International Journal of Food, Agriculture and Veterinary Sciences ISSN: 2277-209X (Online)
An Open Access, Online International Journal Available at http://www.cibtech.org/jfav.htm
2017 Vol.7 (3) September-December, pp.83-89/Soni et al.
Review Article

SORGHUM BICOLOR (L.) MOENCH: A MODEL SYSTEM TO STUDY DROUGHT TOLERANCE IN PLANTS

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ABSTRACT
In nature, plants are continuously exposed to various types of abiotic stress and it adversely affects the growth and development of plants. Drought is the most commonly found abiotic stress. It is the main restrictive factor affecting agriculture and is considered as the most important cause of yield reduction in crop plants. Sorghum [*Sorghum bicolor* (L.) Moench] is a drought tolerant crop and is an excellent model plant for evaluating drought resistance mechanisms. It is highly adapted to areas with too low rainfall, where it is very unfavourable to grow other crops and it ranks fifth amongst worldwide crops. The drought tolerant characteristics of sorghum make it one of the most important food and feed crops in the regions with low rainfall. In future it will become more important in arid regions all over the world as global warming trends and the demand for limited fresh water is increasing day by day. Therefore, it is considered as a model crop for characterizing drought tolerance.

Keywords: *Abiotic Stress, Sorghum Bicolor, C_4 Photosynthesis, Drought Tolerance*

INTRODUCTION
Environmental stress adversely affects plant growth and productivity. It involves two kinds of stress: biotic and abiotic. Abiotic stress includes flooding, drought, metal toxicity, salinity, mineral deficiency, increased temperature, adverse pH and air pollution. All these kinds of abiotic stresses are, however, rarely seen apart and crops are subjected to various adverse situations, especially, in arid and semi-arid regions of the world. Increase in drought has become a major constraint due to change in climate. The drought is considered as the most severe abiotic stress and it directly affects plant productivity (Borlaug and Dowswell, 2005). It is a period of increased dryness in soil and is the most common limiting factor. Drought is the main reason for yield reduction in crop plants and it occurs when water level decreases in the soil and atmosphere which causes continuous water loss by transpiration or evaporation. It can be defined as a period without significant rainfall. Drought is a condition of moderate water loss, which results in the closure of stomata and decreased gas exchange in plants. It is a dominant abiotic factor limiting growth and productivity of plants in various regions of the world (Kramer and Boyer, 1997).
Drought stress is multidimensional which affects plant at different organizational levels. It decreases plant growth by affecting various physiological and biochemical processes, for example, respiration, photosynthesis, ion uptake, translocation etc. Severe drought stress leads to decreased rate of photosynthesis, interruption in metabolism leads to death of the plant (Jaleel *et al.*, 2008). Against these abiotic stresses, plants modify themselves by various mechanisms which include variation in developmental and morphological pattern as well as biochemical and physiological processes (Bohnert *et al*., 1995). Sorghum, for example, is thought to be well adapted to drought as compared to other crops.

Reactive Oxygen Species and Antioxidants
Plants adapt themselves to drought stress by a variety of mechanisms which include changes in morphology, developmental pattern, biochemical and physiological processes. Drought response in plant relies on the inherent strategy of plant species, time and extremity of drought period. Prolonged drought stress results in oxidative damage because of increased yield of reactive oxygen species (Smirnoff, 1993). There are basically four types of cellular ROS, singlet oxygen ($^1O_2$), superoxide radical, hydrogen peroxide (H_2O_2) and hydroxyl radical (HO^-). They cause oxidization of various cellular components, e.g. proteins and lipids, RNA and DNA. Plants possess a well developed antioxidant system which prevents

them from ROS. Reactive oxygen species cause cellular injury, for example, lipid peroxidation and nucleic acid modification can be easily detoxified by the help of antioxidants (McKersie and Leshem, 1994). The key antioxidative enzymes are catalase (CAT), peroxidases, dehydroascorbate reductase (DHAR), superoxide dismutase (SOD), monodehydroascorbate reductase (MDHAR), glutathione reductase (GR).

Sorghum Bicolor (L.) Moench]

S. bicolor commonly known as sorghum and also named as great millet, *durra*, jowari, or milo and it belongs to family Poaceae (Gramineae) which is large and is a pervasive family of monocotyledonous plants possessing flowers which are known as grasses. It is a dryland crop, which is often grown in areas with marginal rainfall and it is highly adapted to areas with low rainfall, where it is very hard to grow other food and feed grains. Sorghum production is limited in arid and semiarid regions because of variable and low rainfall during the season. It is a major cereal food crop used in many regions of the world and it is characterized as a famous crop in the areas with low rainfall, which is highly irregular and erratic. It ranks fifth amongst the crops like wheat, rice, maize and barley. From an economic point of view, it is a very important crop as it is used as food, fodder, fencing, building material and for making brooms (House, 1985; Rooney and Waniska, 2000) and it feeds more than 500 million people in 98 countries (Pennisi, 2009). Drought-stress causes decline in sorghum productivity worldwide. However, sorghum is drought tolerant and it is a C_4 crop which is well adapted to semiarid regions (Quinby, 1974). The C_4 crops, for example, sorghum, evolved from the tropics are generally, more drought and heat tolerant as compared to C_3 plants, e.g., wheat, which is originated from arid regions (Chapman and Carter, 1976; Blum *et al*., 1990). Further, its drought tolerance characteristic makes it an excellent model crop for studying the biochemical and physiological mechanisms of drought tolerance.

In sorghum, drought tolerance is a complicated characteristic affected by various environmental factors. The drought adaptation in sorghum relies on structural and biochemical features, *i.e.* deep root architecture, C_4 photosynthesis and a thick waxy cuticle which helps in gaining efficiency of water use. This crop exhibits various physiological responses that allow continued growth during drought. Hence, sorghum is one of the most drought tolerant crops.

Sorghum is a multipurpose crop and because of its unusual tolerance to adverse environmental conditions, it is grown all over the world. However; it has a wide range of other uses also which are explored as renewable resources due to worldwide interest. The most commonly cultivated types are grain sorghum. Economically, it is a very important crop and it is utilized as food, fodder and is also used in production of syrup and ethanol. It is a principal food crop in the drier regions of Africa and central-western India, where people need stable food production and it also provides food and fodder security for millions of rural families in the semi-arid regions. It is a very important crop from an agricultural, ecological and atmospheric perspective, and it contributes 20% to the world's primary productivity (Ehleringer *et al*., 1997).

In sorghum drought resistance is attributed to a dense root system and during decreased leaf water potential its osmotic adjustment is maintained by stomatal opening (Wright *et al*., 1983). This crop exhibits several physiological responses, *i.e*., stay-green, osmotic adjustment, etc. that allow continued growth during drought. Sorghum, like sugarcane and maize, carries out C_4 photosynthesis, which enables these grasses to adapt themselves from adverse environments, *i.e*., increase drought and temperature (Edwards *et al.*, 2004). C_4 plants have a major role in the universal carbon budget, and C_4 crops, like sorghum and maize, are crucial to current and future international food security (Lloyd and Farquhar, 1994; Ehleringer *et al*., 1997; Brown, 1999; Pingali, 2001).

Drought Tolerance in S. Bicolor

Understanding how crop plants protect themselves from drought and evaluation of plant responses to drought at the physiological and molecular level are the most prevalent topics in plant sciences (Shao *et al.*, 2007). For the improvement in crop productivity, it is important to know about the mechanism of plant responses to water limiting conditions with the ultimate goal of improving performance in various regions of the world where low or unreliable rainfall occurs.

Under water limiting conditions plants adapt themselves by two types- firstly drought avoidance and the other one is drought tolerance. Drought avoidance is a process in which turgidity and volume of plant cell are maintained at lower water status in plant tissues during drought. Plants avoid drought by rapid phenological development, leaf shading, leaf rolling, decreased leaf area and increased cuticular and stomatal resistance (Morgan, 1984; Turner, 1986). After the launch of genome sequencing project, this crop became a model for utilizing C_4 photosynthesis and it has gained the attention of scientists all over the world (Paterson *et al.*, 2009).

Sorghum is a C_4 plant and increased water use efficiencies is specific character of C_4 plants. In arid and semi-arid conditions, the C_4 crops resist drought by osmotic adjustment (Slatyer, 1963) and it enables sorghum to grow at lower leaf water potential (Craufurd *et al.*, 1993). Osmotic adjustment means active acquisition of solutes in response to decreased water potential. It helps in water uptake to continue during increased drought stress in plants. The stomatal conductance and net photosynthetic rate of sorghum decreases with decline in water potential of leaf (Akerson *et al.*, 1980, Garrity *et al.*, 1984, Massacci *et al.*, 1996). The dry land genotypes of this crop have epicuticular wax values closer to the maximum (Jordan *et al.*, 1984). The epicuticular wax indicates hydraulic permeability of the leaf surface. Thus, this crop has relatively increased epicuticular resistance which prevents further loss of water when the stomata are closed.

The primary physiological results of drought are photosynthetic inhibition in plants (Chaves, 1991). Drought causes decrease in photosynthesis, transpiration and stomatal conductance of sorghum (Premachandra *et al*., 1994, Massacci *et al.*, 1996). In water deficit condition, synthesis of abscisic acid (ABA) occurs, which triggers stomatal closure, thus it reduces transpirational water loss. In sorghum drought stress results in decreased photosynthesis because of malate accumulation, an intermediate of the C_4 cycle, in mesophyll tissue (Beyel and Bruggemann, 2005). Mesophyll cells in sorghum are the main source of fluorescence signals coming out from photosystem II (Edwards *et al.*, 2001). PSII is very crucial in photosynthesis, and is abnormally operated under environmental stress. It is a very sensitive constituent of the photosynthetic apparatus to drought (Havaux and Strasser, 1992).

In water limiting condition, plants with C_4 photosynthesis increases the efficiency of water use and restrains photorespiration; thus, C_4 plants are more competitive as compared to C_3 plants in drought-proneregions (Edwards and Ku, 1987). In sorghum drought stress causes non-stomatal limitations in photosynthesis combined with aggregation of malate and consequent *in situ* inhibition of PEPC, and by the decline in phosphate, pyruvate dikinase activity (Beyel and Bruggemann, 2005). It is a very important crop which is highly efficient in the assimilation of carbon (at current atmospheric CO2concentrations) at high temperatures and in water deficit conditions than crops *i.e*., wheat and rice (Kresovich *et al*., 2005).

In sorghum drought response is common in pre- and post-flowering stages. In plants the former response occurs under moist conditions before flowering, especially from differentiation of panicle to flowering and the later one is expressed during moisture stress which occurs on the grain developmental stage. The 'stay-green' term express an important element of post-flowering drought response in this crop (Rosenow and Clark, 1981) and it provides resistance to premature senescence under water limiting conditions at the time of grain filling. In sorghum leaf senescence is frequently induced to restrict the transpiring leaf area and water loss under drought condition (Stout and Simpson, 1978).

Plant response to drought varies respectively at various levels of organization depending upon its duration and intensity of stress as well as plant species and its stage of growth (Chaves *et al*., 2002; Jaleel *et al*., 2008). Plants show response to stress by various adaptive mechanisms which allow the biochemical and the photochemical system to handle stress (Yordanov *et al*., 2000). The plant organ which primarily detects limitation in supply of water is the root system. It prevents plants from drought stress by declining the leaf expansion and promoting root growth. In limited water conditions, the root: shoot ratio increases due to less sensitivity of roots as compared to shoots to growth inhibition by decreased water potentials (Wu and Cosgrove, 2000). The most common effect of water restriction is reduced plant growth, which is mainly caused due to leaf inhibition and elongation of stem when water potential declines below a threshold which varies in plant species (Pelleschi *et al.*, 1997).

In plants long term drought causes oxidative destruction because of the increased yield of reactive oxygen species (ROS). They cause oxidation of multiple cellular components, *i.e*. DNA and RNA, proteins and lipids, which is lethal to plant cell. Drought-induced limitation of photosynthesis causes lack of energy dissipation which results in oxidative stress (Loggini *et al.*, 1999). Plants have evolved a lot of protective mechanisms to reduce and completely eliminate (Mehdy *et al.*, 1996) it by the help of antioxidative system. They are the most important elements which cause ROS scavenging. Antioxidants and the activities of ROS scavenging enzymes are directly related with the tolerance to environmental stresses. Antioxidative system is divided into two groups: enzymatic and non-enzymatic antioxidants. The enzymatic antioxidants involve peroxidase (POD), superoxide dismutase (SOD) and catalase (CAT) while carotenoids, glutathione and ascorbate are non-enzymatic components (Hall, 2002; Caregnato *et al*., 2008). They interact with cellular components of plant and provides defense against the ROS (Foyer and Noctor, 2005).

In C_4 plants the antioxidative enzymes are present in the middle of mesophyll cells and bundle sheath cells (Foyer, 2002). Drought tolerant *S. bicolor* has higher antioxidant capacity in water deficit conditions than drought-susceptible varieties (Jagtap and Bhargava, 1995). It also accumulates glycine betaine and proline in rejoinder to water deficit. Therefore, sorghum is a drought tolerant crop, as it is highly adapted to dry regions of the world.

Ogbaga *et al.*, (2016) examined the biochemical responses of two sorghum cultivars of differing drought tolerance, Samsorg-17 (more drought tolerant) and Samsorg-40 (less drought tolerant), to sustained drought.

Drought tolerant Samsorg-17 was found be more drought tolerant due to up-regulation of protective proteins- HSPs, DHNs- sugars and sugar alcohols. Various components of root system architecture are known to influence drought tolerance in sorghum without any negative impact on productivity. The growth angle of nodal roots is an important target trait for improving drought tolerance (Joshi *et al.*, 2016).

Conclusion

Drought is the main environmental obstacle which limits crop yield in various regions of the world. *S. bicolor* is the most important multipurpose cereal crop grown in dry regions of the world and it is thought to be well adapted to drought than most other crops. It is a drought resistant crop because of specific characteristics which includes osmotic adjustment, transpiration efficiency, root depth, epicuticular wax and stay-green trait. Stay-green is the most important trait of drought-adaptation in sorghum. Therefore, sorghum as a drought-tolerant crop species with a compact genome size can be an excellent model for investigating physiological and biochemical mechanisms which are involved in drought tolerance and plant adaptation to harsh environmental conditions.

ACKNOWLEDGEMENT

V. Soni is grateful to Prof. P.L. Swarnkar, Prof. Reto Strasser and Prof. B. Robert for constant blessing and academic encouragement. M. Rathore is thankful to University Grant Commission for providing grant in the form of BSR fellowship.

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