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SORGHUM PHYSIOLOGY AND ADAPTATION TO ABOTIC STRESSES

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 peroxidase (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 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.

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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 (1993) [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,

31 photosynthesis, and seed size during post-flowering dryness [9]. It possesses a deep root
32 system, the capacity to minimise transpiration by leaf folding and stomatal closure, and the
33 ability to slow metabolic activities to near dormancy under acute drought. As a result,
34 sorghum can endure dry spells and resume development once soil moisture is restored.
35 Despite its drought tolerance, sorghum experiences yield losses of 60–90% depending on
36 the severity of the drought [10].

37 **2. STRESS AND ITS TYPES**

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

46 **3. IMPACT OF ABIOTIC STRESSES ON CROP PRODUCTION**

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

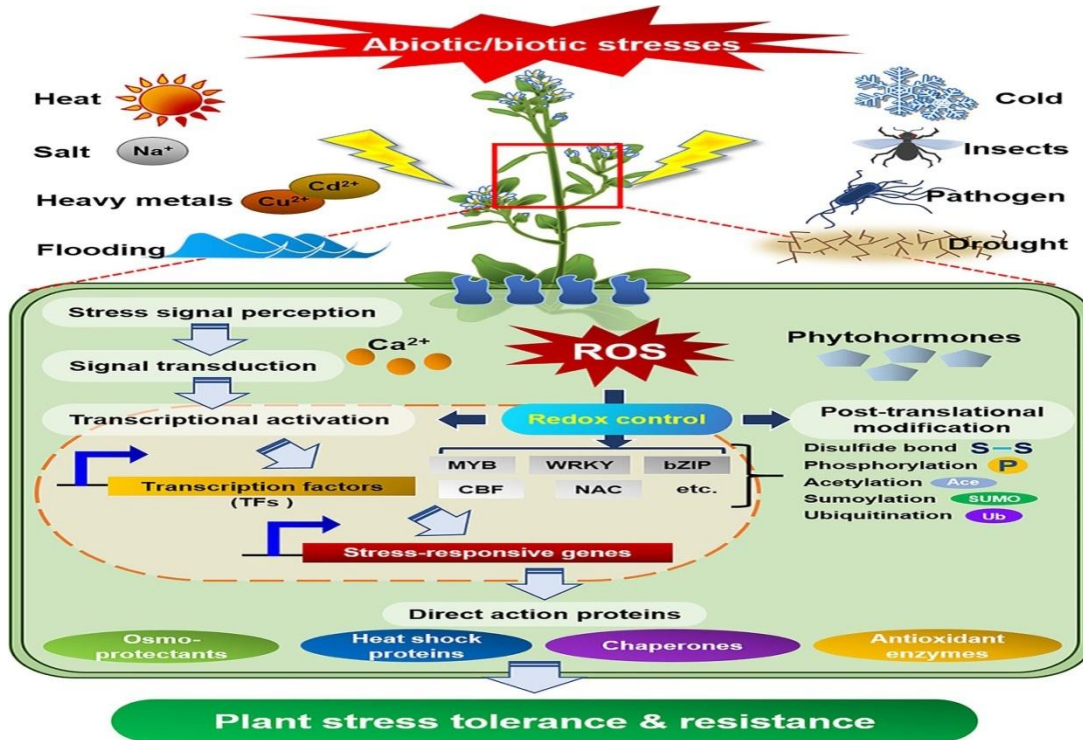
60 **4. RESPONSE OF PLANT TO ABIOTIC STRESSES**

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

71 External stress stimulates a variety of defence mechanisms, along with the formation of
72 reactive oxygen species (ROS), alterations in redox potential or cellular Ca^{2+} ion levels, ion
73 homeostasis interruption, and membrane fluidity adjustment, among others. [16]. These
74 external stress signals are sensed through specific receptors which are mostly present in the
75 cell membrane. The plants transduce those foreign signals into intracellular downstream
76 signalling pathways through secondary messengers like Ca^{2+} ions etc. which ultimately leads

77 to the activation of transcription factors like protein kinase or phosphatase like MYB and CBF
 78 etc. The stimulation and biosynthesis of downstream target proteins and phyto-hormones
 79 eventually determine the plant's growth and development under a stressed environment
 80 (Figure.4). Crosstalk between these complex signalling networks, in particular, precisely
 81 controls the expression of stress-responsive genes while also shielding plants from external
 82 shocks [17].

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84

85 **Figure.2. [Defence signalling in plants against diverse abiotic and biotic external**
 86 **stresses].** Specific receptors in plant cells perceive external stresses and transduce the
 87 signal into downstream components, which activate or express defence molecules to protect
 88 plants from the stresses [17].

89 5. PHYSIOLOGY OF SORGHUM UNDER ABIOTIC STRESSES

90 5.1. SUBMERGENCE STRESS IN SORGHUM

91 Two types of environments cause submergence: flash flooding and deep water. A
 92 flash flood occurs when the water level rises quickly and lasts just a few weeks (2 weeks)
 93 and is not particularly deep. Water levels might rise to 50 cm. With a water depth of more
 94 than 100 cm, it can last for months [19]. Flooding/water logging occurs where there is
 95 stagnation of water on the top of the soil that leads to excessive water in the plants' root
 96 zone, which decreases the availability of O² to roots, limiting respiration. The level of CO²
 97 is also hampered, which limits photosynthesis. Water logging can inhibit plant productivity and
 98 growth, and in severe cases, submergence might result in death [20]. The fully or almost
 99 nearly saturated soil under this condition reduces the movement of gases to and away from

100 plant surfaces. Intolerant cultivars show symptoms like chlorosis and extreme leaf
101 elongation, which are caused by less ethylene being moved away from the plant [21].

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

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

126 **5.2 LOW TEMPERATURE STRESS IN SORGHUM**

127 Low temperature stress, which can be characterised as: a) chilling stress:
128 Temperatures above 0°C but below 15°C cause substantial damage to plants. b) Freezing
129 stress: When temperatures fall below 0°C, ice forms in plant tissue intercellular gaps. Low
130 temperatures have an impact on several elements of crop development [27]. Sorghum,
131 maize, rice, tomato, cucumber, and other tropical crops are considered vulnerable to
132 temperatures below 20°C. Plants are damaged by low temperatures in one of two ways: by
133 chilling, which causes physiological and developmental defects; or by freezing, which causes
134 cellular damage directly or indirectly through cellular dryness. Cold stress inhibits plant
135 growth and development by altering the physiochemical structure of the cell membrane,
136 causing electrolyte leakage and reducing protoplasmic streaming and metabolic processes
137 [28]. Cold responses (PSII) include changes in nucleic acid and protein synthesis, the
138 balance of nutrients and water, the affinity and shape of enzymes, and the amount of
139 photosynthesis, especially the slowing down of Photosystem II and its damage by light.

140 Cooling stress thermodynamically affects plant physiological and metabolic kinetics.
141 Thermophilicity and lower root water cause a shoot water deficit. It lowers root length,
142 biomass, and morphology, reducing the root system's volume for seeking nutrients and
143 water. It promotes tissue necrosis by overproducing ROS in plant cells, which alters
144 membrane characteristics and enzyme activity [29]. Due to over-excitation of thylakoid
145 membranes and consequent impairment of photosynthetic activity, photosynthetic
146 efficiencies are lowered while photo-inhibition processes are enhanced. Wilting of leaves,
147 bleaching owing to photo-oxidation of pigments, water plugging of the intercellular spaces,

148 browning of leaf necrosis, and plant death are all visible indications of low-temperature
149 damage. The ability of some plants to survive under chilling stress or during extracellular ice
150 formation and recover and regrow is called stress tolerance. Lipids, the most essential
151 element of plasma and endo-membranes, affect the body's cold sensitivity. Changes in
152 protein and lipid membrane structure help restore metabolite balance and make cells feel
153 chilly.

154 **5.3 SALINITY STRESS IN SORGHUM**

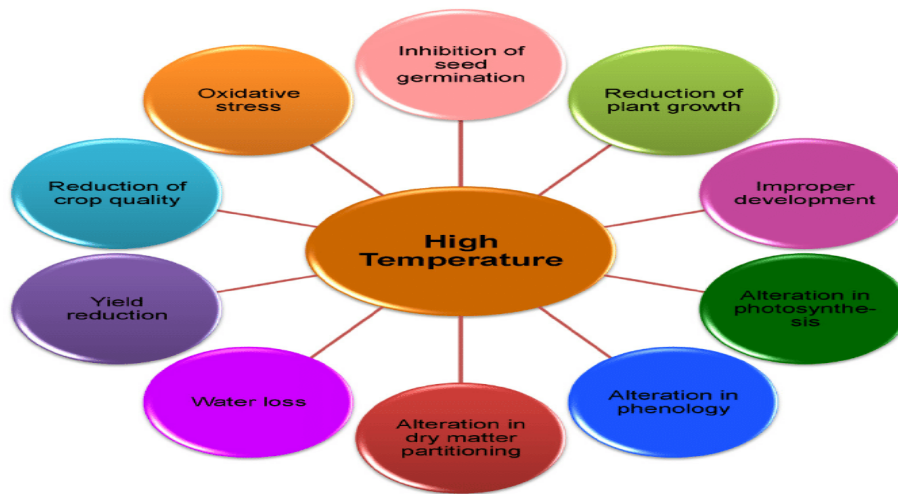
155 The presence or accumulation of excessive amounts of soluble salts in the soil
156 eventually affects the normal functioning of plant growth and development. 10% of global
157 arable land is affected by salinity (higher accumulation of Ca, Mg and their SO₄, NO₃, CO₃,
158 HCO₃ and Cl salts) or sodicity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

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

187 **5.4 HIGH TEMPERATURE (HEAT) STRESS IN SORGHUM**

188 High temperature stress alters structure, biochemistry, and physiology, affecting
189 plant growth and productivity. Rising stress can damage proteins, disrupt synthesis,
190 inactivate enzymes, and destroy membranes [28]. It impacts cell division. This damage can
191 hinder plant growth and induce oxidative damage. Short exposure to high temperatures
192 during seed filling might cause fast filling and decreased quality and yield. Heat stress
193 reduces plant weight, root development, and availability of water and nutrients above
194 ground. PSII is particularly temperature sensitive and partially shuts down under high heat.
195 High temperatures impair the oxygen-evolving complex, leading to unbalanced electron

196 transport to the PSII acceptor site. In many plants, reduced Rubisco activation inhibits net
 197 photosynthesis [33]. Rubisco's catalytic activity grows with temperature, but its poor CO₂
 198 affinity and O₂ binding abilities restrict net photosynthesis. Canopy cooling, photosynthetic
 199 rate, cell membrane thermo-stability, stomatal conductance, chlorophyll fluorescence
 200 (photosystem II efficiency), leaf curling and reflectivity, floret fertility, pollen endurance, etc.
 201 [34] Higher temperatures impact a plant's physiology, survival, growth, and maturity. Some
 202 of the physiological effects are potent inhibitors of metabolic functions due to catalytic protein
 203 denaturation, alteration in membrane permeability, overabundance of reactive oxygen
 204 species (ROS), more CO₂ loss via photorespiration (30-80%), enhanced respiration,
 205 lowered chlorophyll content, chlorophyll a fluorescence, photosynthetic rate, antioxidant
 206 enzyme activities, and increased oxidant production and membrane damage [36, 37].
 207 Sorghum is C₄ plant and PEP carboxylase, working in C₄ plants has high affinity to CO₂, as
 208 well as photorespiration in these plants is low. Ultimately sorghum plant has greater ability to
 209 cope with the high temperature stress as compare to other crops.



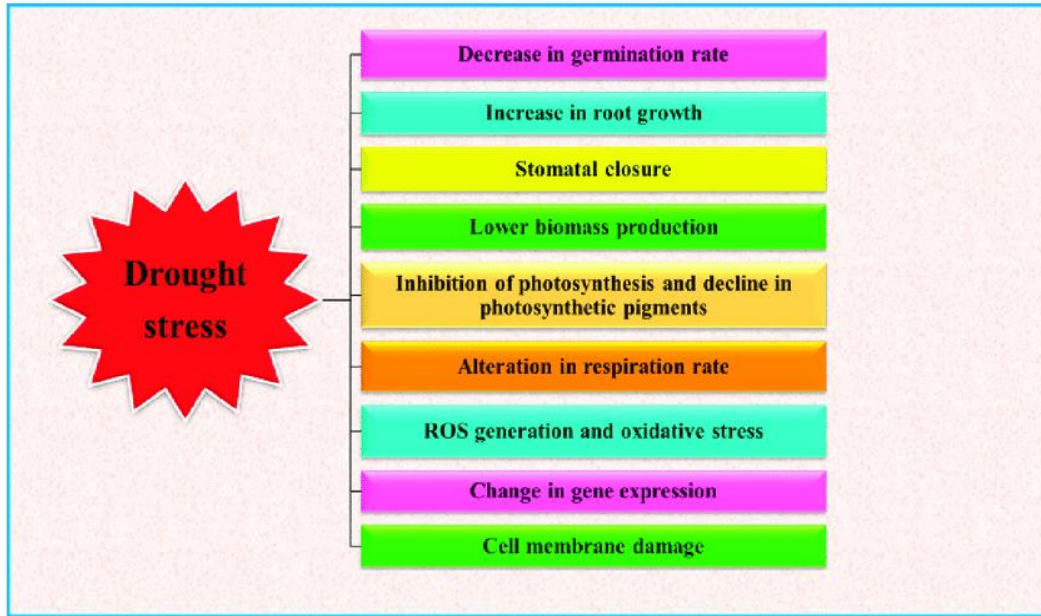
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211 **Figure: 3 Major effects of high temperature on plants [37].**

212 **6. DROUGHT STRESS IN SORGHUM**

213 A drought is an event of prolonged shortages in the water supply, whether
 214 atmospheric (below-average precipitation), surface water, or ground water. Researchers
 215 tend to define droughts in the following main ways: a) Meteorological drought occurs when
 216 precipitation falls below average for an extended period of time. Meteorological drought
 217 usually precedes other kinds of drought [38]. b) Droughts in agriculture have an impact on
 218 crop production or range ecology. This condition can also arise independently of any change
 219 in precipitation levels when either increased irrigation or soil conditions and erosion triggered
 220 by poorly planned agricultural endeavours cause a shortfall in water available to the crops.
 221 However, in a traditional drought, it is caused by an extended period of below-average
 222 precipitation [39]. C) A hydrological drought occurs when the available water reserves in
 223 sources such as aquifers, lakes, and reservoirs fall below a locally significant threshold.
 224 Hydrological drought tends to show up more slowly because it involves stored water that is
 225 used but not replenished. Like an agricultural drought, this can be triggered by more than
 226 just a loss of rainfall. d) Socioeconomic Drought considers the impact of drought conditions
 227 (meteorological, agricultural, or hydrological drought) on the supply and demand of some
 228 economic goods such as fruits, vegetables, grains, and meat. A socioeconomic drought
 229 happens when there isn't enough water to meet the demand for an economic good because
 230 of the weather.
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232 According to one estimate, a 40% drop in land water might result in a 21% decrease
 233 in plant production. Some of the causes of major drought output losses in crops are reduced
 234 cell division and development, reduced photosynthesis, membrane degradation, loss of
 235 water and nutrient absorption and movement, improper biological growth, and oxidative
 236 stress [40].
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241 **Figure: 4 Effect of drought stress on plant growth and development [40].**

242 **6.1 EFFECT OF DIFFERENT LEVELS OF DROUGHT STRESS ON SORGHUM**
 243 **CROPS**

244 The drought stress in sorghum was classified into different types based on the
 245 intensity and was given as follows: a) No stress: normal metabolism with a healthy balance
 246 of antioxidants and ROS. b) Mild stress causes stomatal closure, leaf curling, a wax layer on
 247 the leaf, reduced stomatal conductance, lower CO₂ assimilation, lipid peroxidation,
 248 membrane damage, NADPH oxidase activation, and increased ROS/RNS production.c)
 249 Severe stress: Osmotic adjustment, increased root-shoe ratio, cell wall modification,
 250 metabolism reorganization, antioxidant system activation Reduced mesophyll capacity; CO₂
 251 metabolism inhibition; RUBISCO inactivation; increased photorespiration; chloroplast ETC
 252 over-reduction; PSII down-regulation; and decreased plant growth and yield [42].
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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%

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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].

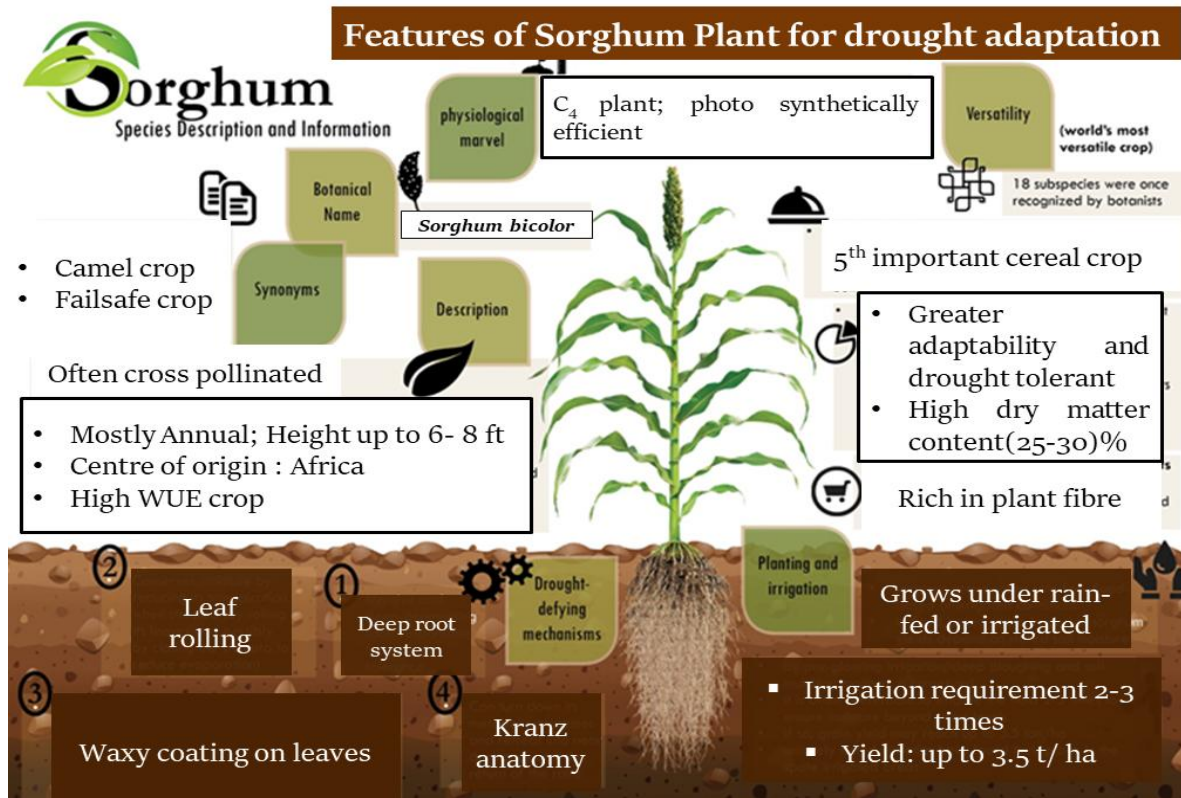
7. PHYSIOLOGICAL, BIOCHEMICAL AND MOLECULAR BASIS OF DROUGHT STRESS TOLERANCE IN SORGHUM CROPS

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 characterise 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 [48].

304 **7.1 PHYSIOLOGICAL MECHANISMS OF DROUGHT TOLERANCE IN**
 305 **SORGHUM**

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

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311 **Figure.5 The significance and mechanism of the sorghum plant in drought adaptation.**
 312 **7.1.1 LEAF ROLLING, STOMATAL CONDUCTANCE AND CANOPY**
 313 **TEMPERATURE**

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

329 cools the leaves. In crops, stomatal closure alone lowers transpiration rates by 70–80%.
330 However, leaf rolling only reduces transpiration rates by 2% [54].
331

332 **7.1.2 ROOT SYSTEM ARCHITECTURE**

333 The quantity of water required to sustain crop output during times of water stress is
334 influenced by root system design [55]. Compact, fine root diameters, long specific root
335 lengths, and a high root length density, especially at depths in soil with adequate water, are
336 root characteristics linked to sorghum crop production during drought [56]. Among the newly
337 planted features, root growth is the one that is least affected by water stress [57]. Longer
338 root growth is more drought resistant and has a greater ability to absorb nutrients and
339 moisture from the soil. When plants are stressed by water, drought-tolerant plants have deep
340 and strong root systems; longer shoot sizes, and less leaf water potential, osmotic potential,
341 and turgidity pressure. Sorghum roots can reach depths of 1 to 2 m and extract water to a
342 lateral distance of 1.6 m from the plant by the booting stage [58].
343

344 **7.1.3 OSMOTIC ADJUSTMENT, DEHYDRATION TOLERANCE AND** 345 **TRANSPIRATION EFFICIENCY**

346 In cells sensitive to water stress, osmoregulation (OA) is a metabolic process that
347 involves a net gain in intercellular solutes. As soil moisture decreases, OA promotes turgor
348 stability and, as a result, metabolic activity fidelity. By prolonging leaf folding and leaf tissue
349 death, osmotic correction promotes agricultural production [59]. The efficient leaf area for
350 photosynthesis rises as leaf curling and ageing decrease. Drought tolerance refers to a
351 plant's ability to sustain a greater turgor tension in its cells under moisture stress. Proline,
352 glycine betaine (GB) and sugars in sorghum act as osmolytes, protecting cells from
353 dehydration. Plants can use GB buildup in cells to help them keep water in their cells or
354 protect biological components from dehydration. The capacity of a genotype to rebound from
355 stress is linked to the development of free proline in water-stressed sorghum leaves,
356 probably due to proline's role as a source of respiratory activity in the healing plant. When
357 sorghum was stressed by drought after anthesis, genotypes with strong osmotic adjustment
358 produced 24% more than genotypes with low adjustment [60]. The total biomass generated
359 per unit of water transpired is known as transpiration efficiency (TE). Increasing TE implies
360 increasing agricultural yield per unit of water utilised.
361

361 **7.1.4 ANATOMICAL MODIFICATIONS**

362 Glaucousness is the waxy coating of the plant canopy that gives a dull-white or
363 bluish-green hue to crops like sorghum and wheat, reducing evaporation loss. In sorghum,
364 the glossy leaf feature has been linked to seedling stage drought resistance. Drought
365 tolerance is aided by leaf pubescence volume and epicuticular wax in sorghum with smaller
366 stomata. In a world where there is less and less water, using C4 photosynthesis has a lot of
367 potential to increase agricultural yield and make sure there is enough food for everyone.
368 Sorghum plants with C4 photosynthesis and kranz anatomy have higher drought tolerance
369 due to lower photorespiration and higher CO₂ fixation capacity.
370

370 **7.1.5 ACCUMULATION OF COMPATIBLE SOLUTES**

371 Osmolytes known as suitable solutes play a protective role against osmotic stress
372 while preserving cytosolic osmotic equilibrium under harsh situations. Amino acids (e.g.
373 proline), polyamins and quaternary amines (e.g. glycine betaine, dimethyl
374 sulfoniopropionate), polyols (e.g. mannitol, trehalose), and sugars like sucrose and
375 oligosaccharids are the three primary families of biocompatible solutes [61]. Suitable solutes'
376 principal role is to prevent water loss in order to sustain turgor pressure and the slope for
377 water absorption into the cell. Proline [62], glycine betaine (GB), and sugars in sorghum act
378 as osmolytes, protecting cells from dehydration. These metabolite accumulations in cells
379 cause a rise in osmotic potential, which leads to increased root water holding efficiency and
380 cell water conservation. Compatible solutes have a variety of features in plants, including

381 safeguarding enzymes and membrane structures and integrity, maintaining protein
382 conformation at low water potentials, scavenging free oxygen radicals, and stabilising
383 cellular macromolecule structures such as membrane constituents. For example, glycine
384 betaine's role in ensuring the safety of the transcriptional and translational machinery under
385 stress. Although hydroxyl radicals are the most harmful of all active oxygen species, no
386 enzyme has been discovered that can breakdown them. Compatible solutes, such as
387 proline, citrulline, and mannitol, operate as scavengers of hydroxyl radicals and may limit
388 contact between these ions and cellular constituents by substituting the water particles
389 around these elements, preventing instability during drought [59]. For instance, betaine and
390 proline protect RuBisCO, while betaine stabilises the PSII super complex. In many species,
391 free proline is thought to play a major role in cytoplasmic tolerance and, as a result, in the
392 plant's overall resilience to severe drought. Sugars can help plants regulate their
393 osmoregulation in dry circumstances.

394 **7.1.6 ACTIVATION OF ANTIOXIDANT SYSTEMS**

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

405 **7.1.7 STAY-GREEN / NON-SENESCENCE**

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

424 **7.1.8 EFFECT OF PHYTO-HORMONE ON DROUGHT TOLERANCE**

425 Drought resistance screening may be done using concentrations of plant hormone
426 secretion during water stress [52]. Auxin and other plant growth hormones, such as abscisic
427 acid, function as chemical messengers. The fundamental regulator of abiotic stress
428 tolerance in plants, abscisic acid (ABA), coordinates a number of processes that allow plants
429 to deal with a variety of challenges. In drought, ABA affects guard cell ion transport,
430 promoting stomatal closure and preventing stomatal opening, hence lowering water loss.
431 In sorghum, ABA has been detected under drought stress circumstances [**Error! Reference**
432 **source not found.**].

433 **7.2 BIOCHEMICAL MECHANISMS OF DROUGHT TOLERANCE IN SORGHUM**

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

445 **7.2.1 AQUAPORIN**

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

451 **7.2.2 LEA (LATE EMBRYOGENESIS ABUNDANT) PROTEINS**

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

460 **7.2.3 REACTIVE OXYGEN SPECIES (ROS)**

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

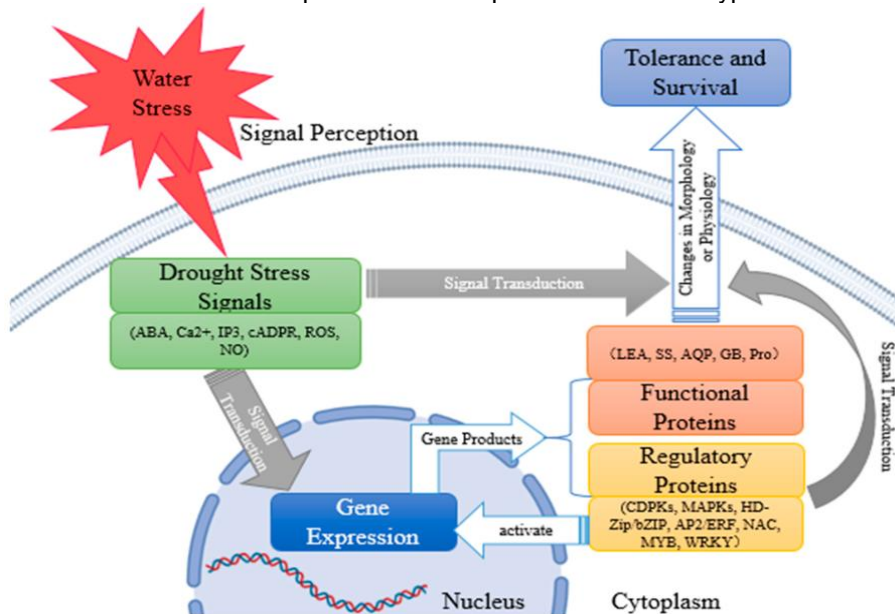
472 **7.2.4 HEAT SHOCK PROTEINS / CHAPERONES**

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

481 **7.2.5 EFFECT OF ABSCISIC ACID (ABA) ON DROUGHT TOLERANCE**

482 ABA is an isoprenoid plant hormone that modulates a variety of physiological
483 processes, from stomatal opening to protein storage, and helps plants respond to a variety
484 of stressors, including drought, salt, and cold [79]. At the cellular and intercellular levels in
485 plants, ABA modulates drought stress responses and tolerance [80]. Seed dormancy and
486 germination, root architecture control, ageing, stomata closure, and other actions of ABA are

487 only a few of them. Abscisic acid is thought to be the main hormone that controls how plants
 488 respond to changes in their environment that are not good for them. This is because the
 489 amount of ABA in plants often goes up when they are under abiotic stress, and more ABA
 490 makes it easier for plants to adapt to different types of abiotic stress [81].

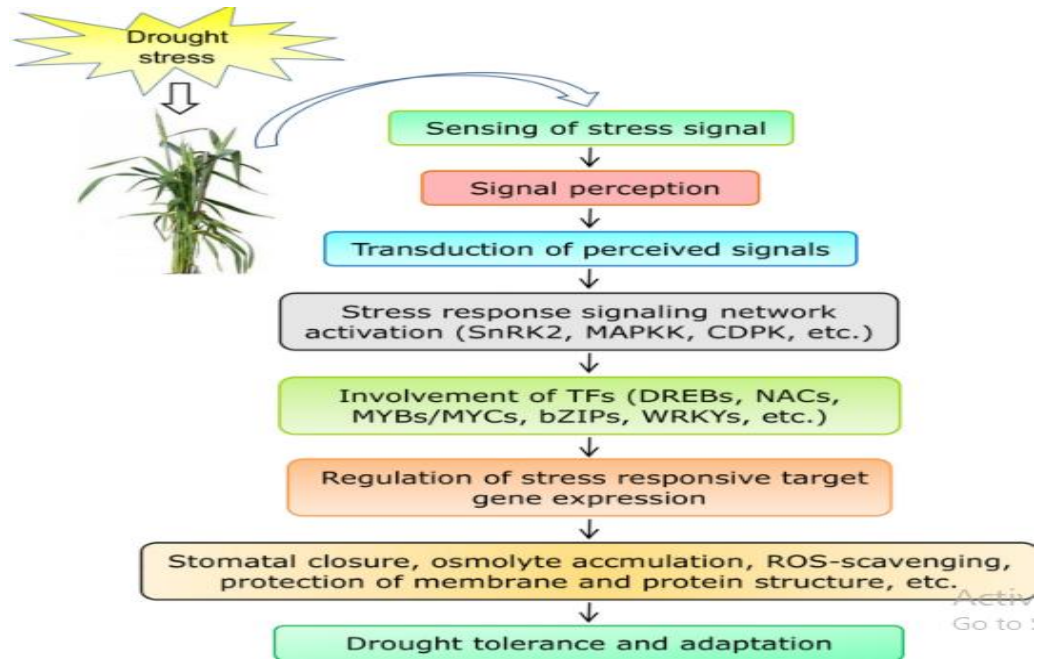


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Figure .6 Process of plant drought-tolerance development [82].
7.3 MOLECULAR MECHANISM OF DROUGHT TOLERANCE

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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. 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].



508

509 **Figure.7 Steps involved in the expression of drought tolerance, starting from the**
 510 **perception of drought stress and transducing the signal through transcription factors**
 511 **for the activation of genes involved in adaptation [824].**

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

526 **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	[867]

		qGW1	[878]
4	Grain yield	qYLD1.1	[89]
5	Pre- Flowering drought	B465/140,tK12/115,bDII/65,tM5/75,tC13/150,bC18/820	[4]
		Stg A, Stg G, Stg J	[55]
6	Stay Green associated traits	Gl 7, Gl 14, Gl 21, Gl 28	[90]
	Stay	Stg1, Stg2, Stg3 and Stg4	[65]

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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.*, (2019) have given a general differentiation between drought tolerance and sensitive crop plants as given below [91].

Table: 3 Difference between drought tolerance and sensitive in Sorghum [901]

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
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533

534 **9. CONCLUSION**

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

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

562

563 **COMPETING INTERESTS**

564

565 The authors declare no conflict of interest.

566

567 **AUTHORS' CONTRIBUTIONS**

568

569 All Authors are equally contributed for the preparation of the manuscript. All authors read
570 and approved the final manuscript.

571

572 **REFERENCES**

573

574 1. Ritter KB, McIntyre CL, Godwin ID, Jordan DR, Chapman SC. An assessment of the
575 genetic relationship between sweet and grain sorghums, within *Sorghum bicolor*
ssp. *bicolor* (L.) Moench, using AFLP markers. *Euphytica*. 2007; 157:161-76.

- 576 2. Motlhaodi T, Geleta M, Bryngelsson T, Fatih M, Chite S, Ortiz R. Genetic diversity
577 in 'ex-situ' conserved sorghum accessions of Botswana as estimated by microsatellite
578 markers. *Aust. Journ. of Crop Sci.* 2014; 8:35-43.
- 579 3. Hossain MS, Islam MN, Rahman MM, Mostofa MG, Khan MA. Sorghum: A
580 prospective crop for climatic vulnerability, food and nutritional security. *Journ. of*
581 *Agri. and Food Res.* 2022:100300.
- 582 4. Tuinstra MR, Ejeta G, Goldsbrough P. Evaluation of near-isogenic sorghum lines
583 contrasting for QTL markers associated with drought tolerance. *Crop Sci.* 1998;
584 38:835-842.
- 585 5. Kebede H, Subudhi PK, Rosenow DT, Nguyen HT. Quantitative trait loci influencing
586 drought tolerance in grain sorghum (*Sorghum bicolor* L. Moench). *Theo. and Appl.*
587 *Gene.* 2001; 103:266-276.
- 588 6. Amelework B, Shimelis H, Tongoona P, Laing M. Physiological mechanisms of
589 drought tolerance in sorghum, genetic basis and breeding methods: a review. *Afri.*
590 *Jour. of Agri. Res.* 2015; 10:3029-3040.
- 591 7. Craufurd PQ, Peacock JM. Effect of heat and drought stress on sorghum (*Sorghum*
592 *bicolor*). II. Grain yield. *Exp. Agri.* 1993; 29:77-86.
- 593 8. Fracasso A, Trindade LM, Amaducci S. Drought stress tolerance strategies revealed
594 by RNA-Seq in two sorghum genotypes with contrasting WUE. *BMC Plant Biol.*
595 2016; 16:1-8.
- 596 9. Wagaw K. Review on mechanisms of drought tolerance in sorghum (*Sorghum*
597 *bicolor* (L.) Moench) basis and breeding methods. *Acad. Res. Journ. of Agri. Sci.*
598 *and Res.* 2019;7:87-99.
- 599 10. Kole C, Muthamilarasan M, Henry R, Edwards D, Sharma R, Abberton M et al.
600 Application of genomics-assisted breeding for generation of climate resilient crops:
601 progress and prospects. *Front. in Plant Sci.* 2015;6:563.
- 602 11. Gonzalez Guzman, M., Cellini, F., Fotopoulos, V., Balestrini, R., & Arbona, V. (2022).
603 New approaches to improve crop tolerance to biotic and abiotic
604 stresses. *Physiologia Plantarum*, 174(1), e13547.
- 605 12. Dos Reis SP, Lima AM, De Souza CR. Recent molecular advances on downstream
606 plant responses to abiotic stress. *Inter. Journ. of Mol. Sci.* 2012;13:8628-8647.
- 607 13. Mantri N, Patade V, Penna S, Ford R, Pang E. Abiotic stress responses in plants:
608 present and future. In *Abiot. Stress Resp. in Plants* 2012;1-19. Springer, New York,
609 NY.

- 610 14. Kogan F, Guo W, Yang W. Drought and food security prediction from NOAA new
611 generation of operational satellites. *Geomat., Natur. Hazar. and Risk.* 2019; 10:651-
612 666.
- 613 15. Bartlett MK, Detto M, Pacala SW. Predicting shifts in the functional composition of
614 tropical forests under increased drought and CO₂ from trade-offs among plant
615 hydraulic traits. *Ecol. Letters.* 2019; 22:67-77.
- 616 16. Choudhury FK, Rivero RM, Blumwald E, Mittler R. Reactive oxygen species, abiotic
617 stress and stress combination. *The Plant Journ.* 2017; 90:856-867.
- 618 17. Nejat N, Mantri N. Plant immune system: crosstalk between responses to biotic and
619 abiotic stresses the missing link in understanding plant defence. *Curr. Issues in Mol.*
620 *Biol.* 2017; 23:1-6.
- 621 18. Akimoto-Tomiyama C, Tanabe S, Kajiwara H, Minami E, Ochiai H. Loss of
622 chloroplast-localized protein phosphatase 2Cs in *Arabidopsis thaliana* leads to
623 enhancement of plant immunity and resistance to *Xanthomonas campestris* pv.
624 *campestris* infection. *Mol. Plant Pathol.* 2018; 19:1184-1195.
- 625 19. Maiti RK, Satya P. Research advances in major cereal crops for adaptation to
626 abiotic stresses. *GM Crops & Food.* 2014;5:259-279.
- 627 20. Tonapi VA, Talwar HS, Are AK, Bhat BV, Reddy CR, Dalton TJ, editors. *Sorghum in*
628 *the 21st Century: Food, Fodder, Feed, Fuel for a Rapidly Changing World.* Springer;
629 2020.
- 630 21. Ella ES, Kawano N, Yamauchi Y, Tanaka K, Ismail AM. Blocking ethylene
631 perception enhances flooding tolerance in rice seedlings. *Funct. Plant Biol.* 2003;
632 30:813-819.
- 633 22. Sharma S, Sharma J, Soni V, Kalaji HM, Elsheery NI. Waterlogging tolerance: A
634 review on regulative morpho-physiological homeostasis of crop plants. *Journ. of*
635 *Water and Land Devel.* 2021.
- 636 23. Oladosu Y, Rafii MY, Arolu F, Chukwu SC, Muhammad I, Kareem I, Salisu MA,
637 Arolu IW. Submergence tolerance in rice: Review of Mech., Breed. and, Future
638 *Prosp. Sust.* 2020; 12:1632.
- 639 24. Li Z, Zhang M, Chow WS, Chen F, Xie Z, Fan D. Carbohydrate saving or biomass
640 maintenance: which is the main determinant of the plant's long-term submergence
641 tolerance?. *Photosyn. Res.* 2021; 149:155-170.
- 642 25. Pradhan C, Mohanty M. Submergence Stress: Responses and adaptations in crop
643 plants. In *Mol. Stress Physiol. of Plants* 2013; 331-357. Springer, India.

- 644 26. Huang YC, Yeh TH, Yang CY. Ethylene signaling involves in seeds germination
645 upon submergence and antioxidant response elicited confers submergence
646 tolerance to rice seedlings. *Rice*. 2019; 12:1-8.
- 647 27. Reinhardt J, Hilgert P, Von Cossel M. Yield performance of dedicated industrial
648 crops on low-temperature characterized marginal agricultural land in Europe—a
649 review. *Biofu., Biopro. and Bioref.* 2022; 16:609-622.
- 650 28. Tari I, Laskay G, Takács Z, Poór P. Response of sorghum to abiotic stresses: A
651 review. *Journ. of Agron. and Crop Sci.* 2013 ;199:264-274.
- 652 29. Bhattacharya A. Low Temperature Stress and Plant-Water Relationship: A Review.
653 *Physiol. Proc. in Plants Under Low Temp. Stress.* 2022:107-197.
- 654 30. Mansour MM, Emam MM, Salama KH, Morsy AA. Sorghum under saline conditions:
655 responses, tolerance mechanisms, and management strategies. *Planta.* 2021;
656 254:1-38.
- 657 31. Amombo E, Ashilenje D, Hirich A, Kouisni L, Oukarroum A, Ghoulam C, El Gharous
658 M, Nilahyane A. Exploring the correlation between salt tolerance and yield:
659 Research advances and perspectives for salt-tolerant forage sorghum selection and
660 genetic improvement. *Planta.* 2022; 255:1-6.
- 661 32. Yang X, Lu M, Wang Y, Wang Y, Liu Z, Chen S. Response mechanism of plants to
662 drought stress. *Horticulturae.* 2021; 7:50.
- 663 33. Ohnishi N, Wacera W F, Sakamoto W. Photosynthetic responses to high
664 temperature and strong light suggest potential post-flowering drought tolerance of
665 sorghum Japanese Landrace Takakibi. *Plant and Cell Physiol.* 2019; 60:2086-2099.
- 666 34. Pandey GC, Mamrutha HM, Tiwari R, Sareen S, Bhatia S, Siwach P et al.;
667 Physiological traits associated with heat tolerance in bread wheat (*Triticum aestivum*
668 L.). *Physiol. and Mol Biol of Plants.* 2015; 21:93-99.
- 669 35. Bokshi AI, Thistlethwaite RJ, Chaplin ED, Kirii E, Trethowan RM, Tan DK.
670 Physiological traits for evaluating heat-tolerance of Australian spring wheat cultivars
671 at elevated CO₂. *Journ. of Agron. and Crop Sci.* 2022 ;208:178-196.
- 672 36. Djanaguiraman M, Prasad PV, Seppanen M. Selenium protects sorghum leaves
673 from oxidative damage under high temperature stress by enhancing antioxidant
674 defense system. *Plant Physiol. and Biochem.* 2010; 48:999-1007.
- 675 37. Hasanuzzaman M, Nahar K, Alam M, Roychowdhury R, Fujita M. Physiological,
676 biochemical, and molecular mechanisms of heat stress tolerance in plants. *Intern.*
677 *Journ. of Mol. Sci.* 2013; 14:9643-9684.

- 678 38. Swain S, Patel P, Nandi S. Application of SPI, EDI and PNPI using MSWEP
679 precipitation data over Marathwada, India. In 2017 IEEE Intern. Geosci. and Remote
680 Sens. Symp. (IGARSS) 2017: 5505-5507. IEEE.
- 681 39. Wang Q, Shi P, Lei T, Geng G, Liu J, Mo X et al. The alleviating trend of drought in
682 the Huang-Huai-Hai Plain of China based on the daily SPEI. Intern. Journ. of Climat.
683 2015; 35:3760-3769.
- 684 40. Hasanuzzaman M, Nahar K, Gill SS, Fujita M. Drought stress responses in plants,
685 oxidative stress, and antioxidant defense. Clim. Change and Plant Abiot. Stress Tol..
686 2013:209-250.
- 687 41. Kapoor D, Bhardwaj S, Landi M, Sharma A, Ramakrishnan M, Sharma A. The
688 impact of drought in plant metabolism: How to exploit tolerance mechanisms to
689 increase crop production. Appl. Sci. 2020; 10:5692.
- 690 42. Laxa M, Liebthal M, Telman W, Chibani K, Dietz KJ. The role of the plant antioxidant
691 system in drought tolerance. Antioxidants. 2019; 8:94..
- 692 43. Hsiao TC. Plant responses to water stress. Annu. Rev. of Plant Physiol. 1973;
693 24:519-570.
- 694 44. Basu S, Ramegowda V, Kumar A, Pereira A. Plant adaptation to water deficit.
695 F1000Research. 2016; 5:1554.
- 696 45. Akman H, Zhang C, Ejeta G. Physio-morphological, biochemical, and anatomical
697 traits of drought-tolerant and susceptible sorghum cultivars under pre-and
698 post-anthesis drought. Physiol. Plantar.. 2021; 172:912-921.
- 699 46. Shao HB, Chu LY, Jaleel CA, Zhao CX. Water-deficit stress-induced anatomical
700 changes in higher plants. Compt. Rend. Biol. 2008; 331:215-225.
- 701 47. Abreha KB, Enyew M, Carlsson AS, Vetukuri RR, Feyissa T, Motlhaodi T et al..
702 Sorghum in dryland: morphological, physiological, and molecular responses of
703 sorghum under drought stress. Planta. 2022; 255:1-23.
- 704 48. Lisar SY, Motafakkerazad R, Hossain MM, Rahman IM. Causes, Effects and
705 Responses. Water Stress. 2012; 25.
- 706 49. Krupa, K. N., Dalawai, N., Shashidhar, H. E., & Harinikumar, K. M. (2017).
707 Mechanisms of drought tolerance in Sorghum: A Review. *International Journal of*
708 *Pure and Applied Bioscience*, 5(4), 221-237.
- 709 50. Tardieu F, Simonneau T, Muller B. The physiological basis of drought tolerance in
710 crop plants: a scenario-dependent probabilistic approach. Annu. Rev. of Plant Biol.
711 2018; 69:733-759.
- 712 51. Geetika G, Van Oosterom EJ, George-Jaeggli B, Mortlock MY, Deifel KS, McLean G
713 et al.. Genotypic variation in whole-plant transpiration efficiency in sorghum only

714 partly aligns with variation in stomatal conductance. *Funct. Plant Biol.* 2019;
715 46:1072-1089.

716 52. Yahaya MA, Shimelis H. Drought stress in sorghum: Mitigation strategies, breeding
717 methods and technologies—A review. *Journ. of Agron. and Crop Sci.* 2022;
718 208:127-142.

719 53. Lopez JR, Erickson JE, Munoz P, Saballos A, Felderhoff TJ, Vermerris W. QTLs
720 associated with crown root angle, stomatal conductance, and maturity in Sorghum.
721 *The Plant Geno.* 2017; 10:plantgenome2016-04.

722 54. Heckathorn SA, DeLucia EH. Effect of leaf rolling on gas exchange and leaf
723 temperature of *Andropogon gerardii* and *Spartina pectinata*. *Botan. Gazet.* 1991;
724 152:263-268.

725 55. Demelash H, Tadesse T, Menamo T, Menzir A. Determination of root system
726 architecture variation of drought adapted sorghum genotypes using high throughput
727 root phenotyping. *Rhizosphere.* 2021; 19:100370.

728 56. Comas L, Becker S, Cruz VM, Byrne PF, Dierig DA. Root traits contributing to plant
729 productivity under drought. *Front. in Plant Sci.* 2013; 4:442.

730 57. Bibi A, Sadaqat HA, Tahir MH, Akram HM. Screening of sorghum (*Sorghum bicolor*
731 var Moench) for drought tolerance at seedling stage in polyethylene glycol. *J. Anim.*
732 *Plant Sci.* 2012; 22:671-678.

733 58. Routley R, Broad IJ, McLean G, Whish J, Hammer G. The effect of row configuration
734 on yield reliability in grain sorghum: I. Yield, water use efficiency and soil water
735 extraction.

736 59. Choudhary S, Wani KI, Naeem M, Khan M, Aftab T. Cellular Responses, Osmotic
737 Adjustments, and Role of Osmolytes in Providing Salt Stress Resilience in Higher
738 Plants: Polyamines and Nitric Oxide Crosstalk. *Journ. of Plant Growth Regul.*
739 2022:1-5.

740 60. Ludlow MM, Santamaria JM, Fukai S. Contribution of osmotic adjustment to grain
741 yield in *Sorghum bicolor* (L.) Moench under water-limited conditions. II. Water stress
742 after anthesis. *Aust. Journ. of Agri. Res.* 1990;41:67-78.

743 61. Ogbaga CC, Stepien P, Dyson BC, Rattray NJ, Ellis DI, Goodacre R, Johnson GN.
744 Biochemical analyses of sorghum varieties reveal differential responses to drought.
745 *PloS One.* 2016; 11:e0154423.

746 62. Sivaramakrishnan S, Patell VZ, Flower DJ, Peacock JM. Proline accumulation and
747 nitrate reductase activity in contrasting sorghum lines during mid-season drought
748 stress. *Physiol. Planta.* 1988; 74:418-426..

- 749 63. Borrell A, Van Oosterom E, Hammer G, Jordan D, Douglas A. The physiology of
750 "stay-green" in sorghum. In Proceedings of the 11th Australian Agronomy
751 Conference 2003; 2-6. Solutions for a better environment, Geelong, Victoria.
- 752 64. Jordan, D.R.; Hunt, C.H.; Cruickshank, A.W.; Borrell, A.K.; Henzell, R.G. The
753 relationship between the stay-green trait and grain yield in elite sorghum hybrids
754 grown in a range of environments. *Crop. Sci.* 2012, 52, 1153–1161
- 755 65. Xu, Wenwei, et al. "Molecular mapping of QTLs conferring stay-green in grain sorghum
756 (*Sorghum bicolor* L. Moench)" *Genome* 43.3 2000:461-469
- 757 66. Subudhi PK, Rosenow DT, Nguyen HT. Quantitative trait loci for the stay green trait
758 in sorghum (*Sorghum bicolor* L. Moench): consistency across genetic backgrounds
759 and environments. *Theo. and Appl. Gene.* 2000; 101:733-741.
- 760 67. Mahalakshmi V, Bidinger FR. Evaluation of stay-green sorghum germplasm lines at
761 ICRISAT. *Crop Sci.* 2002; 42:965-974.
- 762 68. Kannagara T, Durley RC, Simpson GM, Seetharama N. Drought resistance of
763 *Sorghum bicolor*. 6. Changes in endogenous growth regulators of plants grown
764 across an irrigation gradient. *Canad. Journ. of Plant Sci.* 1983; 63:147-155.
- 765 69. Chakhchar A, Lamaoui M, Aissam S, Ferradous A, Wahbi S, El Mousadik A,
766 Ibsouda-Koraichi S, Filali-Maltouf A, El Modafar C. Physiological and biochemical
767 mechanisms of drought stress tolerance in the Argan tree. In *Plant Metabol. and*
768 *Regul. Under Environ. Stress* 201; 311-322. Academic Press.
- 769 70. Shinozaki K, Yamaguchi-Shinozaki K, Seki M. Regulatory network of gene
770 expression in the drought and cold stress responses. *Curr. Opin. in Plant Biol.* 2003
771 ;6:410-417.
- 772 71. Shinozaki K, Yamaguchi-Shinozaki K. Gene networks involved in drought stress
773 response and tolerance. *Journ. of Exp. Botany.* 2007; 58:221-227.
- 774 72. Zargar SM, Nagar P, Deshmukh R, Nazir M, Wani AA, Masoodi KZ, Agrawal GK,
775 Rakwal R. Aquaporins as potential drought tolerance inducing proteins: Towards
776 instigating stress tolerance. *Journ. of Proteom.* 2017; 169:233-238.
- 777 73. Hong-Bo S, Zong-Suo L, Ming-An S. LEA proteins in higher plants: structure,
778 function, gene expression and regulation. *Colloids and surfaces B: Biointerfaces.*
779 2005; 45:131-135.
- 780 74. Liang Y, Kang K, Gan L, Ning S, Xiong J, Song S, Xi L, Lai S, Yin Y, Gu J, Xiang J.
781 Drought-responsive genes, late embryogenesis abundant group3 (LEA 3) and
782 vicinal oxygen chelate, function in lipid accumulation in *Brassica napus* and
783 *Arabidopsis* mainly via enhancing photosynthetic efficiency and reducing ROS. *Plant*
784 *Biotech. Journ.* 2019; 17:2123-2142.

- 785 75. Carvalho MD. Drought stress and reactive oxygen species. *Plant Sig.l Behav.* 2008;
786 3:156-165.
- 787 76. Waraich EA, Ahmad R, Halim A, Aziz T. Alleviation of temperature stress by nutrient
788 management in crop plants: a review. *Journ. of Soil Sci. and Plant Nutrit.* 2012;
789 12:221-244.
- 790 77. ul Haq S, Khan A, Ali M, Khattak AM, Gai WX, Zhang HX, Wei AM, Gong ZH. Heat
791 shock proteins: dynamic biomolecules to counter plant biotic and abiotic stresses.
792 *Intern. Journ. of Mol Sci.* 2019; 20:5321.
- 793 78. Nagaraju M, Reddy PS, Kumar SA, Kumar A, Rajasheker G, Rao DM, Kishor PK.
794 Genome-wide identification and transcriptional profiling of small heat shock protein
795 gene family under diverse abiotic stress conditions in *Sorghum bicolor* (L.). *Intern.*
796 *Journ. of Biol. Macromol.* 2020; 142:822-834.
- 797 79. Sah SK, Reddy KR, Li J. Abscisic acid and abiotic stress tolerance in crop plants.
798 *Front. in Plant Sci.* 2016;7:571.
- 799 80. Takahashi F, Kuromori T, Urano K, Yamaguchi-Shinozaki K, Shinozaki K. Drought
800 stress responses and resistance in plants: From cellular responses to long-distance
801 intercellular communication. *Front. in Plant Sci.* 2020:1407.
- 802 81. Tuteja N. Abscisic acid and abiotic stress signaling. *Plant Signal. & Behav.* 2007;
803 2:135-138.
- 804 82. Yang Z, Li JL, Liu LN, Xie Q, Sui N. Photosynthetic regulation under salt stress and
805 salt-tolerance mechanism of sweet sorghum. *Front. in Plant Sci.* 2020:1722.
- 806 83. Gupta PK, Balyan HS, Gahlaut V. QTL analysis for drought tolerance in wheat:
807 present status and future possibilities. *Agronomy.* 2017; 7:5.
- 808 84. Xiong L, Wang RG, Mao G, Koczan JM. Identification of drought tolerance
809 determinants by genetic analysis of root response to drought stress and abscisic
810 acid. *Plant Physiol.* 2006; 142:1065-1074.
- 811 85. Manavalan LP, Nguyen HT. Drought tolerance in crops: Physiology to genomics.
812 *Plant Stress Physiol.* 2017:1-23.
- 813 86. Abou-Elwafa SF, Shehzad T. Genetic identification and expression profiling of
814 drought responsive genes in sorghum. *Environ. and Exper. Botany.* 2018; 155:12-
815 20.
- 816 87. Zou G, Zhai G, Yan S, Li S, Zhou L, Ding Y et al. Sorghum qTGW1a encodes a G-
817 protein subunit and acts as a negative regulator of grain size. *Journ. of Exper*
818 *Botany.* 2020; 71:5389-53401.

- 819 88. Han L, Chen J, Mace ES, Liu Y, Zhu M, Yuyama N et al. Fine mapping of qGW1, a
820 major QTL for grain weight in sorghum. *Theor. and Appl. Gene.*. 2015; 128:1813-
821 1825.
- 822 89. Mwamahonje A, Eleblu JS, Ofori K, Feyissa T, Deshpande S, Garcia-Oliveira AL et
823 al. Introgression of QTLs for Drought Tolerance into Farmers' Preferred Sorghum
824 Varieties. *Agriculture*. 2021; 11:883.
- 825 90. Kiranmayee KN, Hash CT, Sivasubramani S, Ramu P, Amindala BP, Rathore A et
826 al. Fine-mapping of sorghum stay-green QTL on chromosome10 revealed genes
827 associated with delayed senescence. *Genes*. 2020; 11:1026.
- 828 91. Sallam A, Alqudah AM, Dawood MF, Baenziger PS, Börner A. Drought stress
829 tolerance in wheat and barley: advances in physiology, breeding and genetics
830 research. *Intern. Jouun. of Mol. Sci*. 2019;20:3137.