20. Hackett C (1972) A method of applying nutrients locally to roots under controlled conditions, and some morphological effects of locally applied nitrate on the branching of wheat roots. *Austr J Biol Sci* 25: 1169-1180.
21. Robinson C, Cruse R, Kohler K, Hatfield J, Karlen D (1994) Soil management. *Sust Agric Syst* pp: 109-134.
22. Lynch JP, Brown KM (2001) Topsoil foraging an architectural adaptation of plants to low phosphorus availability. *Plant Soil* 237: 225-237.
23. Manschadi AM, Christopher J, deVoil P, Hammer GL (2006) The role of root architectural traits in adaptation of wheat to water-limited environments. *Funct Plant Biol* 33: 823-837.
24. Manschadi A, Christopher J, Hammer G, Devoil P (2010) Experimental and modelling studies of drought-adaptive root architectural traits in wheat (*Triticum aestivum* L.). *Plant Biosys* 144: 458-462.
25. Richards R (1996) Increasing the yield potential of wheat: Manipulating sources and sinks. Increasing yield potential in wheat: Breaking the barriers. (Edns MP Reynolds, S Rajaram, A McNab) pp: 134-149.

26. Zheng B, Yang L, Zhang W, Mao C, Wu Y, et al. (2003) Mapping QTLs and candidate genes for rice root traits under different water-supply conditions and comparative analysis across three populations. *Theor Appl Genet* 107: 1505-1515.
27. Miyamoto N, Steudle E, Hirasawa T, Lafitte R (2001) Hydraulic conductivity of rice roots. *J Experm Bota* 52: 1835-1846.
28. Fang S, Yan X, Liao H (2009) 3D reconstruction and dynamic modeling of root architecture in situ and its application to crop phosphorus research. *Plant J* 60: 1096-1108.
29. Iyer-Pascuzzi AS, Symonova O, Mileyko Y, Hao Y, Belcher H, et al. (2010) Imaging and analysis platform for automatic phenotyping and trait ranking of plant root systems. *Plant Physiol* 152: 1148-1157.
30. Bengough A, Gordon D, Al-Menaie H, Ellis R, Allan D, et al. (2004) Gel observation chamber for rapid screening of root traits in cereal seedlings. *Plant Soil* 262: 63-70.
31. Weaver JE, Bruner WE (1926) Root development of field crops.
32. Böhm W (2012) *Methods of studying root systems*. Springer Sci Busi Media.
33. Gärtner H, Wagner B, Heinrich I, Denier C (2009) 3D-laser scanning: A new method to analyze coarse tree root systems. *Fore Snow Landsca Res* 82: 95-106.
34. O'toole J, Bland W (1987) Genotypic variation in crop plant root systems. *Adv Agron* 41: 91-145.
35. Wright G, Smith R, McWilliam J (1983) Differences between two grain sorghum genotypes in adaptation to drought stress. I. Crop growth and yield responses. *Austr J Agric Res* 34: 615-626.
36. 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.
37. Paterson AH, Bowers JE, Bruggmann R, Dubchak I, Grimwood J, et al. (2009) The *Sorghum bicolor* genome and the diversification of grasses. *Nature* 457: 551-556.
38. Lopez JR, Erickson JE, Munoz P, Saballos A, Felderhoff TJ, et al. (2017) QTLs associated with crown root angle, stomatal conductance, and maturity in Sorghum. *Plant Geno* 10: 1-12.
39. Bowers JE, Abbey C, Anderson S, Chang C, Draye X, et al. (2003) A high-density genetic recombination map of sequence-tagged sites for sorghum, as a framework for comparative structural and evolutionary genomics of tropical grains and grasses. *Genetics* 165: 367-386.
40. Mace E, Singh V, Van-Oosterom E, Hammer G, Hunt C, et al. (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.
41. Fakrudin B, Kavil S, Girma Y, Arun S, Dadakhalandar D, et al. (2013) Molecular mapping of genomic regions harbouring QTLs for root and yield traits in sorghum (*Sorghum bicolor* L. Moench). *Physiol Molec Biol Plan* 19: 409-419.
42. 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.
43. Hochholdinger F, Woll K, Sauer M, Dembinsky D (2004) Genetic dissection of root formation in maize (*Zea mays*) reveals root-type specific developmental programmes. *Annals Bota* 93: 359-368.
44. Hebert Y, Barriere Y, Bertholeau J (1992) Root lodging resistance in forage maize: Genetic variability of root system and aerial part. *Maydica* 37: 173-183.
45. Thompson D (1968) Field evaluation of corn root clumps 1. *Agronomy J* 60: 170- 172.
46. Kumar B, Abdel-Ghani AH, Reyes-Matamoros J, Hochholdinger F, Lübberstedt T (2012) Genotypic variation for root architecture traits in seedlings of maize (*Zea mays* L.) inbred lines. *Plant Breed* 131: 465-478.
47. Tuberosa R, Sanguineti MC, Landi P, Giuliani MM, Salvi S, et al. (2002) Identification of QTLs for root characteristics in maize grown in hydroponics and analysis of their overlap with QTLs for grain yield in the field at two water regimes. *Plant Molec Biol* 48: 697-712.
48. Lynch JP (2011) Root phenes for enhanced soil exploration and phosphorus acquisition: Tools for future crops. *Plant Physiol* 156: 1041-1049.
49. Ali ML, Luetchens J, Nascimento J, Shaver TM, Kruger GR, et al. (2015) Genetic variation in seminal and nodal root angle and their association with grain yield of maize under water-stressed field conditions. *Plant Soil* 97: 213-225.
50. Lebreton C, Lazić-Jančić V, Steed A, Pekić S, Quarrie S (1995) Identification of QTL for drought responses in maize and their use in testing causal relationships between traits. *J Exper Bota* 46: 853-865.
51. Tuberosa R, Salvi S, Sanguineti MC, Landi P, Maccaferri M, et al. (2002) Mapping QTLs regulating morpho-physiological traits and yield: Case studies, shortcomings and perspectives in drought-stressed maize. *Annals Bota* 89: 941-963.
52. Sanguineti M, Li S, Maccaferri M, Corneti S, Rotondo F, et al. (2007) Genetic dissection of seminal root architecture in elite durum wheat germplasm. *Annals Appl Biol* 151: 291-305.
53. Ribaut JM, Hoisington D (1998) Marker-assisted selection: New tools and strategies. *Trend Plant Sci* 3: 236-239.
54. Tuberosa R, Sanguineti M, Ribaut J, Landi P, Giuliani M, et al. (2000) QTL analysis of root characteristics in maize grown in hydroponics as related to field performance under drought conditions. *Proc Intern Confer 'Plant Animal Genom'* 8: 9-12.
55. Tuberosa R, Salvi S, Sanguineti MC, Maccaferri M,

- Giuliani S, et al. (2003) Searching for quantitative trait loci controlling root traits in maize: A critical appraisal. *Plant Soil* 255: 35-54.
56. Guingo E, Hébert Y, Charcosset A (1998) Genetic analysis of root traits in maize.
57. De-Datta SK (1981) Principles and practices of rice production. *Int Rice Res Inst*.
58. Rebouillat J, Dievert A, Verdeil JL, Escoute J, Giese G, et al. (2009) Molecular genetics of rice root development. *Rice* 2: 15-34.
59. Henry A, Cal AJ, Batoto TC, Torres RO, Serraj R (2012) Root attributes affecting water uptake of rice (*Oryza sativa*) under drought. *J Experim Bota* 63: 4751-4763.
60. Nicou R, Seguy L, Haddad G (1970) Comparison of rooting in four upland rice varieties with and without soil tillage. *Agron Trop* 25: 639-59.
61. Yoshida S, Hasegawa S (1982) The rice root system: Its development and function. *Drought Resistan Crops Emph Rice* 10: 97-134.
62. Ingram K, Bueno F, Namuco O, Yambao E, Beyrouty C (1994) Rice root traits for drought resistance and their genetic variation.
63. Lafitte H, Champoux M, McLaren G, O'Toole J (2001) Rice root morphological traits are related to isozyme group and adaptation. *Field Crop Res* 71: 57-70.
64. Lilley J, Fukai S (1994) Effect of timing and severity of water deficit on four diverse rice cultivars I. Rooting pattern and soil water extraction. *Field Crop Res* 37: 205-213.
65. Courtois B, Ahmadi N, Khowaja F, Price AH, Rami JF, et al. (2009) Rice root genetic architecture: Meta-analysis from a drought QTL database. *Rice* 2: 115-128.
66. Tang L, Tan F, Jiang H, Lei X, Cao W, et al. (2010) Root architecture modeling and visualization in wheat. *Proc. International conference on computer and computing technologies in agriculture*. Springer 5: 479-490.
67. 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.
68. Richard CA, Hickey LT, Fletcher S, Jennings R, Chenu K, et al. (2015) High- throughput phenotyping of seminal root traits in wheat. *Plant Metho* 11: 13.
69. De-Dorlodot S, Forster B, Pagès L, Price A, Tuberosa R, et al. (2007) Root system architecture: Opportunities and constraints for genetic improvement of crops. *Trends Plant Sci* 12: 474-481.
70. Hamada A, Nitta M, Nasuda S, Kato K, Fujita M, et al. (2012) Novel QTLs for growth angle of seminal roots in wheat (*Triticum aestivum* L.). *Plant Soil* 354: 395-405.
71. Christopher J, Christopher M, Jennings R, Jones S, Fletcher S, et al. (2013) QTL for root angle and number in a population developed from bread wheats (*Triticum aestivum*) with contrasting adaptation to water- limited environments. *Theor Appl Genet* 126: 1563-1574.
72. Fao W (2014) The state of food insecurity in the world 2012: Economic growth is necessary but not sufficient to accelerate reduction of hunger and malnutrition. *FAO, Rome*.
73. Passot S, Gnacko F, Moukouanga D, Lucas M, Guyomarc'h S, et al. (2016) Characterization of pearl millet root architecture and anatomy reveals three types of lateral roots. *Frontiers Plant Sci* 7: 829.
74. Bidinger F, Serraj R, Rizvi S, Howarth C, Yadav RS, et al. (2005) Field evaluation of drought tolerance QTL effects on phenotype and adaptation in pearl millet [*Pennisetum glaucum* (L.) R. Br.] top cross hybrids. *Field Crop Res* 94: 14-32.
75. Robinson H, Hickey L, Richard C, Mace E, Kelly A, et al. (2016) Genomic regions influencing seminal root traits in barley. *Plant Genom* 9: 1-13.
76. Franckowiak J, Fox G (2016) Genomic regions influencing seminal root traits in barley. *Plant Genom* 9: 113.