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Progress on the Effect of Drought on Sorghum Growth and Its Response Mechanisms

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Abstract **Review Article**

Sorghum is the fifth most important cereal crop globally, with multiple uses including food, feed, fiber, brewing and bio-energy feedstocks. With the increasing frequency of extreme weather events globally, the risk of sorghum suffering from drought stress is increasing, leading to reduced sorghum yields. This study summarized the effects of drought stress on sorghum growth, discussed the response mechanisms of sorghum to drought stress from stomatal regulation, osmotic regulation and antioxidant defense system regulation, and explored the pathways to enhance sorghum's drought resistance.
Keywords: Sorghum, Drought stress, response mechanism.

1. INTRODUCTION

Drought is the most widespread natural disaster in the world [1], severely affecting plant growth and development [2], reducing crop yields [3], and thus causing serious losses in agricultural production. Over the past decade, the loss of crop production caused by drought globally has amounted to approximately $30 billion [4].

Sorghum (*Sorghum bicolor* (L.)) is the fifth most important cereal crop globally [5], with multiple uses including food, feed, fiber, brewing and bio-energy feedstocks [6, 7]. It also has multiple resistances such as salt-alkali tolerance, drought tolerance, and flood tolerance [8]. Warming world has led to an increase in the intensity and frequency of droughts [9], which seriously affects the growth and yield of sorghum. This study reviews the effects of drought stress on seed germination, leaves and roots during the growth process of sorghum. It discusses the response mechanisms of sorghum to drought stress from the perspectives of stomatal regulation, osmotic regulation, and antioxidant defense system regulation, and provides insights into pathways to improve the drought tolerance of sorghum.

2. Effects of drought stress on sorghum growth

2.1 Effects of drought stress on sorghum seed germination

Drought leads seeds to insufficient water absorption, hindering seed germination [10]. Studies have found that under drought stress, the germination potential, germination index, and vigor index of forage sorghum are all lower than those of forage sorghum not subjected to drought stress [11]. In experiments simulating drought stress conditions using polyethylene glycol 6000 (PEG-6000), it was also observed that the germination potential of sweet sorghum FH59 decreased, and the lengths of the radicle and germ shortened when the PEG concentration was 50g/L, 100g/L, 150g/L, and 200g/L, respectively. Furthermore, the germination potential, radicle length, and germ length all gradually decreased with increasing PEG concentration [12]. These findings indicate that drought stress is detrimental to the germination of sorghum seeds.

2.2 Effects of drought stress on sorghum leaves

During drought stress, sorghum leaves exhibit phenomena such as yellowing, wilting, and curling. Studies have found that the total chlorophyll content, as well as the content of chlorophyll a and chlorophyll b in sorghum leaves decreased under drought stress [13]. When leaves encounter drought, chlorophyll synthesis slows down, decomposition accelerates, and the amount decreases, gradually revealing the colors of carotenoids and anthocyanins that were previously concealed by chlorophyll, thus causing the leaf color to turn yellow [14]. Research has found that after being treated with 25% PEG for 24 hours, the relative water content (RWC) of the leaves of four sorghum varieties T14, T33, S4 and S4-1 all decreased [15]. Drought stress also leads to the accumulation of reactive oxygen species (ROS) in leaves, thereby causing oxidative damage to the leaves [16].

2.3 Effects of drought stress on sorghum roots

The roots is an important organ for plants to absorb water and nutrients [17]. Under drought stress, the decrease of soil moisture leads to difficulties in water absorption by plant roots, resulting in water shortage for plants [18]. Drought stress can also cause changes in the morphological structure of plant roots [19]. Studies have found that under drought stress, the root length of sorghum increases with increasing drought severity [20]. Pei Dong *et al*. found that the root length density of sorghum under dryland treatment was greater than that of sorghum under full water supply treatment at different soil depths [21], indicating that the growth of sorghum roots increases under drought conditions, which is beneficial for water absorption. Under drought stress, changes also occur in the root/shoot ratio, and root surface area of sorghum. Study on the effects of drought stress on the root morphology and vitality of stay green sorghum B35 and normal sorghum Sanchisan during flowering and filling periods found that the root/shoot ratio and root surface area of both stay green sorghum B35 and normal sorghum Sanchisan decreased under drought stress [22].

3. Response mechanism of sorghum to drought stress

3.1 Stomatal regulation

Stomata are tiny pores formed by a pair of guard cells on the epidermis of plants, controlling gas exchange and water loss between plants and the atmosphere [23]. Stomatal regulation is one of the important mechanisms for plants to resist drought stress and adapt to the environment [24]. When sorghum is subjected to drought stress, its leaves can regulate water transpiration through stomata to achieve drought resistance, which is an important mechanism for sorghum's drought tolerance [25].

The stomatal conductance (stomatal opening size) and transpiration rate of sweet sorghum seedlings decreased gradually with the increase of drought stress intensity [26], and the stomatal conductance and transpiration rate of seedlings of the eight sorghum varieties decreased under drought stress [27], indicating that sorghum can resist drought by adjusting stomatal opening and reducing transpiration rate when subjected to drought stress.

Relevant research has found that calcium-dependent protein kinase (CDPKs/CPKs) in sorghum not only regulate the expression of drought-responsive genes, especially those involved in ion transport, but also participate in regulating the activity of the stomatal-related protein slow anion channel 1 (SLAC1), thereby mediating stomatal closure under drought stress. Simultaneously, under drought stress, abscisic acid (ABA) accumulated in the roots and stems of sorghum is subsequently transported to the guard cells. Activated sucrose non-fermenting-1-related protein kinase 2 (SnRK2) interacts with SLAC1, promoting anion efflux and facilitating stomatal closure in response to drought stress. K uptake transporter 6/8（KUP6/8） is also regulated by SnRK2s and contributes to stomatal regulation [28].

3.2 Osmotic regulation

Osmotic regulation is an important physiological mechanism of plant stress resistance [29]. Under drought stress, plants can reduce cell osmotic potential through osmotic regulation, thereby increasing water absorption and enabling cells to maintain normal physiological metabolic activities to adapt to the drought environment [30].

Osmotic regulation substances include organic osmotic regulation substances and inorganic osmotic regulation substances [31-33]. Proline is an important organic osmotic regulation substance [34]. Generally, when plants suffer from drought stress, proline accumulates significantly, reducing the water potential within the plants and thus maintaining water balance [35]. It also plays an important role in maintaining the stability of biological membranes [36]. Under drought stress, sorghum can enhance its osmotic regulation ability by increasing the content of proline, soluble sugar, and other substances, thus maintaining cell water retention [37]. Zhang Yuxia and others found that when simulated drought stress was applied using 15% PEG, the proline and soluble sugar contents of eight forage sorghum varieties increased [38]. Wang Zhiheng and others also found that the contents of proline, soluble sugar and soluble protein in the leaves of sweet sorghum seedlings under drought stress were higher than those under non-stress treatment, and gradually increased with prolonged stress duration [39].

K^+ is an inorganic osmotic regulation substance that maintains cell osmotic pressure in plants, playing a crucial role in sorghum's adaptation to drought conditions.

Wang Yuguo *et al*. studied the relationship of osmotic regulation to elongation growth of sorghum leaves under water stress, and found that K^+ is one of the osmotic regulation substances that contribute most significantly to osmotic regulation [40]. Shao Yanjun and others found that the K^+ content of two sorghum varieties "Jinzhong 405" and "Jinza 12" changed under drought stress, indicating that K^+ might act as an osmotic regulation substance to participate in the drought resistance response of sorghum [41]. Tang Zhangcheng *et al.* found that during water deficit in the seedling stage of sorghum, K^+ can promote the accumulation of proline [42].

3.3 Regulation of antioxidant defense system

Drought stress can lead to a significant accumulation of reactive oxygen species (ROS) in plants, and plants utilize antioxidant defense systems to reduce the excessive accumulation of ROS under drought stress [43]. The antioxidant defense system of plants includes both enzymatic antioxidants and non-enzymatic antioxidants [44]. Enzymatic antioxidants include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and so on. While non-enzyme antioxidants include ascorbic acid (AsA), glutathione (GSH), carotenoids, and so on [45, 46].

Sorghum can cope with drought conditions through its antioxidant defense mechanism and its ability to scavenge reactive oxygen species (ROS) [47]. Research on the physiological characteristics of seedlings of two sweet sorghum varieties (native species and Xingaoliang 2) revealed that under simulated drought stress induced by PEG at different concentrations, the activities of SOD, CAT, and APX were higher than those in non-stress treatments [48]. The study on the impact of drought stress on the physiological characteristics of seedlings of 22 glutinous sorghum varieties also revealed that the activities of SOD and POD were significantly higher than those in non-drought-treated treatments [49]. This indicates that sorghum can resist harm by activating its antioxidant system and enhancing the activity of antioxidant enzymes when subjected to drought stress.

4. Pathways of sorghum resistance to drought stress

4.1 Variety improvement

Research has found that under drought stress, the chlorophyll content, FV/FM ratio, POD, and SOD activities in transgenic sorghum lines overexpressing *SbNAC9* are higher than those in wild-type sorghum. The roots of transgenic lines are more developed than those of wild-type sorghum, and the contents of H^2O^2, O^{2-}, and MDA are lower. This indicates that overexpression of *SbNAC9* can improve the drought tolerance of sorghum by maintaining relative high photosynthesis, strengthening root architecture, and enhancing the ability to scavenge reactive oxygen species [50].

Yan Mengyuan and others also demonstrated through physiological analysis that *GhCDPK60* enhances drought stress tolerance by improving osmoregulation capacity and reducing the accumulation of reactive oxygen species (ROS) in plants [51]. Therefore, genetic engineering and other related technologies can be utilized to overexpress or introduce relevant genes into sorghum, thereby improvingthe variety of sorghum, thus enhancing its tolerance to drought.

4.2 Reasonable fertilization

Nitrogen, phosphorus, potassium, magnesium, and other mineral elements are required for plant growth. Research has found that the application of nitrogen, phosphorus, and potassium fertilizers can enhance the drought tolerance of plants [52-54]. However, excessive fertilization can inhibit plant growth and even increase the mortality rate of seedlings under drought conditions [55]. Therefore, it is necessary to improve the osmotic and stomatal regulation abilities of sorghum through reasonable fertilization, thereby increasing its tolerance to drought and ultimately improving its yield.

4.3 Application growth regulators or antitranspirants

Plant growth regulators are chemical substances that can regulate the growth and development of plants [56], which are beneficial for improving the drought resistance of plants [57]. Commonly used plant growth regulators include gibberellin (GA), cytokinin (CTK), abscisic acid (ABA) and so on.

Relevant research has found that under drought stress, the application of exogenous spermidine can promote the growth of sweet sorghum seedlings, enhance photosynthetic efficiency, increase the content of organic osmotic regulation substances, enhance antioxidant enzyme activity, and reduce MDA content, thereby enhancing the drought tolerance of sweet sorghum seedlings [58].

Antitranspirants are a class of chemical substances that act on the surface of plant leaves, reducing transpiration intensity and water loss [59]. Antitranspirants can be categorized into three types: film-forming, reflective and metabolic [60]. Commonly used antitranspirants include fulvic acid (FA), abscisic acid (ABA), etc. Under drought conditions, reflective antitranspirants can be applied to sorghum to reduce transpiration and maintain life [61]. In summary, by applying plant growth regulators and antitranspirants to sorghum, we can enhance its drought resistance, thus increasing the yield of sorghum.

4. SUMMARY

This study reviewed the effects of drought stress on the growth of sorghum, as well as its response mechanisms under drought stress. It also explored pathways to enhance the drought resistance of sorghum, aiming to provide new insights for mitigating the impact of drought on sorghum production and addressing the increasingly severe challenges posed by drought stress.

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