E-ISSN: 2788-9297
P-ISSN: 2788-9289
www.agrijournal.org
SAJAS 2022; 2(2): 41-47
Received: 20-04-2022
Accepted: 23-05-2022

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Growth, yield and seed quality of soybean under drought stress: A review

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Abstract
Soybean is a drought-sensitive crop and drought is one of the serious problems for crop production in many regions of the world, leading to a huge production loss. Drought stress affects soybean growth as well as yield by reducing all yield components and deteriorating the quality of seed. Therefore, crop growth, yield, and quality improvement under drought is an important goal of plant science research. In this review, we will discuss the currently available information on changes in phenology, yield components, and quality of seed under drought stress. It is presumed that this review will help in formulating future research by understanding the physio-morphological changes of soybean under drought stress.

Keywords: Growth, yield, seed quality, drought stress, soybean

Introduction

Drought refers to the lack of adequate moisture which is necessary for growing plants and completing its life cycle. It is the major yield-limiting factor of crops. World statistics showed that drought affected areas increased more than double during the last 40 years and the losses of crop production due to drought stress exceeded the total losses occurred by all other abiotic stresses (FAO, 2021) [21]. Area by percentage of cultivated drought affect zones in the world were approximately 29% of the total agricultural land (Statista, 2022) [68]. Soybean is the most drought-sensitive crop (Maleki *et al.*, 2013) [39] and its water requirement is very high. The drought stress negatively affects emergence, leaf area, root, tiller, and stem growth and development, dry matter production, floral initiation, panicle development, pollination, fertilization, seed development, seed yield as well as quality of seed (Du *et al.*, 2020) [20]. Therefore, drought stress is considered as the most important constraining factor for soybean cultivation.

Drought stress affects crop growth and development through a complex mechanism of physiological, biochemical and metabolic processes at the genetic and molecular levels (Basu *et al.*, 2016; Hura *et al.*, 2022) [5, 29]. How drought influences plant growth and development, physiological procedures, and improvement of yield is the topmost issue of soybean research. A better understanding of the growth and developmental responses of soybean plants to drought stress is an extreme significance to increase soybean production areas and yield. Although the above-named topic is the well-recognized, this review, connected with morphological, physiological and biochemical mechanisms, is still far from complete.

Many reports stated that drought stress significantly decreases the seed yield of soybeans (Liu *et al.*, 2004a; De *et al.*, 2022) [36, 16]. More specifically, severe drought stress reduced the total seed yield of soybean (Ogunkanmi *et al.*, 2022) [52]. Wei *et al.* (2018) [76] evaluated the effects of drought stress at different stages in soybean and found that all growth and yield parameters were significantly affected by the drought stress during all reproductive growth stages. An understanding of how soybean plants respond to drought stress during different growth stages is important in maximizing yields in the drought-affected zone.

Drought stress is mostly responsible for shriveled, shrunken, misshaped and quality of seeds in soybean (Abdelhamied *et al.*, 2021) [1]. Samarah *et al.* (2009) [58] also reported that the soybean seeds had lower germination under drought stress. Ahmed *et al.* (2011) [2] reported that drought stress reduced quality of seed by increasing the production of small and medium seeds as well as by decreasing seed vigor.

Since the reported facts on the importance of drought on soybean crop are found sporadic, this review paper is prepared with the aim to provide crucial information for enhancement of

Soybean production in the drought-prone areas. To achieve the purpose, we attempted to provide available information on the effect of drought on growth, different growth stages, yield, yield components, and quality of seed in soybean.

Initial response of plant to drought stress

The primary symptom is expressed in the roots located in the upper soil layers of soybean. First stimulating the synthesis of the abscisic acid (ABA) hormone in roots under drought stress. Many reports stated that the ABA is translocated from root to leaves by endogenous signals that operate at long distances (Osakabe *et al.*, 2014; Zhang *et al.*, 2021) [53, 81]. Plant adapts through stomatal movement under drought stress by the alteration of ABA accumulation and ABA induces a string of signaling cascades comprising not only of receptors, kinases, and transcription factors but also transporters and other membrane localized factors (Roychoudhury and Basu, 2021) [54]. In addition, it is also found that the stomatal closure influences the activities of turgor and volume reduction of guard cells, which diminish the gas exchange vis a vis photosynthetic activity during drought stress (Hu *et al.,* 2010) [28]. The ultimate visible effects of drought damage could be wilting, scorching, irreversible shrinkage of cell membranes and increased synthesis of ABA as well as, in case of long-term symptoms, dieback of branches and death of the plant (Kujawski, 2011) [33].

Effect of drought stress on vegetative growth

The survival of plants relies on photosynthesis, nutrient uptake, and transportation. It is a pivotal system for the initiation of growth and development processes throughout the plant's life. The growth and development of the plants depend on cell division. Drought stress damage is most commonly associated with the physiological changes in cell division hampering meristematic regions (Tiwari *et al.,* 2022) [73]. Furthermore, turgor is another drought-sensitive physiological process that causes stunted growth. Low turgor occurred due to lack of water resulting slow or limited cell development of soybean (Mutava *et al.*, 2015) [46].

Stomatal control decreased by 60% under severe drought stress and affected soybean growth (Hao *et al.,* 2013; Mak *et al.*, 2014; Mutava *et al.,* 2015) [26, 38, 46]. Lei *et al.* (2006) [34] noticed that under severe drought stress stomatal conductance, transpiration rate, and photosynthetic rate were reduced by 92%, 85.4%, and 78.4% respectively, in soybean. According to Mak *et al.* (2014) [38] the transpiration rate decreased by 57% under drought stress, consequently growth and plant height were decreased noticeably. Furthermore, drought stress can interfere with oxidative stress (Reddy *et al.*, 2004) [55], membrane integrity (Zhang *et al.*, 2019) [80], and enzyme activity (Xu *et al.,* 2015) [78], all of which inhibit soybean plant growth.

Leaf senescence is a common phenomenon under drought stress. Leaf senescence is the normal process of the soybean plant at which the plant diminishes its life cycle. Leaf senescence and death rate of leaves hasten under drought stress, and it is considered as an adaptive process of survival (Munne-Bosch and Alegre, 2004) [45]. Older leaves decrease water loss through transpiration by causing stomatal closure, consequently younger leaves hold restricted amounts of water. Under drought stress, leaf senescence happens from older to younger leaves, and plant under such condition remobilizes its supplements from the source (senescing leaves) to the sink (younger leaves). As drought hastens leaf senescence, the early remobilization of resources from vegetative to reproductive growth causes speedy completion of the vegetation cycle (Munne-Bosch and Alegre, 2004) [45].

Effect of drought stress on root growth

Generally, soybean has two types of root systems, namely primary root (taproot) and lateral (basal) roots. Thu *et al.* (2014) [71] reported root lengths and dry biomass accumulation decreased in soybean under drought conditions stress. Few researchers reported that drought changes root architecture (root depth, root branching density, and root angle) together with the partitioning of root to shoot biomass (Fenta *et al.*, 2014; Dubey *et al.*, 2021) [22, 19]. The soybean which has a larger root mass at depth and a larger lateral root system with more root hairs gets advantage for better water uptake to maintain photosynthesis under drought stress (Tanaka *et al.,* 2014; Vadez, 2014) [70, 84].

As a leguminous crop soybean produces nodules through the symbiotic interaction. Nodule activity and biological nitrogen fixation are closely related to each other. High-yielding soybeans produce sufficient nodules and increase biological nitrogen fixation capacities. It is reported that nodule numbers were significantly decreased under severe drought stress, resulting in a change in the normal growth of roots (Fernandez-Luquen *et al.*, 2008; Marquez-Garcia *et al.*, 2015) [23, 41].

Furthermore, Manavalan *et al.* (2009) [40] reported that nitrogenase activity was reduced (70%) at the first four days of drought. This phenomenon occurs because the respiration is connected to the nitrogenase activity, and the respiration substrates are diminished by the increased oxygen diffusion resistance for bacteria (Naya *et al.*, 2007) [50]. Other reports also stated that under drought stress ureides and free amino acids increased and the activity of sucrose synthase is decreased. As a consequence, the reduction of the carbon flow to the nodes and availability of oxygen inhibits nitrogen fixation in legumes nodules (king *et al.,* 2009) [32]. Thus, the drought affects seriously nodulation activities in soybean.

Effect of drought stress on nitrogen (N) metabolism

It is well recognized that the regulation of nitrogen (N) metabolism is caused by drought stress (Cao *et al.*, 2018; Zhong *et al.,* 2018) [10, 82]. Plant uptakes N through roots in the form of NO_3^- and transports to the leaves for N assimilation. In cytoplasm NO_3^- is transformed to NO_2^- by nitrate reductase, and NO_2^- is transported to the chloroplast, and then converted into NH_4^+ by nitrite reductase. Xu and Zhou (2006) [78] reported NH_4^+ is converted to glutamate and glutamine through the glutamine synthetase (GS), glutamate synthetase (GOGAT). The accumulation of NO_2^- and NH_4^+ in the nitrogen metabolism process is crucial for maintaining the activities of key enzymes, such as GS and GOGAT for plant growth and development (Nguyen *et al.*, 2005) [51]. The activities of GS and GOGAT are regarded as important metabolic indicators of drought tolerance (Nagy *et al.,* 2013; Singh *et al.*, 2013) [48, 61].

Proline is another important product of nitrogen metabolism and plays a vital role in maintaining the integrity of the cytomembrane and protein structure. Few researchers reported that under drought stress condition nitrogen assimilation products, including NO_3^-, NH_4^+, and proline can regulate the selective absorption and transport of ions in plants and maintain the balance of physiological metabolism in soybean (De Souza *et al.,* 2016; Singh *et al.,* 2016) [16, 62].

Effect of drought on flowering in soybean

Flowering is the most essential growth stage of plant which is affected by drought in soybean. Many researchers reported that drought stress during flower formation led to a shorter flowering period and fewer flowers production (Cohen *et al.,* 2021; Soba *et al.,* 2022) [14, 64]. Drought stress interferes not only flower period but also flower opening and turgor maintenance of floral organs (Ram and Rao, 1984). Few reports documented that flowers abortion may occur by affecting pollination in soybean under drought stress (Trueman and Wallace, 1999; Basal and Szabo, 2020) [72, 4]. It is also stated that flowers may prematurely get dry reducing pollination, and the capability to produce pods under drought stress (ICM, 2017) [30].

Effect of drought on pod set and seed development in soybean

Drought stress is the main constraint of soybean production all over the world. In soybean, the pod number per plant is a prime yield trait. It is well recognized that pod set was positively correlated with photosynthetic rate (Liu *et al.,* 2004b; Djanaguiraman *et al.,* 2019) [35, 18]. The rate of pod abortion and early pod development were very high during drought stress, resulting in decreased seed yield of soybeans (Siebers *et al.,* 2015) [60]. Pod abortion rangewas 21% to 65% in soybean under drought stress (Mwanamwenge *et al.,* 1999) [47]. Liu *et al.* (2004a) [36] reported that a low availability of carbohydrate flux occurred from leaves to pods under drought stress, contributing to high pod abortion in soybeans. Therefore, the low pods set of soybeans under drought stress is occurred mostly due to pod abortion.

Pod development is another important stage for yield determination. It is well known that pod development potentiality depends on water availability in soybean. It is reported that the active cell division in the young ovule, responsible for pod expansion, is affected by drought stress (Subbaramamma *et al.,* 2017) [69]. The greatest reduction in the number of pods occurred under drought stress at the early pod formation stage (Sionit and Kramer, 1977) [63]. Liu *et al.* (2004a) [36] reported that pod development depends on the hexose to sucrose ratio. They also stated that pod development was hampered under drought stress by decreasing the hexose to sucrose ratio in soybean.

Desclaux *et al.* (2000) [17] reported that early stress during the seed filling period reduced the number of seeds per pod, while the late stress decreased seed weight. Brevedan and Egli (2003) [9] reported a short period of water stress during seed filling might have larger negative effects on yield in soybean. At the seed filling stage, the balance between N accumulation and distribution in soybean is very important to seed yield and quality (Zhou *et al.,* 2019) [83]. During this stage, different kinds of energy substances e.g., amino acids and sugars are rapidly transported, synthesized, and stored in seeds by utilizing sufficient amount of water. Several studies have shown that drought stress at the reproductive stage significantly decreased soybean seed yield or even resulted in total yield loss (Liu *et al.,* 2004b; Lobato *et al.,* 2009; Masoumi *et al.,* 2010) [35, 37, 42].

Effect of drought on seed yield in soybean

Soybean is sensitive to drought stress during both vegetative and reproductive (flowering to seed filling) stages. Root growth during vegetative stages is very important for potential yield in soybean. Soybean roots grow mostly in the dry surface layer. However, a maximum root proliferation in the deeper layer under drought stress is detrimental for yield (Xiong *et al.,* 2021) [85]. Drought stress during the reproductive stage affects soybean yield by decreasing yield components. It is reported that drought stress during reproductive stage led to a shorter flowering period and production of fewer flowers, and pods, and consequently, a few numbers of seeds per plant (ICM, 2017) [30]. Rudy and Coto (2003) [57] stated that yield loss starts due to a decrease in pod number per plant and gradually increases the yield loss during critical periods of drought during pod formation and seed filling. The seed set period reduces seed number under drought stress consequently, reducing seed yield in soybean (Rotundo and Westgate, 2010; Sehgal *et al.,* 2018) [56, 59]. Basal and Szabo (2019) [4] reported that soybean seed yield significantly reduced when drought stress was imposed during seed filling. Drought stress induces decreased photosynthetic carbon assimilation capacity and seriously affects seed weight in soybean. Our understanding is that soybean seed yield was reduced when exposed to drought stress at any stage.

Effect of drought on seed quality of soybean

Seed quality is the prime concern to maintain the potential next generation. Drought stress produces shriveled, shrunken, and misshaped seeds in soybean (Vieira *et al.,* 1991; Vieira *et al.,* 1992) [68]. Samarah *et al.* (2009) [58] found that the germination and vigor of small-sized category seeds (produced under drought stress) had lower germination than large seeds (good viability). Drought stress at the pod filling stage reduced seed vigor in soybean (Jumrani and Bhatia, 2018) [31]. Besides, the protein and oil contents of soybean seed are the major parameters determining the nutritional value. Drought stress affects protein concentrations increasing them in the soybean seeds (Bellaloui. and Mengistu, 2008; Wang and Frei, 2011; Miransari, 2016) [6, 75]. However, few studies showed no effect (Sionit and Kramer, 1977) [63] or lower protein concentration (Specht *et al.,* 2001, Boydak *et al.,* 2002; Carrera *et al.,* 2009; Chathurika *et al.,* 2019) [66, 8, 11, 12].

In general, many studies indicated that the drought stress reduced oil content in the soybean seed (Specht *et al.,* 2001; Bellaloui and Mengistu, 2008; Rotundo and Westgate, 2009; Sobko *et al.,* 2020) [66, 6, 56, 65], whereas few other reports showed increased oil content with the water deficit (Specht *et al.,* 2001; Boydak *et al.,* 2002) [66, 8]. However, Gao *et al.* (2009) [24] reported that drought stress had little effect on the oil content.

Hlahla *et al.* (2022) [27] reported that drought stress did not significantly affect the starch content for some cultivars and starch content of some cultivars significantly decreased under drought stress. The fatty acid composition differed when drought stress was exposed to soybean. The lipid content increased by 11.4% under drought stress conditions (Navari-Izzo *et al.,* 1990) [49]. Bennet *et al.* (2004) [7] reported that isoflavones were reduced 2.5-fold under drought stress. Drought stress decreased the nonstructural carbohydrate quantity in soybean pods (Liu *et al.,* 2004a) [36]. A significant decrease in seed isoflavones was noticed in soybean seeds under drought stress compared to control (Bennett *et al.*, 2004; Al-Tawaha *et al.*, 2007) [7, 3]; percentage of the reduction of isoflavones increased as the stress increased (Gutierrez Gonzalez *et al.*, 2010) [25]. Therefore, an overall decrease in seed quality in soybean occurred considerably under drought stress.

Conclusion

This review article focused on the effects of drought on soybean growth, yield, and quality of seed. The primary response of soybean under drought stress is slower photosynthetic activity. Drought stress can alter the normal physiological processes of vegetative growth which could lead to plant growth inhibition. It also affects seriously root growth in soybean by changing physiological activities. During regulation of nitrogen (N) metabolism under drought stress, NO_3^-, NH_4^+, and proline can regulate the selective absorption and convey ions in plants, and keep the balance of physiological activities in soybean. Inhibit nitrogen fixation in soybean nodules under drought may happen mainly by the reduction of the carbon flow to the nodes and the reduced availability of oxygen. Drought stress severely hampers the plant growth and development when exposed to any stage in its life cycle. The reduction in crop yield under drought stress at different reproductive stages could be due to the shortening of flowering period and decrease in the pod set and pod development. During the late seed filling stages, drought stress seriously affects yield due to the lack of different kinds of energy substances e.g., amino acids and sugars sucrose transported from leaves to seeds. Plants also undergo developmental and phenological changes when exposed to drought stress such as hastened leaf senescence and the early remobilization of resources from vegetative to reproductive growth, resulting in speedy completion of the vegetation cycle. Seed quality deteriorates under drought stress due to reducing germination percentage, seed vigor, protein concentration, oil content, and isoflavones. Understanding the responses of physio-morphological traits under drought stress is essential for crop improvement under water limiting conditions and this review is presumed to be useful to get a comprehensive updated information on the issue. However, the limited information in this review on the physiological, biochemical and genetic mechanisms of drought defense is supposed to be focused in future.

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