

Genetic tools uncovered root system variation under drought stress in wheat - A review

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Abstract: Sustainable crop productions are the foremost important practices to meet food demands for the fast-growing world population. However, crop production is being constrained by the occurrences of recurrent droughts. Plant roots are the most significant organ for adaptation to stress environment with a particular function of plant anchorage and acquisition of soil resources. Therefore, understanding and dissecting the genetic components of root system variations and considering them for trait selection under drought stress conditions would help in future breeding programs. This review highlighted the natural variations, roles of root system traits, and genetic tools to overcome the challenges of water scarcity in the era of climate change. Additionally, we compile and comprehend the potential QTLs that are responsible for root system trait variation under drought stress conditions and facilitate future comparative genomic analyses of wheat root system traits. We then described the contributions of genetic tool for root trait improvement, and selection at genetic level and investigate the natural root trait diversity as a basis for future genome editing. Lastly, we summarized breeding strategies to establish pioneering root-based selection and breeding to develop resilient crop varieties in the future.

Keywords: Adaptation, drought stress, natural variations, root system traits.

1. INTRODUCTION

Abiotic stresses are the leading environmental factor for excessive arable land degradation. Thus, this collection is disturbing the overall plant growth and development with devastating effects on crop yield and production across the world (Checker *et al.*, 2012; Fahad *et al.*, 2017). Abiotic stresses are the principal cause of about 50–70% of crop yield loss in the globe (Francini and Sebastiani, 2019). Drought stress is the major driving factor that affects the broad range of agro-climatic production and productivity of crop plants (Sallam *et al.*, 2019).

Drought stress affects the biochemical, physiological, and molecular components of the crop plant (Sallam *et al.*, 2019). Hence, advanced genetic tools are emerging to improve the performance of crops under drought stress by uncovering the genetics of root system responses to generate resilient cultivars and to sustain future food security (Mwadzingeni *et al.*, 2016). It has been recognized that multiple root system traits are vital to mediate drought tolerance in plant growth, and are directly contributing to crop grain yield. The 20th century has a historical indication for exclusive shoot trait research and improvement (Zhu *et al.*, 2019). Although roots have a crucial role to improve the drought tolerance ability of crop plants, crop breeders were mostly focusing to investigate the aboveground trait due to the difficulty of root sampling and phenotyping (Oyiga *et al.*, 2020). However, now a day researchers are researching crop plant root systems and architecture due to the emerging of high throughput root phenotyping and imaging methods (“e.g. Shovelomics”) (York *et al.*, 2018).

In the past decades, a lot of conventional breeding approach was applied to increase the grain yield and quality of crops, and it was satisfactory to increase the grain yield. Currently, for a deeper understanding of the root system traits, genomic and phenomics strategies have been targeted for better utilization of root traits in crop breeding programs (Nguyen and Stangoulis, 2019) as the root system is the most important plant organ for crop adaptation under water stress (Khan *et al.*,

2016). Hence, advanced genomic approaches such as association, GWAS, and QTL mapping were applied to dissect the genetic basis of the wheat root system for drought stress tolerance (Crespo-Herrera *et al.*, 2017; Sukumaran *et al.*, 2018). Association mapping (AM) or genome-wide association mapping (GWAS) is a popular genomic tool to dissect the genomic regions that are responsible for the variability of a phenotypic trait under extreme environments (Qaseem *et al.*, 2018).

However, the genetic dissection of the wheat root system has been limited for several years when compared to other crops due to its genetic complexity. Since then, following the expansion of sequencing technologies and high throughput phenotyping, wheat genomes were subjected and considered for genomic research (Cavanagh *et al.*, 2013; Wang *et al.*, 2014). This genomic analysis established several SNP markers and candidate genes that are related to root traits for drought tolerance and identified genomic regions with constant effects in diverse environmental conditions. Recently, the mega-study showed that more than 660k SNP Array has been developed from the wheat genome, which can identify > 630,000 SNPs with high efficiency and genome specificity (Zhou *et al.*, 2018). Therefore, genomic researches are being emerged as an essential tool to identify QTLs/alleles related to wheat root system traits and functional gene discovery (Li *et al.*, 2019). Also, recently, newer methods, such as transcriptomics, proteomics, metabolomics, and ionomics ('molecular phenotyping'), have been employed to determine root trait inheritance at the phenotypic and physiological levels. Therefore, this review will address the following issues related to the genomics of wheat root systems and their contribution under drought-stressed conditions. 1) How drought stress affects wheat production? 2) How root system architecture of cereal crops responds to drought stress? 3) How and what genetic tools dissect root systems under drought stress? 4) What is the role of root architectural traits to confer water-deficit stress?.

2. CROP PRODUCTION IS THREATENED BY DROUGHT STRESS

Plant growth and productivity are affected by the incidence of drought stress and are posing a significant threat to crop yield loss (He *et al.*, 2018). The occurrence of recurrent drought affects 60% of wheat production in high-income countries and 32% in low-income countries (Chen *et al.*, 2012).

In recent years, drought stress has become the most vital cause of crop yield reductions (Lamaoui *et al.*, 2018). The whole agroecosystems may suffer from frequent drought risks as a consequence of the global increase in temperature (Leng and Hall, 2019). According to the FAO (2018), >60% of the global population will inhabit areas with water deficiencies by 2025, and currently 70% of the world's freshwater

With the dramatic increase in the global population, water requirements are rising at an alarming rate, resulting in an increasing need to breed water-efficient crops (Ruggiero *et al.*, 2017; Blankenagel *et al.*, 2018). The breeding of drought-tolerant cultivars requires improved root system architectural attributes as a necessity for the crops to cope with the changing climatic conditions.

Plants experience drought stress either when the water availability near the root zone is limited or when there is an imbalance between water uptake and loss through transpiration that hinders plant growth and development during the plant life cycle (Anjum *et al.*, 2011). Under drought stress conditions, plants exhibit a wide variety of disorganization that may result in an alteration from high sensitivity to viable tolerance (Joshi *et al.*, 2016). A drought restricts various crucial physiological processes, including growth performance, correlations between nutrients and water, photosynthesis, and assimilates partitioning, which consequently results in significant reductions in biomass production and yield (Hussain *et al.*, 2018). A lower absorption rate of photosynthetically active radiation, decreased radiation use efficiency and a decline in the harvest index are leading factors of yield reduction under limited soil moisture conditions (Randhawa *et al.*, 2017). Evolution has shaped the inherent potential of plant populations for morphological and physiological adjustments that mitigate the detrimental impacts of drought stress (Farooq *et al.*, 2009; Basu *et al.*, 2016).

3. THE ROOT SYSTEM ARCHITECTURE OF CEREAL CROPS

The root systems of cereal crops in the soil have their shape, spatial arrangement and are defined as root system architecture (RSA). It is configured by changing the root type, rate of growth, and root angle (Grossman and Rice, 2012). It is classified into four different groups (Figure 1.); the first is coarse (tap) roots (Wasaya *et al.*, 2018), it is the primary root that grows during the seedling stage and helps the plant to grow on the surface of the soil by managing the growth of RSA and root depth (Marden *et al.*, 2018; Montagnoli *et al.*, 2020). The second is the lateral root or fine root; it is the

branching of root from another root which is the main part of the root system that is used for mechanical attachment of the plant to the soil mainly for nutrient acquisition (Baesso *et al.*, 2018). The shoot-born roots are also the third part of the root system which is emerged from hypocotyls and it is a stress-induced trait (Koevoets *et al.*, 2016; Wasaya *et al.*, 2018). The types of the root systems are variable according to the types of the crop; for instance, bread wheat has two major types of root system like Seminal root (the first root emerge from the seed) and nodal root which is helpful for high root depth of wheat crop (Slack *et al.*, 2018).

According to Lynch, (1995) root architecture is the general term to describe root morphology, root topology, and root distribution. Root morphology described the exterior appearance of a particular root axis as a part of the root system, such as root diameter, root cap, root hairs, the structure of tiny roots, and cortical senescence. Root topology also expresses the association of individual roots with branching and it is easy to measure after digging from the soil because root topology is constant and flexible to move. On the other side root distribution also shows the belongings of roots in the soil in its positional grid such as the comparison of two or more plants by their root biomass and root length. To compare that root describing root architecture help to examine more root axis than root topology and root distribution. On the other side roots, architecture is difficult to measure than root topology and distribution.

The cereal crop RSA consists of multiple embryonic (primary and seminal) and postembryonic (lateral, crown, and brace) roots (Lehmensiek *et al.*, 2009). These parts of RSA have their importance; for instance, primary and seminal roots which are produced at the basal limit of the embryo would help for plant healthy growth, nutrient and water acquisition from the soil (Khan *et al.*, 2016). In wheat, the RSA traits such as root growth angle, seminal root number, and length are basic for adaptation of plants during water deficit, and they are determined at the early growth stage in the soil (Figure 1.) (Zhu *et al.*, 2019). Other RSA parts are also formed aboveground and underground of the shoot node, which is known as crown and brace roots (nodal roots); are important for lodging resistance with a role of water and nutrient uptake (Ahmed *et al.*, 2018). Lateral roots have also emerged in all parts of roots within the soil and it has a decisive role in water and nutrient uptake (Rogers and Benfey, 2015).

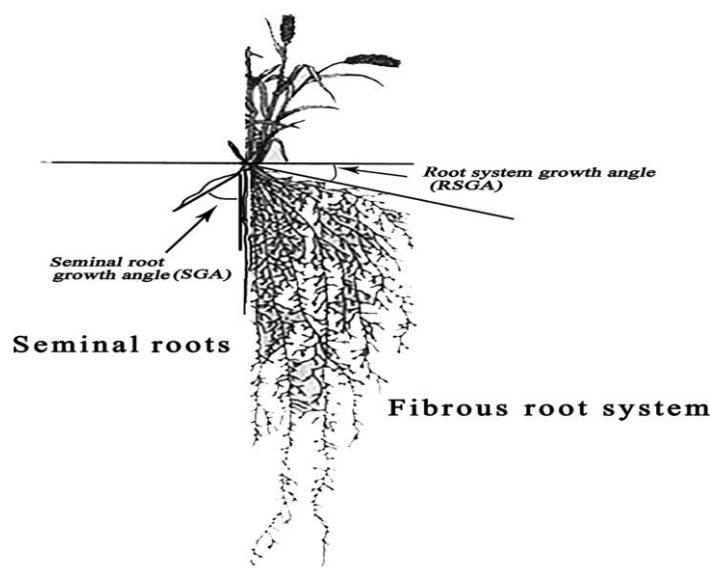


Figure 1: Wheat root system to show root growth angle in the seminal and fibrous root (Zhu *et al.*, 2019)

4. HOW DO ROOT ARCHITECTURAL TRAITS CONFER WATER-DEFICIT STRESS?

Roots are essential organs of the plant that played a major role in anchoring the plant and optimizing soil resources (Dietrich, 2018). The plant increases its root surface area by growing lateral root and root hairs directionally for the improved acquisition of soil moisture and to avoid water deficit stress (Dietrich, 2018). Roots are evolved to be responsive and intensely accommodative to the native surrounding; so their morphology, growth, and physiology are closely associated with plant genotype and growing medium properties, for example, the elongation rate and the number of lateral roots can be decreased by a high amount of soil water content or soil density and this can also be associated with

shoot growth reduction (Bengough *et al.*, 2011). As such, the root system is crucial to improve plant adaptation to various environmental stress conditions such as drought, salinity, waterlogging, and nutrient deficiencies (Chen *et al.*, 2020).

The wheat root system has a fundamental role in the drought adaptation mechanism; Lateral roots which are emerging from the primary and nodal root are used for the absorption of water and nutrient (Zarebanadkouki *et al.*, 2013). Each root trait has its function for adaptation to drought stress (Wasaya *et al.*, 2018). When the primary root has a small growth angle it can reach deeper soil and it helps to absorb available water from deeper soil at the lateral growing season (Trachsel *et al.*, 2013). The depth of the root will also help for the adaptation of crops under water stress conditions (Wasson *et al.*, 2012). The deep rooting of the plant is called root vigor which assists by the length of the root system (Comas *et al.*, 2013). A high rate of cell divisions and extensions occur within the root tip for rapid root growth (Rahni and Birnbaum, 2019). Root vigors are affected by the amount of water on the root tip (Colombi *et al.*, 2017), photo assimilation (Hauer-Jákli and Tränkner, 2019), and the shoot growth or shoot traits such as shoot tiller number or branching (Ito *et al.*, 2018). The reduction of tiller number in the shoot of wheat provides an opportunity for the root to become deeper and longer (Slack *et al.*, 2018). The root growth angle also influences root depth, for example, the narrow root angle in wheat the deeper rooting system and consequently increase the yield (Nguyen and Stangoulis, 2019).

The root density contributes to plant adaptation during water deficit stress by easily penetrating the compact soil layer for better absorption of water (Friedli *et al.*, 2019) The higher number of root hair increases the physical contact of the root into the soil and increases the moisture content absorption of the soil (Choi and Cho, 2019). The nodal root and its lateral roots also spread in the deep soil to maximize water uptake and nutrient acquisition (Ehdaie *et al.*, 2012). So the root traits are highly determined by environmental factors and also a combination of the genotype and environmental interactions. Therefore, it is important to examine the root traits in the soil and their relation with the genetic variation that influences the wheat yield during drought stress, and also it is critical to examine root traits in soil from the respective target environments (Fleury *et al.*, 2010).

5. GENETIC DISSECTIONS OF WHEAT ROOT SYSTEM VARIATION

Considering as an important type of grain crop from an economic point of view, wheat was examined in detail for root structure variations. Recently, numerous spring wheat collections showed improved root systems of deep rooting and root biomass (Narayanan *et al.*, 2014). The origins and growing environment of the wheat genotypes would also have a momentous effect on the depth of root penetration. The wheat subgroups collected from Australia, the Mediterranean, and western Asia have a greater root depth compared to subgroups of South Asia, Mexico, and Canada. The elongated root length could be an important adaptive trait of genotypes to improve water uptake and that were cultivated in moderately drier environments. The biparental RIL population and a derivative of Xiaoyan 54 and Jing 411 (a Chinese wheat variety) were considered for QTL mapping and major QTLs responsible for root length was discovered (Table 1), and this trait was originated from the older variety Xiaoyan 54 having a larger and deeper root system (Table 1) (Ren *et al.*, 2012). A study reported by Ma *et al.* (2017) identified 15 QTLs related to root traits using a population of Q1028 and ZM9023. The efficient QTL alleles came from the parent Q1028, which are recognized by a longer root system (Table 1).

Genetic studies to explore the major QTL effects on root architectural traits under different water regimes have been carried out in wheat mapping populations. Liu *et al.* (2013) mapped seven consistently expressed QTLs that were associated with seminal root traits, including total root length, seminal root number, project root area, root surface area, and seminal root angle, and the individual QTLs manifested phenotypic variations ranging from 4.98% to 24.31% under different water regimes. This study importantly noticed that one chromosomal region at the interval *Xgwm644.2-P6901.2* on chromosome 3B harbored nine QTLs affecting most of the root morphological traits. Recently, favorable alleles of eight QTLs linked to root length were mapped to the wheat RILs derived from a cross between 'W7984' (synthetic) and 'Opata 85' under hydroponic conditions, with two of the eight QTLs being contributed from the drought-resistant parent 'W7984' (Ayalew *et al.*, 2017) (Table 1).

According to Maccaferri *et al.*, (2016) report a GWAS analysis for different root traits was considered using a panel of 183 durum wheat cultivars by growing on vertical black screening plates to identify a possible candidate's gene for future marker-assisted selection in root based breeding. Also, the genome-wide analysis conducted by Alahmad *et al.*, (2019) recognized seven marker-trait associates across chromosome 6A of durum wheat which is responsible for the seminal root angle (Table 1). Ayalew *et al.*, (2018) reported that a collection of winter wheat was assessed for rooting depth under PEG

induced water deficit stress and normal conditions, and the LD analysis showed 15% of the total marker were significant, and GWAS discovered five major root length QTLs clustered on chromosomes 2B, 3B, and 5B, indicating that the B genome contributes a significant role to control root growth and can be potential for marker-assisted selection. According to Beyer *et al.*, (2019) a GWAS analysis was conducted to identify the candidate gene and loci for five root traits using 201 winter wheat accessions having 200 years of selection and breeding record at the seedling stage by growing on the hydroponic system and using a total of 20,881 polymorphic SNP markers and come with 63 marker-traits association with seven for root length, 24 for root branching, four for seminal root length, eight for root dry weight, and 20 for root diameter. Alahmad *et al.*, (2019) reported that an association mapping for 100 wheat lines together with well-conditioned wheat cultivars were evaluated using 102 simple sequence repeat markers to identify the genetic markers that are related with quantitative trait loci for root traits, and the results indicated the presence of two novel QTLs that are related with drought stress tolerance within a group of wheat and this finding will help to develop drought tolerance wheat germplasm. Therefore, the above scientific report shows that genome-wide tools are powerful for the identification of important traits in wheat such as root-related traits (Ahmad *et al.*, 2017) and enhancing abiotic stress (Kumar *et al.*, 2018). The GWAS approach also identified three drought-responsive pleiotropic single nucleotide polymorphism (SNP) markers associated with root dry biomass in a panel of 100 bread wheat genotypes selected based on their breeding history for drought tolerance (Mathew *et al.*, 2019). Another study identified five significant markers causing extended rooting lengths under drought stress conditions using a mapping population consisting of two introgressed populations (Bhatta *et al.*, 2018).

Table 1: List of genome-wide identified major QTL/genes associated with root system traits to drought-stress in wheat.

Root trait	QTL/genes	Chr. No	Position (cM)	Reference
Root length	<i>Qrls.uwa-1AS</i>	1	36.6	Ayalew <i>et al.</i> , 2017
	<i>Qrls.uwa-3AL</i>	3	92.2	Ayalew <i>et al.</i> , 2017
	<i>Qrls.uwa-7BL.1</i>	7	38.9	Ayalew <i>et al.</i> , 2017
	<i>Qrls.uwa-7BL.2</i>	7	44.7	Ayalew <i>et al.</i> , 2017
Root dry weight	<i>Qrdws.uwa-4AL</i>	4	65.7	Ayalew <i>et al.</i> , 2017
	<i>Qrdws.uwa-5AL</i>	5	53.8	Ayalew <i>et al.</i> , 2017
Seminal root number	<i>QSRN.cgb-2B</i>	2	0.3	Liu <i>et al.</i> , 2013
	<i>QSRN.cgb-3B</i>	3	-1.7*	Liu <i>et al.</i> , 2013
Total root length	<i>QTRL.cgb-3B</i>	3	-7.7*	Liu <i>et al.</i> , 2013
Projected root area	<i>QPRA.cgb-3B</i>	3	-0.6*	Liu <i>et al.</i> , 2013
Root surface area	<i>QRSRA.cgb-3B</i>	3	-0.6*	Liu <i>et al.</i> , 2013
Seminal root angle	<i>QSRA.cgb-2B</i>	2	3.0*	Liu <i>et al.</i> , 2013
Seminal root angle	<i>QRA.qgw-2A</i>	2	80.2	Christopher <i>et al.</i> , 2013
	<i>QRA.qgw-3D</i>	3	9.1	Christopher <i>et al.</i> , 2013
	<i>QRA.qgw-6A</i>	6	5.3	Christopher <i>et al.</i> , 2013
	<i>QRA.qgw-6B.2</i>	6	149.9	Christopher <i>et al.</i> , 2013
Seminal root number	<i>QRN.qgw-4A.1</i>	4	3.3	Christopher <i>et al.</i> , 2013
	<i>QRN.qgw-6A</i>	6	40.7	Christopher <i>et al.</i> , 2013
Root volume	<i>QRv.D84-2A.a</i>	2	52.5	Ibrahim <i>et al.</i> , 2012
	<i>QRv.D84-5D.a</i>	5	82.0	Ibrahim <i>et al.</i> , 2012
	<i>QRv.D84-3A.a</i>	3	83.3	Ibrahim <i>et al.</i> , 2012
Surface root area	<i>QSra.D84-2A.a</i>	2	52.5	Ibrahim <i>et al.</i> , 2012
	<i>QSra.D84-2D.a</i>	2	48.2	Ibrahim <i>et al.</i> , 2012
	<i>QSra.D84-5B.a</i>	5	14.3	Ibrahim <i>et al.</i> , 2012
	<i>QSra.D84-7D.a</i>	7	28.2	Ibrahim <i>et al.</i> , 2012
Total root length	<i>QTrl.D84-7A.a</i>	7	144.0	Ibrahim <i>et al.</i> , 2012
	<i>QTrl.D84-2D.a</i>	2	48.2	Ibrahim <i>et al.</i> , 2012
Root length	<i>wPt6278</i>	2	83.9	Ayalew <i>et al.</i> , 2018
	<i>wPt1159</i>	3	44.4	Ayalew <i>et al.</i> , 2018

Chr. No.; Chromosome number; cM, Genetic distance between putative QTL and the nearest flanking marker, Positive values are between the QTL and the left flanking marker, negative values are between the QTL and the right flanking marker; QTL, Quantitative loci

6. FUTURE PERSPECTIVES ON ROOT SYSTEM VARIATIONS FOR BREEDING PROGRAMS

Roots and shoots are the two most important organs of the plant anatomy. However, for varietal selection only shoot traits were targeted, whereas root traits were neglected in breeding programs. Hence, a future breeding objective should be considered and target the root system traits together with shoot traits for crop yield improvement.

Several studies have also shown that root system traits leading to improve shoot traits for yield and this is indicating that roots traits are the foremost breeding target of the future (Li *et al.*, 2018). Understanding the genomic diversity of root system traits would be an opportunity to comprehend the drought adaptation mechanisms with the final objectives of selecting genotypes based on the favorable root traits. Currently, QTLs associated with root system variation including root length, biomass, number, angle, and density under drought stress conditions are identified and reported (Table 1.). More importantly, the root diversity of wild relatives of a crop has been investigated and showed a significant role in drought stress adaptation (Reinert *et al.*, 2016).

The improvement of drought stress adaptation based on the root system traits underlying classical breeding is difficult due to the complexity of root traits (Van Oosten *et al.*, 2016). Hence, both genomic and phenomics strategies are emerging as an important breeding tool to dissect in-depth analyses of root traits under drought stress adaptation. However, the biggest challenge in molecular breeding and genetic dissection is the events of G×E interactions to determine the precise genetic regions of complex root traits under field conditions. Hence, to overcome these challenges there is a need to conduct QTL expression analysis for the particular dissection of responsible root traits across varying environments. Also, the advancements of NGS and bioinformatics tools provide an extra opportunity to discover novel genes controlling root traits (Taunk *et al.*, 2019). Using comparative genomics tools have also been applied to identify stress-responsive expressed genes for root system traits in rice (Lou *et al.*, 2017), wheat (Hu *et al.*, 2018), maize (Li *et al.*, 2017), and barley (Kwasniewski *et al.*, 2016). Genetic modifications and editing provided the single prospect to edit the targeted genome for particular breeding traits. The above described genomic strategies may help to dissect complex traits and for targeted selection in breeding (such as genomic selection), as well as gene function analyses of genes controlling root dynamics and breakthroughs in the determination of yield responsible genes in cereals production.

In summary, we recommend to employ the following multistep root breeding approaches to ascertain drought stress adaptations in cereals: (i) evaluate genome-wide diversity of the natural populations related with root traits; (ii) applying advanced genomics and phenomics strategies for powerful quantitative dissection of root traits; (iii) using high-throughput root phenotyping; (iv) combining high throughput genome-wide tools to identify QTL using commutative models; (v) considering wild relatives and landraces to dissect root system variations for drought stress adaptations via genomics strategies; (vi) identifying stable and major QTL effects and combine phenotype, genotype, and environment to develop breeding varieties; (vii) functional classification of the underlying root related genes; (viii) applying RNA-sequencing based QTL expression analyses for high-resolution gene trait analyses; (x) manipulating gene functions using CRISPR/Cas9; (xi) establishing an interdisciplinary research network among geneticists, biotechnologists, agronomists, breeders, and crop physiologists to merge scientific knowledge on root system variation. These efforts will allow us to combine and interchange scientific knowledge in breeding programs for the objectives of developing resilient crops and sustaining food security under changing climatic conditions.

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Author contributions

MT: conceptualization, writing and draft preparation, writing review, editing and validation.

Conflict of interest

The author declares that no conflict of interest

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