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Drought Effects on Soybean Cultivation - A Review

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Authors' contributions

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

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ABSTRACT

The soybean crop is exposed to many adverse environmental conditions; among them, it is the drought stress, which is responsible for great losses on crop yield. The crops productivity improvement may have a limit due stress factors, as noted by its stabilization in the past years in 80% of their theoretical yield potential. These stress factors may be biotic or abiotic, affecting the plants growth and development. Among the abiotic factors, the drought is considered the most devastating, affecting all plants growth and development stages causing huge losses in soybean yield. In the field, such stresses occur simultaneously, limiting the plants growth and development, compromising sustainable agriculture. This review article focused on Drought effects on soybean cultivation. Field studies that indicate the performance of cultivars in different drought patterns are

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necessary to identify the genotypes response mechanisms. Recent studies in southern Brazil on drought response soybean were generated under greenhouse conditions and fields showing that plants can modulate the metabolism in response to this adverse drought circumstance by targeting different mechanisms, aiming to survival and keep productivity. Studies have shown that cultivars with lower daily water use before flowering, but higher use after flowering had higher grain yield and higher water use efficiency. In the future, since the drought events tend to become more severe and frequent in Brazil and worldwide, the study and obtainment of drought resistant cultivars is necessary.

Keywords: Glycine max; drought tolerance; ABA; water deficit; yield.

1. INTRODUCTION

Among the major international commodities, soybean has a great prominence and it generates huge amounts of money from the exportation and by-products [1]. Possessing excellent nutritional properties, it became widely used as a source of protein, mineral nutrients, oils and natural products. It also has a high content of secondary metabolites such as isoflavones [2], oligosaccharides, phytic acid, goitrogens [3] and phytoestrogens [4]. Soybean is widely used in animal and human consumption [5], especially in foods such as tofu, soy milk, fermented bean paste, soy sauce, tempeh, etc [6]. In addition, it presents health-promoting properties such as prevention of diabetes and obesity and cholesterol reduction [5] besides other industrial and pharmaceutical applications [7].

The damage caused by droughts is extensive and has become a serious global problem [8]. In Brazil, droughts often damage the production of soybean [1], and severe droughts have occurred there four times (2004/2005, 2008/2009, 2011/2012, and 2013/2014 seasons) in the past 10 years [1,9].

One of the main ways to maintain the high soybean productivity in drought conditions is to make use of more drought tolerant varieties. Such crops can be obtained by classical breeding or by biotechnology. Countries like China used this technique and observed an increase in productivity by up to 79% [10]. Thus, lineages with genetic background for drought tolerance have been used in several studies, as in the case of the Brazilian Embrapa 48 [11] and RD29:DREB2A CA plants [12].

Plants have due to their classical genetic origin, different responses to drought stress: 1) avoidance, 2) escaping and 3) drought tolerance [13]. Thus, it becomes important to study the phenotyping and characterization of more drought-tolerant plants. In this way, some studies involving a physiological approach related to drought avoidance mechanisms [14,15] have considered the best effective use of water is associated with the roots depth, smaller transpiration rates, quickness in root development and increase of conducting tissues.

Cultivars with background for drought tolerance have been applied in gene prospecting studies for detecting genes involved in the response to drought [16,17]. To understand the plants transcriptional behavior under these conditions, it is important the use and development of selection tools, such as the molecular and expression markers to drought identified in maize [18], chickpeas [19] and soybeans [17].

In order to make plants respond to drought, many genes are differentially expressed. These genes present in their promoter regions several cis-elements in response to dehydration and heat. During the drought stress, there is a transduction cascade signal which can be dependent or independent of abscisic acid (ABA) [20]. In the genes promoters belonging to the ABA-dependent cascade, there are several cis-regulatory elements, such as ABRE [21,22] recognition MYC sites, [23], MYB [24], NAC [25] and for the ABA-dependent cascade, the DRE cis-element [20].

Drought is the main abiotic stress factor that affects crop productivity, and it is of particular importance in soybean [*Glycine max* (*L.*) *Merril*] due to the susceptibility of this crop to drought, particularly during the reproductive growth stage [26,27,28]. In Brazil, which is the second highest soybean producer worldwide, the occurrence of prolonged periods without rain during the summer has become increasingly common in recent seasons. Losses due to drought events during the period of 2003/2004 and 2014/2015 crop seasons are estimated to be in the US$46.6

billion range [1]. In southern Brazil (Rio Grande do Sul), the 2012 crop is the most recent example of this, with a loss of approximately 10 million tons (72% of affected municipalities) and break in the soybean crop of 36% [29].

Thus, in order to use soybean cultivars in regions with different drought patterns, it is necessary to identify the response mechanism of soybean cultivars and field studies that indicate their performance in the different environmental conditions.

2. ABIOTIC STRESSES WITH EMPHASIS IN DROUGHT

The improvement in crop yields of major grain crops may have a basic limit because of stressful factors, as noted by the stabilization of this improvement [30]. These stressors may be biotic or abiotic and affect the plants growth and development [31]. Among the abiotic factors, the drought is considered the most devastating, affecting all the plants growth and development stages and reducing the soybean yield [31]. The most critical phase for the water deficit affection is during flowering or right after this period [28,31,32]. In reduced conditions of available water, there is a shortening of the grain filling period, it decreases the transference of assimilates to the grain, which means that there is a reduction in the soybean grains weight [33].

[34] observed among the eight soybean genotypes, two recent cultivars (J19 and ZH) with lower daily water use before flowering, but higher use after flowering had the best yield performance in the water stress and terminal water stress treatments in the pot experiment and in the field. These two soybean genotypes and J19, another recent cultivar, had higher grain yield, hundred-grain weights and water use efficiency for grain yield in the water stress treatments than the other genotypes, and higher hundred grain weights, higher water use efficiency, higher pod numbers and the only significant grain yield in the terminal water stress treatment.

Often the term "drought" is not defined based on the plant tissue hydration, but in soil changes and weather conditions [35]. In fact, the water stress implies the interaction of the atmosphere, plant shoot and root system with the soil, all elements connected as a resistance transference series where the water flow occurs. Thus, the unbalance between water transport in the soil-root system and the evapotranspiration potential generates the drought, which normally occurs when the ambient temperature is high and relative humidity and soil is low [35]. The drought along with heat stress often affects the plants, and the effects on crop yields of both factors combined are even more harmful than the isolated effects. Especially in the field, such stresses occur simultaneously, limiting the growth and development of plants, thus compromising sustainable agriculture [35].

According to forecasts, over the next few years, due to global climate change, droughts will become more frequent and severe [36]. Completing the future scenario, increases in the CO_2 concentration, heat waves events, intra and inter-seasonal variations may also increase the complexity of plant drought stress [35,36].

3. PLANTS PERCEPTION AND INITIAL RESPONSE TO DROUGHT

To improve crop productivity in stressful or unfavorable conditions, we must considerer that plants when exposed to water stresses respond and adapt themselves in molecular, cellular, physiological and biochemical levels [37]. In plants, the first step in this adaptation is the perception of drought by the roots located in the upper soil layers. Lack of water decreases the soil water potential, stimulating the synthesis of the abscisic acid (ABA) hormone in root. From the roots, the ABA is translocated to leaves by endogenous signals that operate at long distances. These signals may be chemical (plant hormones and pH), hydraulic or electrical [38,39]. It is recognized that ABA produced in leaves vascular tissues, may affect stomatal closure by transport via passive diffusion and ABA carriers. It particularly happens for members of the subfamily ABC G (ATP-binding cassette) and thus, together with anions and cations (Cl^- and K^+), it induces turgor and volume reduction of guard cells, promoting stomatal closure [39,40], which decreases the gas exchange and results in reduced photosynthetic activity.

In addition to stomatal closure, an increase of endogenous ABA also induces the gene expression response to stresses [39,41]. This induction firstly happens because carriers located in the plasmatic membrane carry out the ABA intracellular transport [42] into the cytosol, in which the ABA induce a variety of molecular events related to a ABA receptor complex [43,44]. When the cell is under drought stress, ABA binds to its receptors (PYR / PYL / RCAR) and activate them by promoting inactivation of PP2Cs and allowing SnRK2s to phosphorylate target proteins, such as type S anionic slow canal, SLAC1 which controls the stomatal response [45,46,47] and transcription factors (FTs) leucine zipper (bZIP) such as members ABF / AREB / ABI5 (ABRE- binding factors / ABRE-binding / ABA insensitive 5) [48,49] involved in activating the expression of ABA cascade downstream genes such as rd29A (dehydration responsive 29A) among others [50,39,43].

Because many genes induced by dehydration are not present in the ABA-dependent cascade, it is suggested the existence of a gene activation cascade independent of this hormone [50]. The largest class of transcription factors of this route are DREB transcription factors (Dehydration Responsive Element Binding protein) who bind to the DRE sequence (Dehydration Responsive Element) also known as CRT (C-repeat and Low-Temperature-Responsive) found in the promoter region of genes responsive to dehydration, salinity, cold and heat, promoting the transcription of these genes [50].

The DREB proteins belong to the family of transcription factors ERF (Ethylene-Responsive Element-Binding Factors) and, within that group, in EREBP subfamily [51]. In *A. thaliana*, the family of transcription factors, DREB / CBF (C-repeat Binding Factor) is classified into two major groups DREB1 and DREB2.

Experiments conducted in greenhouse in genetically modified soybean plants (GM) containing the AtDREB1A gene controlled by the stress induced promoter rd29A demonstrated that plants had higher stomatal conductance, photosynthetic rate and transpiration compared with non-transgenic control plants, suggesting the activation of mechanisms that can lead to increased drought tolerance [52]. Lineages of soybeans containing the same construction were evaluated both in the greenhouse and in field conditions and some yield components were higher when the drought was imposed during the growing season [53,1].

In addition to the DREB1A gene, another transcription factor in the DREB family, the DREB2A gene has been used in obtaining higher tolerant plants to drought, salinity and heat [54,55,56].

In soybeans, GM lineages containing the genetic construct rd29A: AtDREB2A CA were obtained with few (P1397 strain) and multiple copies (P2193 strain) inserted [12]. Both lineages after being subjected to dehydration, showed high levels of expression in root tissue, with reduced photosynthetic rate (A) and stomatal conductance (GS) [12].

4. GENE TRANSCRIPTION IN DROUGHT CONDITIONS

In general, genes that have differential expression under drought stress, transcriptional regulation by FTs, and post transcriptional as RNAi and micro RNAs are classified into two categories: genes encoding functional proteins, and genes encoding regulatory proteins [57]. Thus, this group consists of proteins such as LEA (Late embryogenesis Abundant), chaperones, key enzymes for osmolytes biosynthesis, osmotin, proline and sugars transporters, binding proteins to mRNA, enzyme detoxifying, anti-freeze proteins and several proteases [58].

On the other hand, the group of regulatory proteins is comprised of several transcription factors, signaling molecules (such as binding proteins, calmodulin), phosphatases, kinases and enzymes involved in phospholipid metabolism, or regulatory proteins and protein factors involved in additional regulation of signal transduction [58].

5. BIOCHEMICAL AND METABOLIC PLANT RESPONSES UNDER DROUGHT STRESS

When the plants are exposed to drought they neutralize the negative effects of this exposure through the activation of biochemical responses including the maintenance of intracellular homeostasis of ions, synthesis and osmolytes accumulation and elimination of reactive oxygen species (Reactive Oxygen Species - ROS) [59]. The water deficit produces oxidative stress in plants because it increases the production of ROS (as singlet oxygens), which consequently causes damage and degradation of proteins, inactivation of enzymes and cells membrane lesions [60,61].

To decrease the toxicity of reactive oxygen species produced under stress conditions, the cells produce antioxidant enzymes such as SOD (superoxide dismutase, EC 1.15.1.1), CAT (catalase, EC 1.11.1.6), and POD (peroxidase, EC 1:11. 1.7). Another way to reduce this toxicity is the application of nutrients as N (nitrogen), K (potassium), Ca (calcium) and Mg (magnesium) that perform the elimination of ROS [62]. Antioxidants molecules as phenolic compounds, flavonoids, anthocyanins and lignin may also be synthesized to minimize cell damage [60,63].

In general, these antioxidants and other compatible osmolytes are produced in response to a signaling cascade, which helps to promote fluid and osmotic balance. The expression of MAPK signaling cascades (Mitogen Activated Protein Kinases) and CDPK (Calcium Dependent Protein Kinase) is increased by the initial effects of stress, namely the induction of Ca^{2+} influx and reorganization of the cytoskeleton [63,64].

Among the compatible osmolytes produced, proline and glycine betaine are accumulated and facilitate water absorption [65,66] in drought conditions. Both methods besides the protection against the increase of ROS in the cytosol and vacuoles (pro vacuole and cytosol), the osmotic adjustment protecting proteins, DNA and membranes [67,68].

During conditions of water stress, proline attenuates the super reduction of photosystem I (PSI), increasing the availability of NADP +, glutamate reduction arising in the synthesis of proline, in the chloroplast, and prevents disruption of redox-sensitive pathways [65]. In addition to performing the elimination of ROS during drought, proline also protects the photosystem II (PSII) and prevents lipid peroxidation [69]. Also acting in the photochemical efficiency of PSII is glycine betaine, which does not directly eliminate the production of ROS during osmotic stress [70], but protects the cells against oxidative damage [70,71]. The glycinebetaine accumulation is more efficient in chloroplasts, as noted by its action on the PSII than in other cellular compartments [71]. Furthermore, Hoque et al. [72] showed that the amino acids proline and glycinebetaine both have roles in the regulation of antioxidant enzymes.

There are in addition, soluble sugars that besides contributing to the regulation of ROS signaling have the role of osmotic adjustments in conditions of abiotic stresses [73,74]. These sugars are involved in the protection and metabolism of the elimination and production ROS pathways, such as pentose-phosphate oxidative pathways, photosynthesis and mitochondrial respiration [75]. Among these sugars is the trehalose, a disaccharide that acts as signaling ABA molecule under stress conditions [76]. In transgenic rice plants expressing the *Escherichia coli* trehalose under drought conditions, the photo-oxidative damage to PSII was lower when compared with non-transformed plants [77].

Another soluble sugar that acts in regulation and signaling of ROS under stress is mannitol, which protects the chloroplastic apparatus against photo-oxidative damage caused by HO· [78], as observed in transgenic tobacco plants, which produced more mannitol directed to the chloroplast, greater HO· elimination capacity and the greater resistance of transgenic plants to oxidative stress [79,80].

6. PHYSIOLOGICAL PLANTS RESPONSES UNDER DROUGHT

6.1 Root System Behavior

The drought affect the plants when the ambient temperature is high and the relative humidity is low and this combination affect the plant and tissue hydration and therefore cannot be defined only as a period of crops harmful dry weather, in which changes in soil conditions and weather are occurring [35].

The emergence of drought occurs when, during the crops growing season, the rains are insufficient to attend the plants demand, or there is insufficient water in the soil [81,36,63,82]. Thus, the water deficit occurs due to an imbalance of the water flow rate and the potential of transpiration because of the disparity in the water transference resistance among the soil, the root system, the shoot and the atmosphere [35].

Under normal conditions, the soil-roots water flow is regulated by the root hydraulics conductance (Lp), which depends on the water potential gradient between the soil and roots and varies among different types of roots, along its length, age, root growth and plasticity [83]. Lp is modeled by the permeability of the cell membrane and water channels (aquaporins), which at the beginning of a short-term drought can cause an increase and then a decrease of Lp [35]. When this drought extends, there is a root exodermis and endoderm suberisation, promoting greater reduction in Lp [84]. The decrease in Lp on short and long term drought, although reducing the plant water flow, it prevents the waste for the dry soil. In longer episodes of drought, Lp value can be further reduced by xylem embolism [35].

The drought conditions begin with the interaction between the soil and the root system, which thought its architecture decreases absorption efficiency by roots agglutination [85,86], also affecting the vertical heterogeneity of available water in the soil [87]. In order to maintain the water absorption for longer period, Lp roots (aquaporins and suberization) modulates the extent and speed of this process, and it helps to increase the absorption of water in wetter areas, compensating for the low absorption in drier ones [88,89]. This increased absorption in wetter areas can be modulated also by roots exudates, mucilage and possibly the solute accumulation [90,91].

In the promulgation of drought, there may be a faster roots grow that are in contact with the wetter regions of the soil [81,92], but if the water deprivation remains, there may be a decoupling between carbon production in leaves and roots, reducing in this way the root growth. Another roots adaption to drought is the growing of the main root in direction to the deeper soil layers in seek for water [31,93]. This indicates that the plasticity of root is fundamental to absorb more water, as observed by increased root ratio: part of aerial resulted from the increased biomass root partition [31]. Research has shown that the deep roots can contribute to the better use of water and nutrients. [94] indicated that the highest soybean yield is only obtained if the root system reach up to 1 m deep. If the roots reach only 60 cm for example, soybean production reaches 70% of maximum. However, when this deep root growth is restricted, it reduces the volume of soil explored by the roots for water and nutrients which, in practical terms, it means that the size of the water reservoir available to plants is substantially reduced.

6.2 Biological Nitrogen Fixation

Studies have shown that in drought conditions the biological nitrogen fixation is reduced as observed by the reduction of nitrogenase activity (70%) during the first four days of drought [31]. This occurs because the respiration connected to the nitrogenase and its activity as well as the accumulation of oxidized lipids, respiration substrates and activation of antioxidant genes, are diminished by increased oxygen diffusion resistance for bacteria, impairing its respiratory activity [95]. Other factors such as increased ureides and free amino acids, decrease the activity of sucrose synthase node, reduction of the carbon flow to the nodes and the reduced availability of oxygen also inhibit nitrogen fixation in legumes nodules [96,97]. Thus, the drought affects directly and significantly the nodulation activity [31]. As a result, the reduction of nitrogen supplement for the production of proteins causes crop yield decrease [98].

In a recent study in Brazil, [99] assessing physiological traits of nitrogen fixation drought-tolerant (R01-581F, R01-416F and R02-1325) and drought-susceptible (CD 215 and BRS 317) genotypes of soybean subjected to drought. The nitrogen fixation drought-tolerant genotypes generally showed higher concentrations of N, K and Mn in shoots, irrespective of the water condition. Exposure to drought increased total soluble sugars in nodules in all genotypes, as well as the concentrations of ureides in leaves and nodules, whereas ureides in petioles increased only in the susceptible genotypes. The R01-581F showed the best performance, with potential for use in breeding programs aiming at drought-tolerant varieties.

6.3 Gas Exchange

Under natural conditions, the plant can switch from a saturated soil with water to a land where there is little water available and this transition phase occurs the decrease in stomatal conductance, depending on the kind and quantity available water in the soil [31]. In a study of soybean in conditions of moderate drought, Liu et al. [100] observed a decrease in stomatal conductance simultaneously with an increase in the amount of ABA in the xylem responding to chemical signals triggered by stress [31]. In drought conditions, the loss of water through the stomata during gas exchange is composed of cuticular conductance (and any residual conductance), since the stomata tend to close under these conditions [31]. Under normal conditions this conductance is too low and is neglected compared to the total conductance [31].

It is important to emphasize that in plants such as soybeans and especially Xerophytic species, the density of the foliar pubescence is responsible for increasing the leaf reflectance, and therefore by the lower temperature in high irradiance conditions [31]. Studies have shown that soybean lines with dense pubescence have deeper root length in addition to greater root density and higher vegetative vigor [101], restriction of water loss by perspiration and increased photosynthesis [102].

The stomata are responsible for co-regulation of the CO_2 flux into the atmosphere and transpiration by water loss [103]. As much of the CO_2 and water exchange is held in the leaf, the stomata are a major component in water use efficiency (WUE) defined by the amount of water used to fix carbon [103]. Thus, this is a measure of the effectiveness of a crop to save water, reflecting how much water can be converted into grains [35,81]. Evaluations conducted in the field had demonstrated variations in the WUE rate of soybean plants, a result that was related to different plants genetic bases [104]. Commonly, high WUE values in drought conditions can help maintain crop yields [31].

A low stomatal conductance, related to the difference in stomatal density (SD) can give a good standard of the conservative use of water [14]. This stomatal density is regulated in *A. thaliana* by a single gene called ERECTA, discovered in studies of gene regulation transpiration [105]. The lowest rate of water loss per unit of leaf area can also be generated by genotypic differences, as demonstrated in millet by [15].

Plants can reduce the consumption of water in the soil (initial vigor), limiting its use during growth, in order to use this reserved water mainly for the grains filling [19,107]. Another mechanism that limits the use of water in plants is the low gas exchanges in normal growth and high VPD as observed in soybean where the VPD > 2.0 kPa limits the growth of some genotypes [109]. Furthermore, the lower transpiration in tolerant plants in comparison to sensitive ones to drought, may be considered a third capping mechanism [106,108,109].

Particularly in drought, the decrease in internal CO_2 reduces photosynthesis by inhibiting the synthesis of photosynthetic enzymes and ATP [60,110]. In this stress the release of calcium and magnesium ions of their connections the removal of external proteins and the decrease in electron transport suppress the photochemical efficiency of photosystem II [60,61].

6.4 Plants Response Mechanisms to Drought

The plants generally use different mechanisms for dealing with drought, which can be classified into three groups [13]: escape, avoidance and tolerance to drought. Plants who use escape as a strategy may have a shorter life cycle, completing its cycle during the water available period, and producing only few seeds [31]. The plants that avoid drought use various mechanisms to maintain high water status during periods of drought stress, such as reducing evaporation and an effective water uptake by roots [31]. Such mechanisms include morphophysiological characteristics as the depth of roots, an increase in the proportion of conducting tissues, the rapid issue of new roots, the osmotic adjustment, leaf rolling, the leaf area reduction, leaf abscission, increased trichome, deposition of epicuticular waxes, early flowering and a hardening of the cell wall. However, as the soil water potential decreases and the stress intensifies, the tolerance mechanisms become critical for survival [111].

Tolerant cells must have the ability to regulate metabolic processes as they dehydrate the cells to repair the damage [112]. Products of uncontrolled metabolism, particularly the ROS, have been identified as causal agents of these damages [78,113,114]. In addition, tolerant plants can also carry out the accumulation of molecular protectors and the remobilization of water soluble carbohydrate in stems, among other processes [115].

According to Lawlor [116] there is also a fourth response mechanism to drought: survival. In this case, organs, tissue and plant cells cease their growth, during drought conditions, conducting the called "state of quiescence". After the deficit period, these plants quickly recover their normal water status and their basic cellular functions return to normal.

7. CONCLUSIONS

This review article focused on Drought effects on soybean cultivation. Field studies that indicate the performance of cultivars in different drought patterns are necessary to identify the genotypes response mechanisms. Recent studies in southern Brazil on drought response soybean were generated under greenhouse conditions and fields showing that plants can modulate the metabolism in response to this adverse drought circumstance by targeting different mechanisms, aiming to survival and keep productivity. Studies have shown that cultivars with lower daily water use before flowering, but higher use after flowering had higher grain yield and higher water use efficiency.

In the future, since the drought events tend to become more severe and frequent in Brazil and wordwide, the study and obtainment of drought resistant cultivars is necessary.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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