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Mechanisms of Drought Tolerance in Sorghum: A Review

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ABSTRACT

Sorghum is the fifth most important cereal crop and occupies the second position among the staple food grains in semi-arid tropics. The adaptation of grain sorghum to a wide range of environmental conditions has led to the evolution and existence of extensive genetic variation for drought tolerance. Accordingly, sorghum is expected to play an increasingly important role in agriculture and meeting world food demand in the face of climate change, land degradation and increasing water scarcity. The crop requires relatively less water than other important cereals such as maize and wheat. However, yield potential of the crop is significantly limited due to drought and heat stresses. Drought is one of the most important factors that affect crop production worldwide and continues to be a challenge to plant breeders, despite many decades of research. Underestimating the different mechanisms underlying drought tolerance is vital for the breeding to alleviate adverse effects of drought in order to boost productivity. In this literature review, the main effects of drought on crop growth and development, and yield are reported.

Key words: *Drought, Sorghum, Physiological mechanisms, Drought tolerance, Breeding.*

INTRODUCTION

Drought stress is a serious agronomic problem contributing to severe yield losses worldwide. This agricultural constraint may nevertheless be addressed by developing crops that are well adapted to drought prone environments. Drought tolerance depends on the plant developmental stage at the onset of the stress syndrome, which in sorghum may happen during the early vegetative seedling stage, during panicle development and in post-flowering, in the period between grain filling and physiological maturity[93,94].

Sorghum is one of the most drought tolerant crop species and is an important model system for studying physiological and molecular mechanisms underlying drought tolerance. It is considered as one of the most important crops for production cereal grains and fodder for humans and animals. Also grain yield used to bridge the deficit in wheat flour to produce bread municipal.

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A biotic stress such as water stress and salinity was the incumbent in the first resistor work to improve the resistance for environmental stresses, especially the problem of water shortage. Sorghum is predictable to play an increasingly significantly function in cultivation and gathering world food desire in the countenance of climate modification, ground degradation and mounting water reduction[4].

Sorghum serves as a dietary staple crop for millions of people, especially in arid and semi-arid farming systems. Additionally, sorghum grain is used as livestock feed and for production of local beverages, while the stalk is used for animal feed, firewood, and as a construction material[68]. Sorghum grows across a wide geographic area at various altitude, day length, rainfall, and temperature regimes. Consequently, it is well adapted to withstand harsh conditions, which are the characteristic feature of tropical regions. The crop requires relatively less water than other important cereals such as maize and wheat. However, yield potential of the crop is significantly limited due to drought and heat stresses within the tropics and subtropics necessitating sorghum breeding for drought tolerance and productivity[14].

Drought can occur at any stages of the crop development. However, in the arid and semi-arid tropics, the probability of drought is highest at the start and end of the growing season. Drought stress at the beginning of the growing season will severely affect plant establishment. If drought occurs at flowering, or in the grain filling stages, it may result in reduced yield, or complete crop failure[12].

Drought contributes to poor crop performance and yield. Countries in arid and semi-arid tropics usually experience insufficient, unevenly distributed, and unpredictable rainfall. At one point rain may be abundant and perhaps wasted through runoff; in some years much rain may fall completely outside the growing season. In other years, in adequate mid-season rain may fall after crops have germinated, causing crop failure. Although drought stress at the beginning of the growing season may severely affect plant establishment, plants tend to recover soon when late rain fall levels are adequate[85]. Consequently, crops are prone to periodic moisture stress in one way or another because of the aforementioned realities[116]. The impact of moisture stress on crop yield is dependent on the stage of plant development[53,111]. Anthesis and grain filling stages appear to be the most vulnerable growth stages; occurrence of drought at these stages may result in reduced yield and/or complete crop failure[128].

Crop production is constrained by several biotic, abiotic and socio-economic factors. Amongst the most important abiotic constraints, drought is the most important. Therefore, understanding of the physiological mechanisms and genetic control of drought in crops is important as a base for improving the production and productivity of crops in the arid and semi-arid tropics. In this article, different mechanism of drought tolerance in crops have been reviewed.

Effects of Drought on Crop Growth and Development

Drought is a combination of stress effects caused by high temperatures[80] and a lack of water[22]. Evapo-transpiration is the major driving force that affects the soil, plant, and atmospheric continuum of the hydrologic cycle. In earlier studies, predictions of drought were mainly based on the amount and distribution of precipitation[13]. However, in recent studies soil moisture balance and soil characteristics have been introduced in the assessment of drought. Lack of adequate soil moisture, or water deficit, affects the ability of plants to grow and complete a normal life cycle[74].

Drought can have major consequences on growth, development and yield of crops by affecting several physiological, morphological and biochemical processes[103]. It is the major cause of poor crop performance and low yields, and sometimes it causes total crop failure. In the tropics, the probability of drought is highest at the start and the end of the growing season.

Drought can occur at both seedling, pre-flowering and post-flowering stages of development, and has the most adverse effect on yield[53,111]. Drought stress at the seedling stage of development will severely affect plant establishment[5]. If it occurs at flowering, or in the grain filling stages, it may cause reduced yields, or complete crop failure[12]. Researchers have classified drought as either pre- or post-flowering stress. The reactions of genotypes to these stresses are variable and controlled by different genetic mechanisms. Pre-anthesis moisture stress has effects on yield components such as stand count, tillering capacity, number of heads and number of seeds per head, while post-anthesis moisture stress affects transpiration efficiency, CO_2 fixation and carbohydrate translocation. The latter factors, in turn, results in low yields and premature plant senescence[109,123].

Physiological Mechanisms of Drought Tolerance

Levitt[58] mentioned that drought resistance mechanisms like drought avoidance, recovery, survival and tolerance, are associated with plant survival and production. Drought avoidance is defined as the ability of plants to conserve water at the whole plant level through decreasing water loss from the shoots or by more efficiently extracting water from the soil[60]. However, drought tolerance is defined as the ability of plants to withstand water deficit while maintaining appropriate physiological activities to stabilize and protect cellular and metabolic integrity at tissue and cellular level[111,124]. Survival is the ability of the crop to survive drought, irrespective of the yield it produces, while production is the ability of the crop to grow and yield under water stress conditions[4].

Ceccarelli *et al*[23]., defined drought tolerance, is a complex quantitative trait influenced by many genetic and environmental factors The responses of different plants, species, or genotypes to drought are variable in relation to developmental stage, duration of drought, and evolutionary adaptation of the crop[97]. In sorghum, for example, varieties that are adapted to arid and semi-arid environments showed higher drought tolerance than varieties of humid origin[9]. Several studies have been conducted in understanding the mechanism of drought resistance in crops and in identifying essential traits for drought tolerance[13]. Drought resistance, therefore, involves the interaction of different morphological structures, physiological functions, and biochemical expressions[20,71].

Stomatal Conductance and Leaf Rolling

In plants, stomatal conductance and leaf rolling have been found to be reliable physiological indicators of drought tolerance[52], which are strongly associated with leaf water potential[7]. These two mechanisms are controlled by different factors, where stomatal conductance is controlled by soil moisture dependent root signals, while leaf rolling is controlled by leaf water potential[28]. The strong correlation of leaf rolling and leaf water potential allows breeders to use leaf rolling as a visual scoring criterion for selecting for drought resistance in plants[46]. The rolling of leaves usually occurs following the reduction in leaf water potential. However, the degree of leaf rolling depends on the ability of the plant to adjust osmotically at low leaf water potential[35]. Plants with high osmotic adjustment develop less leaf rolling, and hence, reduced leaf rolling is considered as an indicator of a greater degree of desiccation avoidance, through a deep root system[46].

Drought tolerant genotypes exhibit lower stomatal conductance associated with increased leaf temperature, which gives rise to high transpiration efficiency and lower carbon isotope discrimination. The drought susceptible genotypes, on the other hand, show higher stomatal conductance and lower leaf temperature results in lower transpiration rates[54].

There is a lack of consensus on the benefits of the two traits of leaf rolling and stomatal conductance as drought resistance mechanisms. Leaf rolling has a detrimental effect on transpiration rate through changes in leaf stomatal conductance, and reduction in effective leaf area[88]. In addition, leaf rolling enhances stomatal closure by increasing leaf resistance to water loss. However, Heckathorn and DeLucia[43] argued that leaf rolling had positive effects on reducing leaf temperature and loss of water by decreasing the incident irradiation. Stomatal closure alone causes a 70-80 % decrease in transpiration rate in crops, where leaf rolling causes a decrease of only 2 % of normal transpiration rate[43]. Therefore, leaf rolling has less value in reducing water loss than stomatal closure and it may increase the survival of plants by enhancing stomatal closure under extreme drought conditions[43]. The significance of using these traits as physiological indicators of plant drought adaptive mechanisms depends on the crop species and the environment. Under conditions where there are no sophisticated instruments to measure transpiration efficiency and stomatal conductance, leaf rolling is good indicator of drought tolerance.

Characteristics of Root

Roots are the primary plant organ affected by drought stress and other environmental stresses of the soil[81]. Sorghum crown roots grow about 2 to 3 cm per day[96] and root growth is mainly affected by the amount of carbon partitioned to the roots, although it varies with environmental and genetic factors[10]. Sorghum roots may grow to depths of 1 to 2 m by the booting stage, and can efficiently extract water to a lateral distance of 1.6 m from the plant[96]. Root growth in sorghum terminates at flowering stage; however, it is more prominent in a senescent than in nonsenescent sorghum genotypes[91].

Bawazir and Idle[6] reported variation in root anatomy and morphology, among sorghum genotypes. Genotypes that have large number of seminal roots, large vessel diameter in both seminal and nodal roots showed better survival rate under drought stress conditions. Similarly, Habyarimana *et al*[39]., found that the drought tolerance traits displayed by the genotypes were related to drought avoidance mechanisms. These, in turn, are associated with deep root system, which enables plants to exploit moisture from the deeper soil horizons.

The root has received less attention than the shoot in the search for characters of use for screening or selection for drought resistance. Esau[32] remarked that in dry soil the restriction of adventitious root growth makes the efficiency of water transport depend more upon the conductivity of the seminal roots. Camacho *et al*[21]., showed that plants with efficient water transport systems avoid dehydration of the leaf tissue during periods of atmospheric drought.

Meyer and Ritchie[70] showed that, the root contributes more resistance than the shoot at least at high transpiration rates. Richards and Passioura[89] demonstrated variation in vessel size related to climatic factors in some wheat accessions, and proposed a selection and breeding programme for small vessels in the expectation of improving the performance of wheat under conditions of limited water supply. Passioura[78] reports encouraging signs in this programme.

Ekanayake *et al*[31]., indicated that drought stress tolerance was found to be highly associated with root characteristics such as root thickness, root length density, number of thick roots, root volume, and root dry weight. It was also found that number of thick root, root thickness, and root length density were highly associated with leaf water potential and field visual drought scoring using drying leaf. Drought stress adapted plants are often characterized by deep and vigorous root systems[15]. Nour *et al*[76]., also reported root weight is the best and easiest attribute to determine drought tolerance in grain sorghum. Matsuura *et al*[67]., on the other hand, reported a positive correlation between drought tolerance and root length in sorghum and millet (*Pennisetum glaucum*). Moreover, Plaut *et al*[79]., and Pace *et al*[77]., reported that seedlings under water stress caused an increase in root length with reduced diameter. Root depth, root length density, root distribution was reported as drought tolerance contributing traits[106].

Drought is often associated with nutrient availability and the capacity of roots to absorb the available nutrients. Ludlow and Muchow[60] indicated that greater root activity under intermittent drought should enhance crop stability by reducing the incidence of water deficits. Egilla *et al*[30]., and HongBo *et al*[45]., reported the significance of potassium (K). in improving drought resistance and root longevity. Shao *et al*[101]., also reported the importance of mineral elements, such as K^+ and Na^+ for root signal transduction function. Shangguan *et al*[98]., further denoted that the hydraulic conductivity of roots can be mainly affected by nitrogen and phosphorous nutrients. Hydraulic conductance in sorghum is primarily dependent on the number of fully functional nodal roots[11]. In moisture stress conditions, plants with sufficient P supply exhibited higher hydraulic conductivity than P deficient plants. Therefore, plants with sufficient P are found to be more droughts tolerant, and also have a higher ability to recover after drought.

Osmotic Adjustment

Under rainfed conditions, plants are exposed to varying degrees of water stress due to lack of an adequate water supply to meet the transpirational demand. The ability of a crop to grow in areas subject to water deficits has been termed drought resistance[115]. Individual plant species differ markedly in the mechanisms utilized to survive when water deficit exist. Adaptations to survive drought may be anatomical, morphological or physiological in nature and they serve either to faciliate the maintenance of favourable water balance (increasing water absorption or decreasing water loss). or to allow desiccation tolerance at low leaf $\psi_{w.}$

Osmotic adjustment is a major drought adaptive mechanism in plants[49]. Sorghum and millet landraces, which are collected either dry or humid environments show variation in osmotic adjustment. Landraces that come from drier regions show greater osmotic adjustment than landraces from humid regions. The assumption is that through the course of evolution the drier environments provided sufficient selection pressure for osmotic adjustment. Landraces with higher osmotic adjustment are characterized by their dwarf nature with high rates of transpiration and low rates of leaf senescence under stress[9]. Osmotic adjustment improves crop productivity through delaying leaf rolling and leaf tissue death[13]. As leaf rolling and leaf senescence decreases, the effective leaf area for photosynthesis increases. In a study by Ludlow *et al*[63]., on sorghum genotypes, those with high osmotic adjustment exhibited a 24 % higher yield than genotypes with low adjustment, when exposed to a post-anthesis drought stress. The yield difference observed was both in grain size and grain number, and it was associated with higher harvest index. Similarly, Amede and Schubert[3] observed that, a 20 % dry matter yield was increased in legume species that maintained turgor through osmotic adjustment. The contribution of osmotic adjustment to reducing yield losses varies with the intensity and duration of the stress[46]. In general, yield reduction of stressed plants compared with non-stressed plants is due to the plant's additional energy requirements for osmotic adjustment[14,71].

Evidence for maintenance of stomatal conductance by turgor maintenance due to osmotic adjustment has been reported for field crops[1,61,62,113,114,122]. Nevertheless, not all data have provided such confirmation. Jones and Rawson[50], Turner *et al*[113]., and Gollan *et al*[37]., working with several species observed a range of stomatal conductance and net photosynthesis at zero turgor. Because of contradictory and limited information on the association of physiological parameters with osmotic adjustment, the question whether osmotic adjustment is beneficial in contributing to productivity or survival mechanism under water stress conditions is not yet answered.

Transpiration Efficiency

Transpiration efficiency (TE). is defined by Xin *et al*[123]., it is a biomass accumulation per unit water transpired. Variation in TE within species has been demonstrated for several C3 plant species such as wheat, barley, rice, cotton, beans, tomato, and sunflower[47,57,69,87,105,108]. Genetic variation in TE has also been found in sorghum using gas-exchange properties, traditional lysimetric assays, and field evaluation[40,73]. Sorghum genotypes with low internal CO_2 concentration and enhanced photosynthetic capacity may be associated with high TE, whereas high TE was strongly correlated with increased biomass accumulation, rather than with reduced water use[123].

Accumulation of Solutes

Solutes are low-molecular-weight and highly soluble compounds that are usually nontoxic even at high cytosolic concentrations. Generally, they protect plants from stress through different means such as contribution towards osmotic adjustment, detoxification of reactive oxygen species, stabilization of membranes, and native structures of enzymes and proteins[33]. In sorghum, proline[104], glycinebetaine (GB).[127] and sugars functions as osmolytes that protect cells from dehydration[120]. GB accumulation in cells can assist plants to either maintain water within cells or protect cellular component from dehydration[127]. However, the genetic and metabolic basis of variation in GB accumulation is not well understood in sorghum[20]. Grote *et al*[38]., reported that a recessive allele of a single locus is associated with non-accumulation of GB in sorghum genotypes.

Accumulation of free proline in water-stressed sorghum leaves is related to the ability of a cultivar to recover from stress, possibly due to proline's role as a source of respiratory energy in the recovering plant[8]. In wheat, accumulation of proline[99] and anti-oxidative enzymes has been reported in both wild and cultivated species. Different wheat genotypes have different visible water threshold levels resulting in diverse responses to drought in terms of proline and anti-oxidative enzyme accumulation[100]. Proline comprises 18 % of the osmotic pool in chickpea[3]. A strong accumulation of proline increases the cell solute concentration, resulting in increased water potential in the tissue through osmotic adjustment. Alternatively, the expression of anti-oxidative enzymes serves as a signal transduction for gene expression, and hence, proteins are synthesized, which control metabolism effluxes. Evaluation of rice genotypes under *in vitro* drought induced conditions revealed a significant accumulation of proline and total soluble sugars in the leaves[117]. The tolerant lines showed a continuous increase in proline level for five weeks after the stress was induced and started to decline after six weeks under drought. The solute concentrations decreased to normal levels when plants were allowed to recover from drought stress[117].

Grain formation and development in crop plants is dependent on assimilates produced by photosynthesis after anthesis or assimilates stored mainly in the stem before anthesis. Wheat genotypes revealed genotypic variation in the relative importance of pre-anthesis assimilates and post-anthesis photosynthesis to drought resistance[48]. A relatively high photosynthetic rate during grain filling under water stress was observed in drought resistant cultivars relative to susceptible cultivars. Moreover, the drought susceptible cultivars were much more reliant on remobilization of pre-anthesis assimilates stored in the stem to fill the grain as opposed to the resistant cultivar[48]. This demonstrates that, under moisture stress, the pre-anthesis assimilates stored in the stem in the drought resistance cultivars are used to maintain a higher photosynthetic rate during the grain filling period.

Remobilization of pre-anthesis assimilates from the leaf and stem is one of the drought escape mechanism. In conditions where photosynthesis is inhibited by stress such as drought, heat, leaf diseases or shading, the demand for nutrient storage usually exists[15]. A large yield sink produces a physiological load on the leaves and stem, and the impact of this load is intensified under drought stress when the demand for carbon from stored reserves increases[55]. However, Blum *et al*[16]., indicated that there are cases where the utilization of stem reserves for grain filling is not dictated by the environmental conditions. Genetically, male sterile plants showed a twofold increase in assimilate storage in the stems, indicating that removal of a grain sink increases stem sugar[36]. Leaf defoliation during anthesis promoted lodging, suggesting that it may be due to depletion of carbohydrates from the stem[83]. Conversely, each plant sink events (plant height, flowering time and tillering) may increase sugar production potential in non-stress environments[75].

Drought Adaptation of Stay-Green Sorghum

Stay-green, is a post-anthesis drought resistance trait in plants that provides resistance to pre-mature leaf senescence to the plant under severe moisture stress condition during grain filling stage. It contributes to an improved yield and yield stability under moisture stress condition[107].

Stay-green is an integrated drought-adaptation trait in sorghum. Delayed leaf senescence during grain filling is an emergent consequence of dynamics occurring earlier in crop growth and is largely due to an improved balance between the supply and demand of water, as well as the efficiency with which the crop converts water to biomass and grain yield[19,51]. On the supply side, crop water use during grain filling can be enhanced by increasing water availability at anthesis or increasing water accessibility during grain filling[118]. On the demand side, crop water use can be reduced by decreasing leaf area and transpiration per unit leaf area. Leaf area can be constrained by reducing tillering[56], leaf number per culm, and individual leaf size[17]. Transpiration per unit leaf area can be limited by stomatal density or aperture, timing of stomatal opening, and hydraulic factors.

There are multiple ways for a plant to remain green[109]. A stay-green phenotype may arise if the onset of senescence is delayed (type A), the rate of senescence is reduced (type B), chlorophyll is retained but photosynthesis declines (type C), greenness is retained due to rapid death at harvest (type D), or the phenotype is greener to begin with (type E). These classifications indicate that staygreen may be functional or cosmetic. Functional stay-green is characterized by the maintenance of leaf photosynthesis during grain filling (types A, B, and E)., while cosmetic stay-green occurs when photosynthetic capacity is disconnected from leaf greenness (types C and D).

Enhanced crop productivity in water-limited environments is dependent on functional stay-green. However, not all functional stay-green is necessarily productive. For example, low sink demand relative to source, created by a small panicle or low grain number, will generate a stay-green phenotype since there is little demand for the crop to translocate carbon and nitrogen from leaves to grain[44,95]. Therefore, selection for both stay-green and grain yield should be undertaken simultaneously in plant breeding programmes to ensure that delayed senescence is not due to low sink demand.

Stay-green improves resistance to diseases and lodging. In sorghum, genotypes with the stay-green trait continue to fill their grain generally under moisture stress conditions[92], exhibit improved resistance to charcoal rot (*Macrophomina phaseolina*) and induced lodging[121].

Genetics of Drought Resistance

The main purpose of studying the genetics of drought resistance in plants is to identify genetic factors that regulates the productivity of crops under drought stress conditions. Advances in crop improvement under water-limited conditions are only possible if drought resistance traits are identified and selected for in addition to yield[17,97]. Quantitative trait loci (QTLs) have been mapped[97] on the 10 linkage groups of sorghum. They are involved in controlling traits related to yield and yield components, root systems, stay-green, plant height, flowering and maturity.

A number of traits related to drought resistance have been identified and mapped; however, the stay-green trait is recognized as the most crucial drought resistance trait in sorghum. Tuinstra *et al*[111]., identified 13 genomic regions associated with post-anthesis drought tolerance in sorghum. Four QTLs were identified for yield and yield stability, seven for duration of grain development and seed weight, and two for the stay-green trait. Kebede *et al*[53]. and Haussmann *et al*[42]., mentioned that there are three stay-green gene sources (B 35, SC 56 and E 36-1) from which QTLs that have been mapped onto 10 linkage groups on sorghum.

Crasta *et al*[26]., and Xu *et al*[125]., identified four stay-green QTLs and mapped two of the QTLs (*Stg1* and *Stg2*) on linkage group A, and the other two, *Stg3* and *Stg4* onto linkage group D and J. The stay-green QTLs were ranked based on their contribution to the stay-green phenotype as *Stg2*, *Stg1*, *Stg3*, and *Stg4* in their order of merit. Likewise, Xu *et al*[125]., mapped three QTLs (*Chl1*, *Chl2* and *Chl3*) for chlorophyll content, and the map position coincides with the stay-green QTLs. The phenotypic association of the stay-green trait and chlorophyll content may be explained by the map position of these QTLs on the genome.

Differences in flowering time, reproductive sink strength together with variation in the environmental factors alter the expression of the stay-green trait[41,107]. Six maturity genes (*Ma1- Ma6)* have been identified, and mapped onto the sorghum genome. The dominant forms of these genes cause extreme lateness[72]. Two maturity QTLs are positioned near a stay-green QTL linkage group and the major independent maturity QTLs were found to be highly correlated with stay-green rating[106,125]. Tropical genotypes are found to be dominant for all four loci (*Ma1-Ma4*) that control the time of flowering[82]. However, substituting the dominant maturity gene, *Ma1*, to recessive *ma1* converts a tropical sorghum to a temperate one that will flower in high latitudes[66]. Tuinstra *et al*[110]., identified that physiological association of the maturity and stay-green trait is not well understood. The indistinct association between the two traits suggests that the earliness trait may work against reproductive sink strength during post-anthesis drought stress.

Van Oosterom *et al*[119]., found that the stay-green trait as a function of green leaf area duration (GLAD), which is affected by green leaf area at flowering, time of onset of senescence, and subsequent rate of senescence. It has been reported that the three stay-green components appeared to be inherited independently. The inheritance of the onset of leaf senescence was additive, and the senescence rate was dominant. Consequently, GLAD was found to be partially dominant. The expression of these three factors is also affected by many environmental factors, and hence, the combined genetic effects of the three factors and the environmental factors should be considered when designing breeding programs for drought resistance[18,65]. Delayed senescence in sorghum is a valuable trait that improves genotypes adaptation to drought stress, grain filling and grain yield under stress.

The expression of genes related to water deficit in plants is found to be induced by water stress, desiccation, and abscisic acid (ABA). Yamaguchi-Shinozaki *et al*[126]., observed a wide variation in the timing of induction and expression of drought related genes classifying the genes into two groups. The first group is responsible for proteins that function directly under stress tolerance, and the second group produces protein factors involved in the regulation of signal transduction and gene expression under drought[126]. Most of these drought-inducible genes are induced by ABA. However, various researchers have reported the existence of ABA-dependent, and ABA-independent, signal transduction cascades between the initial signal of drought stress and the expression of the genes[102]. Inhibition of lateral root development under moisture stress condition is reported as one mechanism of drought tolerance in plants[124]. The drought-induced inhibition of lateral root growth is partly mediated by abscisic acid. Plants that are sensitive to abscisic acid in lateral root growth are more drought tolerant than those insensitive to abscisic acid[124]. It was also found that abscisic acid insensitive plants have higher transpiration rates and lose water much faster than abscisic acid sensitive plants[126].

Mace *et al*[64]., and Rajkumar *et al*[84]., identified four QTLs for nodal root angle (*qRA1_5*, *qRA2_5*, *qRA1_8*, *qRA1_10*), three QTLs for root dry weight (*qRDW1_2*, *qRDW1_5*, *qRDW1_8*) and eight QTLs for root volume, root fresh weight and root dry weight. Additionally, one of the root angle QTL are co-located with QTL for stay-green in sorghum and associated with grain yield[64]. Recently two QTLs (*qRT6* and *qRT7*) associated with brace roots have been mapped on sorghum Chromosome 6 and 7. Brace roots significantly contribute to effective anchorage and water and nutrient uptake during late growth and development and have a substantial influence on grain yield under water limited conditions[59]. Ekanayake *et al*[31]., found that the inheritance of root characters was controlled equally by both additive and dominant genetic effects.

Drought Tolerance Through Breeding

The major objective of plant breeding is generating and selecting for new combinations of genes to produce genotypes with superior trait performances than those of existing genotypes, within the target environment[25]. In any breeding programme, defining the critical traits to improve grain yield in a given target environment is critical[34]. Identification of important traits depends on the degree of influence of a trait on yield, expression of the trait at a whole plant level, the nature of the target environment which includes, rainfall amount, distribution, onset and cessation, available soil water, nutrient status of the soil, and diseases, and economic environment. In maize, for example, it has been found that early flowering, crop water use efficiency and early vigour are important traits to breed for improve yield under drought condition[90].

The greater flexibility of sorghum in adapting to diverse climatic conditions has resulted in the evolution of tropical and temperate sorghum varieties. The tropical varieties are characterized by being tall, late maturating with low harvest indices, photoperiod sensitivity and poor population performance. They are generally adapted to low population levels and exhibit little response to improved agricultural practices (fertilization and mechanized harvesting). The temperate sorghum varieties, on the other hand, are characterized by dwarf stems, early maturity, high yields, and less dry matter per plant[86]. In the early sorghum improvement programme, conversions of tropical varieties to temperate varieties were made by substituting two dominant alleles for height and three for maturity for their recessive counterparts. The conversion programme started with hybridization of tropical and temperate varieties followed by successive backcrossing[2].

The most sorghum breeding programmes after the discovery of stable and heritable cytoplasm-nuclear male sterility systems in the crop is exploitation of heterosis by the production of hybrids. This discovery further enables large-scale production of commercial hybrid seed to be commercially viable[27]. One study of the expression of hybrid vigour in grain sorghum by Doggett[29], revealed that there was an 84 % increase in number of seed per plant, an 82 % increase in grain weight, and a 12 % increase stover weight in the hybrids relative to the better parent.

Plant breeders have two basic approaches for breeding for drought resistance, direct and indirect breeding. Direct selection for drought is conducted under conditions where stress factors occur uniformly and predictably whereas indirect selection involves selection of genotypes under managed stress environments. However, environmental factors such as temperature and moisture are highly variable from one location to another and hence difficult to predict. Moreover, variation for stress tolerance actually exhibits a large environmental component or large genotype-by-environment interaction making direct selection for a physiological trait in a single environment difficult. As a result, indirect selection breeding is used as a preferred method where selection is made based on based on developmental traits or based on assessment of plant water status and plant function[60].

Earlier drought resistance screening was done under optimal conditions, because the maximum genetic potential of yield can only be realised under optimum conditions.

Additionally, it was believed that a high positive correlation exists between performance under optimum and stress conditions[39,111]. However, a high genotype by environment interaction may restrict the expression of the yield potential under drought condition[24]. Although, there is a yield penalty when selecting plants under drought condition in contrast to optimal environmental conditions.

Richards[90] and Tuinstra *et al*[111]., suggested that selection under both optimal and drought conditions represents the ideal trial design to select for yield and yield stability, drought tolerance and expression of drought related traits. Hence, drought resistance and its impact on yield involve interaction between plant water relations and plant physiological functions. The interactions are further complicated by the frequency and duration of the drought, plant development stage and other stress factors such as low soil fertility and biotic stress factors.

CONCLUSION

Understanding the different drought resistance mechanisms in plants is essential when breeding for drought resistance. Stay-green is a valuable trait that improves genotype adaptation to drought stress, grain filling and grain yield under stress[18,65], without a yield penalty under moisture deficit conditions as compared to osmotic adjustment and early maturity[17]. The balance among these characters maintains adequate productivity by providing a spectrum of effective drought tolerance mechanisms. An early maturing genotype yields less compared to a late maturing genotype in a favourable environment. This is because drought escape by shortening the growing period is made at the expense of the crops genetic yield potential.

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