

Sugar and Sucrose metabolism in Soybean (*Glycine max*) leaves and roots: Impact of Drought and heat stress at different growth stages

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Abstract

High temperature, water deficiency, and rapid fluctuations in climate damage plant growth, maturation, yield, and seed characteristics in soybean (*Glycine max*). Drought stress and high-temperature stress are major environmental attributes that restrict plant development; these two issues frequently take place alongside nature. Therefore, the major focus of this overview is to demonstrate the analysis of the effect of these issues in combination and independently in soybean. Drought stress decreases photosynthetic carbon assimilation capacity, contents of glucose, starch, and fructose in seeds during the filling stage also reduce shoot biomass and leaf photosynthetic rate. Drought stress decreased the starch contents but enhanced the quantity of soluble sugar and sucrose in leaves, but all of these contents are increased in the roots. Sucrose transport genes and enzymes are triggered and up-regulated during the early stages of seed development under water stress which can be one of the functional mechanisms for soybean plants to restrict water scarcity issues. Sucrose is involved in responding to many abiotic stresses. These stresses not only affect the current status of the plant's production but also generated after-effects that's why the confirmation of adequate water supply is important, especially at the flower blooming and pod forming phase to ensure rich biomass production potential in soybean. When water deficiency is imposed at high temperatures it not only affects the reproductive stage but also seed degradation is worse as compared to it prescribed at the vegetative stage. Elevated heat disturbs the structural and functional vigor of protein storage bodies that collect seed storage proteins, plasmolysis also takes place.

Keywords: Drought, plant development, carbon assimilation capacity, pod filling stage, starch.

Introduction

Soybean (*Glycine max* L. Merr) was introduced as a forage crop in the United States but has emerged as a rich protein source and oilseed legume for food, feed, and various industrial products (Hari B., et al, 2020). Soybean is an annual crop. Agriculture heat stress and drought stress are natural disasters all over the world that threaten social activities and food security. In addition this increase in global warming to the activities of human beings like industrialization, more chemicals usage, etc. which affect social and economic development in many countries. Soybean plant development and yield potential are down-regulated by many biotic and abiotic stresses but modern breeding techniques have increased yield. (Cui, Y., et al, 2020). Soybean is approximately heat tolerant rather than other crops with a vegetative ideal temperature of ~30 C but pollination and seed development are extra delicate to increase in temperature the optimal reproductive temperature is 22–24C. Soil compaction is also a major drawback in those fertilized areas under the zero-tillage system (Chebrolu., et al, 2016). The basic source of the establishment of compressed soil is the absence of crop rotation, plants with a shallow root system, the nature and amount of straw in the upper layers of soil, improper use of mechanical chiseling, and the absence of soil conservation practices. Different biological chemicals and physical factors like rhizosphere micro-biome, pathogens, mineral elements' insufficiency, temperature, water, mechanical obstruction, and oxygen which has an impact on root development and plant nourishment. These limitations caused heat and drought stresses (de Moraes., et al, 2021). High temperature and shortage of water are major abiotic stresses that retard plant maturation, these two problems occur side by side in nature. Water deficiency and elevated temperature strongly interact with each other and their collective effect has more dangerous impacts instead of separate stress (Jumrani., et al, 2018). Drought stress is one of the main climate fluctuation issues that not only decrease plant production but also the standard of the crop and becomes a serious hazard to agriculture. Seed composition, weight, size, and moreover final soybean plant production are regulated by the seed filling phase which is the main growth phase of a plant. Seed filling phase contains the process of carbohydrate mobilization, and transport along with the biochemical composition of lipids and proteins in the development of seeds (Du, Y., et al, 2020). Seed standard is affected by many components like seed size, seed moisture level, seed deterioration, mechanical harm, pathogens, genetic constitution, soil fertility, and other environmental components. (Jumrani., et al, 2018). Forced seed maturation is very common in soybean because of high temperature besides temperature, water deficiency during the seed fill

stage also have an unfavorable effect on soybean complexity. Its intrinsic features such as thin seed coat, high content of unsaturated fatty acids, vulnerability to the environmental position of hilum, etc. make soybean seed vulnerable to conditions of the environment. Tetrazolium test, seedling vigor index has also been broadly used for evaluating the vigor of the seed.

Tetrazolium test is faster and more extensive in addition to germination potential also discloses the sources of seed delicacy such as field and storage declining, mechanical harm, and any other biotic or abiotic factor and also aids in discrimination of seed into many classes based on their viability. And based on heat and drought stress combined effect on soybean is necessary for improving growth, development, and yield. Seeds produced in different areas under different environmental conditions exhibit a broad range of vigor and viability (Jumrani., et al, 2018). Drought originates a lot of symptoms in plants such as a change in metabolism, increased oxidative stress, and inhibition of plant photosynthesis. Protein and oil are major components in soybean seed their proper maintenance is also very essential as both elements are accumulated in distinguished bodies in soybean seed, protein storage vacuoles possess seed storage proteins while oil is collected in lipid bodies.

The stress at the vegetative phase plays an important role in the decline in photosynthesis, leaf area, and root/shoot biomass once the stress over a plant can recover up to a fixed limit but the loss ultimately occurs (Du, Y., et al, 2020). The possibility of betterment in the reproductive phase is less because of disturbance in reproductive processes such as reproductive capability and seed maturation when the stress is being applied to plants. Sucrose is not only the major photosynthetic by-product of complex plants but also the carbon base of physiological metabolism and also a signaling molecule that correlates the link within plants as a source and sink which plays a necessary part in seed development and plant maturation (Cui, Y., et al, 2020). Seeds are major storing bodies in soybean plants their final phenotypic and genotypic attributes and traits are observed by the nutrient reserved accumulation and seed filling process. Sucrose is the carbon base of energy metabolism and amino acid synthesis for seed development and maturation. Non-adapted landraces are an outstanding genetic resource for stress-tolerant varieties in soybean germplasm. Sudden climate change and changes in precipitation patterns could increase the severity of water and high-temperature stress. The essential vegetative part of the plant is the root, which provides water, minerals, essential nutrients, salts, soluble sugar, sucrose contents, and aboveground

strength to the plant for better survival and growth (Wei, Y., et al, 2018). The root/shoot ratio is the relative dissemination ratio of root and shoots and above and underground biomass, and is also a necessary component to measure approximate drought tolerance in plants. Changes in root\shoot ratio in soybean seedlings under water scarcity can help us to acknowledge the flexibility of soybean cultivars under stress conditions (Du, Y., et al 2020). Photosynthesis is one of the necessary main functions that balanced carbon fixation and metabolism. Drought stress alters the distribution of carbon in plants, and lowers the photosynthetic rate, leading to depleted energy and ultimately yield loss (Du, Y., et al 2020).

The Impact of Drought Stress on Plant height

The impacts of water scarcity during various phases of soybean maturation are being observed. All treatments experienced rapid height development early in the growth cycle it peaked at the end of the setup phase under (FPS) and then ceased. The plant that was grown in the water deficient environment had shorter height than the plants that were being grown on normal irrigated land. Water scarcity stress that is applied at the early stage of growth has a worse effect than drought stress on the final height (Wei, Y., et al, 2018).

The effect of water stress on above and underground dry matter accumulation:

Drought stress badly affects the photosynthetic rate and biomass collection of shoots and roots of soybean. It seems that the root/shoot ratio of the soybean plant is enhanced under drought stress. The root/shoot ratio is higher in plants on which the severe drought is applied rather than the plants on which the mild drought is applied. The ratio of root and shoot growth indicates that the relationship between the root/shoot ratio and drought stress is related to the levels of severity of stress (Du, Y., et al, 2020). When the water applied to soybean plants is less than its normal watering level, the stress effect is more adverse at the reproductive stage than in the vegetative phase. The accumulation of aboveground biomass at growth is less than at the beginning during drought stress. Water scarcity at the flowering-podding stage causes irreversible damage to biomass accumulation in soybean, as biomass cannot be restored when water is being reapplied at the seed filling stage. (Wei, Y., et al, 2018). If the drought stress occurs at the flowering and pod filling stage, the yield is decreased and, the size of the seed would be decreased. The scarcity of water along with high

temperature adversely affected the growth and development in the reproductive phase than in the vegetative phase (Cui, Y., et al, 2020).

The leaf area per plant (LAP)

Leaf area per plant development is extremely slow at the seedling stage, but this development is followed by a huge increase in the LAP at the flowering and pod setting stage and then a huge decline in LAP is observed. The fact of this happening is that soybean is an annual crop and when soybean enters the pod filling stage, its pods and leaves turn yellow and die quickly. Water scarcity at the R2 (full bloom) stage down-regulated the leaf area index by 52% when the comparison was done with the control soybean plants (Wei, Y., et al, 2018).

The effect of drought stress on soluble sugar, sucrose, starch and their mechanism in leaves and roots

The drought stress increases the soluble sugar and sucrose content in leaves as compared to the plants in which the normal water is being applied. The drought stress does not affect the sugar and sucrose content in the roots and if drought affects the sugar contents in the roots, the effect will be the same as the effect of drought in the leaves (Du, Y., et al, 2020). But the starch content in leaves decreases due to the drought stress. While water scarcity shows a significant increase in the starch amount in roots than in the leaves (Ruan, Y.L., et al, 2012).

1. Enzyme activity in drought conditions

For a better understanding of the function of sucrose and sugar contents in leaves and roots, the study of enzymes that are included in the mechanism and functioning of these sugars are being studied and these enzymes including SPS (for sucrose synthesis), SuSy (for sucrose cleavage), α -amylase and β -amylase (for starch hydrolysis). The activity of these enzymes is analyzed under drought conditions and controlled conditions and these enzymes' activity is higher in conditions under drought stress than the control conditions (Du, Y., et al, 2020).

2. Role of key genes of sugar and sucrose metabolism in drought

Many genes that are controlling the demonstration of different amounts of carbohydrates products and their transcript levels show how these genes code for the sucrose and sugar synthases.

3. Impact of water scarcity on GmSPS1, GmSPS2, GmSPS3, and GmSPS4 in Leaves and Developing Seeds

All these genes show different responses under water deficiency and normal conditions. Drought stress notably increases the transcript level of GmSPS1 at 15-45 days after flowering of soybean as compared to the controlled conditions of water level. While the expression levels of GmSPS2, GmSPS3, and GmSPS4 are suppressed at 15-45 days after flowering in soybean. But in the development, the expression of GmSPS genes are different at different seed filling stages. The expression levels of the four GmSPS genes have been suppressed at some stage in 30 to 45 DAF in plant life that is water deficit, besides that no widespread differences are discovered among the manage and water scarce remedies in GmSPS4 transcript stage were found at 45 days after flowering and at 30ys after flowering (Ruan, Y.L., at el, 2014).

4. Expression levels of GmSusy1 and GmSusy2 in Leaves and Developing Seeds

Water scarcity notably stimulated the transcript levels of GmSusy1 at some point of 15–45 DAF by a mean of 1.84-fold in soybean leaves. The transcript tiers of GmSusy2 were stimulated underneath water deficiency in leaves throughout 15–45 DAF as compared to managed plants. In seeds, the transcript tiers of GmSusy1 and GmSusy2 underneath drought stress behaved distinctively throughout seed filling levels. Drought stress extensively enhanced the expression tiers of GmSusy1 and GmSusy2 at 15 DAF compared to control flowers. However, GmSuSy1 and GmSuSy2 transcripts have been rapidly suppressed in drought-confused vegetation throughout 30 to 45 DAF (Xie Futi., et el, 2020).

5. Expression Levels of GmA-INV and GmC-INV in Leaves and Developing Seeds

Drought stress extensively up-regulated the expression levels GmA-INV and GmCINV during 15 days after flowering in the vegetative parts of plants. Except that there were notably no distinctions between the control and water deficit treatments in GmC-INV transcript levels at 45 DAF and at 15 DAF, respectively. In seeds, the expression levels of GmA-INV and GmC-INV under water scarcity behaved distinctively across seed filling stages. Drought stress notably enhanced the transcript levels of GmA-INV and GmC-INV at 15 DAF in comparison with the plants that were

grown under normal conditions. However, GmA-INV and GmC-INV transcripts were all abruptly suppressed in water-scarce seeds during 30 to 45 DAF (Du Yanli et al, 2020).

The Impact of Water Deficit and the high temperature on Yield and Its Components

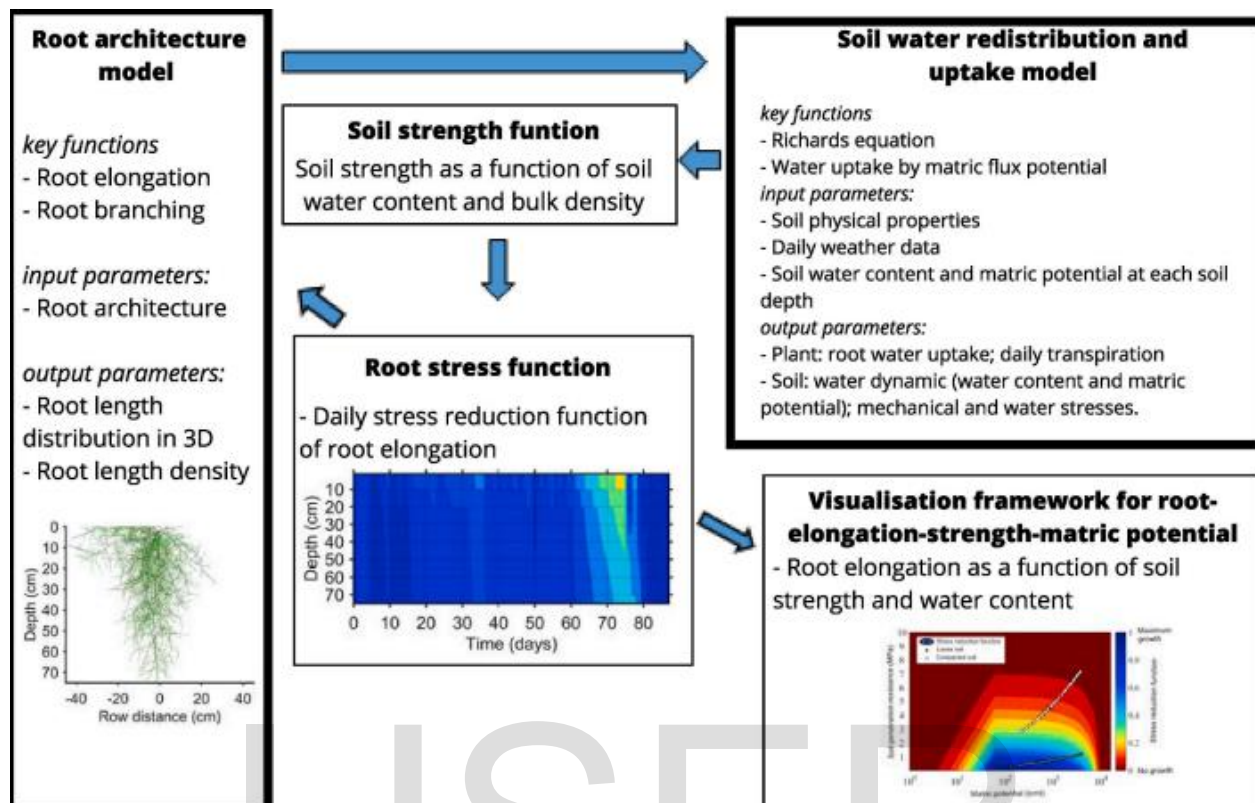
The average yield of soybean is 2.79 metric tons per hectare. Yield is being compared between the plants that were grown under normal conditions and drought conditions. There is a significant decrease in the yield at the flowering-podding stage and the pod-filling stages under drought stress. Underwater scarcity, developmental stages at vegetative and reproductive phases are also inhibited (Wei Yanqi., et al, 2018). Yield loss will be greater if the water stress is applied at the reproductive stage and vegetative stage (pod-filling stages) than at the early stage of growth. There was an irreparable loss in the yield of soybean when the soybean is grown at high temperatures, i.e. 34/24C (Jumrani., et al, 2018).

The combined effect of heat and drought on relative water content (RWC) of leaves and roots

The rate of evapotranspiration at proper irrigation and under water stress is compared and the evapotranspiration rate is too declined in the plants, which were being grown in the water deficit soil (Jumrani et al, 2017). Transpiration rate under drought conditions is observed at different stages the of seedling stage (R I), branching stage (R II), flowering-podding stage (RIII), and seed-filling stage(R IV), and a significant difference is observed in transpiration rate at these stages by 48.54%, 52.40%, 48.78%, and 61.26%, respectively. The plants have to close their stomata to avoid the extra transpiration under water scarce-conditions and due to, this a significant loss occurs in evapotranspiration (Cui et al, 2020).

Effect of Drought and Elevated temperature on root elongation and growth

Osmotic potential is reviewed as a physical element affecting root extension and is being utilized for the calculation of the accessibility of water in the soil. The root extension ratio decreased considerably while water potential was reduced from zero to – 500 kPa, and there was a decrease in the relative percentage of root elongation of soybean by 60%. Water stress directly affects root elongation. The soil does not store the water in its pores and water is no longer available to the roots for its growth and intake of nutrients from the water, when the water is being applied to the soybean in scarce amount.



Function of root elongation in soil strength and water quantity (Moraes., et al. 2018).

Thus, water consumption by the roots underneath drought situations and can be raised through (i) deep rooting (Gao et al., 2016), (ii) an up-regulation in the adequate depth of the root system (Fan et al., 2016), and (iii) enhanced root length density (Bodner et al., 2015; Tron et al., 2015). Therefore, the existence of bio pores in the soil texture can diminish the influence of mechanical and water deficiency to root extension (Bengough, 2012; Bertollo et al., 2021), which prefers fast root development in deep soil horizons (Han et al., 2015b; Uteau et al., 2013), enhancing the soil volume accessible to root intake water and nutrients, especially during drought period (Gao et al., 2016; Lynch and Wojciechowski, 2015).

Conclusion

This overview of the effect of drought stress on different growth stages and developmental phases depicts that the plant height is more in early growth stages rather than in the later growth stages and height is inhibited in final growth stages. Water scarcity will cause the plants to wither and the

dry leaves' pods will be shed off, hence it results in increased dry mass accumulation and a decrease in fresh biomass accumulation. Plant mechanism reduces the leaf area to decrease the enhanced transpiration and hence there will be no excess evapotranspiration. This study showed that the impact of water scarcity increases the metabolism of enzymes and genes of soluble sugar, sucrose, and starch amount in leaves and roots. The metabolism of these enzymes and genes behaves differently at different growth stages under water scarcity. The combined effect of drought and high temperature decreases the yield and also reduces the relative water amount of leaves and roots. Root elongation is also affected due to the water unavailability of water in soil pores.

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