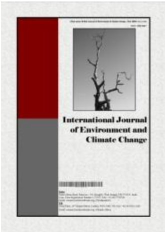

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Sorghum Physiology and Adaptation to Abiotic Stresses

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

Sorghum (*Sorghum bicolor* (L.) Moench) is the world's fifth most important cereal and a staple crop for nations in Sub-Saharan Africa and Asia, with great biomass production potential. In the dry and semi-arid tropics, it may be considered as a source of human food, grain, and pasture for cattle, as well as fuel. Abiotic stress factors such as drought, warmth, salt, and submergence remain key limitations to crop growth and yield as a result of climate change. Although sorghum can resist a variety of conditions such as heat, drought, salt, and floods, in dry and semi-arid areas, this crop is typically damaged by water stress at the post-flowering stage. Drought tolerance is a result of morphological and anatomical characteristics (thick leaf wax, leaf rolling, deep root system, and kranz anatomy), as well as physiological responses such as osmotic adjustment via osmoprotectants, stay green traits, quiescence, and ROS-scavenging enzymes such as catalases (CAT), superoxide dismutase (SOD), peroxidases (POD), and ascorbate peroxida (APX). Drought resistance is enhanced by functional proteins such as aquaporin, late embryogenesis abundant (LEA) proteins, heat shock protein, and regulatory proteins such as protein kinase, various transcription factors such as DREB2, bZIP, and phytohormones such as ABA and ethylene. Drought-tolerant sorghum genotypes contain greater osmolyte, chlorophyll, RWC decrease, leaf rolling, and up-regulation of various enzymes and regulatory proteins. When breeding for drought resistance, it's crucial to understand the various drought tolerance mechanisms in plants. The key to

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generating abiotic stress-tolerant agricultural plants in the future is to understand the physiological underpinning of crop production, crop responses, and crop adaptability in stress-prone locations under sustainable agriculture.

Keywords: Abiotic stress; sorghum physiology; drought stress; drought resistance and adaptation mechanisms.

1. INTRODUCTION

After wheat, rice, maize, and barley, sorghum (*Sorghum bicolor*) is the world's fifth most important crop [1,2]. It is a versatile plant with high biomass production potential. In the subtropical and semi-arid tropics, it may be considered as a source of human food, grain, and fodder for cattle, as well as fuel. Adequacy in sorghum production is challenged by growing population urbanization/ industrialization, and climate change. Drought, warmth, salt, and submergence are all key abiotic stressors for crop growth and yield as a result of climate change [3]. Sorghum can endure a variety of conditions, including heat, drought, salt, and floods, but in dry and semi-arid environments, this crop is typically damaged by water stress during the reproductive stage, especially after blooming [4,5]. Drought is a combination of stress effects caused by high temperatures and deficient soil moisture [5]. Craufurd and Peacock [7] reported grain yield loss in sorghum due to water stress, which they attributed to variance in total biomass buildup. Sorghum is a prominent drought-tolerant crop in such places and a suitable model for investigating moisture stress tolerance mechanisms among C4 cereals. Drought tolerance is a combination of morphological and anatomical features (thick leaf wax, deep root system) as well as physiological effects (osmotic adjustment, remain green, quiescence) [8]. Greater cell growth, photosynthesis, and biomass accumulation under pre-flowering stress; high pollen survivability; seed set and seed counts during blooming; and better stay green, photosynthesis, and seed size during post-flowering dryness [9]. It possesses a deep root system, the capacity to minimise transpiration by leaf folding and stomatal closure, and the ability to slow metabolic activities to near dormancy under acute drought. As a result, sorghum can endure dry spells and resume development once soil moisture is restored. Despite its drought tolerance, sorghum experiences yield losses of 60–90% depending on the severity of the drought [10].

2. STRESS AND ITS TYPES

Stress is any adverse environmental factor or condition that affects normal metabolic or physiological processes [10]. There are two broad categories of stresses occurring in plants, *viz.,* biotic and abiotic stress. A living organism's detrimental influence on other living species in a certain environment is known as biotic stress. Pathogens that cause disease are mostly found therein. The negative influence of non-living forces on living organisms in a given environment is known as abiotic stress. Abiotic pressures include extreme light intensity, strong wind velocity, heavy metal stress, dietary stress, contaminants, and human problems.

3. IMPACT OF ABIOTIC STRESSES ON CROP PRODUCTION

Abiotic stressors are one of the most significant environmental factors that influence crop yield and distribution all over the world. Almost 90% of arable lands are vulnerable to one or more of the aforementioned stresses [12], which can result in up to 70% production losses in important food crops [13]. Abiotic stressors have severely limited agricultural productivity in recent years. Abiotic stressors are responsible for almost half of all agricultural productivity losses. Climate change is anticipated to exacerbate their severity and harmful repercussions. Drought (9%), temperature conditions (7%), and other kinds of stress account for the majority of the losses (20%). Drought is a severe danger to the world's food production systems because of rapidly changing climatic dynamics [14]. Plant growth and yield development are both impacted by drought stress [15]. Plants, as sessile organisms, are persistently confronted with harmful factors that arise from an ever-changing environment. Plants have developed sophisticated and delicate ways to protect themselves from environmental stresses that hurt their growth and development.

4. RESPONSE OF PLANT TO ABIOTIC STRESSES

Abiotic stressors have a significant impact on agricultural plant growth, development, and productivity, leading to lower crop yields. Some of the notable changes are: a) Germination inhibition b) Growth reduction c) Premature senescence d) Reduction in productivity. Decreased water intake, changed transpiration rate, reduced photosynthesis, altered respiration, reduced nitrogen incorporation, metabolic toxicity, and the build-up of growth inhibitors are all physiological responses to abiotic stress. Abiotic stresses influence the various aspects of plant reproductive development at the molecular level as well. Common abnormalities include changes in gene expression, the breakdown of macromolecules, less activity of essential enzymes, less protein synthesis, and a mess in the membrane system.

External stress stimulates a variety of defence mechanisms, along with the formation of reactive oxygen species (ROS), alterations in redox potential or cellular Ca2+ ion levels, ion homeostasis interruption, and membrane fluidity adjustment, among others. [16].These external stress signals are sensed through specific receptors which are mostly present in the cell membrane. The plants transduce those foreign signals into intracellular downstream signalling pathways through secondary messengers like Ca^{2+} ions etc. which ultimately leads to the activation of transcription factors *like* protein kinase or phosphatase like MYB and CBF etc. The stimulation and biosynthesis of downstream target proteins and phyto-hormones eventually determine the plant's growth and development under a stressed environment (Fig.1). Crosstalk between these complex signalling networks, in particular, precisely controls the expression of stress-responsive genes while also shielding plants from external shocks [17].

Specific receptors in plant cells perceive external stresses and transduce the signal into downstream components, which activate or express defence molecules to protect plants from the stresses [17].

5. PHYSIOLOGY OF SORGHUM UNDER ABIOTIC STRESSES

5.1 Submergence Stress in Sorghum

Two types of environments cause submergence: flash flooding and deep water. A flash flood occurs when the water level rises quickly and lasts just a few weeks (2 weeks) and is not particularly deep. Water levels might rise to 50 cm. With a water depth of more than 100 cm, it can last for months [19]. Flooding/water logging occurs where there is stagnation of water on the top of the soil that leads to excessive water in the plants' root zone, which decreases the availability of O^2 to roots, limiting respiration. The level of CO^2 is also hampered, which limits photosynthesis. Water logging can inhibit plant productivity and growth, and in severe cases, submergence might result in death [20]. The fully or almost nearly saturated soil under this condition reduces the movement of gases to and away from plant surfaces. Intolerant cultivars show symptoms like chlorosis and extreme leaf elongation, which are caused by less ethylene being moved away from the plant [21].

To overcome the submergence and post-submergence effects, the plants have developed certain adaptations that allow them to survive under such adverse conditions. The occurrence of gas-filled cavities in the roots of many plant species, known as aerenchyma, is assumed to be a crucial physiological adaptation for living under flood circumstances. The aerenchyma allows oxygen to diffuse from aerial phytoconstituents to roots or rhizomes. Also, some crops have been shown to grow longer internodes and petioles that are longer than the water level, as well as a radially root oxygen loss barrier and changes in chlorophyll fluorescence parameters [22].

Various physico-chemical phenomena, as well as multiple physiological adaptations, occur after water stress stress, followed by the commencement of an adaptive mechanism. Changes occurring in the energy utilisation and maintenance along with the impact of various plant hormones are given here under:- a) Energy maintenance: Plants' ability to reserve and maintain a high level of carbohydrates in shoots before, during, and after submergence is an important characteristic of tolerant varieties [23]. Because biomass incorporates all sustainable and environmental processes leading to fitness, it is theorised that plant submergence tolerance might be controlled by the fall of plant biomass owing to submergence [24]. Quick regeneration following submergence and efficient ROS scavenging also determine the survival of the plant post- submergence [25]. b) Plant hormone-induced submergence: The plant hormones ethylene, GA, and ABA all play important roles in a plant's survival under submerged conditions. Because of higher production and entrapment under anaerobic conditions, the concentration of ethylene in plant tissue rises [26]. Increased ethylene concentration controls the favourable and unfavourable regulators of shoot elongation, gibberellins and ABA, respectively. Susceptible genotypes have lower ABA concentrations but higher GA levels, which result in longer shoots.

5.2 Low Temperature Stress in Sorghum

Low temperature stress, which can be characterised as: a) chilling stress: Temperatures above 0°C but below 15°C cause substantial damage to plants. b) Freezing stress: When temperatures fall below 0°C, ice forms in plant tissue intercellular gaps. Low temperatures have an impact on several elements of crop development [27]. Sorghum, maize, rice, tomato, cucumber, and other tropical crops are considered vulnerable to temperatures below 20°C. Plants are damaged by low temperatures in one of two ways: by chilling, which causes physiological and developmental defects; or by freezing, which causes cellular damage directly or indirectly through cellular dryness. Cold stress inhibits plant growth and development by altering the physiochemical structure of the cell membrane, causing electrolyte leakage and reducing protoplasmic streaming and metabolic processes [28]. Cold responses (PSII) include changes in nucleic acid and protein synthesis, the balance of nutrients and water, the affinity and shape of enzymes, and the amount of photosynthesis, especially the slowing down of Photosystem II and its damage by light.

Cooling stress thermodynamically affects plant physiological and metabolic kinetics. Thermophilicity and lower root water cause a shoot water deficit. It lowers root length, biomass, and morphology, reducing the root system's volume for seeking nutrients and water. It promotes tissue necrosis by overproducing ROS in plant cells, which alters membrane characteristics and enzyme activity [29]. Due to over-excitation of thylakoid membranes and consequent impairment of photosynthetic activity, photosynthetic efficiencies are lowered while photo-inhibition processes are enhanced. Wilting of leaves, bleaching owing to photo-oxidation of pigments, water plugging of the intercellular spaces, browning of leaf necrosis, and plant death are all visible indications of low-temperature damage. The ability of some plants to survive under chilling stress or during extracellular ice formation and recover and regrow is called stress tolerance. Lipids, the most essential element of plasma and endo-membranes, affect the body's cold sensitivity. Changes in protein and lipid membrane structure help restore metabolite balance and make cells feel chilly.

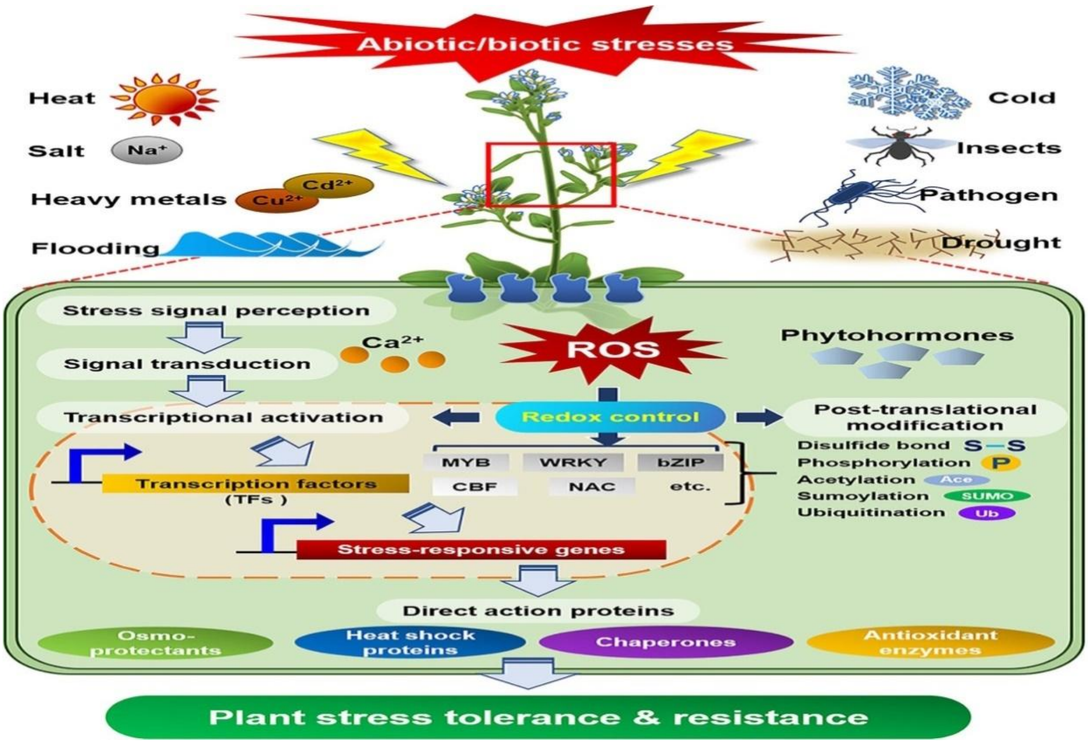

Fig. 1. Defence signalling in plants against diverse abiotic and biotic external stresses [17]

5.3 Salinity Stress in Sorghum

The presence or accumulation of excessive amounts of soluble salts in the soil eventually affects the normal functioning of plant growth and development. 10% of global arable land is affected by salinity (higher accumulation of Ca, Mg and their SO4, NO3, CO3, HCO3 and Cl salts) or sodicity (higher concentration of Na). Out of 1.5 billion ha of global cultivated land, 23% is saline, while 37% is affected by sodicity. Salt stress affects sorghum growth and causes several physical and biochemical changes [30]. The following are some of the impacts of salt on crops: a) Osmotic effect or scarcity of water: lowers the plant's ability to absorb water, leading to delayed development. b) Salt-specific activator ion exchange: Salts permeate the evaporation stream and damage cells in transpiring leaves, further reducing growth. C) Effects on development and growth: slowed rate of leaf surface expansion; significant plant stunting; lower fresh and dry weights of leaves, stems, and roots; sterility and reduced seed set; high incidence of infertile florets and pollen survivability; severity increases with salt. d) Increased respiration, ion toxicity, imbalanced mineral distribution, decreased membrane permeability, lower photosynthetic efficiency, and increased generation of reactive oxygen species are all effects of excessive salt content in the plant. e) Significant changes in leaf anatomy include increased epidermal width, mesophyll thickness, palisade cell size, palisade dimension, spongy cell diameter, and a decrease in intercellular gaps. f) Biochemical changes: nitrate reductase (NR) is more sensitive to NaCl stress in vivo and in vitro than nitrite reductase (NIR), and anionic salt concentration is also salt-induced buildup of betaine and betaine aldehyde dehydrogenase (BADH) mRNA occurs concurrently with the presence of ABA, implying that these enzymes help plants cope with stress [31].

Responsive strategies in sorghum to salt stress, particularly sorghum seedlings' remarkable potential to recover following salt stress alleviation, appear to be connected to an appropriate allocation of carbon between roots and shoots and to modifications in absorption, transport, and re-translocation of salts [28]. Overexpression of reactive oxygen species-scavenging enzymes, such as glutathione-S-transferases and L-ascorbate peroxidase, is common in plant stress responses. Sorghum plants adapt to salinity stress by using avoidance mechanisms like salt exclusion, salt extrusion, salt dilution, and ion separation, as well as threshold processes like osmoregulation, hormone production (especially ABA, which makes plants more resistant to too many salts), balance, detoxification, and control of growth [32].

5.4 High Temperature (Heat) Stress in Sorghum

The regulation of temperature is an important phenomenon of plants in growth and development and also in adaptation. The major effects of high temperature are given in the Fig. 2. High temperature stress alters structure, biochemistry, and physiology, affecting plant growth and productivity. Rising stress can damage proteins, disrupt synthesis, inactivate enzymes, and destroy membranes [28]. It impacts cell division. This damage can hinder plant growth and induce oxidative damage. Short exposure to high temperatures during seed filling might cause fast filling and decreased quality and yield. Heat stress reduces plant weight, root development, and availability of water and nutrients above ground. PSII is particularly temperature sensitive and partially shuts down under high heat. High temperatures impair the oxygen-evolving complex, leading to unbalanced electron transport to the PSII acceptor site. In many plants, reduced Rubisco activation inhibits net photosynthesis [33]. Rubisco's catalytic activity grows with temperature, but its poor CO2 affinity and O2 binding abilities restrict net photosynthesis. Canopy cooling, photosynthetic rate, cell membrane thermo-stability, stomatal conductance, chlorophyll fluorescence (photosystem II efficiency), leaf curling and reflectivity, floret fertility, pollen endurance, etc. [34,35] Higher temperatures impact a plant's physiology, survival, growth, and maturity. Some of the physiological effects are potent inhibitors of metabolic functions due to catalytic protein denaturation, alteration in membrane permeability, overabundance of reactive oxygen species (ROS), more CO2 loss via photorespiration (30-80%), enhanced respiration, lowered chlorophyll content, chlorophyll a fluorescence, photosynthetic rate, antioxidant enzyme activities, and increased oxidant production and membrane damage [36, 37]. Sorghum is C4 plant and PEP carboxylase, working in C4 plants has high affinity to CO2, as well as photorespiration in these plants is low. Ultimately sorghum plant has greater ability to cope with the high temperature stress as compare to other crops.

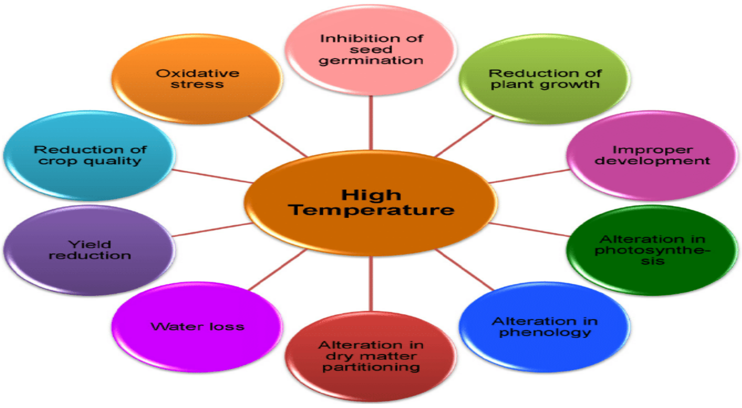

Fig.2. Major effects of high temperature on sorghum plants [37]

6. DROUGHT STRESS IN SORGHUM

A drought is an event of prolonged shortages in the water supply, whether atmospheric (below-average precipitation), surface water, or ground water. Researchers tend to define droughts in the following main ways: Meteorological drought occurs when precipitation falls below average for an extended period of time. Meteorological drought usually precedes other kinds of drought [38], Droughts in agriculture have an impact on crop production or range ecology. This condition can also arise independently of any change in precipitation levels when either increased irrigation or soil conditions and erosion triggered by poorly planned agricultural endeavours cause a shortfall in water available to the crops. However, in a traditional drought, it is caused by an extended period of below-average precipitation [39]. A hydrological drought occurs when the available water reserves in sources such as aquifers, lakes, and reservoirs fall below a locally significant threshold. Hydrological drought tends to show up more slowly because it involves stored water that is used but not replenished. Like an agricultural drought, this can be triggered by more than just a loss of rainfall. Socioeconomic drought considers the impact of drought conditions (meteorological, agricultural, or hydrological drought) on the supply and demand of some economic goods such as fruits, vegetables, grains, and meat. A socioeconomic drought happens when there isn't enough water to meet the demand for an economic good because of the weather.

According to one estimate, a 40% drop in land water might result in a 21% decrease in plant production. Some of the causes of major drought output losses in crops are given in Fig. 3 and are reduced cell division and development, reduced photosynthesis, membrane degradation, loss of water and nutrient absorption and movement, improper biological growth, and oxidative stress [40].

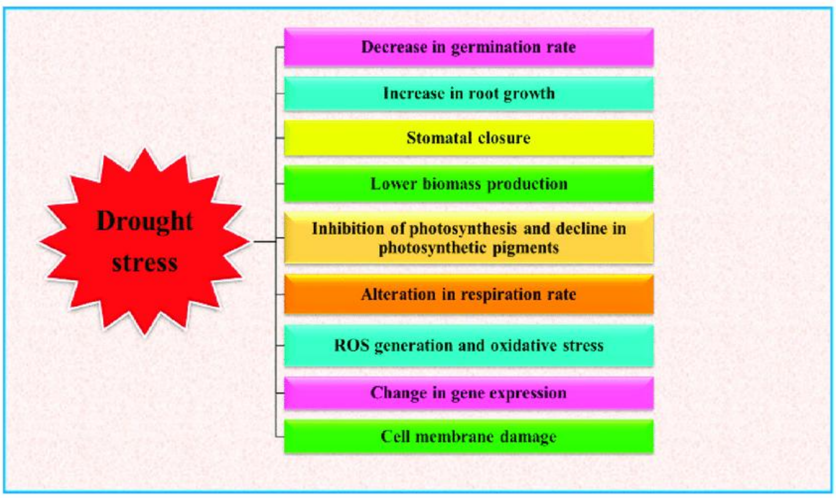

Fig. 3. Effect of drought stress on plant growth and development [40]

6.1 Effect of Different Levels of Drought Stress on Sorghum Crops

The drought stress in sorghum was classified into different types based on the intensity and was given in the (Table 1) as follows: a) No stress: normal metabolism with a healthy balance of antioxidants and ROS. b) Mild stress causes stomatal closure, leaf curling, a wax layer on the leaf, reduced stomatal conductance, lower CO_2 assimilation, lipid peroxidation, membrane damage, NADPH oxidase activation, and increased ROS/RNS production.c) Severe stress: Osmotic adjustment, increased root-shoe ratio, cell wall modification, metabolism reorganization, antioxidant system activation Reduced mesophyll capacity; CO_2 metabolism inhibition; RUBISCO inactivation; increased photorespiration; chloroplast ETC over-reduction; PSII down-regulation; and decreased plant growth and yield [42,43].

Table 1. Classification of drought [43]

Types of stress	Water potential (MPa)	Reduction in RWC
Mild Stress	0.1	8-10%
Moderate Stress	(-1.2) – (-1.5)	>10<20%
Severe Stress	>(-1.5)	>20%

6.2 Mechanism of Natural Drought Adaptations in Sorghum Crops

Due to their drought endurance, plants in typically dry circumstances maintain a considerable amount of organic matter and may be categorised into four adaption categories: a) Drought-escaping plants: annuals that only germinate and thrive when there is enough humidity to accomplish their life span. b) Drought-evading plants: non-succulent perennials that grow only during seasons of high moisture supply. c) Drought-enduring plants: also known as xerophytes, these everlasting shrubs have large root systems as well as morpho - physiological changes that allow them to continue growth even in the face of severe drought. d) Drought-resisting plants: also known as succulent perennials, drought-resistant plants conserve water in their leaf tissue for emergency usage. Alterations of the stomata to minimise water loss (like fewer of them, submerged pits, and waxy surfaces), cutting the number of leaves and their surface area, storing water in succulent above-ground portions or water filled tubers, and crassulacean acid metabolism (CAM metabolism), which lets plants get carbon dioxide at night and store malic acid during the day so that they can photosynthesize during the day [44].

6.3 Mechanism of Drought Tolerance in Sorghum

Drought tolerance is described as a plant's capacity to survive water shortages while sustaining necessary physiological activities to safeguard and enhance cellular metabolic viability at the tissue and cellular levels. Drought avoidance, on the other hand, is described as a plant's capacity to manage water at the whole plant level by reducing water loss from the shoots or absorbing water from the soil more efficiently. Drought tolerance involves a number of activities and engagements, including stomatal conductance, carotenoid breakdown and anthocyanin accumulation, osmoprotectants (such as sucrose, glycine, and proline), and ROS-scavenging enzymes. Transcriptional factors like dehydration-responsive element-binding protein (DREB), abscisic acid (ABA)-responsive element-binding factor (AREB), and NAM (no apical meristem) control drought tolerance at the molecular level [45].

7. PHYSIOLOGICAL, BIOCHEMICAL AND MOLECULAR BASIS OF DROUGHT STRESS TOLERANCE IN SORGHUM CROPS

The physiology of plants' drought adaptations at the whole plant level is extremely complicated, including both harmful and adaptive alterations. Plant species and variation, the dynamics, length, and severity of soil water deficiency; variations in water requirements from the environment, climatic circumstances; plant development; and the morphological stage in which water deficit develops are all elements that contribute to the obscurity of this process [46]. Sorghum is a drought-tolerant crop that may be used to study moisture stress tolerance processes. Drought tolerance in sorghum is a composite feature controlled by numerous genes coding for different properties. Drought tolerance is a result of morphological and anatomical features (thick leaf wax, deep root system) as well as physiological responses (osmotic adjustment, remaining green, quiescence) [8]. To maximise productivity in drought circumstances, plants optimise the morphology, physiology, and metabolism of their organs and cells [9]. Drought tolerance is acquired by physiological, biochemical, and molecular processes unique to cells and tissues, such as particular gene expression and protein accumulation [47]. Fundamental alterations in water relations, metabolic and physiological processes, membrane structure, and ultrastructure of subcellular organelles characterize the dehydration process in drought-tolerant plants. Some plants respond to drought stress by closing their stomata, letting some of their tissues age, slowing the growth of their leaves, making structures that store water, and making their roots longer and denser that is shown in (Fig. 4) [48].

7.1 Physiological Mechanisms of Drought Tolerance in Sorghum

Drought tolerance systems work in many different ways, both in space and in time, from quickly closing stomata to keeping crops from dying [49, 50]. Some of the physiological mechanisms of drought tolerance are discussed here [6,49,9].

7.1.1 Leaf rolling, Stomatal conductance and Canopy temperature

The curling of leaves is generally triggered by a decrease in leaf water potential. The degree of leaf curling, on the other hand, is determined by the plant's capacity to adapt osmotically at low leaf water potential. Plants with a high degree of osmoregulation have less leaf rolling, which is assumed to suggest a higher degree of decalcification avoidance via a deep root system. The role of stomatal conductivity in leaf temperature regulation is well understood. It's frequently used as a sorghum drought screening test [51, 52]. Low stomatal conductance is related to increased leaf temperature in drought-tolerant genotypes, resulting in high evaporation effectiveness and decreased carbon isotope selectivity. Two QTLs have been identified for stomatal conductance, one on chromosome 7 that explains 4.32 percent of phenotypic variation and the other on chromosome 10 that explains 1.25 percent of phenotypic variation [53]. The regulated transpiration cooling system brought on by stomatal closure is responsible for the high leaf temperature and transpiration percentage. Plants having a high stomatal conductance transpire more, keeping the canopy temperature lower. In the warm and humid weather that is generally linked with drought stress, canopy temperature and its decrease relative to ambient temperature reflect how much transpiration cools the leaves. In crops, stomatal closure alone lowers transpiration rates by 70–80%. However, leaf rolling only reduces transpiration rates by 2% [54].

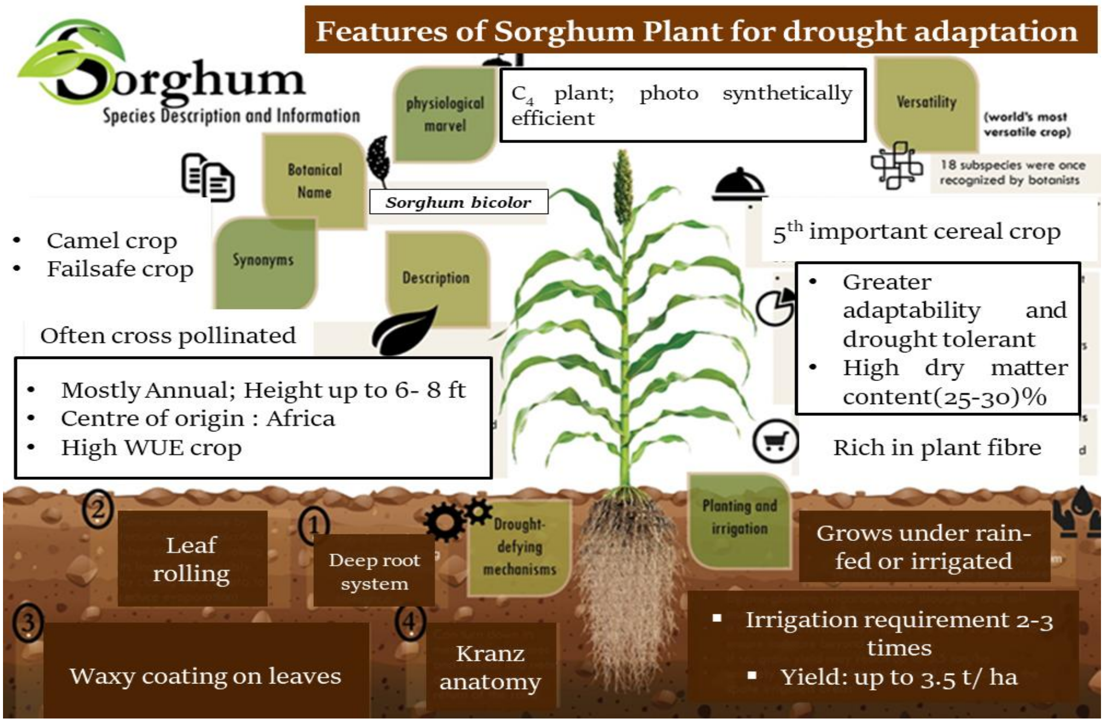

Fig.4. Significance and mechanism of the sorghum plant in drought adaptation

7.1.2 Root system architecture

The quantity of water required to sustain crop output during times of water stress is influenced by root system design [55]. Compact, fine root diameters, long specific root lengths, and a high root length density, especially at depths in soil with adequate water, are root characteristics linked to sorghum crop production during drought [56]. Among the newly planted features, root growth is the one that is least affected by water stress [57]. Longer root growth is more drought resistant and has a greater ability to absorb nutrients and moisture from the soil. When plants are stressed by water, drought-tolerant plants have deep and strong root systems; longer shoot sizes, and less leaf water potential, osmotic potential, and turgidity pressure. Sorghum roots can reach depths of 1 to 2 m and extract water to a lateral distance of 1.6 m from the plant by the booting stage [58].

7.1.3 OSMOTIC adjustment, dehydration tolerance and transpiration efficiency

In cells sensitive to water stress, osmoregulation (OA) is a metabolic process that involves a net gain in intercellular solutes. As soil moisture decreases, OA promotes turgor stability and, as a result, metabolic activity fidelity. By prolonging leaf folding and leaf tissue death, osmotic correction promotes agricultural production [59]. The efficient leaf area for photosynthesis rises as leaf curling and ageing decrease. Drought tolerance refers to a plant's ability to sustain a greater turgor tension in its cells under moisture stress. Proline, glycine betaine (GB) and sugars in sorghum act as osmolytes, protecting cells from dehydration. Plants can use GB buildup in cells to help them keep water in their cells or protect biological components from dehydration. The capacity of a genotype to rebound from stress is linked to the development of free proline in water-stressed sorghum leaves, probably due to proline's role as a source of respiratory activity in the healing plant. When sorghum was stressed by drought after anthesis, genotypes with strong osmotic adjustment produced 24% more than genotypes with low adjustment [60]. The total biomass generated per unit of water transpired is known as transpiration efficiency (TE). Increasing TE implies increasing agricultural yield per unit of water utilised.

7.1.4 Anatomical modifications

Glaucousness is the waxy coating of the plant canopy that gives a dull-white or bluish-green hue to crops like sorghum and wheat, reducing evaporation loss. In sorghum, the glossy leaf feature has been linked to seedling stage drought resistance. Drought tolerance is aided by leaf pubescence volume and epicuticular wax in sorghum with smaller stomata. In a world where there is less and less water, using C4 photosynthesis has a lot of potential to increase agricultural yield and make sure there is enough food for everyone. Sorghum plants with C4 photosynthesis and kranz anatomy have higher drought tolerance due to lower photorespiration and higher CO_2 fixation capacity.

7.1.5 Accumulation of compatible solutes

Osmolytes known as suitable solutes play a protective role against osmotic stress while preserving cytosolic osmotic equilibrium under harsh situations. Amino acids (e.g. proline), polyamins and quaternary amines (e.g. glycine betaine, dimethyl sulfoniopropionate), polyols (e.g. mannitol, trehalose), and sugars like sucrose and oligosacharids are the three primary families of biocompatible solutes [61]. Suitable solutes' principal role is to prevent water loss in order to sustain turgor pressure and the slope for water absorption into the cell. Proline [62], glycine betaine (GB), and sugars in sorghum act as osmolytes, protecting cells from dehydration. These metabolite accumulations in cells cause a rise in osmotic potential, which leads to increased root water holding efficiency and cell water conservation. Compatible solutes have a variety of features in plants, including safeguarding enzymes and membrane structures and integrity, maintaining protein conformation at low water potentials, scavenging free oxygen radicals, and stabilising cellular macromolecule structures such as membrane constituents. For example, glycine betaine's role in ensuring the safety of the transcriptional and translational machinery under stress. Although hydroxyl radicals are the most harmful of all active oxygen species, no enzyme has been discovered that can breakdown them. Compatible solutes, such as proline, citrulline, and mannitol, operate as scavengers of hydroxyl radicals and may limit contact between these ions and cellular constituents by substituting the water particles around these elements, preventing instability during drought [59]. For instance, betaine and proline protect RuBisCO, while betaine stabilises the PSII super complex. In many species, free proline is thought to play a major role in cytoplasmic tolerance and, as a result, in the plant's overall resilience to severe drought.

Sugars can help plants regulate their osmoregulation in dry circumstances.

7.1.6 Activation of antioxidant systems

Free oxygen radicals, which are created as a common side effect of environmental stress, are extremely hazardous to cell constituents and must be carefully controlled. To neutralise these harmful chemicals, all plants have developed a variety of antioxidant mechanisms, both enzymatic and non-enzymatic. Catalases (CAT), superoxide dismutase (SOD), peroxidases (POD), ascorbate peroxidases (APX), glutathione reductase (GR), and mono dehydro ascorbate reductase (MDAR) are some of the most important antioxidant enzymes. Antioxidant molecules such as ascorbic acid (AA), glutathione, tocopherols, flavanones, carotenoids, and anthocyanins are also present. Other things, like osmolytes (like proline), proteins (like peroxiredoxin), and amphiphilic molecules (like tocopherol), that can get rid of ROS can also work as antioxidant [42].

7.1.7 Stay-Green / Non-Senescence

Staying green is a drought-adaptive and continuous characteristic of sorghum. Drought and other environmental stress conditions cause leaf senescence, which is a planned necrosis. The depletion of chlorophyll and a gradual decrease in photosynthetic ability are the hallmarks of this condition. The capacity of a plant to retain a photosynthetically effective leaf area beyond physiological development often referred to as "stay green" or "non-senescence," is an indicator of post-flowering drought resistance. Stay green genotypes had larger quantities of cytokinins, leaf nitrogen, and basal stem carbohydrates than senescent genotypes [52]. The delay in the commencement of leaf senescence or the pace at which leaf senescence progresses is linked to the functionality of keeping green [63; 64]. Stg1, Stg2, Stg3, and Stg4, which account for approximately 54 percent of the phenotypic diversity seen in stay green sorghum genotypes, were discovered using quantitative mapping to uncover the QTLs associated with this trait [65]. The QTLs Stg1 and Stg2 on the third chromosome, and Stg3 and Stg4 on the second and fifth sorghum chromosomes, have been identified using chromosomal mapping. Stg2 is the most significant QTL influencing stay green, accounting for the greatest amount of phenotypic variance [66], out of all four stay green QTLs. The most promising line with the "stay green" trait is Sorghum line B35, which comes from a cross between Ethiopian durra and a Nigerian landrace and is often used as a source of traits in different parts of the world [67].

7.1.8 Effect of phyto-hormone on drought tolerance

Drought resistance screening may be done using concentrations of plant hormone secretion during water stress [52]. Auxin and other plant growth hormones, such as abscisic acid, function as chemical messengers. The fundamental regulator of abiotic stress tolerance in plants, abscisic acid (ABA), coordinates a number of processes that allow plants to deal with a variety of challenges. In drought, ABA affects guard cell ion transport, promoting stomatal closure and preventing stomatal opening, hence lowering water loss. In sorghum, ABA has been detected under drought stress circumstances [68].

8. BIOCHEMICAL MECHANISMS OF DROUGHT TOLERANCE IN SORGHUM

Drought is a complicated physicochemical process involving nucleic acids (DNA, RNA, microRNA, and so on), proteins, carbohydrates, lipids, plant hormones, ions, free radicals, and mineral elements [69]. Functional proteins and regulatory proteins are the two types of proteins generated in response to abiotic stress. The first group includes proteins that are thought to play a role in stress tolerance, such as chaperones, late embryogenesis abundant (LEA) proteins, osmotin, antifreeze proteins, and others, while the second group contains protein factors implicated in signal transduction and stress-responsive gene expression. DREB2, AREB, MYC, MYB, bZIP, and other transcription factors, as well as protein kinases, phosphatases, enzymes involved in phospholipid metabolism, and other signalling molecules [70; 71]. The following are some of the biochemical pathways that have been discussed:

8.1 AQUAPORIN

It's an intrinsic water channel transmembrane glycoprotein that's abundantly found in the plasma and vacuolar membranes and is principally responsible for regulating cellular water homeostasis. Root aquaporin expression is tightly controlled and is influenced by the root plant's shape and amount of water stress. Because aquaporin closes when affected by water stress, root flow rate is reduced [72].

8.2 LEA (LATE EMBRYOGENESIS ABUNDANT) Proteins

They are a broad collection of extremely hydrophilic, highly soluble, globular proteins that accumulate in seeds as they mature and desiccate. They inhibit protein accumulation and preserve cellular constituents and cell membrane structure from dehydration [73]. By limiting protein misfolding and denaturation, they help safeguard enzymatic activity. Dehydrins are group 2 LEA proteins that minimise the damage caused by dehydration. LEA-type proteins may operate as water-binding molecules, helping to stabilise macromolecules and membranes while also assisting in ion sequestration. LEA3 proteins influence lipid formation primarily by increasing photosynthetic efficiency and lowering ROS levels [74].

8.3 REACTIVE OXYGEN SPECIES (ROS)

The fractional breakdown of ambient O2 produces reactive oxygen species (ROS), also known as active oxygen species (AOS) or reactive oxygen intermediates (ROI). Singlet oxygen (1O2), superoxide radical (O2-), hydrogen peroxide (H2O2), and the hydroxyl radical (HO•) are the four types of biological ROS. ROS, especially singlet oxygen and the hydroxyl radical, are very reactive. Unlike normal oxygen, they can oxidise many parts of living things, like proteins, lipids, DNA, and RNA [75]. In drought-stressed cells, ROS generation increases. If drought tolerance is extended, ROS production will overwhelm the antioxidant system, causing cellular injury and destruction. These plants feature a flexible ROS-scavenging mechanism. Superoxide dismutase (SOD) fights ROS. It absorbs superoxide quickly. SOD dismutes active oxygen species into H2O2 and oxygen. APX converts H2O2 to water [76].

8.4 Heat Shock Proteins / Chaperones

As chaperones, plant heat shock proteins (HSPs) play a critical role in establishing biotic and abiotic stress tolerance. By favorably controlling the antioxidant enzyme system, HSP improves membrane stability and detoxifies reactive oxygen species. It also employs ROS as a signal to molecules to get them to produce HSP [77]. A genome-wide scan has found the presence of 47 sHsps in Sorghum (SbsHsps), dispersed over 10 subfamilies, with the P (plastid) group having the most genes (17), and promoter findings show that they are linked to both biotic and abiotic stressors, as well as plant growth. Expression analysis also showed that it plays a key role in regulating responses to environmental stress [78].

8.5 Effect of ABSCISIC ACID (ABA) on Drought Tolerance

ABA is an isoprenoid plant hormone that modulates a variety of physiological processes, from stomatal opening to protein storage, and helps plants respond to a variety of stressors, including drought, salt, and cold [79]. At the cellular and intercellular levels in plants, ABA modulates drought stress responses and tolerance [80]. Seed dormancy and germination, root architecture control, ageing, stomata closure, and other actions of ABA are only a few of them. Abscisic acid is thought to be the main hormone that controls how plants respond to changes in their environment that are not good for them. This is because the amount of ABA in plants often goes up when they are under abiotic stress, and more ABA makes it easier for plants to adapt to different types of abiotic stress [81].

8.6 Molecular Mechanism of Drought Tolerance

Drought resistance is a multi-gene characteristic that is affected by the timing and degree of moisture stress. As a result, it is among the most challenging characteristics to research and characterize. . The complete step wise procedure and gene expression in the development drought tolerant sorghum cultivar are given in (Fig. 5 &6).One of biologists' and plant breeders' main efforts have been to figure out how plants can withstand drought [83]. Research into the fundamental molecular concepts has been hampered by a lack of understanding of particular features associated with drought resistance. Drought stress solutions are also challenging to administer quantitatively and consistently. The unpredictability of the testing environment, as well as the interplay between stages of plant growth and the environment, makes drought tolerance selection problematic [9]. Plant drought tolerance research has been severely hampered as a result of these issues. As a result, little is known about the biological basis of drought tolerance, and few drought resistance factors have been discovered. The slow pace of identifying drought tolerance pathways has hampered conventional breeding efforts as well as the application of current genetics techniques in improving drought tolerance of agricultural plants [84].

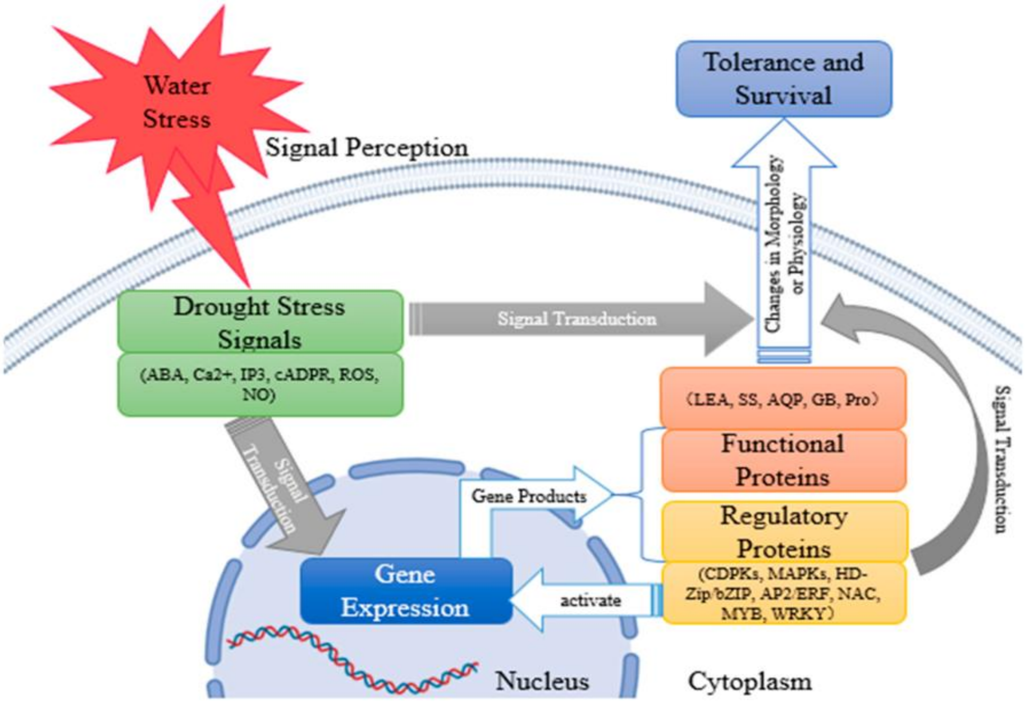

Fig. 5. Process of plant drought-tolerance development [82]

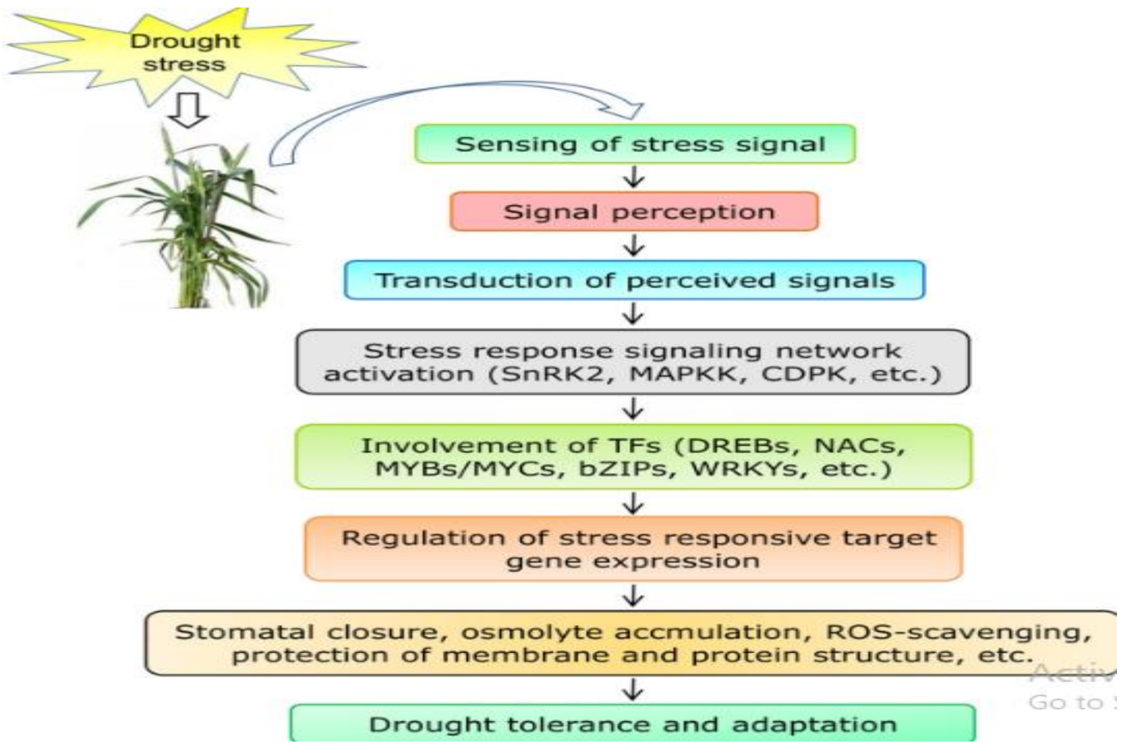

Fig. 6. Steps involved in the expression of drought tolerance, starting from the perception of drought stress and transducing the signal through transcription factors for the activation of genes involved in adaptation [83]

Drought resistance in crops might be significantly improved using molecular breeding techniques such as QTL discovery and marker-assisted wide selection. Two cutting-edge technologies are being intensively exploited to build impetus for the advancement of breeding for drought tolerance. One method is to employ molecular biomarkers to better understand the genetic basis of drought resistance and to select for this characteristic more efficiently. The other approach, collaborative plant breeding, allows farmers to play a more active role in plant selection by closely monitoring plant performance and contributing to selection for higher drought resistance. The establishment of genetic hotspots in chromosomes using genome mapping across crop species will assist in prioritising the genes to be employed for drought-resistant crop development. Drought-tolerant rice and sorghum were effectively bred using a mix of the following techniques described above [85]. The discovery of QTLs for drought tolerance features in numerous crops has been made possible through linkage mapping with molecular markers. Sorghum-specific QTLs have been identified and given in the Table 2.

From the above literature, we can summarise the different characteristics of drought-tolerant sorghum plants and get a clear-cut idea regarding the difference between drought-tolerant and sensitive sorghum plants. Ahmed Sallam*et al.* have given a general differentiation between drought tolerance and sensitive crop plants as given below in the (Table 3), that is also applicable to sorghum crop [91].

Table 2. A lists of some QTLs identified for drought stress related traits in Sorghum

Sl No.	Trait(s)	QTLs	References
1	Drought Tolerance	SbAGS01, SbAGB03,Xtxp69	[86]
2	Root Angle trait	qRA1 5,qRA2 5, qRA1 8,qRA1 10	[55]
3	Grain weight	qTGW1a	[87]
		qGW1	[88]
4	Grain yield	qYLD1.1	[89]
5	Pre- Flowering drought	B465/140,tK12/115,bDIl/65,tM5/75,tC13/150,bC18/820	[4]
		Stg A, Stg G, Stg J	[55]
6	Stay Green associated traits Stay	Gl 7, Gl 14, Gl 21, Gl 28	[90]
		Stg1, Stg2, Stg3 and Stg4	[65]

Table 3. Difference between drought tolerance and sensitive in Sorghum [91]

Sl.no	Drought tolerance plants	Drought Sensitive plants
1.	Up-regulation of hormonal signalling	Disturbance of hormonal signalling of ABA.
2.	Rich in stress metabolites like GSH, ASA, Poly amines, Glycine betaine	Degeneration of stress metabolites like GSH, ASA, Poly amines, Glycine betaine
3.	Limited reduction in leaf area and itsefficiency	Severe reduction in leaf area and its efficiency.
4.	Low effect on membrane stability traits.	Poor in anti- oxidant thus deteriorate the membrane
5.	Limited reduction on chlrophyll-a, chl-b and carotenoids	Increased reduction on chlrophyll-a, chl-b and carotenoids
6.	Maintained RWC & WUE and reduced LWLR and residual transpiration rate	Depletion of RWC & WUE and increased LWLR and residual transpiration rate.
7.	Oxidative stress limited capacity	Destructive Oxidative damage through ROSproduction
8.	Managing primary metabolites like sugars, protein, amino acid, lipids and proline	Down-regulation of primary metabolites like sugars, protein and amino acid etc.
9.	Maintainance of macro and micro nutrients uptake and translocations	Limited uptake and translocations of macro and micro nutrients.
10.	Longer root system	Reduced root system.
11.	Limited reduction on yield traits.	Higher reduction on yield traits

9. CONCLUSION

Sorghum is a resilient plant that can thrive in even the worst conditions. Sorghum is vulnerable to water stress, salinity, and drought stress, and is sensitive to freezing and temperature changes. Crops are subjected to a variety of changes as a result of biotic and abiotic stressors, which can have negative impacts on plant expansion and maturation. By safeguarding photosystem assembly and improving sucrose biosynthesis to deal with salt, the sorghum crop enhances Na+ exclusion capacity and maintains a high sugar content in shoots. Plants have three general survival strategies under drought situations: flight, avoidance, or tolerance. Sorghum's root architecture, capacity to maintain stomata open at lower leaf water potentials, high osmotic adjustment, waxy bloom material in the leaves and stems, greater leaf angle adjustment, and leaf rolling make it more drought-tolerant than other crops. Sorghum cultivars provide a source of drought-resistant hybrids. Stay-green is a useful feature that, when contrasted to osmotic compensation and early development, enhances genotype adaptability to drought stress, grain filling, and grain production under stress without a yield penalty under moisture deficiency situations. When breeding for drought tolerance, it's essential to understand the various drought tolerance mechanisms in plants. Understanding the physiological basis of agricultural production, crop responses, and crop adaptability in areas of organic farming that are prone to stress is important if we want to grow crops that can handle abiotic stress in the future.

More studies on stress adaptation and yield enhancement are needed because it is a neglected crop. Breeders can use the investigation of abiotic stress-induced transcriptomes, proteomes, and metabolomes to increase stress tolerance in sorghum. Abiotic stress in sorghum may now be screened across a broader region with less time and labour because of the advent of high-throughput phenotyping techniques. In high-productive cultivars, the incorporation and combining of physiological features into quantitative trait loci (QTL) and genes underlying these qualities would prolong yield during drought conditions. A full metabolic monitoring method can show how a cell's physiology and biochemistry are changing in real time.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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