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The effects of drought stress on soybean (*Glycine max* L. Merr.) growth, physiology and quality – Review

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SUMMARY

Abiotic stresses are one of the most limiting factors inhibit plant's growth, leading to a serious production loss. Drought stress is one of the most destructive abiotic stresses and is still increasing year after year resulting in serious yield losses in many regions of the world, consequently, affecting world's food security for the increasing world population. Soybean is an important grain legume. It is one of the five major crops in the world, an essential source of oil, protein, macronutrients and minerals, and it is known as the main source of plant oil and protein. Harvested area of soybean is increasing globally year after year. However, soybean is the highest drought stress sensitive crop, the water deficit influences the physiology, production and seed composition of this crop. We introduce a review for literatures concerning the changes of the above traits of soybean exposed to drought stress, with past explanations for these changes.

Keywords: *soybean, production, quality*

DROUGHT STRESS

Biotic and abiotic stresses are one of the most limiting factors inhibit plant's growth, leading to a serious production loss (Kang et al. 2002, Mahajan and Tuteja 2005).To adapt with such stresses, plants get morphological, physiological and molecular changes (Bray 1993, Seki et al. 2003, Yamaguchi-Shinozaki and Shinozaki 2006). Water scarcity is a major factor limiting agricultural production all over the world, consequently, many efforts were and should be made to adapt edible crops preventing drought stress from making critical harms to them.

SOYBEAN

Soybean is an important grain legume. It is one of the five major crops in the world, an essential source of oil (18–22%), protein (35–40%), macronutrients and minerals, and it is known as the main source of plant oil and protein (Lei et al. 2006, Maleki et al. 2013). Among crops, soybean is the highest drought stress sensitive (Maleki et al. 2013). Its water requirement is relatively high (Yang et al. 2003), so it is quite important to use the genotypes which best exploit available water and use it more effectively.

EFFECTS OF DROUGHT STRESS ON SOYBEAN

Effects of drought stress on soybean morphological and physiological traits

Drought stress was demonstrated to affect soybean morphology and physiology. Navari-Izzo et al. (1990) found that drought-stressed soybean resulted in a 25% reduction in leaf water potential (LWP). Five days of drought stress during pre-flowering stage resulted in adrop of the LWP to -2.2 MPa, compared to -1.4 MPa for control plants (Lei et al. 2006), which was consistent with Liu et al. (2003) results by which a decrease of WLP was recorded for drought-stressed soybean compared to watered control. Many studies reported similar results (Pennypacker et al. 1990, Siddique et al. 2000, Fu and Huang 2001, Shaw et al. 2002, Liu et al. 2004ab, Liu et al. 2005, Hao et al. 2013). Moreover, it was concluded that drought stress affected not only soybean leaf water potential, but also pod water potential causing both to fell (Liu et al. 2004c). Makbul et al. (2011) recorded a significant decline of soybean leaf water potentialfrom -0.88 MPa in unstressed leaves to -1.18 MPa in drought stressed ones, moreover, they suggested that this decline may have resulted in the significant decrease chlorophyll content by 28% in drought-stressed soybean. Hao et al. (2013) found that the chlorophyll content of the drought-stressed soybean decreased by 31% compared to control plants. Similar results were provided by Atti et al. (2004).

Schulze (1993) reported that drought stress decreased the leaf water potential, resulting in a reduction of the swelling pressure and consequently causing the stomatal closure. Giorio et al. (1999) also reported good positive relationships between leaf water potential and stomatal conductance. Stomatal control was considered as a main physiological factor for optimizing water use under drought conditions (Makbul et al. 2011), preventing excessive water loss under extended drought conditions (Ku et al. 2013). Stomatal conductance, as compared to control, decreased 60% under drought stress (Hao et al. 2013), this result was consistent with previous studies (Liu et al. 2005, Makbul et al. 2011), and was confirmed later (Mak et al. 2014, Mutava et al. 2015). Lei et al. (2006) noticed that the stomatal conductance decreased as the drought progressed, confirming the conclusion that the impact of moisture deficit was greater at the severe stress than at the medium stress (Atti et al. 2004), who demonstrated a reduction in stomatal conductance, transpiration rate and photosynthetic rate by 92%, 85.4% and 78.4%, respectively, under water stress. They showed that stomatal conductance was correlated with transpiration rate more than with photosynthetic rate, which was reported earlier (De Souza et al. 1997).

Transpiration rate decreased 53% (Hao et al. 2013), and 57% (Mak et al. 2014) under drought stress, this decrease was duemainly to a decrease of stomatal conductance which was controlled by root-originated ABA, as a 50-fold xylem ABA was measured under drought stress (Liu et al. 2005), that, however, was reported earlier (Samet et al. 1984, Liu et al. 2003) with a significant increase as the stress became severe (Liu et al. 2004b). Moreover, Mutava et al. (2015) reported a significant ABA increase in a drought tolerant soybean genotype more than in a drought susceptible one under drought stress conditions.

Photosynthetic rates, after 9 days of drought stress, were significantly lower than in the control plants (Liu et al. 2004a). Similar results were obtained for soybean seedlings (Hao et al. 2013). These results were consistent with other reports at different soybean growing stages (Lei et al. 2006, Mak et al. 2014, Mutava et al. 2015).

Soybean seedling height decreased 4.3% under drought stress (Navari-Izzo et al. 1990), which was reported later at different stages (Atti et al. 2004, Hao et al. 2013, Mak et al. 2014). Particularly, drought stress at V4 stage reduced the plant height more than at R2 (full flowering), R4 (full pod formation) and R6 (full seed filling) stages (Li et al. 2013, Maleki et al. 2013). Although Sionit and Kramer (1977) reported no significant differences on plant height under drought stress, most researchers reported the opposite (Brady et al. 1974, Kadhem et al. 1985, Demirtas et al. 2010, Maleki et al. 2013). This reduction might be caused by a drought tolerance mechanism, as cell swelling, cell wall and synthesis enzymes are reduced, consequently, growth and plant height are decreased (Levitt 1980, Austin 1989).

It was concluded that drought stress increased the root length as the roots searched for water, in addition to the formation of fine roots able to penetrate smaller soil pores (Turner 1986, Komatsu and Hossain 2013, Maleki et al. 2013, Khan and Setsuko Komatsu 2016). However, the root weight of the drought-stressed soybean plants was reduced as compared to the controls (Kausar et al. 2012, Mohammadi et al. 2012, Hao et al. 2013, Oh and Komatsu 2015, Khan and Setsuko Komatsu 2016).

Moreover, root to shoot ratio increased under water deficit conditions, because roots are less sensitive than shoots to growth inhibition by drought stress (Wu and Cosgrove 2000, Franco et al. 2011). Soybean shoot dry matter was reduced under drought stress (Liu et al. 2005, Hao et al. 2013, Mak et al. 2014). The reduction was higher when stress was applied during podding than during seed filling stage, which in part was higher compared to drought stress application during flowering stage (Li et al. 2013).

Relative water content decreased 33% under drought stress (Hao et al. 2013), and it was decreased more for a drought susceptible soybean genotype compared to drought tolerant one (Mutava et al. 2015).

Karam et al. (2005) reported a reduced soybean leaf area index under drought stress conditions by an average of 30% compared to controls. Similar results were obtained later (Atti et al. 2004, Demirtas et al. 2010, Li et al. 2013).

Both establishment and activity of the legume–Rhizobium symbiosis were reported to be extremely sensitive to drought stress (Zablotowicz et al. 1981, Kirda et al. 1989). Consequently, legume productivity can be greatly reduced both by moderate and severe drought (Saxena et al. 1993, Subbarao et al. 1995). Smith et al. (1988) reported substantial decreases in nodule mass in drought-stressed soybean. However, Sinclair et al. (1988) noticed a decrease in nodule number and dry weight only after a severe drought.

Samarah et al. (2009) and Heatherly (1993) reported the germination rate to be reduced for soybean under drought stress during seed filling period. Flowering period, podding period, flower number and leaf number were reported to be reduced under drought stress (Atti et al. 2004, Mak et al. 2014, He et al. 2016).

Effects of drought stress on soybean production traits

Frederick et al. (2001) noticed a large effect of drought stress on the final number of soybean branches formed. Later, Atti et al. (2004) reported that water reduced the mean number of branches by 28% compared to the controls. The number of pods per plant was reported to be reduced under drought stressby many researchers (Kadhem et al. 1985, Desclaux and Roumet 2000, De Costa and Shanmugathasan 2002, Demirtas et al. 2010, Sadeghipour and Abbasi 2012, Li et al. 2013, Mak et al. 2014). At the beginning of pod development, drought stress reduced pod number by 92.7%, while during pod lengthening, the reduction was 81.6% compared to the controls, due to the cumulative effects of reductions in pod induction, young pods [due to abortion – Kokubun (2011)] and pod enlargement (Atti et al. 2004) and to the reductions in flower number (He et al. 2016).

Reduced seed number per plant under drought stress was recorded (Demirtas et al. 2010, Li et al. 2013, He et al. 2016), this results, however, was reported earlier (Kadhem et al. 1985, Karam et al. 2005). Highest reduction in seed numbers per plant occurred in flowering stage (Sionit and Kramer 1977, Smiciklas et al. 1992, Maleki et al. 2013). Bord and Hartville (1998) suggested that drought stress during flower formation led to a shorter flowering period and produced fewer flowers, fewer pods, and consequently, significantly smaller numberof seeds per plant. However, it was concluded earlier that drought stress during the seed set period reduces seed number (Meckel et al. 1984, Rotundo and Westgate 2010).

Weight of soybean seeds was affected by drought stress (Sionit and Kramer 1977, Rose 1988, Liu et al. 2003, Karam et al. 2005, Demirtas et al. 2010, Sadeghipour and Abbasi 2012, Li et al. 2013). 15.2% reduction in the weight of 100 seeds grown under drought stress during R5 (beginning of seed filling) stage was noticed compared with non-stressed plants (Gutierrez-Gonzalez et al. 2010), which was confirmed later by He et al. (2016). It was suggested that the weight of grain is determined in the late reproductive stage, and therefore, more affected by drought stress at R5 (beginning of seed filling) stage, this decrease could be due to loss of assimilate to seeds (Yordanov et al. 2003), or to a shortened seed filling period (Demirtas et al. 2010).

Soybean seed yield, when exposed to drought stress, was reduced (Rose 1988, Kokubun et al. 2001, Sadeghipour and Abbasi 2012, Li et al. 2013). More specifically, severe drought stress reduced the seed yield of soybean more than moderate drought stress (Dornbos and Mullen 1992).

The soybean genotype was found to have a role on yield loss (Bellaloui and Mengistu 2008, He et al. 2016), which is consistent with the conclusions of Brown et al. (1985) who found the reduction to be significant (Maleki et al. 2013).

Doss et al. (1974) and Sionet and Kramer (1977) found that the drought stress during R3 (beginning of pod formation) and R4 (full pod formation) stages resulted in greater yield reduction than that occurred during R1 (beginning of flowering) and R2 (full flowering) stages. Moreover, Demirtas et al. (2010) and Maleki et al. (2013) concluded that drought stress during R5 (beginning of seed filling) stage caused the most reduction, which was previously reported (Ashley and Ethridge 1978, Huck et al. 1983, Eck et al. 1987, Foroud et al. 1993, Karam et al. 2005). It was suggested that drought stress during R5 (beginning of seed filling) stage shortened the seed-filling period and reduced seed yield (Meckel et al. 1984, Frederick et al. 1991, Smiciklas et al. 1992). Others suggested it to be due to the reduction of pod numbers per plant (Atti et al. 2004), seeds number (Dornbos et al. 1989), and seeds weight (Samarah et al. 2006, Demirtas et al. 2010, Maleki et al. 2013). However, seed yield was found to have a significantly positive correlation with plant height, number of pods and seeds per plant, seed weight, harvest index and days to maturity (Georgiev 2004, Maleki et al. 2013). A reduction in soybean biomass due to drought stress was early reported (Read and Bartlett 1972), and confirmed lately (Khan and Setsuko Komatsu 2016). Particularly, the biomass was significantly decreased, when drought stress was applied in the pod filling period (Demirtas et al. 2010) more than V4 stage (Maleki et al. 2013).The effect of drought stress on harvest index was significant, as drought occurrence at R5 (beginning of seed filling) stage reduced it by 27.9% compared to control (Maleki et al. 2013). Ashley and Ethridge (1978) suggested that the harvest index was reduced due to the loss of flowers and the decrease in seed numbers per plant.

$WUE_{yield, biomass}$(Water Use Efficiency) for soybean was improved under a certain range of drought stress (Liu et al. 2005, Lei et al. 2006, Demirtas et al. 2010, Li et al. 2013). Moreover, Karam et al. (2005) found that soybean WUE at R2 (full flowering), R6 (full seed filling) stage was 13 and 4% higher than the control, respectively, whereas at R5 (beginning of seed filling) was 17% lower than the control. That was recently demonstrated (He et al. 2016).

Effects of drought stress on soybean quality traits

The protein and oil contents of soybean seed are the major parameters determining the nutritional value (Chung et al. 2003). The relationship between drought stress and soybean seed composition, however, still remains controversial (Medic and Atkinson 2014). Dornbos and Mullen (1992), Kumar et al. (2006) and Rotundo and Westgate (2009, 2010) reported 2–23% increased protein contents under drought stress compared to controls. Environmental factors affect protein concentrations increasing them in the harvested parts (Rose 1988, Dornbos and Mullen 1992, Bellaloui and Mengistu 2008, Wang and Frei 2011). However, few studies showed no effect (Sionit and Kramer 1977) or lower protein concentration (Rose 1988, Specht et al. 2001, Boydak et al. 2002, Carrera et al. 2009). Differences among the reported conclusions were suggested to be due to the timing and intensity of the drought stress during the different stages (Carrera et al. 2009). Bellaloui and Mengistu (2008) suggested that the plant's response to drought stress might be cultivar-dependent.

In general, soybean seed protein content is negatively correlated with the amount of seed oil (Chung et al. 2003). Results of most studies indicated that the drought stress reduced oil content in the seed (Rose 1988, Specht et al. 2001, Bellaloui and Mengistu 2008, Rotundo and Westgate 2009), whereas few other reports showed increased oil content with the water deficit (Specht et al. 2001, Boydak et al. 2002). However, Gao et al. (2009) reported that drought stress had little effect on the oil content. The effect of drought stress at different stages was significant on oil content, and the lowest oil percentage was obtained when drought stress was applied at V5 stage (Dornbos and Mullen 1992, Smiciklas et al. 1992, Maleki et al. 2013).The oil content had a significantly positive correlation with seed weight (Maleki et al. 2013).

The fatty acid composition differed when soybean was subjected to drought stress; a decrease in Palmetic, Linoleic Linolenic acid and an increase in Stearic and Oleic acid were noticed (Bellaloui and Mengistu 2008, Gao et al. 2009). The lipid content also increased 11.4% under drought stress conditions (Navari-Izzo et al. 1990), particularly,an increase in glycolipids, diacylglycerols, triacylglycerols and free sterols was recorded while free fatty acids and phospholipids decreased by drought stress (Navari-Izzo et al. 1990). Dornbos and Mullen (1992) suggested that the increase in triacylglycerols and diacylglycerols of stressed soybean increased the proportion of stearic acid, while oleic acid content decreased.

Bennet et al. (2004) found that isoflavones were reduced 2.5-fold under drought stress applied on soybeans. These results were confirmed as unstressed soybean seeds were found to have increased total isoflavone, daidzein, and genistein contents by 1.2-folds but without differences in the content of glycitein (Lozovaya et al. 2005).

Britz and Kremer (2002) concluded that the tocopherol content of soybeans was insignificantly affected by the drought stress. Drought stress decreased the non-structural carbohydrate quantity in soybean pods (Liu et al. 2004c).

Free proline increased in drought stressed soybean plants (De Ronde et al. 2004) because of the increase in the of enzymes involved in proline biosynthesis and the decrease of those involved in proline degradation (Kiyosue et al. 1996).

Significant decrease in seed isoflavones in soybean seeds under drought stress compared to control was noticed (Bennett et al. 2004, Al-Tawaha et al. 2007); the reduction increased as the stress increased (Gutierrez Gonzalez et al. 2010). Drought stress increased alfa-tocopherol concentration (Britz and Kremer 2002).

CONCLUSIONS

Drought stress is an important abiotic stress affecting soybean traits, resulting in considerable yield losses by different mechanisms. More studies should be generated in order to better understand the soybean seed quality under water deficit conditions, as the past studies demonstrated different results. In addition, different soybean genotypes need to be compared in order to find tolerant genotypes.

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