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Impact of Drought Stress in Sorghum (Sorghum Bicolor (L.) Moench) Production and Drought Genetic Resistance Mechanisms

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ABSTRACT: *Over half a billion people in Sub-Saharan Africa and Asia utilize sorghum as a staple food. It grows in semi-arid to desert environments around the world. Grain sorghum's adaptation to a wide range of environmental conditions has resulted in the evolution and existence of considerable sorghum genetic polymorphism for drought tolerance. As a result, sorghum is expected to play an increasingly important role in agriculture and meeting global food demand in the face of climate change, land degradation, and increased water shortages. Drought is a complicated phenomenon that affects agricultural production all around the world. It is the world's largest sorghum production constraint, resulting in high yield losses every year. Plant breeders continue to face challenges despite decades of research. To reduce the negative effects of drought and boost production, it is vital for breeding to underestimate the genetics and physiological systems that underpin drought resistance. The sorghum crop requires less water than other important cereals such as maize and wheat. The crop's yield potential, however, has been severely hampered by drought and heat stress. Drought causes plants to reprogram their gene expression, which controls a range of biochemical and physiological processes. Sorghum is a drought-resistant crop that is increasingly being utilized as a model grain for identifying tolerance genes. Furthermore, drought resistance varies greatly across different sorghum genotypes due to natural variation. Sorghum is the world's most significant cereal crop, with great drought tolerance and adaptability. Plant breeding requires the identification and characterization of sorghum germplasm that has desired traits for genetic improvement. Sorghum is a high-yielding, nutrient-efficient, and drought-tolerant crop that can be grown on more than 80% of the world's farmland. Drought is a significant limiting factor for agriculture, and it is the leading cause of crop yield reduction. The identification of genetic factors involved in plant responses to drought stress will pave the way for breeding drought-resistant plants. Sorghum is one of the most significant food and feed crops in the world's arid and semi-arid regions due to its excellent drought tolerance. Sorghum is a valuable resource for the economic growth of the country, therefore determining the genetic diversity of current sorghum germplasm is critical for improved conservation, utilization, and crop improvement. Generally, sorghum is a drought-resistant crop that supports the livelihoods of millions of people residing in isolated regions.*
KEY WORDS: drought stress; sorghum; tolerance mechanism; food security; genetic bases

INTRODUCTION

Sorghum [Sorghum bicolor (L.) Moench, 2n=2x=20] is the emerging model crop species for the tropical grasses with C_4 photosynthesis. In the semi-arid tropics, sorghum is the fifth most important cereal crop and the second most important staple food grain. Sorghum is a self-pollinating crop that belongs to the poaceae family and has a genomic size of 730 megabytes (Paterson *et al*., 2009). Sorghum stalks are used as animal feed, fuel, and construction material, while the grain is used to feed livestock and make local beverages (McGuire, 2000). Sorghum can be grown in a multitude of altitudes, day lengths, rainfall, and ambient temperature. As a result, it has evolved to withstand the harsh conditions seen in tropical climates. The crop requires less water than other important grains such as maize and wheat. The crop's yield potential is substantially diminished in the tropics and subtropics due to drought and heat stress, necessitating sorghum breeding for drought tolerance and productivity (Blum, 2005).

Sorghum is a vital source of food for about half a billion people, particularly in the semi-arid and desert tropics. It's rich with protein, fiber, and is gluten-free (Impa *et al*., 2019). It is used as a feedstock for bio-ethanol production as well as for human consumption (Mathur *et al*., 2017). Drought stress from a shortage of water has an impact on sorghum's soil-nutrient absorption capacity, as well as nutrient mobilization and transport (Sarshad *et al*., 2021). Sorghum can adapt and tolerate a broad variety of conditions, including high temperatures, high evaporative demand, insufficient and unpredictable rainfall, and soils with poor structure, low fertility, and low water holding capacity (Teshome *et al*., 2007). Sorghum is the principal staple food crop for over 500 million people in Africa, Asia, and Latin America, especially in semi-arid tropical regions where food production is limited by drought (Ejeta, 2005). In underdeveloped countries, almost a third of the sorghum grain produced is consumed for human consumption (Ejeta, 2005).

Drought is the most common abiotic stress that sorghum faces in its primary production areas (Assefa *et al*., 2010). As a result, much research has been conducted to better understand the impacts of drought stress on sorghum, as well as its stress tolerance mechanisms, in order to develop drought-tolerant cultivars and implement efficient sorghum mitigation measures. In the field, a variety of biotic and abiotic stressors confront crops under varying environmental conditions. As a result of global climate change, temperatures and CO_2 levels in the atmosphere are rising, and droughts are becoming more often and widespread. One of the most common abiotic factors limiting crop yield and productivity is drought. It affects all major crops and is a common occurrence in many parts of the world. Drought has a significant impact on crop productivity and quality, and it can lead to famine in food-insecure areas. Crops, on the other hand, vary in their drought resilience, and even within a crop species, there is variation.

The stress has an impact on sorghum growth and development, from germination to reproductive and grain filling phases, as well as the plants' physicochemical characteristics, resulting in a considerable loss in grain yield and quality (Queiroz *et al*., 2019). The plant's response to stress includes changes in water usage efficiency, transpiration rate, and remobilization of photosynthetic assimilates, as well as biochemical alterations involving proline and other metabolites (Zhang *et al*., 2019a). The stress response, which is linked to energy and fitness costs as well as the direct effects of stress, can devastate an entire crop, but it most usually manifests itself in the form of severe grain yield loss and nutritional quality deterioration (Fischer *et al*., 2019). As a result, drought stress could lead to malnutrition in food-insecure and drought-prone areas where sorghum is an important crop. Drought can reduce sorghum grain-protein digestibility even more (Impa *et al*., 2019), resulting in poor nutritional absorption from sorghum grown in drought (Duodu *et al*., 2003).

Drought is one of the most devastating abiotic stresses to plant growth and productivity (Ahuja *et al*., 2010). Between 2005 and 2015, it was the major cause of food shortages in several countries (Kogan *et al*., 2019), costing over $29 billion in losses (Conforti *et al*., 2018). Drought resistance comes in three forms for plants: drought escape, drought avoidance, and drought tolerance (Osmolovskaya *et al*., 2018). To cope with drought stress, plants reprogram a wide range of responses at the molecular, biochemical, and physiological levels (Thatcher *et al*., 2016). Depending on the tissue type, developmental stage, and stress level, these changes can happen rapidly and with a lot of precision. At the molecular level, drought stress causes transcriptional and post-transcriptional regulation of gene expression (Takahashi *et al*., 2018). Differential expression of genes involved in various metabolic pathways is caused by transcriptional modulations, resulting in changes in metabolite flow and physiological changes associated to cellular damage protection (Knight H and Knight M.R, 2001).

Drought stress is a critical agronomic issue that causes severe production losses around the world. Developing crops that are well adapted to drought-prone environments could help to alleviate this agricultural constraint. The mechanisms that allow this crop to thrive in such severe environments are complicated and poorly understood. Drought in agriculture, specifically water scarcity, has a negative impact on plant and crop productivity by reducing leaf size, stem extension, and root proliferation, disrupting plant water and nutrient relationships, and diminishing water-use efficiency. During periods of severe drought, these losses can be significantly larger, and crop failure is a distinct possibility. Drought is a major constraint in sorghum production around the world, and it is the leading cause of crop yield reduction (Sabadin *et al*., 2012).

Sorghum is a desirable crop in tropical, warmer, and semi-arid regions of the world with high temperature and water stress due to its drought tolerance. With the effects of climate change on crop productivity looming large, sorghum, a drought-resistant crop will play a significant role in food, feed, and fodder security in the dry land economy (Mishra *et al*., 2017). Pre-flowering (panicle differentiation to flowering) and post-flowering (flowering to grain growth) drought responses have been identified in sorghum (Sanchez *et al*., 2002). Decreased panicle size, seed number, grain yield, seed set, plant height, leaf rolling, irregular leaf erectness, delayed flowering, and flower abortion are all examples of pre-flowering drought tolerance responses in sorghum. Stalk lodging, reduced seed size, susceptibility to charcoal rot, reduced biomass, loss of chlorophyll, degradation of photosynthesis, reduced seed weight, reduced grain number, reduced hundred seed weight, and premature leaf and stalk senescence are all examples of post-flowering drought resistance (Burke *et al*., 2010). Drought stress during anthesis is regarded to be more detrimental to grain yield, regardless of severity, because photosynthesis per unit leaf area is reduced, resulting in yield losses of up to 70%. (Abraha *et al*., 2015).

Generally, drought is a periodic phenomenon that endangers crop yields and threatens the livelihoods of populations all over the world (Liedtke *et al*., 2020). The development of drought-resistant crop varieties through breeding or biotechnology is a major challenge for agriculture. Understanding how drought affects plants is therefore crucial for designing superior cultivars with consistent high yields. Plant responses to drought stress, on the other hand, are complicated and vary based on environmental conditions, stress frequency and duration, plant species and variety, and physiological stage at the time of stress. It is required to identify genes whose expression is connected with drought resistance and about which little is known in order to generate drought-resistant sorghum lines, either by genetic engineering or molecular breeding. Increased expression of rapidly triggered transcription factors discovered in drought-resistant genotypes in drought-sensitive genotypes could lead to the development of drought-resistant cultivars via genetic engineering technology (Salah *et al*., 2020). The objective of the paper was to understand the role of sorghum in ensuring food security under moisture stress areas.

EFFECT OF DROUGHT ON YIELD AND YIELD COMPONENTS OF SORGHUM

Impact of Drought Stress on Growth and Development of Sorghum

Drought is one of the most important factors affecting crop productivity worldwide. As a result of climate change, droughts and floods will become more common, particularly in many African countries. According to some data, droughts may become more frequent and severe as a result of climate change. By 2050, droughts are expected to affect 67 percent of the world's population (Ceccarelli *et al*., 2004). Drought can strike at any time throughout a crop's development. Drought risk is highest in the dry and semi-arid tropics at the beginning and end of the growing season. Early in the growing season, drought stress will have a substantial impact on plant development. Drought during the crop's flowering or grain filling stages may result in lower yields or crop failure (Tumwesigye and Musiitwa, 2002).

Drought (prolonged dry periods or delayed rainfall), nutrient deficiencies, weeds, insects, wet weather at planting and harvest, lodging, excessive rainfall, early frost, snow, extreme cold conditions, high temperature, and bird assaults are all factors that limit sorghum yields (Assefa and Staggenborg, 2010). Drought, on the other hand, is by far the most important yield limiting factor, adversely affecting crop productivity around the world (Hussain *et al*., 2011). Drought decreases photosynthesis and, as a result, the amount of photosynthetic assimilate and energy available to the plant. Drought stress, according to El-Kholy *et al*. (2005), modifies plant growth and development patterns by inhibiting cell division, organ growth, net photosynthesis, protein synthesis, and hormonal balances in important plant tissues, resulting in severe yield reductions. Drought tolerance is high in sorghum, both before and after flowering (Phuong *et al*., 2013).

Despite its higher genetic adaptability, both stages have the potential to result in severe yield losses or crop failure. Drought during the anthesis and grain filling stages might result in lower yields or crop loss (Moradi and Younesi, 2009). Furthermore, post-flowering dryness frequently results in early plant death, lodging, seed size decrease, and yield losses (Borrell *et al*., 2014a). Drought stress is predicted to worsen in the future years, with drought-affected areas potentially doubling by 2050 (Rauf *et al*., 2016). Drought stress early in the growing season can be harmful to plant development; but, when late rain fall levels are enough, plants recover swiftly (Ramu *et al*., 2016). As a result of the above realities, crops are regularly subjected to moisture stress in one form or another (Twomlow *et al*., 2008). Depending on the stage of plant development, moisture stress has a different impact on crop yield (Kebede *et al*., 2001).

Drought appears to be especially vulnerable during anthesis and grain filling; occurrence of drought at these periods may result in decreased yields and/or crop loss (Moradi and Younesi, 2009). Crop yield is limited by a number of biotic, abiotic, and social factors. Drought is the most serious abiotic constraint among the major abiotic constraints. In the arid and semi-arid tropics, understanding the physiological mechanisms and genetic regulation of crop dryness is crucial for enhancing crop production and productivity. Seedling death is a major issue in dry land areas where drought stress is common, and it is most prevalent during seedling emergence and establishment when drought and heat stress are present (Ndlovu *et al*., 2021). Stand losses in sorghum can occur after full emergence but before seedling establishment due to drought (Queiroz *et al*., 2019). Drought stress affects plants more acutely in their early phases of development (germination, emergence, and seedling establishment). As a result, the impact of a drought-induced shortage of water on sorghum production in the early stages has gotten a lot of attention. However, the responses of sorghum genotypes to varied degrees of drought stress differ significantly.

Drought stress induced by polyethylene glycol (PEG) has been shown to significantly reduce sorghum seed germination in several studies (Queiroz *et al*., 2019). Similarly, water shortages at different levels of soil water content (60 percent and 40% field capacity) significantly reduced the percentage of seed emergence (Bayu *et al*., 2005). The osmotic potential was lowered from zero to -0.8 MPa, which significantly reduced percent germination (PG), germination rate index (GRI), and the amount of water absorbed by seedlings (Oliveira and Gomes-Filho, 2009). The germination rate index was much greater in a high osmotic potential environment, and the mean germination time (MGT) was significantly longer. Drought stress decreases seedling vigor, germination rate index, and percent germination through increasing respiration rate, which affects starch synthesis and energy generation (adenosine triphosphate (ATP) (Queiroz *et al*., 2019).

Sorghum genotypes have different starch content, according to research. However, the adaptation mechanisms of these genotypes and how the water deficit affects starch production during seed germination have yet to be fully studied. The delay in germination was shown to be caused by a strongly negative osmotic potential, which hampered the seeds' water intake, or imbibitions, the first step in the germination process (Queiroz *et al*., 2019). During the imbibitions phase, seeds must achieve an acceptable amount of moisture to revive the seed metabolic activities and encourage the growth of the embryonic axis for effective germination. Plants that are severely drought-stressed need longer time to adapt their internal osmotic potential to match the external environment.

Drought stress can stunt radicle, hypocotyl, and plumule (including coleoptiles and mesocotyl) growth after germination (Queiroz *et al*., 2019). According to Queiroz *et al*. (2019), the limitation of radicle appearance and growth under water shortage conditions could be related to a reduction in the turgor of the radicle cells, which affects cell division and elongation. This could have an impact on the plant's growth and development in the future. Under mild and severe water deficiency situations, for example, Bayu *et al*. (2005) found that the length of the coleoptiles and mesocotyl was shortened. For proper emergence and early plant vigor, the mesocotyl and coleoptiles are required. Under water-stressed conditions, poor elongation of the mesocotyl and coleoptiles indicates poor seedling emergence and establishment. Furthermore, a lack of water reduces shoot elongation and dry weight, as well as root growth to some extent (Bobade *et al*., 2019). Similarly, Bayu *et al*. (2005) discovered an increase in the root-to-shoot ratio as well as an increase in osmotic potential levels, which researchers believe is an adaptive response to water shortages.

Furthermore, a reduction in one or both of the primary cellular growth parameters: wall extensibility and cell turgor, could result in a decrease in shoot growth rate (Queiroz *et al*., 2019). Drought-sensitive sorghum cultivars have a more significant effect of water shortage on vegetative growth than drought-tolerant sorghum cultivars, according to studies. Fadoul *et al*. (2018) found that under drought stress, the drought-sensitive cultivar's shoot and root length were shorter than the drought-tolerant genotypes. This shows that cultivars with long and wide root systems may have a better chance of establishing seedlings because their root systems may rapidly penetrate the upper soil layers and reach moist soil layers for water intake, reducing the stress caused by a lack of water. When searching for drought-tolerant sorghum genotypes, it's critical to evaluate traits including seed vigor, imbibitions, germination potential, germination rate, plumule and radicle development, as well as root and shoot growth at an early stage of plant growth and development.

The Effect of Drought Stress on Sorghum Grain Yield

Drought stress, caused by a lack of water in the soil, is one of the most severe abiotic stresses influencing agricultural yields around the world. Drought stress can cause floral initiation to be delayed greatly, as well as affect panicle development and the formation of new leaves (Ndlovu *et al*., 2021). Photosynthesis, chlorophyll content (Soil Plant Analysis Development; SPAD), photo assimilate translocation, and soil nutrient uptake are all reduced, resulting in lower grain yield and quality (Sehgal *et al*., 2018). Drought stress affects crops in different ways and through different mechanisms. Drought tolerance involves physiological and molecular mechanisms (Sabadin *et al*., 2012) for activation of relevant genes and pathways, energy and resource allocation for cellular functioning, and stomatal conductance and transpiration modification, as well as increasing water use efficiency and promoting stay-green (Tovignan *et al*., 2020). Drought tolerance is the outcome of a variety of physico-chemical changes (Sehgal *et al*., 2018), which result in fitness costs that reduce crop productivity.

Drought stress reduces seed size, quantity, and weight per panicle, as well as other agronomic characteristics, reducing grain yields significantly (Sarshad *et al*., 2021). In other words, it raises direct and indirect expenses for crops, limiting their yield and productivity. Despite the fact that sorghum is one of the most drought-tolerant crops adaptable to a variety of agro-ecologies and low-input agriculture, drought stress can still cause considerable production losses (Sabadin *et al*., 2012). This can be thought of as the tolerance mechanisms' fitness cost, reflected as a reduction in grain yield. Grain yields are frequently reduced in water-stressed areas due to unpredictable and insufficient precipitation (Hattori *et al*., 2005). Drought stress can affect grain yields at any stage of crop development, according to Gano *et al*. (2021). However, practically all previous research has concentrated on the impact of stress that occurs during a specific developmental stage, despite the fact that stress is prevalent at all phases in nature.

Drought stress lowered grain yield by more than 36% and 55% in the vegetative and reproductive stages, respectively (Assefa *et al*., 2010). The stress imposed during the booting and flowering stages reduced grain yield by 87 percent, but only substantially longer and more extreme drought stress at the vegetative stage may cause such a significant yield loss (Crafurd and Peacock, 1993). As a result, whereas drought stress can reduce grain yield at any developmental stage, it has a greater impact on grain yield during reproductive phases. This is because during the reproductive stages, there is a stronger link between the environment and grain yield and quality than during the vegetative stages. Flowering, pollination, microsporogenesis, and seed filling (Sarshad *et al*., 2021) have been found to be crucial reproductive phases that can negatively affect grain yield (Kebede *et al*., 2001). Seed filling, which involves a variety of metabolic processes, enzymes, and transporters found in the leaves and seeds, is the stage of the plant that is most vulnerable to drought stress (Sehgal *et al*., 2018).
Drought stress affects sorghum production both before flowering (panicle formation) and after flowering (between flowering and grain development) (Adugna and Tirfessa, 2014). Drought stress both before and after flowering affects grain yield and quality, according to a study on sorghum (Kapanigowda *et al*., 2013). Drought stress during the flowering stage can also reduce the quantity of grains per panicle, which is a characteristic that directly affects grain yield (Manjarrez-Sandoval *et al*., 1989). A drought during the post-flowering stages, on the other hand, has a greater influence on grain yield than a drought during the pre-flowering stages. Drought during the post-flowering periods, for example, is a major sorghum production constraint, according to sorghum growers in Ethiopia and Burkina Faso (Derese *et al*., 2018).

Drought stress during the post-flowering growth stage, according to Burke *et al*. (2018), had a significant impact on sorghum productivity due to early plant death and smaller seed size. Drought stress during the post-flowering stage lowered grain yield by about 50%, according to a two-year classic study including 30 sorghum varieties (Batista *et al*., 2019). Due to the heterogeneity in their responses to stress, the effect of drought stress on different sorghum genotypes may differ. When genotypes with a high growth rate and a short length of grain filling were exposed to drought stress at the terminal post-flowering stage, they produced larger grains than genotypes with a longer duration of grain development (Tuinstra *et al*., 1997). To understand how water deficit affects starch production, germination, and metabolic response of sorghum seeds, metabolic and enzyme experiments are necessary.

Drought stress during the pollination stage might result in a considerable reduction in grain yield due to a lack of egg insemination inside the ovary (Sarshad *et al*., 2021). This is due to the fact that pollen grains must be transferred from male to female organs and must come into contact with the eggs in the ovary, which necessitates sufficient moisture, which is a limiting factor in drought-stricken areas. According to Manjarrez-Sandoval *et al*. (1989), significant drought stress prior to microsporogenesis resulted in a drop in grain number per panicle (but a modest increase in grain size), resulting in decreased grain production. Drought stress following grain filling, on the other hand, had no substantial negative effect on gain yield, according to a study by Sarshad *et al*. (2021). Overall, research has shown that drought stress lowers grain yield; however, the severity of the stress is dependent on a number of parameters. Differences in the degree of the damage caused by drought stress are influenced by stress severity and duration, plant development stage and genotype, the presence of other confounding stresses, and seasonal fluctuations.

The Effect of Drought Stress on Nutritional Quality

Drought stress changes the relationship between morpho-physiological traits on the one side and source activity and sink strength on the other (Yu *et al*., 2017), changes grain physico-chemical characteristics (Impa *et al*., 2019), reduces nutrient mineralization, and impairs membrane permeability (Impa *et al*., 2019). Various researches have revealed how drought stress affects the nutritional content and composition of sorghum, in line with these changes in plants. Growing sorghum genotypes in dry conditions, for example, resulted in lower grain micronutrient content (Zn, Fe, Mn, and Cu) (Impa *et al*., 2019). Drought stress induced during the flowering stage resulted in lower total starch, amylase, and amylopectin accumulation, which is linked to enzymes' activities on sugar nucleotide precursors during grain filling, such as starch synthase (SSS), granule-bound starch synthase (GBSS), starch branching enzyme (SBE), and starch debranching enzymes (DBE) (Bing *et al*., 2014).

Drought stress imposed on sorghum at various phenological stages, from flowering to late seed filling, did not significantly alter glucose levels and subsequent ethanol generation, according to Ananda *et al*. (2011). However, because the plants were stressed at each phenological stage individually, the results might not be definitive because this scenario might not arise in natural field conditions. Plants respond to water deficits by activating a variety of signaling pathways, with the phytohormone abscisic acid (ABA) playing a key role in biosynthetic buildup of certain metabolites (amino acids, sugars, indoles, phenolics, and glucosinolates) primarily in drought-tolerant genotypes (Stagnari *et al*., 2016). Drought-tolerant genotypes, for example, have higher grain K and Fe concentrations than susceptible genotypes (Abu Assar *et al*., 2002). Drought-induced stress increased sugar and sugar alcohol content in one sorghum genotype and amino acid concentration in another, according to Ogbaga *et al*. (2016). Drought stress raised total protein content and had a beneficial effect on total soluble carbohydrate, crude protein, and proline content in sorghum in other research (Sarshad *et al*., 2021).

The increasing number of these molecules suggests their role in drought stress tolerance, whereas genotype-specific tolerance mechanisms are shown by changes in their accumulation levels. Drought stress may also have an impact on nutrient availability. Impa *et al*. (2019), for example, found that protein derived from sorghum produced under drought stress was less digestible. This could be linked to an increase in starch levels as a result of drought stress (Stagnari *et al*., 2016). In terms of grain nutrient content, there is a lot of variance across sorghum genotypes. Sorghum varieties differed significantly in total starch, amylose, and mineral content, with two varieties (Tx430 and AR-3048) having significantly higher protein content than the rest (Ng'uni *et al*., 2016). Protein and nutrients (Ca, Fe, K, Mg, Mn, Na, P, and Zn) have considerable variability between sorghum accessions, according to Motlhaodi *et al*. (2018), and these traits have a strong broad-sense heritability ranging from 0.62 to 0.85.

Nonetheless, the influence of drought stress on the amounts of these nutrients in different sorghum genotypes was not investigated in these experiments. When grown under drought stress circumstances, however, Abu Assar *et al*. (2002) found that sorghum genotypes showed significant diversity in mineral composition, with drought-tolerant genotypes containing higher K and Fe content than susceptible genotypes. As a result, even when grown under water deficit conditions, the tolerant genotypes could retain appropriate mineral and other nutrient compositions. The availability of genotypes with greater Fe and Zn concentrations, as well as consistent nutrient content heritability (Motlhaodi *et al*., 2018), suggests that sorghum genotypes with higher concentrations of these nutrients can be used to improve micronutrient composition in elite sorghum materials. The substantial positive connection between micronutrients (Phuke *et al*., 2017) and their high heritability in some genotypes suggest that these key quality attributes are under strong genetic influence.

MECHANISMS OF DROUGHT TOLERANCE IN SORGHUM

Sorghum is C_4 crop used for food, feed, and fiber, is one of the best-adapted cereals to water-limited conditions, ranking among the most drought-tolerant of all US crops (Ludlow M.M and Muchow R.C, 1990). Heritable morphological and anatomical traits (such as thick leaf wax and a deep root system), physiological responses (such as osmotic adjustment and the stay-green trait), and adaptive mechanisms all contribute to its drought tolerance (Tari *et al*., 2013). Farmers and plant breeders chose today's sorghum cultivars and hybrids for its high grain yields, early flowering, drought tolerance, and bioenergy production from sorghum species that separated 50 million years ago in different parts of Africa's Sahara Desert (Doebley *et al*., 2006).

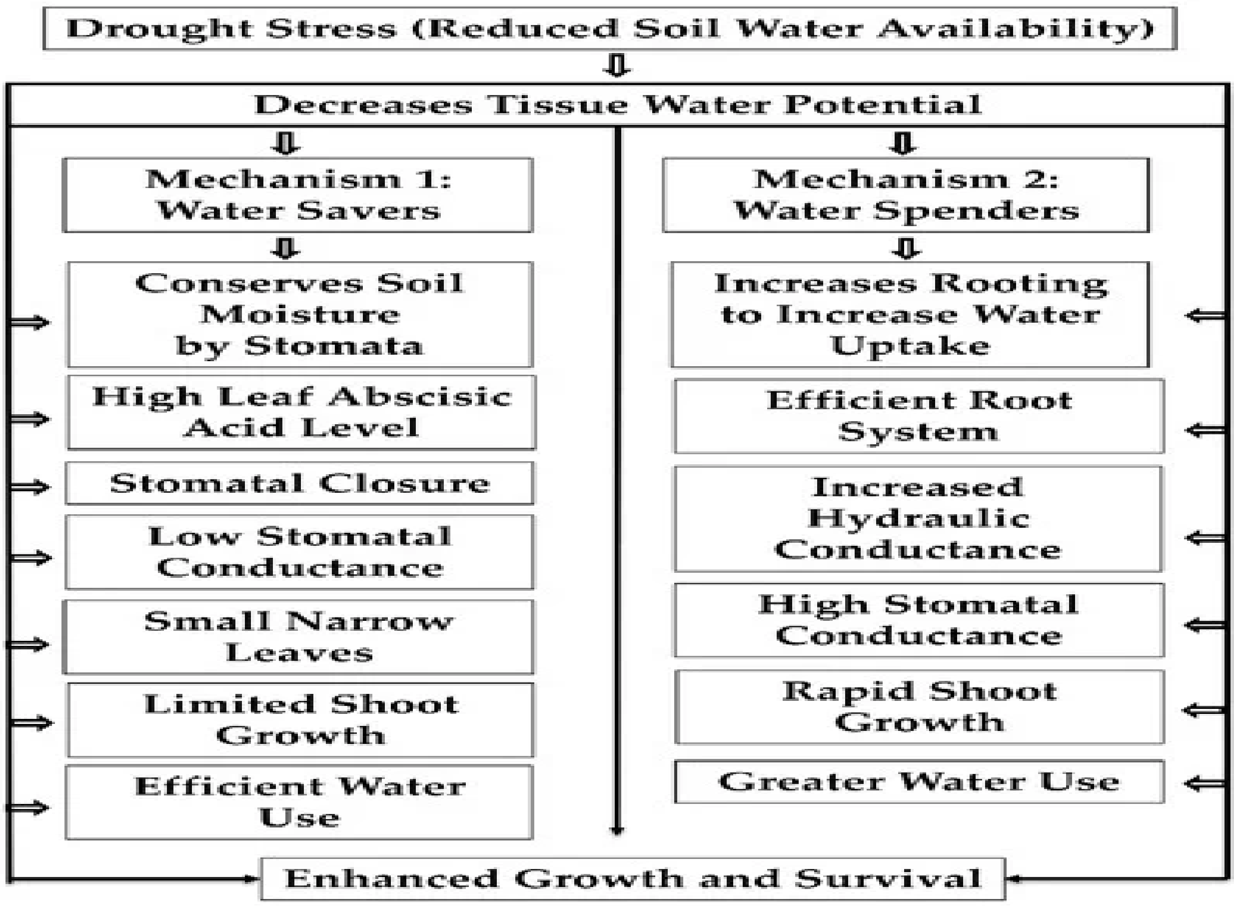

Figure 1: Drought tolerant mechanisms in crop plants

Physiological Mechanisms of Drought Tolerance in Sorghum

The physiological, biochemical, genomic, proteomic, and metabolomic changes that occur in plants in response to drought stress and drought tolerance are the consequence of complex biological processes (Ngara *et al*., 2021). Drought is mitigated by plants through processes such as avoidance, recovery, survival, and tolerance. Drought avoidance refers to a plant's ability to conserve water by minimizing water loss from the shoots or absorbing water more effectively from the soil (Osmolovskaya *et al*., 2018). Plants also survive drought stress by expanding its root system, closing their stomata, curling their leaves, waxing their stems, remaining green, and having high transpiration efficiency (Badigannavar *et al*., 2018).

Drought escape, which refers to plants completing their life cycles before a dry season begins in order to maintain reproduction, is a more successful strategy (Manavalan and Nguyen, 2017). Early flowering and maturity, high leaf N_2 levels, high photosynthetic capacity, and remobilization of assimilates are all drought-resistant strategies (Badigannavar *et al*., 2018). Drought tolerance, on the other hand, refers to a plant's ability to resist water stress while maintaining key physiological functions that maintain and protect metabolic integrity at the tissue and cellular levels (Tuinstra *et al*., 1997). Osmotic adjustments, protective solutes, high proline, desiccation resistant enzymes, and high stomatal conductance are examples of this (Badigannavar *et al*., 2018).

Photosynthetic Rate, Transpiration and Stomatal Conductance

Under stress conditions, stress-induced physiological changes such as a shift in photosynthetic rate were identified in drought sensitive sorghum genotypes (Fracasso *et al*., 2016). Photosynthetic rate (A), transpiration rate (E), water usage efficiency (WUE), and stomatal conductance are all affected by drought stress. The Fv/Fm ratio, which corresponds to the maximal quantum yield of photo system II, is a useful measure for determining how drought stress affects photosynthesis (Husen *et al*., 2014). It's utilized as a measure of photosynthetic efficiency, which is much lower in sorghum cultivated in drought-stricken conditions (Johnson *et al*., 2014). Drought stress reduces photosynthetic rate in sorghum by decreasing stomatal conductance and transpiration rate (Zhang *et al*. 2019b), quantum yield and increasing leaf temperature (Kapanigowda *et al*., 2013), reduction in chlorophyll and Rubisco, increase in O_2 evolution, and decrease in PEPCase activity (Kapanigowda *et al*., 2013), reduction in chlorophyll and Rubisco (Bao *et al*., 2017).

Drought-tolerant sorghum genotypes have much greater Fv/Fm and photosynthetic rate than non-tolerant sorghum genotypes, according to much research (Fracasso *et al*., 2016). In addition to a plant's ability to avoid and/or survive drought stress, the photosynthetic recovery that occurs after rehydration is critical in determining drought tolerance and minimizing grain production decline (Chaves *et al*., 2009). A primary method by which tolerant genotypes sustain grain yield in sorghum is increased photosynthetic rate, which provides raw material and energy required for growth and development during drought stress (Getnet *et al*., 2015). Under normal and drought stress conditions, several studies have found significant genetic variation in sorghum in terms of net carbon absorption rate (A), transpiration rate (E), A: E ratio, and WUE.

Several studies have found that increasing A: E and WUE during the pre-flowering stage of sorghum improves drought tolerance (Vadez *et al*., 2011b). In drought-tolerant sorghum genotypes, transpiration efficiency did not differ between control and drought stressed plants, however in drought sensitive genotypes, there was a statistically significant difference between control and drought stressed plants (Fracasso *et al*., 2016). Furthermore, during the drought stress period, drought-tolerant genotypes had a considerably higher WUE than drought-sensitive genotypes (Fracasso *et al*., 2016). In sorghum, transpiration efficiency and water extraction were found to be highly related to grain yield (Vadez *et al*., 2011b). Given the importance of the genetic basis of tolerance mechanisms in producing drought-tolerant sorghum genotypes, selecting attractive genotypes based on this trait is critical. Drought tolerant genotypes have lower stomatal conductance and reduced transpiration rate (E) during the vegetative phase, which conserves water that can be utilized during the grain filling stage in water-limited environments (Lopez *et al*., 2017). Lopez *et al*. (2017) found that QTL for stomatal conductance were linked to lower E but not A or shoot biomass in this fascinating study.

Chlorophyll Content and Stay Green

Drought adaptation is determined by a plant's capacity to sustain normal chlorophyll content under drought stress conditions (Chen *et al*., 2016). The amount of total chlorophyll, as well as chlorophyll a and b, in a plant directly influences its ability to absorb light for photosynthesis. A considerable fall in chlorophyll content in sorghum cultivated under drought stress has been reported in several investigations (Fadoul *et al*., 2018). When compared to equivalent genotypes grown under control conditions, remain green genotypes had a 23 percent loss in total chlorophyll content while senescent genotypes had a 75 percent reduction in total chlorophyll content (Xu *et al*., 2000). Another study found that stressed plants had 4.3 percent lower total chlorophyll content than control plants (Devnarain *et al*., 2016).

In addition to chlorophyll, reduced concentrations of certain carotenoids have been documented under extreme drought stress (MunnéBosch *et al*., 2001). Drought tolerance lowered both chlorophyll and carotenoid concentration in drought-tolerant sorghum during the pre- and post-flowering stages, according to Takele (2010). In drought-sensitive genotypes, a drop in carotenoids is likely due to down-regulation of genes involved in terpenoid and carotenoid production (Fracasso *et al*., 2016). Drought stress causes down-regulation of genes involved in the biosynthesis of carotenoids and chlorophyll, which has a significant impact on light reaction and carbon fixation processes. At the flowering and maturity stages, the chlorophyll concentration had a substantial positive association with the number of green leaves and the area of green leaves. As a result, grain yield was highly linked with both leaf features at both phases (Reddy *et al*., 2014). The loss of chlorophyll and a progressive decline in photosynthetic capacity characterize leaf senescence (Borrell *et al*., 2000). Stay-green is a well-studied trait that contributes to sorghum's adaptability to post-flowering dry conditions by delaying leaf senescence and increasing grain yield. Several researchers have attempted to decipher the physiological basis behind sorghum's ability to stay green. Staying green is linked to a higher leaf nitrogen concentration, cytokinin, and chlorophyll content during drought stress, according to early assumptions and investigations. Borrell *et al*. (2000), for example, found a link between staying green and greater leaf nitrogen concentrations, particularly throughout the flowering stage. Another study found that stay green sorghum genotypes maintain high amounts of cytokinin, indicating that the stay green genotypes have a decreased senescence rate (Thomas and Howarth, 2000). Additionally, stay green genotypes have higher chlorophyll concentration than senescent genotypes (Xu *et al*., 2000).

In response to drought, the stay green trait of sorghum is related with increased leaf chlorophyll content, a slower rate of loss of green leaf area (Kassahun *et al*., 2010), less tillering, and smaller upper leaves (Kassahun *et al*., 2010). (George-Jaeggli *et al*., 2017). Increased transpiration efficiency (TE) and water extraction are also linked to the trait (Vadez *et al*., 2011a). The introgression of stay green QTLs from B35 to senescent variety R16 under drought stress resulted in higher leaf chlorophyll levels at flowering and a greater percentage green leaf area during grain filling stages, as well as a higher relative grain yield during the post-flowering stages (Kassahun *et al*., 2010). At flowering phases, the Stg QTL controls canopy size by reducing tillering and the size of higher leaves, enlarging the size of lower leaves, and in some cases reducing the number of leaves per culm.

Reduced canopy size at flowering reduces pre-flowering water demand, allowing more water to be available during the grain filling stage, resulting in higher biomass production and grain yield (Borrell *et al*., 2014a). Accelerated age-related senescence of lower leaves in stay green lines prior to flowering causes shedding of old leaves at flowering, resulting in a reduced canopy (George-Jaeggli *et al*., 2017). Any water saved during the pre-flowering stages increases the amount of water available during the post-flowering stages, allowing plants to keep their photosynthetic potential for longer and "stay green" during grain filling (George-Jaeggli *et al*., 2017). Stay green could be considered as a post-flowering drought tolerance mechanism that facilitates the availability of water essential for overall development and grain production, based on these and similar research results.

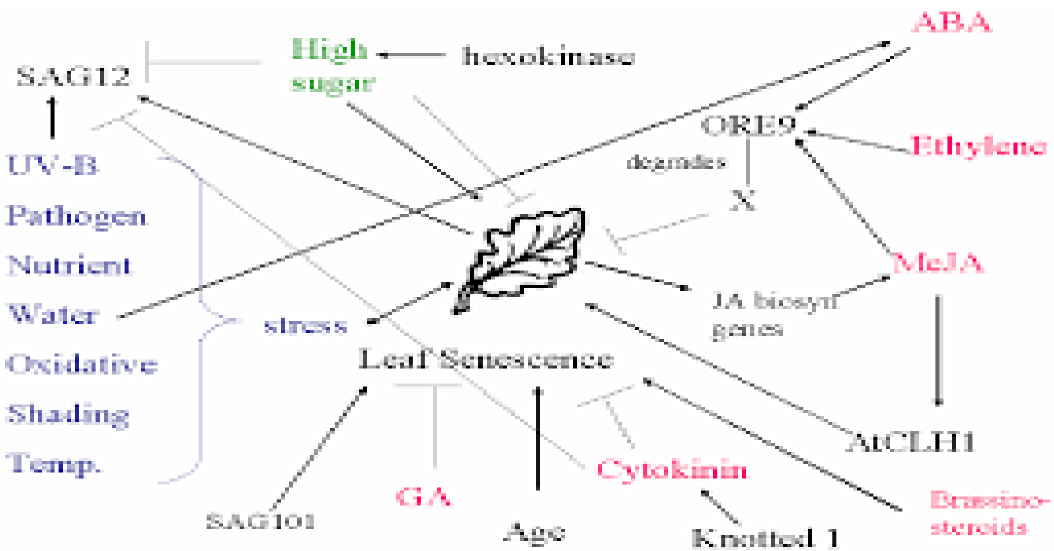

Figure 2: Genetic analysis of sorghum stay-green drought tolerance trait

The Genetic Basis of Drought Tolerance Traits

The purpose of researching the genetics of drought resistance in plants is to find genetic factors that influence crop productivity under drought stress. Drought resistant traits must be found and chosen for in addition to yield to make progress in crop improvement under water limited conditions (Borrell *et al*., 2000a). On the ten linkage groups of sorghum, quantitative trait loci (QTLs) have been mapped. They are in charge of controlling yield and yield components, root systems, plant height, flowering, and maturity traits (Sanchez *et al*., 2002). A multitude of drought-resistant characteristics have been identified and mapped, however the stay-green trait is often considered as the most significant drought resistance trait in sorghum. Tuinstra *et al*. (1997) identified 13 chromosomal areas in sorghum that are linked to post-anthesis drought resistance. Four QTLs for yield and yield stability, seven for grain development duration and seed weight, and two for the stay-green characteristic were identified. QTLs have been mapped into 10 linkage groups on sorghum from three stay-green gene sources (B 35, SC 56, and E 36-1) (Kebede *et al*., 2001).

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Two stay-green QTLs were identified on linkage groups B and I by Tao *et al*. (2000). Similarly, Crasta *et al*. (1999) and Xu *et al*. (2000) identified four stay-green QTLs, two of which (Stg_1 and Stg_2) were mapped to linkage group A, and the other two (Stg_3 and Stg_4) to linkage groups D and J, respectively. The stay-green QTLs were ranked in order of merit based on their contribution to the stay-green phenotype: Stg_2, Stg_1, Stg_3, and Stg_4. Xu *et al*. (2000) also mapped three QTLs for chlorophyll content (Chl_1, Chl_2, and Chl_3), and the map position aligns with the stay-green QTLs. The map position of these QTLs on the genome may explain the phenotypic association of the stay-green trait and chlorophyll content.

Stay green, chlorophyll content, leaf number, leaf length, leaf width, and leaf area, as well as root characteristics, are all controlled by many genes contained inside chromosomal areas known as quantitative trait loci (QTLs). For the development of drought-tolerant sorghum cultivars, identifying and understanding the QTLs linked with these traits is critical. In sorghum, multiple QTLs associated with drought-related phenotypes have been found, and several QTLs connected with these traits have been mapped. However, bi-parental linkage mapping was used to find the majority of these QTLs. Future research should focus on genome-wide association mapping using high-density SNP markers to correctly identify QTLs linked to characteristics. Stay-green, which is correlated with chlorophyll content and is considered a very significant characteristic for sustainable grain yield under drought stress, particularly during the grain filling period, is the best characterized of the drought tolerance related traits in sorghum.

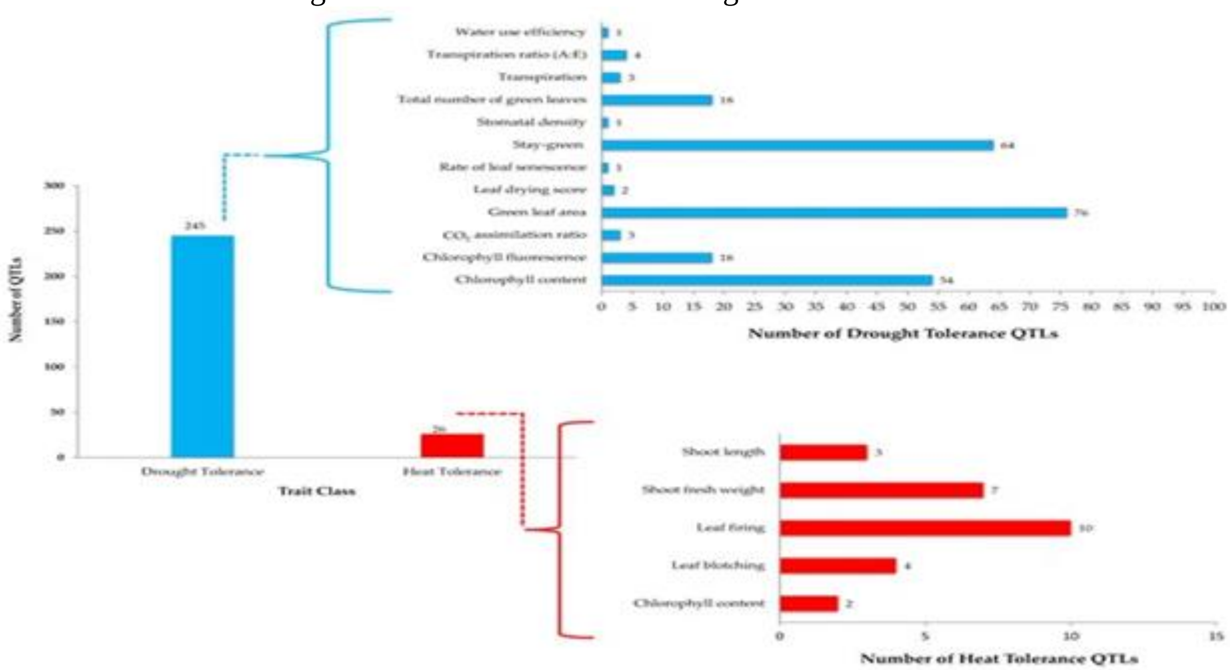

Figure 3: Quantitative traits and Quantitative Trait Loci (QTLs) identified for drought or heat stress in sorghum

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CONCLUSION

Sorghum is a vital food crop for people living in drought-prone areas. Rainfall is the main limiting factor in major sorghum-growing areas, reducing productivity and production significantly. In dry lowland areas, drought is one of the key abiotic restrictions to reduced or entire loss sorghum grain yield production. As a result, plant breeders must focus their efforts and research on enhancing sorghum's drought tolerance in order to reduce yield losses caused by drought stress. Drought resistance is a complex trait whose expression is influenced by the action and interaction of different morphological (earliness, reduced leaf area, leaf rolling, wax content, efficient rooting system, awn, stability in yield and reduced tillering), physiological (reduced transpiration, high water use efficiency, stomatal closure and osmotic adjustment) and biochemical (accumulation of proline, polyamine, trehalose, increased nitrate reductase activity and increased storage of carbohydrate) characters.

Crop yield enhancement is essential to fulfill the needs of future population growth, however abiotic stressors reduce yields significantly over the world. Several abiotic and biotic environmental elements influence plant development and productivity. Drought stress is one of the most important abiotic stresses, negatively influencing crop growth and limiting agricultural productivity around the world. Drought stress causes total alteration of crop metabolism and cellular structure by reducing the availability of sufficient water, which results in stomatal closure, which restricts gas exchange. Drought is the most significant abiotic factor affecting growth and crop yield, particularly in hot and dry climates. Drought in agriculture has a negative impact on crop production by reducing leaf size, stem expansion, and root multiplication, disrupting plant water and nutrient relationships, and diminishing water use efficiency. During times of severe drought, there are significant yield losses that can lead to crop failure.

Drought is the greatest yield-reducing factor in areas where rainfall is erratic and unevenly distributed, and water supply is inadequate for crop plants to survive and produce the expected yields. Developing drought resistant or tolerant varieties, in addition to inherent drought resistance mechanisms in plants, is critical in balancing future population expansion and food demand all over the world. Drought is a major limiting factor in crop production around the world. Because sorghum is widely grown in the dry and semi-arid tropics, it is a dependable crop for farmers in those areas. However, there are a number of obstacles that impede the global sorghum product and production system. Crop breeding can increase a crop's ability to tolerate adverse environmental conditions. In the case of sorghum, several cultivars are currently being developed with the support of plant breeding efforts to increase yield by tolerating drought. Despite the fact that drought is a limiting factor, sorghum may adapt to hard conditions through a variety of strategies. The most crucial events for drought resistance in the sorghum crop are stay greenness, solute accumulation, leaf rolling, and root characteristics.

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