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Review Article

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Drought Resistance Mechanism and Adaptation to Water Stress in Sorghum [*Sorghum bicolor* (L.) Moench]

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Abstract

Drought is a major constraint in sorghum production worldwide. Drought adversely affects growth and yield of crops to various extents. Growing of drought tolerant crops is a good option to obtain economical yields from water stress areas for which quick method to screen drought tolerant plants, particularly in early stages of their growth is important. Sorghum is one of the most important cereal crops and also the major staple food crop of millions of people in semi-arid tropics (SAT). Now-a-days, Sorghum grain is mainly used for human food, fodder, feed and fuel purposes. Moreover, seeds are used for popcorn and preparing delicious food. Sorghum is C4 plant which native to Sub-Saharan Africa. Drought-stress in sorghum has been characterized at both pre-flowering and post-flowering stages resulting in a drastic reduction in grain yield. Various drought-related traits, including root traits, leaf traits, osmotic adjustment capabilities, water potential, ABA content, and stability of the cell membrane, have been used as indicators to evaluate the drought resistance of plants. There are four different mechanisms which help in survival of plants under moisture deficit conditions viz., drought escape, drought avoidance, drought tolerance, and drought recovery. Drought stress can occur at any stage of crop growth ranging from seedling establishment, vegetative stage, panicle development post-flowering, period between grain filling and physiological maturity. Water stress responses in sorghum can be of physiological, morphological and phenological in nature.

Keywords: Sorghum, grain yield, drought stress, drought resistance and adaption

1. Introduction

Drought is an extended abnormal dry period that occurs in a region consistently receiving a below-average rainfall. Globally, agriculture is the biggest consumer of water. The growth, development, and reproduction of plants require sufficient water. Drought is a complex environmental stress and major constraint to crop productivity (Mishra and Singh 2010; Farooq et al., 2012). It is a global problem that may have profound effects on agriculture and food security, especially upon agricultural systems which are dependent on rain as their primary source of water (Bray et al., 2000; Rosegrant et al., 2002). Sorghum [*Sorghum bicolor* (L.) Moench, [2n=2x = 20] is the emerging model crop species for the tropical grasses with C4 photosynthesis. Sorghum a crop native to Sub-Saharan Africa, has been cultivated for centuries in Africa and Asia. It is an important grain crop and food source in many developing countries (Doggett, 1988). Sorghum is the fifth most important Cereal crop and occupies the second position among the staple food grains in semi-arid tropics. Sorghum grows across a wide geographic area at various altitude, day length, rainfall, and temperature regimes. Sorghum is recognized as a remarkably drought tolerant species and is favoured for subsistence farming in water scarce, impoverished regions of the world (House, 1985; McKersie and Leshem, 1994; Wani et al., 2012). 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 (Mc Guire, 2000). Grain sorghum exhibits resilience to the effects of water stress, particular growth stages in its lifecycle are susceptible to drought stress. The early vegetative stage and reproductive stages (pre flowering and post flowering) of sorghum are vulnerable to the effects of water deficit (Tuinstra et al*.,* 1997; Kebede et al,. 2001; Wani et al., 2012). A drought period during the early seedling stage of sorghum may inhibit establishment of the crop, whilst water deficit during pre-flowering and post flowering stages impacts grain development and yield of the crop (Mc Kersie and Leshem 1994). Therefore, the ability to withstand water deficit at these stages is critical to productivity. Plants may exhibit various biochemical and physiological mechanisms to ameliorate the effects of drought (Tuinstra et al., 1997; Bray et al., 2000). Approximately, one-third of the earth's land area is arid and semi-arid, while periodically unexpected climatic droughts often occur in most of the other land areas. Water scarcity can be lethal to plants and lead to enormous social problems and economic losses.

2. Mechanisms of Drought Resistance

Drought Resistance is the ability of a plant to maintain favorable water balance and turgidity even exposed to drought conditions there by avoiding stress and its consequences. Stress avoidance due to morphological anatomical characteristics which themselves are the consequences of the physiological processes induced by drought these zerophytic characteristics are quantitative and vary according to environmental conditions. The growth, development, and reproduction of plants require sufficient water. These drought tolerance mechanisms are associated with plant survival and production. Various drought-related traits, including root traits, leaf traits, osmotic adjustment capabilities, water potential, ABA content, and stability of the cell membrane, have been used as indicators to evaluate the drought resistance of plants.

There are four different mechanisms which help in survival of plants under moisture deficit conditions. There are:

2.1. Drought escape

Drought Escape refers to natural or artificial adjustment of the growth period, life cycle, or planting time of plants to prevent the growing season from encountering local seasonal or climatic drought (Mitra, J., 2001; Manavalan et al., 2009). Farmers usually choose crop varieties with short life cycles which complete their life cycle by avoiding the seasonal drought stress in agricultural production. The simplest way of survival under drought conditions is to escape drought. Generally, drought occurs either in the mid or late crop season. Drought escape is most common in case of plants grown in desert regions. They complete their life cycles in 4 to 6 weeks (Figure 1). Drought escape also plays an important role in some crop plants. For example, yields of early varieties of wheat, sorghum, maize, and rice are less affected by severe drought than late maturing ones. All these crops have determinate growth habit. In spring wheat, late maturing varieties give higher yield than early types especially when drought occurs early in the season and is over before anthesis (Figure 2).

Figure 1: "Stay green" (left) and "normal" (right) cultivars of sorghum under post-flowering drought stress (Sources: Blum, 2011)

Figure 2: "Stay green" (left) and "normal" (right) cultivars of sorghum under post-flowering drought stress (Sources: Blum, 2011)

2.2. Drought avoidance

Drought avoidance refers to ability of the plant to maintain a favourable internal water balance under moisture stress. In other words, plants which avoid drought retain high water contents in their tissues. Drought avoidance is 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). Drought avoidance can permit a longer growth period in the crop through reduced water use or increased water uptake. The root system plays a critical role in response to water deficit stress. Some plants have the robust ability to increase root growth at the early stage of drought stress to absorb the water in deep soil (Hu and Xiong, 2014). Drought avoidance is principally characterized by the maintenance of high plant water potentials in the presence of a water shortage (Mitra, 2001; Luo, 2010) (Table 1 and 2).

2.3. Drought Tolerance:

Drought tolerance refers to the ability of plants to sustain a certain level of physiological activities under severe drought stress conditions through the regulation of thousands of genes and series of metabolic pathways to reduce or repair the resulting stress damage (Mitra, 2001; Luo, 2010; Passioura, 1997). In other words, Drought tolerance is 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). Plants accumulate a variety of organic and inorganic sub- stances (such as sugars,

Table 1: Grain sorghum drought tolerance/avoidance mechanisms, how the mechanisms contribute to drought tolerance, and limits of the mechanisms

Drought tolerance/avoidance mechanism in grain sorghum	How the mechanism help	Limits of the mechanism
Deep root system	Increases water extraction depth	Up to 2.50 meters
Higher root density (secondary roots)	Increases water extraction area	Root density of about 4.1 cm per cm soil
Stomata remain open at wide range of leaf turgor	Maintain CO_2 exchange (photosynthesis)	from 11 bars to 1 bar
Stomata closing at higher level of stress	Avoids further water loss	About −14 bar to −15 bar is lowest leaf water potential where stomata closes
Leaf roll	Avoids further water loss by decreasing surface area of leaf	Starts after about 10 to 14 days of water stress
Forming small vacuoles from large central vacuoles	contact with radiation Avoids cell rapture by maintaining tonoplast integrity	At about a leaf water potential of −37 bar
Production of antioxidant	Protect from lipid peroxidation	Until late in the drought stage
Cuticle and epicuticular wax (waxy bloom substance)	Checks transpiration (decreases water lose from leaves by obstructing the path)	It can check up to 30% of transpiration lose

(Sources: Assefa et al., 2010)

polyols, amino acids, alkaloids, and inorganic ions) to increase their concentration in the cytochylema, reduce the osmotic potential, and improve cell water retention in response to water stress. This phenomenon is defined as osmotic adjustment (OA) (Morgan, 1984; Rhodes and Samaras, 1994) a significant strategy for plant drought tolerance.

2.4. Drought recovery

Drought recovery refers to the plant capability to resume growth and gain yield (for crops) after exposure to severe drought stress which causes a complete loss of turgor pressure and leaf dehydration (Luo, 2010). Levit (1980) pointed out that the determination of drought resistance is much more difficult than that of other stress resistances.

Table 2: Difference between Drought Avoidance and Drought Tolerance

Sl. No.	Drought Avoidance	Drought Tolerance
1	Plants maintain favourable tissues water content.	Plants do not maintain favourable tissue water content.
2	Plants can not withstand low tissue water content.	Plants can withstand low tissue water content.
3	In cereals, it operates during vegetative phase.	In cereals, it operates during reproductive phase.
4	It reduces photosynthesis and increase root development.	Better seed germination, seedling growth and photosynthesis.
5	It involves various morphological and anatomical features of plant which reduce water loss through transpiration.	It generally involves those characters which support for better photosynthesis under drought conditions.

3. Sorghum Adaptation to Water Stress

The effect of drought stress depends on the plant developmental stage at the onset of stress. Under field conditions, drought stress can occur at any stage of crop growth ranging from seedling establishment, vegetative, panicle development and post-flowering, and the period between grain filling and physiological maturity (Rosenow and Clark 1995, Rosenow et al., 1996). Sorghum is reputed for its ability to tolerate water stress, both intermittent and terminal stress. This is mostly attributed to its dense and prolific root system, ability to maintain relatively high levels of stomatal conductance, maintenance of internal tissue water potential through osmotic adjustment and phenological plasticity (Tsuji et al., 2003). Water stress responses in sorghum can be of physiological morphological and phenological in nature.

3.1. Physiological adaptation

Ability to maintain key physiological processes, such as photosynthesis, during drought stress is indicative of the potential to sustain productivity under water deficit. Sorghum exhibits physiological responses that allow a continued growth under water stress (Dugas et al., 2011). Delayed senescence, high chlorophyll content and chlorophyll fluorescence as well as low canopy temperature and high transpiration efficiency are physiological traits that confer drought tolerance to sorghum (Harris et al., 2006; Kapani gowda et al., 2013).

3.2. Morphological adaptation

Plants constantly obtain water (and nutrients as well) from the soil through their roots. Hence, the root system plays a critical role in response to water deficit stress. Some plants have the robust ability to increase root growth at the early stage of drought stress to absorb the water in deep soil (Hu and Xiong, 2014). The root system is the plant organ in charge of capturing water and nutrients, besides anchoring the plant into the ground. It is naturally viewed as a critical organ to improve crop adaptation to water stress (Vadez, 2014).

Long, narrow, pointy leaves reduce the contact surface area with direct sunlight during high temperatures, hence preventing desiccation. Sorghum leaves and stem are covered by a waxy cuticle and epicuticular wax (Saneoka and Ogata, 1987) preventing excessive water loss during water stress. Leaf rolling is a common response of plants to water deficit, and it is a mechanism to reduce water consumption when water stress is present (Begg et al., 1980). 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 (Borrell et al., 2009; Jordan et al., 2012).

Tillering ability is commonly associated with sorghum in regions with limited rainfall. Tillering is generally recognized as one of the most plastic traits affecting biomass accumulation and ultimately grain yield in many field crops (Kim et al., 2010).

3.3. Phenological adaptation

Sorghum utilizes quiescence adaptive mechanisms to allow for extreme drought tolerance (Dugas et al., 2011). Water stress affects sorghum at both pre- and post-flowering stages of development. Pre flowering drought stress response occurs when plants are under significant water stress prior to flowering, particularly at or close to panicle differentiation and until flowering (Kebede et al., 2001). The most adverse effect of water stress on yield occurs during and after anthesis (Blum, 2004). Post flowering drought stress significantly reduces the number and size of the seeds per plant (Rosenow and Clark, 1995), which are the main causes for lower grain yield in sorghum (Assefa et al., 2010).

Breeding for varieties with drought tolerance under rainfed / soil moisture situations (shallow-medium and deep soils and under irrigated condition) is a high priority to improve productivity in large drought prone area of India.

Four genotypes, *viz*., IS 19153, IS 23514, IS 29392 and RS 585 showed consistent better post-flowering drought response over two years. Of these, IS 23514, a red sorghum line was found to be promising as it recorded lowest Drought Susceptibility Index (DSI). The evaluation of key adaptive traits for post-flowering drought tolerance revealed that water extraction in pre-anthesis period was negatively correlated to the water extracted in the post-anthesis period**.** In addition, a two-fold variation in transpiration efficiency indicated that there is a large scope for improving the water-use efficiency of *rabi* sorghum. The genotype IC 392124 recorded the highest drought tolerance efficiency (DTE) of 92.8 and 90.5% under water deficit and rainfed conditions, respectively. Based on DSI and DTE values, the genotypes IC 392124, IC 392147, IC 343584 and IC 343573 were found to be drought tolerant.

Productive genotypes identified for grain yield under drought stress include SPH 1644 (hybrids), and C 43 and CSV 20 (inbreds/variety). As regards to DSI, the genotypes CSH 16 (0.102), 27B (0.217), SPH 1644 (0.364), SPH 1655 (0.386), and 463B (0.486) were stable and tolerant to mid-season (pre-flowering) drought stress. (Sources: DSR -Annual Report 2013-14).

Thirty-two genotypes were evaluated in lysimeter for the key physiological drought adaptive traits. For Pattern of water use, water extraction in pre-anthesis period was negatively correlated to the water extracted in the post anthesis period under both well watered and water stressed conditions. The genotypes like IC392140, IC 343586, CRS 20 and Phule Maulee recorded highest ability to extract the water from the soil profile. Similarly, for transpiration efficiency, a two-fold variations (3.5 to 7.7 g kg^{-1} water transpired) in transpiration efficiency indicate that there is large scope for improving the TE of *rabi* sorghum to adapt to water scarcity during the post-flowering growth period. The genotypes which recorded the higher TE under the WS conditions are Phule chi-tra, CRS20, IC392140, Phule Maule, Phule Suchitra and IC343586. (Sources: ICAR-IIMR, Annual Report 2015-16).

Stress Susceptible Index (SSI) value for yield per plot (g) underone irrigation ranged from 0.01 (CRS7) to 3.57 (PKR Kranti) while under two irrigation ranged from 0.49 (BRJ62×RS585) to 1.31 (Phule Chitra). SSI value for fodder yield per plot under one irrigation ranged from 0.00 (Sangola hondi×BRJ62) to 3.56 (IC343583) and under two irrigation ranged from 0.00 (Sangola Hondi×BRJ62) to 1.69 (Phule Anuradha×BRJ62). In addition to Drought Susceptible Index (DSI) values, drought tolerant genotypes were judged based on weighted means. The highest weight of 5 was given to treatment under rainfed condition as yield under less soil moisture condition is more advantageous than yield under irrigated condition followed by 3.5 and 1.5 weights were given to the treatments under water deficit and assured irrigated conditions respectively according to economic benefit in relation to moisture condition. For grain yield, weighted means ranged from 334.35 (IC 343583) to 743.1 (BRJ 62 x RS 585) and for fodder yield, it ranged from 3201.66 (CSV22) to 1236.66 (Phule Anuradha×SLR 24). Based on DSI for grain and fodder yield under one irrigation and two irrigations, the genotypes, Phule Anuradha x Sangola Hondi, Sangola Hondi ×BRJ 62, SLR 24×BRJ 62, IC 392155, CRS7, CRS20, CRS48, Selection 3 and EP 87 were drought tolerant. The genotypes Sangola Hondi x BRJ 62, SLR 24×BRJ 62, and CRS7 showed lower DSI and higher weighted mean value indicating these are drought tolerant as well as high yielder also. The trais viz., early flowering, long peduncle length and less reduction in leaf area at the time of flowering are desirable to enhance drought tolerance in rabi sorghum. (Source: ICAR-IIMR - Annual Report 2016-17)

4. Conclusion

These drought tolerance mechanisms are associated with plant survival and production. Determining the water requirement of a crop is not as easy as determining the nutrient requirement because the former is highly dependent on the environmental requirement. Maximum grain sorghum yield requires 450 to 650 mm of water. Sorghum is more drought tolerant than other crops because of its root system, ability to maintain stomatal opening at lower levels of leaf water potential, high osmotic adjustment, waxy bloom substance in leaves and stem, better adjustment in leaf angle, and leaf rolling in low water conditions. Therefore, this variation among varieties of sorghum should be well utilized as a source for drought tolerant hybrids selection.

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