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Minireview

Root dynamics and drought stress management in plants — An overview

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Drought is a predominant factor responsible for yield reduction throughout the world. The current scenario of climate change and global warming are further causing frequent and severe droughts, which emphasize the need to understand the response of plants to drought stress. Hence, it is imperative to develop a system wherein water utilization in agriculture is managed more efficiently. In this context, the plant root system which is in close association with soil assumes greater importance and they play an important role in plant growth and development by exploiting soil water and nutrients. Root traits such as root diameter, length, specific area, angle, length and density are considered useful traits for improving plant growth under drought conditions. This review on root dynamics under drought stress presented here provides readers with the latest information on root system architecture, genetics, physiology and molecular responses of roots under drought stress.

Keywords: Abiotic stress, Climate change, Global warming

Introduction

Drought stress is an important factor limiting in realization of the yield potential of any crops. In developing countries, the larger cultivable area experiences moisture stress. With an increase in global temperature, it has been predicted that the occurrence of moisture stress will be more frequent and severe in future years[1]. Hussain *et al*.[2] who had reviewed both cold and drought stresses in crop plants, reported that drought stress negatively influences the plant growth through physiological and biochemical functions such as photosynthesis, respiration, ion uptake and translocation, and carbohydrates metabolism stages of the plant. Not only drought, even low temperature may also trigger turgor stress at cellular level due to to poor root hydraulic conductance and diminished root activity[2]. Even though the common methods like direct selection and heterosis breeding are employed for developing new tolerant varieties, they are time-consuming and labour intensive. The alternative strategy that has succeeded in many crops is using secondary traits like root-related traits[3].

The role of deeper roots, lengthier roots and root system architecture in moisture absorption and physiology and genetics of root traits under drought stress gains importance. Hence, we present here, a critical review on root traits and its importance in drought stress.

Root dynamics and drought stress tolerance

Generally, plants will take up water from the deeper soil layers under water limited conditions and roots are the first organ in plants that are in close association with soil to respond to drought. Different types of plants have different types of root traits *viz*., number and length of primary roots, lateral roots, crown root number, root diameter, root length density, root angle and number of root hairs which are important in water absorption under dry conditions.

Deeper root system

The ability of the plant to change its architecture to have thicker and deeper roots under drought condition is an important adaptation to avoid drought stress, which depends on the crop genotype. The availability of water to a plant is decided by its root system and its morphological and physiological characteristics. Plants with deeper root systems can be able to absorb more water from deeper soil layers under drought stress. The root system of a plant determines its ability to capture available water and nutrients, and therefore it is critical for drought tolerance. Generally, deeper and more profuse root

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systems could be able to tap extra water from the deeper soil and thereby helps to alleviate drought effects. Under mild water stress, plants extract soil water from the 15-30 cm soil depth and when the drought stress becomes severe, roots at the mid soil zones (30-45 and 45-60 cm depth) gain importance[4]. A well-known phenomenon is the development of more roots with a smaller diameter to increase surface area while saving carbon investment in response to drought, which has been shown to increase drought tolerance[5]. Deeper rooting and a higher proportion of deeper roots have also been recognized as an important root trait for the terminal drought to access stored water in deeper layers of soil[6,7].

Root length density

Root traits, especially length, number and depth of roots were viewed as important traits which enhance the efficiency of crops under drought stress. Root length is an important trait against drought stress i.e., crop varieties with longer root system have more tolerance[8]. Generally, at the seedling stage itself, the root length gives a fair idea about later root growth under field condition. Similarly, under drought stress condition, root distribution is low in the surface layer and high in the deep soil layers to absorb more water from the deeper layers of soil. Efficient uptake of water which is essential for yield improvement under drought stress depends on size and activity of the root system i.e., number of roots, root length and penetrating ability of the roots.

Root proliferation at the early stage of growth decides further growth of roots and root proliferation is ultimately responsible for recording higher biomass and grain yield under drought stress. The root systems having thin xylem vessels will have more capillary forces which are helpful in water and nutrient uptake from dry soils[9]. It has been reported that water deficit significantly reduced RLD in wheat[10].

Roots with a small diameter and high specific root length increase the surface area of roots which are in contact with soil moisture, thereby increase the soil volume that can be explored for water. Generally, more root hairs help in absorbing more water from the soil. Root hairs, in general play a major role in the absorption of water and nutrients, since they are the first organs facing the soil stresses[11].

Root system architecture (RSA)

It has been reported that when plants are under drought stress, they inhibit primary root growth and there is a significant RSA alteration[12]. RSA is defined as the system of primary, adventitious and accessory roots, which is determined by root parameters *viz*., root number, length and angle[7]. The root system architecture (RSA) greatly affects crop growth and yield. Moderate water stress results in reduction of lateral root growth but with an increase in primary and secondary root growth while with the advancement of severe water stress, there will be more emphasis for direct root growth and root branching for water scavenging[13]. Even though the root length and surface area are the main factors that determine the absorption of water from the soil, the diameter of xylem vessels influence the root hydraulic conductivity which decides the crop yield under drought stress[14]. Root architecture is critically important for soil water acquisition, in which, the rooting angle has the advantage i.e., vertical root growth angle helps for deep root systems without any change in the distribution of root biomass. Rooting angle is associated well with deep root systems in beans[5], and larger genetic diversity for the same was reported in rice[15].

Response of roots to drought stress in plants

The deeper root system for acquiring more moisture from soil layers has been noted in rice, wheat, beans and other short-statured plants that were grown under drought conditions. Significance of a deep root system for uptake of water from deeper soil layers under water-stressed environments was observed in many plants *viz*., rice (*Oryza sativa* L.)[15,16] and maize (*Zea mays* L.)[6]. The potential ability of roots to recover under drought stress is an important factor that will decide the growth of rice[17]. Increase in root length density and decrease in adventitious roots was observed in rice under drought[18], which modifies the root architecture so that more water can be taken up from deeper soil layers. Significant response in root branching, particularly in capillary lateral roots was noted in rice in drought condition[19]. A positive correlation of root diameter and depth with plant vigour was noticed in rice under drought stress[20]. It has been found that rice plants with deeper roots are more tolerant to water stress, which also helps to maintain crop growth in such situations[16]. Multiple root traits identified could confer wheat genotype RAC 875 advantage in drought tolerance. Higher growth of new nodal roots was seen in drought-tolerant RAC 875[21]. A general association of drought tolerance with the growth of nodal roots has been shown in pearl millet[22].

Legumes play a major role in providing a balanced dietary protein in the diet of the people. They also play a major role in crop rotation, diversification and enriching the soil fertility in respect of nitrogen and organic matter. Increased absorption of soil water by efficient root system is one of the promising approaches for drought tolerance in legumes[23]. Moisture stress largely affects production and yield stability of pulse crops particularly black gram. Field experiments were conducted with ninety-four genotypes of black gram to study their response under induced moisture stress condition. All the root parameters *viz*., the number of roots, root length, root diameter, dry weight of root and root volume were observed along with root penetration ability. Based on the root parameters and root penetration, two genotypes, T 9 and CBG-09-13 were selected as drought tolerant[3] (Table 1).

Similar studies were conducted in eighty nine green gram genotypes based on root characters and root penetration ability and observations on root traits were recorded for screening for drought tolerance. Root penetration study was conducted to screen drought tolerant and susceptible genotypes. In this study, a thin layer of paraffin wax and white petroleum ether were mixed in 2:1 ratio to simulate a hard pan. A thermocol was made with holes and its bottom was covered with wire mesh. Then the wire mesh was wrapped with aluminium foil to prevent leakage of paraffin wax solution. The 2:1 mixture of paraffin wax and white petroleum ether was poured into the holes of thermocol to form 2-3 mm thin layer and the entire set up was kept in room temperature for 30 min to allow it to cool. Then the aluminium foil was removed. Two-third of the holes in thermocol was filled with sand and sowing was taken up. The entire set up was kept in coarse sand bed for allowing root development. After 18 days, thermocol set up was removed and root penetration and root growth were observed. The roots of the genotypes which penetrated 2:1 mixture of paraffin wax and white petroleum ether, and which had longer and a greater number of roots were identified as drought tolerant[1](Table 1).

In terminal drought, the root system during early growth stage has significantly contributed to the seed yield in chickpea. The increased rooting depth will increase the uptake of water and yield in chickpea, even though it may be more expensive. In chickpea, increasing drought avoidance through deeper and profuse root system is one of the traits helpful in producing higher yield under terminal drought stress[24]. Significant correlations between drought resistance and various root traits has been reported in soybean[25]. The members of the Cactaceae family under extreme drought condition avoid drought stress by senescence of primary root tips resulting in rapid branching and growth of shallow root system[26]. Low-moisture regimes may develop a more extensive root

Table 1 — Root parameters in black gram and mung bean under drought stress

Parameters	No. of Genotypes		Mean		Range	
	Black gram	Green gram	Black gram	Green gram	Black gram	Green gram
No. of Roots						
1.00-2.00	-	1				
2.01-3.00	12	6				
3.01-4.00	23	26				
4.01-5.00	21	34	4.28	4.44	2.25 -7.42	1.17-8.99
5.01-6.00	6	15				
6.01-7.00	9	2				
7.01-8.00	2	2				
8.01-9.00	-	3				
Root Length (cm)						
10.00-20.00	-	-				
20.01-40.00	11	22	46.29	44.11	27.06-69.20	26.22-58.82
40.01-60.00	45	67				
60.01-80.00	16	-				
Root Diameter (cm)						
0.20-0.30	19	21				
0.31-0.40	33	47				
0.41-0.50	16	11	0.36	0.37	0.22-0.59	0.21-0.68
0.51-0.60	5	6				
0.61-0.70	-	4				
Root Volume						
0.00-1.00	4	7				
1.01-2.00	18	15				
2.01-3.00	16	23				
3.01-4.00	18	21				
4.01-5.00	11	9	2.77	3.13	0.50-5.71	0.48-9.52
5.01-6.00	6	12				
6.01-7.00	-	1				
7.01-8.00	-	-				
8.01-9.00	-	-				
9.01-10.00	-	1				
Root DMP (g)						
0.000-0.100	1	-				
0.101-0.200	6	2				
0.201-0.300	17	11				
0.301-0.400	11	14				
0.401-0.500	13	28	0.497	0.463	0.047-1.674	0.169-0.888
0.501-0.600	6	19				
0.601-0.700	5	7				
0.701-0.800	3	4				
0.801-0.900	2	4				
< 0.901	9	-				

[Adapted from Prakash *et al*. 2017[1] and Prakash *et al*. 2018[3]] system and also observed changes in the characteristics of root systems of horticultural plants when subjected to drought stress[27].

Physiological responses of roots under drought stress

Physiological studies were started at IRRI even during the 2000s towards the function of roots for water uptake. Root:shoot ratio was found to be closely associated with drought resistance. Three adaptive mechanisms have been found for rice under drought stress: (i) osmotic adjustment in roots, if possible, in conditions with a relatively small soil water reservoir (ii) increased root penetration into the soil, and (iii) increased root density, depth and the root to shoot ratio in conditions with a relatively larger soil water reservoir[28]. It has been reported that lower root pressure is associated with drought sensitivity[29]. It was found that with limited rooting depth, root attributes limit rice performance more than shoot attributes under drought[30]. Higher proline and antioxidant enzymes were noted in roots under drought conditions[31].Gradual water depletion reduced shoot growth, with the maintenance of root growth resulting in an increased root to shoot ratio[32]. Similarly, under drought conditions, the root biomass is also reduced, along with root length and root tip frequency[33]. However, other root traits, such as root tissue density and root area index remain unchanged, when oak (*Quercus* sp.) saplings were exposed to drought[34].

Several root traits in cereals have been reported to be associated with drought tolerance[35]. Smaller metaxylem diameter of primary roots might restrict water extraction during early plant growth, leading to conservative use of available water, which is considered to be an important trait under drought environments with stored water in deep soil[36]. A DNA-based method was developed to assess DNA concentrations of wheat roots in soil[37]. Generally, root DNA concentrations in soil are used to quantify root responses to abiotic stress *viz*., drought stress in wheat[37].

Genetics of root traits under drought stress

Genetic studies were started even in the 1980s to improve selection methods for root characters. Root traits are considered to be complex, which is controlled by polygenes having a quantitative effect and are difficult to quantify under field conditions and they are highly prone to environmental effects. Multiple genes with small effects control most of the root traits and their interaction varies with the prevailing environment. Identification of drought tolerance-related QTLs and mapping of QTLs of root traits for drought-tolerance is inevitable in marker-assisted selection (MAS). Even though the use of molecular markers in drought tolerance is challenging, molecular markers with the desired QTL for root traits or genes must be identified for a successful breeding program[35].

Several genes and quantitative resistance loci associated with root response to various stresses were identified. The identification of QTLs and genes for drought resistance is advancing both at IRRI and in other institutes. For the root traits, associated QTLs had already been mapped in a few crops. For example, four major QTLs affecting root traits in rice and a major QTL for leaf ABA concentration for effective root architecture in sorghum were reported[38,39]. QTLs for five traits (root thickness, maximum root depth, root dry weight (RDW), RDW, root: shoot ratio) were identified in an IR64 × Azucena population[40]. Common QTLs for root penetration ability was also found[41]. Kinandang Patong has now been used as a source for a gene controlling deep root angle, and it also shows improved root elongation ability and yield under drought[42]. N22 is the source of a major-effect drought-yield QTL, qDTY 1.1 Root systems were improved by using QTLs in marker-assisted back cross-breeding program in rice[43] and a gene for deeper rooting (DRO1) has been identified on the chromosome 9 in rice[16]. The accuracy of the number and location of the identified QTLs have been refined by recent developments in meta-QTL analysis and genome-wide association mapping approaches[39].

Studies on drought stress in rice revealed 139 QTLs in just five studies for root traits[44]. Introgression of rice DRO1 gene by backcrossing to rice variety IR64 recorded higher drought resistance without reduced yield under normal conditions. More uptake of water due to deeper root system and a specific root length associated with a QTL, which also helped to maintain yield under moisture stress was reported n rice[45]. The drought-tolerant rice cultivar Birsa Vikas Dhan 111 was developed by marker-assisted backcross breeding, targeting four donor-parent chromosomal regions related to root traits. Different combinations of the QTL promoted water uptake in different environments, signifying their role in crop improvement programs in rice under drought conditions[43].

Table 2 — Genes involved in drought tolerance

Gene	Expression analysis	Role in drought tolerance
DRO1	Upregulated	Influnces root angle, induces root elongatiuon and deeper rooting[16]
OsDRE-B2B	Upregulated	Increses root number and length[48]

Presence of multiple QTLs for different root traits *viz*., root number, length, angle, biomass, and surface area were observed with a molecular mapping of root traits in wheat[46]. A 'QTL hotspot' for root traits introgressed into a chickpea cultivar proved its yield potential in different environments under terminal drought conditions[23]. Root trait-based seedling stage screening helped in mapping QTLs in soybean[47].

Molecular responses of roots under drought stress

Drought stress generally activates the ABA-dependent signalling pathway. Research studies proved that rice DREB transcription factors work as vital regulators in ABA-independent drought responses[48]. Among the five DREB-2 type genes, OsDREB2A and OsDREB2B are upregulated by abiotic stress and OsDREB2B generates OsDREB2B1 and OsDREB2B2 transcripts. Drought stress accumulates OsDREB2B2 transcripts, indicating its key role in the abiotic stress response in rice through the alternative splicing system. The OsDREB1F regulates the ABA-dependent pathway and the rice plants which over express this gene increased drought tolerance[48]. Few examples of the genes involved in drought resistance in rice are furnished in Table 2.

When five segments on different chromosomes were introgressed into rice lines, the one carrying a recessive gene for aroma, caused a marked increase in root length under drought stress conditions[43]. A field upland rice introgressed with root QTL resulted in increased root length and also recorded yield benefit of 1 t/ha in comparison to the control[43].

Conclusion

Among the various environmental stresses, drought is one of the major environmental stresses which has a negative effect on crop yield and productivity. With the advent of climate change and global warming, the effect of drought stress will certainly have a major impact on agriculture in future years. For the effective management of drought stress, even though several tools are employed like heterosis breeding, molecular breeding and genetic engineering, they require a lot of time and costlier also. But the study of root traits, their genetics and physiological response and dynamics under drought stress is helpful in drought management. Based on this review, it is observed that different root traits such as deeper roots, root length, root area, root system architecture and root length density are useful in improving adaptation of plant's productivity under drought stress conditions. Identification of genes or molecular markers linked with root architecture and root growth is useful to improve root traits through breeding and molecular selection methods. Hence, it is suggested that all these root traits may be included in any crop improvement programs to improve crop yield and productivity under drought stress conditions.

Conflict of Interest

Authors declare no competing interests.

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