

Review

Physiological mechanisms of drought tolerance in sorghum, genetic basis and breeding methods: A review

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Sorghum is grown in semi-arid to arid regions of the world and serves as the staple food for about half a billion people in sub-Saharan Africa and Asia. 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. Consequently, 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. Drought is a complex phenomenon, and is considered one of the most significant factors limiting crop yields around the world and continues to be a challenge to plant breeders, despite many decades of research. Underestimating the genetics and the physiological mechanisms underlying drought tolerance is vital for the breeding to alleviate adverse effects of drought in order to boost productivity. In this literature review, research findings from the 1970s up to present are included. Most of the basic researches on the mechanism of drought tolerance were done in the early 1980s, and most of the current researches focus on verification and fine-tuning of methodologies. The paper outlines the main effects of drought on crop growth and development, and yield. It then examines the basic information on physiological mechanisms of drought in crops. Subsequent discussion is given on the genetic control of drought tolerance, and breeding methods in sorghum.

Key words: Moisture stress, drought tolerance, breeding, genetics, mechanisms, *Sorghum bicolor*.

INTRODUCTION

Sorghum [*Sorghum bicolor* (L.) Moench, [2n = 2x = 20] is the emerging model crop species for the tropical grasses with C4 photosynthesis. Sorghum is the fifth most important

Cereal crop and occupies the second position among the staple food grains in semi-arid tropics. It remains a critical component of food security for more than 300 million

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in Africa. 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 (McGuire, 2000). 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 (Blum, 2005).

Drought is one of the most important factors that affect crop production worldwide. Climate changes will increase the frequency of drought and flood, particularly in many countries in Africa. There is indication that climate change may lead to a change in the frequency and severity of drought events. For instance, by 2050, water shortages are expected to affect 67% of the world's population (Ceccarelli et al., 2004). 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 (Tumwesigye and Musiitwa, 2002).

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 (Ramu et al., 2008). Consequently, crops are prone to periodic moisture stress in one way or another because of the aforementioned realities (Twomlow et al., 2008). The impact of moisture stress on crop yield is dependent on the stage of plant development (Tuinstra et al., 1997; Kebede et al., 2001). 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 (Younesi and Moradi, 2009).

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, physiological mechanisms, genetic control and breeding methods of drought tolerance in crops have been reviewed.

EFFECTS OF DROUGHT ON GROWTH AND DEVELOPMENT OF CROPS

In the semi-arid tropics where dryland farming is practiced, drought is a common phenomenon that occurs at different periods during the growing season (Blum, 1988). There is also a high season-to-season variability of rainfall, temperature, and radiation in the tropics. Agricultural conditions greatly vary in topography, soil, existing agricultural practices, and other associated biotic stress factors (Chapman et al., 2000b).

Drought is a combination of stress effects caused by high temperatures (Prasad et al., 2008) and a lack of water (Campos et al., 2004). 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 (Blum, 2011). 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 (Moussa and Abdel-Aziz, 2008). Drought can have major consequences on growth, development and yield of crops by affecting several physiological, morphological and biochemical processes (Simpson, 1981). 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 (Tuinstra et al., 1997; Kebede et al., 2001). Drought stress at the seedling stage of development will severely affect plant establishment (Baalbaki et al., 1999). If it occurs at flowering, or in the grain filling stages, it may cause reduced yields, or complete crop failure (Blum, 1996). 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, CO₂ fixation and carbohydrate translocation. The latter factors, in turn, results in low yields and premature plant senescence (Thomas and Howarth, 2000; Xin et al.,

2008).

PHYSIOLOGICAL MECHANISMS OF DROUGHT TOLERANCE

Levitt (1980) defined drought resistance as mechanisms of drought avoidance, recovery, survival and tolerance. These drought tolerance mechanisms 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 (Ludlow and Muchow, 1990). 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 (Tuinstra et al., 1997; Xiong et al., 2006).

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 (Levitt, 1980). Drought tolerance is a complex quantitative trait influenced by many genetic and environmental factors (Ceccarelli et al., 2004). 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 (Sanchez et al., 2002). In sorghum, for example, varieties that are adapted to arid and semi-arid environments showed higher drought tolerance than varieties of humid origin (Blum and Sullivan, 1986). Several studies have been conducted in understanding the mechanism of drought resistance in crops and in identifying essential traits for drought tolerance (Blum, 2011). Drought resistance, therefore, involves the interaction of different morphological structures, physiological functions, and biochemical expressions (Mitra, 2001; Borrell et al., 2006).

LEAF ROLLING AND STOMATAL CONDUCTANCE

In plants, stomatal conductance and leaf rolling have been found to be reliable physiological indicators of drought tolerance (Kadioglu and Terzi, 2007). Stomatal conductance and leaf rolling are strongly associated with leaf water potential (Bittman and Simpson, 1989). On the other hand, these two mechanisms are controlled by different factors because stomatal conductance is controlled by soil moisture dependent root signals, while leaf rolling is controlled by leaf water potential (Dingkuhan et al., 1999). 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 (Hsiao et al. 1984). 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 (Flower et al., 1990). 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 (Hsiao et al., 1984).

Drought tolerant genotypes exhibit lower stomatal conductance associated with increased leaf temperature, which gives rise to high transpiration efficiency and lower carbon isotope discrimination (Khan et al., 2007). The increased leaf temperature and transpiration rate are due to a controlled transpirational cooling system induced by stomatal closure. The drought susceptible genotypes, on the other hand, show higher stomatal conductance and lower leaf temperature results in lower transpiration rates (Khan et al., 2007). The yield difference in stress and stress-free genotypes may be due to the negative relationship between yield potential and drought resistance in cereals. It is most likely explained by reduced assimilate translocation, due to drought resistance mechanisms, such as stomatal closure and reduced leaf area.

However, 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 (Redmann, 1985). In addition, leaf rolling enhances stomatal closure by increasing leaf resistance to water loss. However, Heckathorn and DeLucia (1991) 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; however, leaf rolling causes a decrease of only 2% of normal transpiration rate (Heckathorn and DeLucia, 1991). Therefore, leaf rolling has less value in reducing water loss than stomatal closure. However, leaf rolling may increase the survival of plants by enhancing stomatal closure under extreme drought conditions (Heckathorn and DeLucia, 1991). 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.

ROOT CHARACTERISTICS

Roots are the primary plant organ affected by drought stress and other environmental stresses of the soil (Prince et al., 2002). Sorghum crown roots grow about 2 to 3 cm per day (Routley et al., 2003) and root growth is mainly affected by the amount of carbon partitioned to the

roots, although it varies with environmental and genetic factors (Blum, 2004). 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 (Routley et al., 2003). Root growth in sorghum terminates at flowering stage; however, it is more prominent in a senescent than in nonsenescent sorghum genotypes (Robertson et al., 1993). Bawazir and Idle (1989) 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. (2004) 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.

Ekanayake et al. (1985) 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 (Blum, 1997). Nour et al. (1978) also reported root weight is the best and easiest attribute to determine drought tolerance in grain sorghum. Matsuura et al. (1996), on the other hand, reported a positive correlation between drought tolerance and root length in sorghum and millet (*Pennisetum glaucum*). Moreover, Plaut et al. (1996) and Pace et al. (1999) reported that seedlings under water stress caused an increase in root length with reduced diameter. Root depth, root length density, root distribution were reported as drought tolerance contributing traits (Taiz and Zeiger, 2006).

Drought is often associated with nutrient availability and the capacity of roots to absorb the available nutrients. Ludlow and Muchow (1990) indicated that greater root activity under intermittent drought should enhance crop stability by reducing the incidence of water deficits. Egilla et al. (2001) and HongBo et al. (2006) reported the significance of potassium (K) in improving drought resistance and root longevity. Shao et al. (2005) also reported the importance of mineral elements, such as K⁺ and Na⁺ for root signal transduction function. Shanguan et al. (2005) 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 (Blum et al., 1977). 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, DEHYDRATION TOLERANCE AND TRANSPIRATION EFFICIENCY

Osmotic adjustment is another major physiological drought adaptive mechanism in plants (Izanloo et al., 2008). Sorghum and millet landraces, which are collected either dry or humid environments show variation in osmotic adjustment (Blum and Sullivan, 1986). 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 (Blum and Sullivan, 1986).

Osmotic adjustment improves crop productivity through delaying leaf rolling and leaf tissue death (Blum, 1996). As leaf rolling and leaf senescence decreases, the effective leaf area for photosynthesis increases. In a study 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 (Ludlow et al., 1990). The yield difference observed was both in grain size and grain number, and it was associated with higher harvest index. Similarly, a 20% dry matter yield increase has been observed in legume species that maintained turgor through osmotic adjustment (Amede and Schubert, 2003). The contribution of osmotic adjustment to reducing yield losses varies with the intensity and duration of the stress (Hsiao et al., 1984). In general, yield reduction of stressed plants compared with non-stressed plants is due to the plant's additional energy requirements for osmotic adjustment (Mitra, 2001; Blum, 2005).

Blum (1988) defined dehydration tolerance as the capacity of the plant to maintain higher turgor potential in the plant cell under moisture stress conditions. Dehydration tolerance is usually measured by tissue's water level, which is expressed in terms of water potential (Blum, 2011). This characteristic is highly associated with cell membrane stability to maintain high level of cell water potential under drought condition (Singh et al., 2008). Crops that exhibit high dehydration tolerance have the capacity to maintain physiological and biochemical functions; regardless of the magnitude of the water stress. In other words, physiological and biochemical activities of the cell, which are essential for growth and yield of the plant are not strictly constrained by water stress (Huang et al., 1997). However, dehydration sensitive plants accumulate solutes and macromolecules in the intracellular membrane, reduced loss of water through dehydration and alteration in the cellular membrane (Chaves and Oliveira, 2004). This, in turn, has

an influence in the performance of the plants in terms of growth and yield.

Transpiration efficiency (TE) is defined as biomass accumulation per unit water transpired (Xin et al., 2008). Variation in TE within species has been demonstrated for several C₃ plant species such as wheat, barley, rice, cotton, beans, tomato, and sunflower (Merah et al., 2001; Rebetzke et al., 2002; Teulat et al., 2002; Lambrides et al., 2004; Impa et al., 2005; Stiller et al., 2005). Genetic variation in TE has also been found in sorghum using gas-exchange properties, traditional lysimetric assays, and field evaluation (Hammer et al., 1997; Mortlock and Hammer, 1999). Among sorghum genotypes significant variation in TE and water treatments has been observed (Mortlock and Hammer, 1999). Sorghum genotypes with low internal CO₂ concentration and enhanced photosynthetic capacity may be associated with high TE (Xin et al., 2008). High TE was strongly correlated with increased biomass accumulation, rather than with reduced water use (Xin et al., 2008).

Solute accumulation and storage sugar

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 (Farooq et al., 2009). In sorghum, proline (Sivaramakrishnan et al., 2006), glycinebetaine (GB) (Yang et al., 2003) and sugars functions as osmolytes that protect cells from dehydration (Wood and Goldsbrough, 1997). GB accumulation in cells can assist plants to either maintain water within cells or protect cellular component from dehydration (Yang et al., 2003). However, the genetic and metabolic basis of variation in GB accumulation is not well understood in sorghum (Borrell et al., 2006). Grote et al. (1994) 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 (Blum and Ebercon, 1976). In wheat, accumulation of proline (Shao et al., 2006a) and anti-oxidative enzymes (Shao et al., 2005) 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 (Shao et al., 2006b). Proline comprises 18% of the osmotic pool in chickpea (Amede and Schubert, 2003). 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 (Shao et al., 2005). Evaluation of rice genotypes under *in vitro* drought induced conditions revealed a significant accumulation of proline and total soluble sugars in the leaves (Vajabhaya et al., 2001). 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 (Vajabhaya et al., 2001).

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 (Inoue et al., 2004). 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 (Inoue et al., 2004). 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 (Blum et al., 1997). 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 (Khanna-Chopra and Sinha, 1988). However, Blum et al. (1994) 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 (Fortmeier and Schubert, 1995). Leaf defoliation during anthesis promoted lodging, suggesting that it may be due to depletion of carbohydrates from the stem (Rajewski and Francis, 1991). Conversely, each plant sink events (plant height, flowering time and tillering) may increase sugar production potential in non-stress environments (Murray et al., 2008).

When demand for storage carbohydrates develops during grain filling, carbohydrate degrading enzymes are activated which degrade the large carbohydrate molecules into simple sugars which are in turn transported

to the caw to fill the grain (Blum, 1997). Consequently, higher non-reducing sugar contents have been observed in the stem juice of high biomass genotypes of sweet sorghum at maturity as compared to the low yielding genotypes (Channappagoudar et al., 2007). This low level of non-reducing sugar in low yielding genotypes has been attributed to a decrease in invertase enzyme activity. This finding corroborates with the suggestion that reduced level of sucrose-degrading enzymes appears to be a requirement for the accumulation of sucrose in the stems of sorghum (Tarpley et al., 1994). However, this decline cannot account for the difference in stem sucrose content between sweet stem and grain sorghum. High sugar accumulation, mainly sucrose, was observed in the stem of non-senescent sorghum genotypes (stay-green) at the flowering stage (Kouressy et al., 2008a). This may delay the onset of senescence and maintain a high photosynthetic rate during the grain filling stage, and hence, reducing competition for assimilates between the grain and vegetative organs. Under conditions of severe terminal drought, this stem sugar reserve may be translocated to the developing grain.

STAY-GREEN / NON-SENESCENCE

Leaf senescence is a programmed cell death resulting from drought and other environmental stress factors. It is characterized by loss of chlorophyll and progressive decline in photosynthetic capacity (Tuinstra et al., 1997; Crasta et al., 1999; Tao et al., 2000). Premature plant tissue death usually occurs when plants are subjected to water stress during the grain filling period in sorghum (Rosenow and Clark, 1981). Stay-green, on the other hand, 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 (Tao et al., 2000). However, it reduces the source-sink translocation from leaves to grain.

Stay-green is associated with a higher level of chlorophyll content, cytokinin, and leaf nitrogen concentration under moisture stress conditions. The stay-green lines show higher levels of chlorophyll content than the normal lines (Xu et al., 2000). The visual scoring of leaf and plant senescence for the stay-green response as proposed by Wanous et al. (1991) was validated by Xu et al. (2000). Stay-green sorghum lines exhibited high levels of cytokinin, suggesting that the reduced senescence rate of the stay-green lines is in part due to a higher level of cytokinin (Thomas and Howarth, 2000). Furthermore, stay-green genotypes are also associated with higher leaf nitrogen concentration, particularly at flowering (Borrell and Hammer, 2000; Borrell et al., 2000a), and basal stem sugars (Duncan, 1984), than senescent genotypes. This

suggests that the stay-green trait may possibly contribute to higher transpiration efficiency of non-senescent genotypes. However, leaf senescence is characterized by a loss of chlorophyll and progressive decline in photosynthetic capacity (Tuinstra et al., 1997; Crasta et al., 1999; Tao et al., 2000).

Greater green-leaf area duration has been observed to occur in stay green varieties during grain filling stage, and therefore, van Oosterom et al. (1996) described that stay-green trait as post-flowering green leaf area duration (GLAD). The stay-green sorghum lines appear to be the combined effect of three distinct factors namely, green leaf area at flowering, time of onset of senescence, and subsequent rate of senescence (Borrell et al., 2000a). Large variations have been reported in the proportions of green-leaf area among different genotypes as a result of combined effects of differences in onset and rate of senescence (Borrell et al., 2000a; Mahalakshmi and Bidinger, 2002). An increase in biomass of about 47% over and above that obtained from senescent genotypes has been reported in genotypes that express the stay-green trait under post-anthesis moisture deficit (Borrell et al., 2000b). A lack of grain yield differences observed by these authors among genotypes grown under irrigated conditions, suggests that the stay-green trait does not reduce yield under zero moisture deficit conditions.

Stay-green improves resistance to diseases and lodging (Tenkouano et al., 1993). In sorghum, genotypes with the stay-green trait continue to fill their grain generally under moisture stress conditions (Rosenow and Clark, 1981), exhibit improved resistance to charcoal rot (*Macrophomina phaseolina*) and induced lodging (Woodfin et al., 1988). However, Tenkouano et al. (1993) reported that the non-senescent and charcoal rot reaction are genetically independent.

GENETICS OF DROUGHT TOLERANCE

The purpose of studying the genetics of drought resistance in plants is to identify genetic factors that determine 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 (Borrell et al., 2000a; Sanchez et al., 2002). Quantitative trait loci (QTLs) have been mapped 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 (Sanchez et al., 2002).

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. (1997) 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. 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 (Kebede et al., 2001; Haussmann et al., 2002).

Tao et al. (2000) identified two stay-green QTLs located on linkage group B and I. Likewise, Crasta et al. (1999) and Xu et al. (2000) 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, respectively. 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. Furthermore, Xu et al. (2000) also 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.

Many secondary factors, such as differences in flowering time, reproductive sink strength together with variation in the environmental factors alter the expression of the stay-green trait (Harris et al., 2007; Tao et al., 2000). Six maturity genes (*Ma₁-Ma₆*) have been identified, and mapped onto the sorghum genome. The dominant forms of these genes cause extreme lateness (Morgan et al., 2002). 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 (Subudhi et al., 2000; Xu et al., 2000). Tropical genotypes are found to be dominant for all four loci (*Ma₁-Ma₄*) that control the time of flowering (Quinby, 1974). However, substituting the dominant maturity gene, *Ma₁*, to recessive *ma₁* converts a tropical sorghum to a temperate one that will flower in high latitudes (Major et al., 1990). Tuinstra et al. (1998) identified two QTLs that conditioned the expression of the stay-green trait. The 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.

Walulu et al. (1994) found that the stay-green trait in sorghum is controlled by a major gene that expresses different levels of dominant gene action, depending on the environment. However, van Oosterom et al. (1996) studied 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 (Borrell et al., 2000b; Mahalakshmi and Bidinger, 2002). Delayed senescence in sorghum is a valuable trait that improves genotypes adaptation to drought stress, grain filling and grain yield under stress.

Several genes are involved in drought stress tolerance in various plant species. The function of these genes is either protecting the cell from water deficit by the production of important metabolic proteins, or regulation of genes for signal transduction. The expression of the dehydrin gene, *dhn1* in sorghum as a response to water deficit was reported by Wood and Goldsbrough (1997). Expression of the *dhn1* gene in seedlings and pre-flowering sorghum was identical among genotypes, but genotypes showed variation in time of expression of the gene. This suggested that the expression of dehydrins is an important drought adaptation mechanism in sorghum.

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. (2002) 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 (Yamaguchi-Shinozaki et al., 2002). 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 (Shinozaki and Yamaguchi, 1997, 2000). Inhibition of lateral root development under moisture stress condition is reported as one mechanism of drought tolerance in plants (Xiong et al., 2006). 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 (Xiong et al., 2006). It was also found that abscisic acid insensitive plants have higher transpiration rates and lose water much faster than abscisic acid sensitive plants (Yamaguchi-Shinozaki et al., 2002).

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 were identified by (Mace et al. (2012) and Rajkuma et al. (2013). Additionally, one of the root angle QTL are co-located with QTL for stay-green in sorghum and associated with grain yield (Mace et al., 2012). 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 (Li et al., 2014). The inheritance of root characters was controlled equally by both additive and dominant genetic effects (Ekanayake et al., 1985).

Leaf rolling is known as a typical response to water deficit in numerous species such as rice, maize, wheat and sorghum. The rolling of leaves is mainly controlled by major genes and several genes (*RL1* to *RL10*) were identified in rice. *RL7*, *RL8* and *RL9* were among those which were assigned to their corresponding chromosomes with molecular markers. Single-recessive alleles of each gene exhibited rolled leaves (Zhang et al., 2009). Luo et al. (2007) identified a dynamically rolled leaf mutant (*RL10*) from a spontaneous mutation in rice. In maize, *RDL1*, a semi-dominant maize mutant gene controlled the upward curling of the leaf blade (Juarez et al., 2004). Zhang et al. (2009) isolated and characterized *SLL1* gene, a key gene controlling rice leaf rolling. *sll1* mutant plants have extremely incurved leaves due to the defective development of sclerenchymatous cells on the abaxial side.

BREEDING FOR DROUGHT TOLERANCE

Generating and selecting for new combinations of genes to produce genotypes with superior trait performances than those of existing genotypes, within the target environment, is the major objective of plant breeding (Chapman et al., 2003). In any breeding programme, defining the critical traits to improve grain yield in a given target environment is critical (Fernandez, 1992). 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 (rainfall amount, distribution, onset and cessation, available soil water, nutrient status of the soil, and diseases), and economic environment (the requirements of grain quality and quantity). 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 (Richards, 1996).

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 maturing 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 (Rao et al., 2002). 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 (Acquaah, 2007).

In breeding for drought tolerance, a pure line selection method has been used in many national and regional sorghum improvement research programmes in Africa and Asia (Acquaah, 2007). However, pedigree and bulk selection methods are commonly used in most international and national breeding institutions. Pedigree selection in segregating populations derived from planned crosses is the dominant breeding strategy to develop pure line varieties and hybrid parents in sorghum (Dar et al., 2006). If the transfer of only a few traits relating to drought resistance to a high yielding cultivar is required, then backcrossing is the appropriate breeding method (Mittra, 2001).

Exploitation of heterosis by the production of hybrids is routine in most sorghum breeding programmes after the discovery of stable and heritable cytoplasm-nuclear male sterility systems in the crop. This discovery further enables large-scale production of commercial hybrid seed to be commercially viable (Dar et al., 2006). One study of the expression of hybrid vigour in grain sorghum 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 (Doggett, 1988).

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 yield *per se*, or based on developmental traits or based on assessment of plant water status and plant function (Ludlow and Muchow, 1990).

In the past 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 (Tuinstra et al., 1997; Habyarimana et al. 2004). However, a high genotype by environment interaction may restrict the expression of the yield potential under drought condition (Chapman et al.,

2000a, b). Although, there is a yield penalty when selecting plants under drought condition in contrast to optimal environmental conditions, Richards (1996) and Tuinstra et al. (1997) 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 genetic and physiological basis of drought resistance in plants is essential when breeding for drought resistance. Lin et al. (1995) and Kouressy et al. (2008b) identified the importance of reduced plant size in terms of small and narrow leaf structures and genetic dwarfing of the plant for drought resistance. Reduction of leaf area index, through reducing the number of leaf and narrowing the leaf structure, also results in the reduction of the effective photosynthesis area. This in turn, reduce the amount of assimilates produced and the grain yield. However, it also reduces the amount of water lost through transpiration. Genetic dwarfing, on the other hand, increases the efficiency of plants in balancing the translocation of assimilates translocation between the developing grain and the vegetative organs (Kouressy et al., 2008b).

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. Short cropping duration may not be an exclusive selection criterion *per se* because other factors may also be involved in affecting genotype performance under water stress (Blum et al., 1989). Stay-green is a valuable trait that improves genotype adaptation to drought stress, grain filling and grain yield under stress (Borrell et al., 2000b; Mahalakshmi and Bidinger, 2002), without a yield penalty under moisture deficit conditions as compared to osmotic adjustment and early maturity (Borrell et al., 2000a). The balance among these characters maintains adequate productivity by providing a spectrum of effective drought tolerance mechanisms. Many researchers have proposed various characteristics related to drought resistance that could be used in breeding and selection programmes. However, comprehensive understandings of the physiological and genetic basis of adaptation in moisture stress conditions are still lacking. Moreover, the interaction between the different characteristics within a plant and the environment makes drought resistance breeding very complicated.

Hence, the chances of breeding drought resistant cultivars with all the important characters are low. The choice of specific traits as selection criteria depend on the crop species, the heritability, and the ease of transfer of the traits. Moreover, since drought resistance is the interaction of different morphological, physiological, and biochemical traits, a combination of different resistance traits, rather than a single trait, should be used as the overall selection criterion.

Conflict of Interest

The authors have not declared any conflict of interest.

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