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Sucrose Metabolism in Plants under Drought Stress Condition: A Review

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ABSTRACT

Drought stress reduces photosynthetic rate and leading to depletion of the energy source and lowers the yield. Under drought stress, reduced turgor pressure cause inhibition of cell elongation and impaired mitosis leads to reduction in growth rate. Role of sucrose metabolism under drought adaptation and response of plants to stress in different tissues and at different developmental stages. Cytoplasmic sucrose synthesis is more under drought condition and there is differential expression in tolerant and susceptible cultivars. Under drought condition, plant start consuming its own sink for its survival thus reducing sucrose concentration. But reduction in sucrose concentration is less in drought tolerant plants. Drought stress induced an increase of the root/shoot ratio, which was due to the increased inhibition of biomass accumulation of shoots compared to roots. Drought stress enhanced the activities of sucrose metabolic enzymes and up-regulated the expression of genes such as *SPS, SuSy* and *INV*. In addition, drought stress up-regulated the expression levels of *SWEET* and *SUC* and promoted the transport of sucrose from source to sink.

Key words: Drought, Enzymes, Sucrose metabolism, Source to sink relation.

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Plants changes its behavior to adapt with stress differently in different organs at different growth stages. Non photosynthetic plant organs such as seed and fruit, comprises more than 75% of global food production (Ruan *et al.*, 2010). Thereby, grasping the mechanisms of their behavioral changes to environmental stress would straightly useful to improve the food security. Plants have the capability to convert CO_2 into organic carbon in photosynthetic leaves by using the solar energy. Sucrose is the key carbon source for growth, development and defense, which is synthesized in photosynthetic leaves (source organ) and translocated to heterotrophic sink organs through the sieve element/ companion cell complex of the phloem. Then sucrose is taken out into various organs for metabolism and storage. Sucrose content in sink organs affected by the photosynthetic activity of source leaves. Turgor pressure difference through the osmotic impact of sucrose by the loading of sucrose into the phloem and its unloading into the sink. This variation in pressure causes mass flow of water, which carries sucrose as assimilate from source to sink. This sucrose dependent phloem translocation is the important pathway through which all components, such as nutrients, water and signaling molecules, are transported to meristematic sinks, including the shoot and root apical meristems. Sucrose cleavage results hexoses essential to generate energy and produce cellulose, starch, fructan, proteins and antioxidant compounds (Wang *et al.,* 2000).

Sucrose synthesis and cleavage are critical to the production of food, fiber and fuel, thus it is vital to agriculture and energy renewability. Carbohydrates that originate from sucrose constitute ~90% of plant biomass, making sucrose a crucial yield determinant. Upon phloem unloading in sinks, sucrose is enzymatically degraded into hexose to power and support the growth of sinks such as developing seeds, fruits, roots, tubers and cotton fibers (Du *et al.*, 2020)

Sucrose metabolism is among the key regulatory systems conferring tolerance to biotic and abiotic stresses. Drought is the most widespread stress that adversely aûects crop growth and yield. Inhibition of plant photosynthesis (Ohashi *et al.*, 2006), increased oxidative stress (Porcel and Lozano, 2004) and changes in metabolism (Valliyodan and Nguyen, 2006) are the reported injury symptoms caused because of drought stress in plants. Plants can generate certain morphological and physiological adaptations to acclimatize with the drought condition (Xu *et al.*, 2015). The root/shoot (R/S) ratio is an important parameter for measuring the drought tolerance of plants, which indicates the relative distribution between root and shoot biomass (Wilson, 1988; Naresh *et al.*, 2018; Nithya *et al.*, 2020). To withstand the adverse environmental condition such as drought, plants changes the location of assimilates like sucrose from source organ to sink organ (Cuellar-Ortiz *et al.*, 2008).

Recently, the target of agricultural research has to develop techniques to improve the productivity with limited resources (Passioura, 2012). Because of the varying climate and increasing water unavailabilty, impacts of drought stress expected to be high (Sheshshayee *et al.*, 2011). Drought results variation in water relations, structure of membrane, biochemical and physiological processes and subcellular organelles (Beena *et al.*, 2012; Manikanta *et al.*, 2020; Rejeth *et al.*, 2020; Nithya *et al.*, 2021). Also, leaf size reduction, stem enlargement, root proliferation impairment and low water uptake is observed (González *et al.*, 2009; Beena *et al.*, 2017; Beena *et al.*, 2018c). During different abiotic stresses, changes in photosynthesis and carbon assimilation are commonly observed characteristics. Here we discuss about sucrose metabolism and its role during drought stress condition in crops.

Sucrose

Sucrose is the main photosynthetic product in plants and acts as a major energy substrate and signaling regulator of plant growth (Du *et al.,* 2020).

Sucrose biosynthesis

Sucrose synthesis takes place in green leaves act as photosynthetic source (Fig 1) (Halford *et al.*, 2010). Fructose 1,6 bisphosphate is the primary product formed by the aldol condensation between dihydroxy acetone phosphate and glyceraldehyde-3-phosphate. Then fructose1,6-bisphosphate converted to fructose-6-phosphate by the enzyme fructose 1,6-bisphosphatase, then by the action of phosphoglucoisomerase fructose 6 phosphate is converted to glucose 6 phosphate, which is get converted to glucose-1-phosphate by phosphoglucomutase. Glucose 1 phosphate combines with uridine triphosphate, forms uridinediphosphate (UDP) glucose with the help of UDP glucose pyrophosphorylase. Sucrose phosphate synthase, which is an important enzyme converts UDP glucose and fructose 6 phosphate into sucrose phosphate. Sucrose phosphate removes the phosphate group and form sucrose molecule by the enzyme sucrose phosphate phosphatase (Halford *et al.*, 2010).

Storage

Sucrose translocation for storage takes place in various sites like apoplasts, the cytosols and vacuoles of storage parenchyma is controlled by invertase as it is results the sucrose concentration gradient, which leads to the phloem uploading (Fig 2) (Chandra *et al.*, 2012). In wheat, storage site of sucrose is in stem internodes (Shiomi *et al.*, 2006). In sugar cane, sucrose was stored in the stem whereas in sugar beet its storage takes place in roots (Halford *et al.*, 2010). In *Beta vulgaris*, sucrose was stored in roots (Turesson *et al.*, 2014). In many plant species, the sucrose concentration gradient helps it to diffuse from mesophyll cells to the vein, resulting in sucrose entry to the apoplast.

Sucrose metabolism in plants

Sucrose synthesis and phloem loading in source leaves

In the chloroplast, leaves fix CO_2 to produce triose phosphate by using solar energy. Triose-phosphate act as the building unit for other metabolism, for which it is exported to cytoplasm. Within the chloroplast, it may also be converted to ADP-glucose for the synthesis of starch. At night starch is cleaved into glucose or maltose and translocated to cytoplasm. Sucrose biosynthesis takes place in the cytoplasm (Fig 3). Sucrose is transport through the phloem either apoplasmically (by sugar transporters) or symplasmically (using plasmodesmata). The mass flow of sucrose through phloem towards the sink organ is carried out because of the accumulation of assimilates (sucrose), which absorb water osmotically and increases the turgor

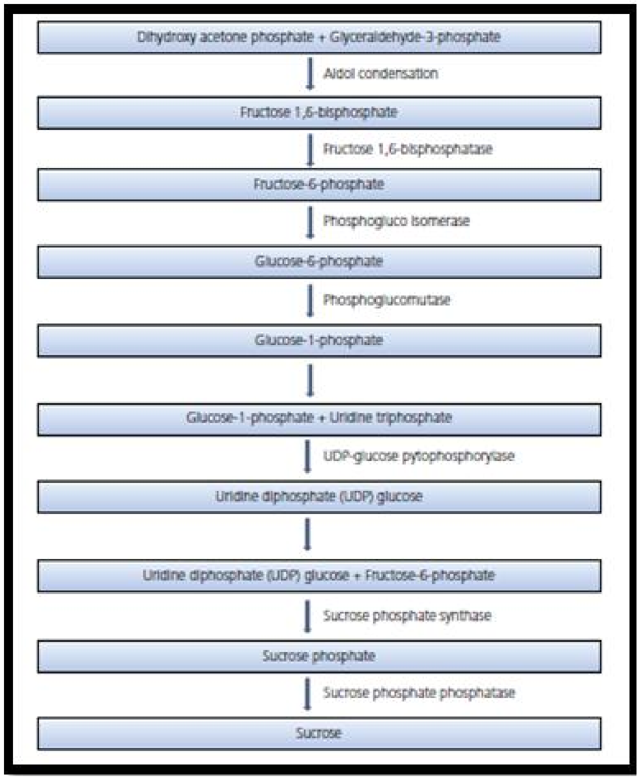

Fig 1: Biosynthesis of Sucrose. (Source: Halford *et al.,* 2010).

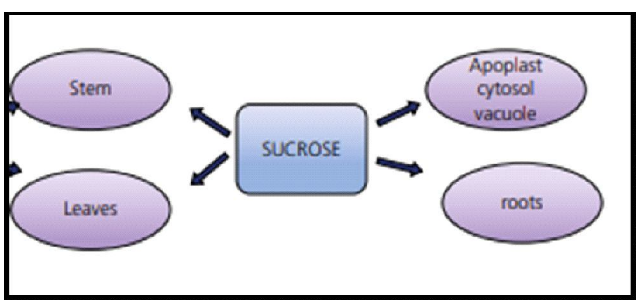

Fig 2: Various storage site of sucrose in plants (Source: Halford *et al.,* 2010).

pressure inside the phloem element. So the molecules attract towards the sink organ, where having low pressure compare to phloem (Ruan, 2014).

Sucrose unloading, transport and metabolism in sink tissues

Unloading of sucrose into various sink organs from the phloem is either apoplasmically or symplasmically (Fig 4). By apoplasmically, cell wall invertase (CWIN) converts sucrose into glucose and fructose. This conversion is take place when the sucrose is before being taken up by the cytoplasm. G protein coupled receptor might be sense the apoplasmically converted glucose for signaling. Cytoplasmic invertase (CIN) and sucrose synthase (Sus) may be degrade sucrose, that unloaded through plasmodesmata (PDs) or taken up by sucrose transporters. For hydrolysis by vacuolar invertase (VIN) sucrose may enter into vacuoles from the cytosol. The intracellular hexose (Hex) formed in the intracellular is further used for glycolysis and synthesis of polymers such as fructan, cellulose and starch. Nucleus-localized hexokinase (HXK) or other proteins sense the hexose level to regulate gene expression (Ruan 2014).

Sucrose metabolising enzymes

Sucrose-phosphate synthase (SPS) is the enzyme which catalysis the synthesis of sucrose in the cytosol, that converts uridinediphosphate (UDP)-glucose and fructose 6-phosphate into sucrose-6-phosphate, then by sucrose-phosphate phosphatase (SPP) dephosphorylate the former and yield sucrose. The rate of sucrose synthesis is related the activity of sucrose phosphate synthase (Fu *et al.* 2010).

Sucrose synthase (SuSy) and invertase are the two major enzyme, which catalysis the cleavage of sucrose molecule into hexose. Sucrose synthase localized in the cytoplasm, that reversibly synthesizes and degrades sucrose. Invertase irreversibly convert sucrose into glucose

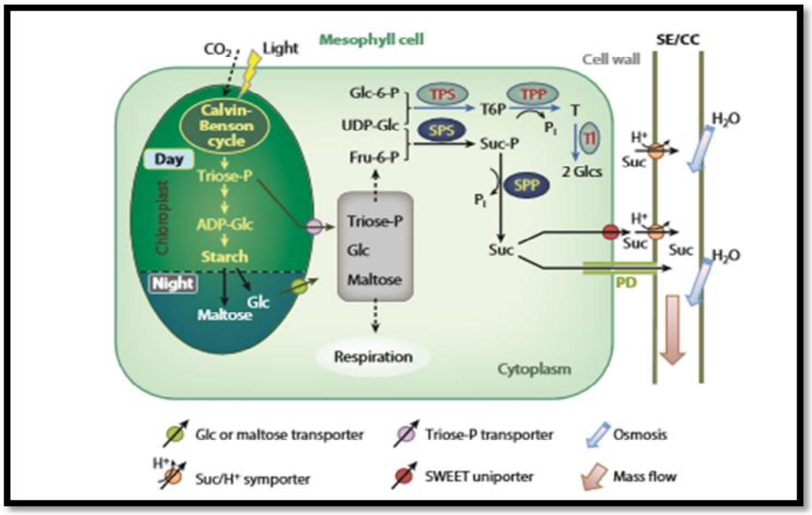

Fig 3: Sucrose synthesis in source (Ruan, 2014).

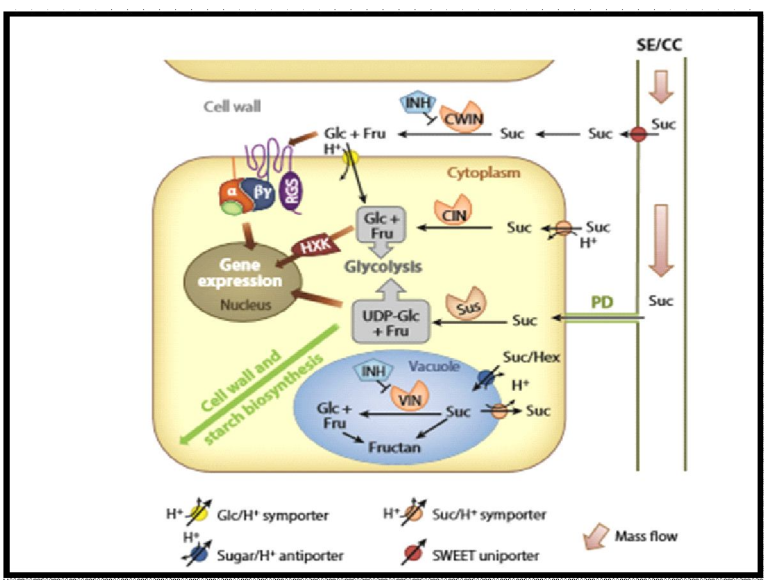

Fig 4: Sucrose unloading in sink organ (Ruan, 2014).

and fructose. Activity of invertase is recognised as an important regulator of assimilation distribution and generation of signals in response to environmental variations (Hammond and White 2011). There are different types of invertase enzymes present in plants. In the vacuole (VI) or cell wall contain acidic invertase (Liao *et al.* 2020), whereas cytoplasm consist of neutral or alkaline invertase. Metabolic fluxes at the early stages of plant development and the regulation of sugar constituents and in sucrose distribution at the later developmental stages are major functions of vacuolar invertase (Roitsch and Gonzalez 2004).

Sucrose transporters

It is proved that tonoplast and plasma membrane of parenchyma cells transport sucrose both as input and output. In plants there are two types of phloem transport systems are present; symplastic and apoplastic pathway. Symplastic pathway is carried out by the plasmodesmata, while the apoplastic pathway requires sucrose transporter proteins, sucrose transporter (SUC) and SWEET (Sugars will eventually be exported transporters) gene family (Ayre, 2011). Sucrose translocated from companion cells to the sieve cells through the plasmodesma and enter into to the sink organs. AtSWEET11 and AtSWEET12 are the transporters present in *A. thaliana* which take up the sucrose into the apoplast (Chen *et al.*, 2012),then sucrose is carried by companion cells though AtSUC2 (H+: sucrose co-transporter) (Gottwald *et al.*, 2000).

Sucrose as signaling molecule

Sucrose act as an indirect signaling molecule, when there islow concentrations of hexoses like glucose and fructose, substitute the effect of sucrose (Ehness *et al.*, 1997). In plant system, hexose sensing is done by two mechanisms: the hexokinase-independent pathway and the hexokinase-dependent pathway (Gupta and Kaur, 2005). Phosphorylation of sugar is required in the case of hexokinase dependent pathway while, that is not required in hexokinase independent pathway (Smeekens, 2000). Hexokinase independent pathway activate the expression of cell wall invertase, sucrose synthase by 6 deoxy glucose, a glucose analogue, but that does not undergo phosphorylation. Sucrose hydrolysing enzyme such as invertase and sucrose synthase have also been reported to have regulatory roles. Studies reported that invertases regulate the gene expressions in the osmotic regulation, organ development, hormonal crosstalk, cell cycle, cell division and reproductive development (Ruan *et al.*, 2010). On the other hand, sucrose synthase involved in the signaling role of shoot apical meristem and leaf development (Pien *et al.*, 2001). This enzyme was found to be the tool in shoot apex expansion andincreasing the initiation of leaf and in cotton plants which represses the seed abortion (Xu *et al.*, 2012).

Roles of sucrose metabolism in coping with drought stress

Sucrose metabolism is the key regulatory mechanism in plants not only to development but also to the responses to abiotic stresses.

Role of sucrose: Osmoregulation under drought stress

Drought stress causes changes in plant metabolism which results osmotic imbalance. It leads to the changes in water relation, so plant cell will experience dehydration. To withstand cell dehydration, assimilates such as sucrose accumulate in the plants by normalizing the osmotic imbalance by regulation of turgor pressure and be the plant cell hydrated during drought stress condition by the accumulation of solute like sucrose is called osmoregulation.

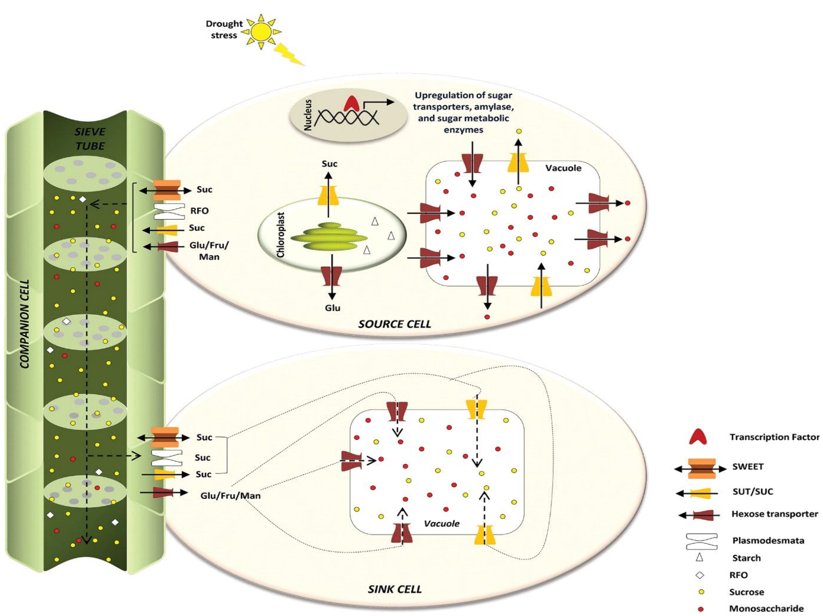

Fig 5: Distribution of sugars from source to sink cells during drought stress. Fru, fructose; Glu, glucose; Man, mannose, RFO, Raffinose family oligosaccharides; Suc, sucrose (Kaur *et al.,* 2021).

Plant resistance by accumulating sucrose under drought stress

Sucrose accumulation during drought condition is a plant adaptation strategy which is widely accepted by the whole (Fig 5). Sucrose play a role both as nutrients and signaling molecules. Accumulation ofsucrose for osmotic adjustment, is a physiological adaptation important for plants to survive under drought conditions. It helps in water extraction from dry soils and in the maintenance of cell turgor, growth and gas exchange under drought (Chaves *et al*., 2003). The increase in the sucrose might be because of the depletion in starch content. Higher concentration of sucrose and low starch content under drought conditions in two *Zea mays* cultivars was reported by Mohammadkhani and Heidari (2008). They suggested that enhanced sucrose content was accompanied by a sharp reduction in the starch level with a decrease in water potential. Sucrose play an important role in plant metabolism as it serve as substrate in biosynthetic processes, energy generation and products of hydrolytic processes and also stabilize cellular membranes under stress conditions. During drought stress, sucrose protect cells in two ways. Firstly, the substitution of water by the hydroxyl groups of sucrose during dehydration maintains proteins and hydrophilic interactions in membranes. Secondly, the prevention of protein denaturation is done by the hydrogen bond interactions of sugars with membranes and proteins. The soluble sugars, fructans, which are fructose polymers and are derived from sucrose, provide resistance to drought (Perez *et al*., 2001). Drought stress increased the content of sucrose (Chegah *et al*., 2013). In the experiments on four clones of Robusta coffee (drought tolerant and drought sensitive), an increase in sucrose and hexose and a decrease in starch content was observed (Praxedes *et al*., 2006). An increase in the amount of sucrose with an increase in the duration of drought conditions was observed by Mohsenzade *et al*., (2006). This increase in the sucrose is correlated with the relative water content. They found that relative water content decreases by 20% and the reduction in the rate of photosynthesisand the increasing of the sucrose content. Slama *et al.* (2011) had also obtained these results in alfalfa under drought stress. They recorded enhanced accumulation of sugars.

The study done by Sperdouli and Moustakes (2012) showed that accumulation of sucrose along with other metabolites under drought stress lead to the enhanced acclimation by maintaining a higher antioxidant protection.

Signaling role of sucrose metabolism under stress condition

Sucrose metabolism is a dynamic process, which contain simultaneous synthesis and cleavage processes during stress. These performed as a regulating the signals and thereby controlling the expression of various genes that is involved in growth and development of plants (Fig 6) (Rolland *et al*., 2006). Presence of soluble sugar in the source tissue downregulate the photosynthesis, which maintains homeostasis (Koch, 2004).Variable source sink effects on metabolic processes induced by abiotic stresses results in variable expression of many proteins involved in sucrose metabolism (Wingler *et al*., 2012). Several signals activated during drought and their response causes either stress avoidance or stress tolerance in plants *via* differential expression of sugar transporters and redistribution of sugars from source to sink (Kaur *et al.,* 2021).

Sucrose metabolism to enhance the plant resistance

Plant adapt to the stress by altering the primary metabolism like changing the enzyme activities. It shows that plants need more energy during stress. In drought stress, enzymes of

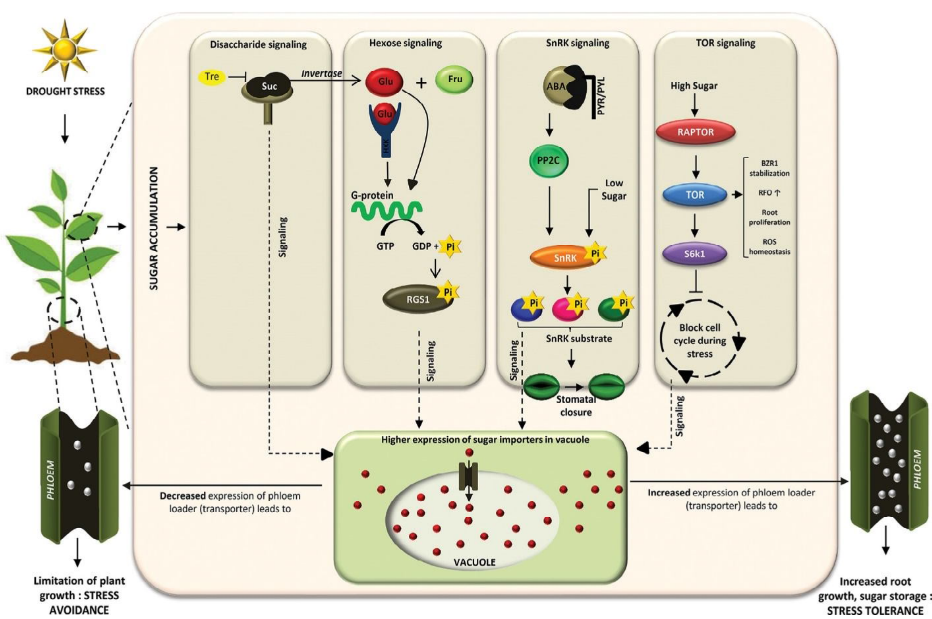

Fig 6: Sugar-mediated signaling in plants during drought stress (Kaur *et al.,* 2021).

sucrose metabolism play a significant role. Sucrose sustain the organization of the cytoplasm and maintain osmotic regulation during drought conditions by serving as companionable solutes. The other way to protect the plant cell from drought by the means of sucrose through the construction of glass. The formation of intracellular glass may protect the embryos from damage due to desiccation. Under water deficient condition, this glass prevents the damage of cell by filling up the space (Koster *et al*., 1991). Sucrose is the main end product of photosynthesis and acts as a most important transport of sugar and in some cases as a direct or indirect controller of gene expression (Winter and Huber, 2000). Drought stress leads to important modifications in sucrose metabolism. For this reason, the expression of various genes is affected by up and down regulating their expression. Protein phosphorylation is a significant system calculating the sucrose phosphate synthase (SPS) action in reaction to a variety of environmental and endogenous signals. Castrillo (1992) evaluated the effects of water stress on sucrose metabolism in bean plants of the Tacarigua variety grown for 25 days. Decreasing water potential and relative water content were observed. Water stress effects resulted in a decline of sucrose phosphate synthase (SPS). An increase in sucrose synthase activity increased the activities of both neutral and acid invertases at moderate water stress and decreased activities at severe water stress. The starch/sucrose ratio declined and the ratio of total glucose/total fructose enlarged. Yang and Zhang (2006) observed that when grain filling in rice starts under water stress conditions, sucrose synthase activation and sucrose amassing in cereal stems results in the remobilization of fructans stored in the stem and compounds are transported to the grain. This hastens the course of grain filling. Legay *et al*., (2011) worked with potato clones differing in resistance and suggested that rearrangement of sucrose is required under drought conditions. However, the chief enzyme of sucrose synthesis, sucrose phosphate synthase, was less active in these experiments, whereas more sucrose was mounting up in the tolerant clone. Activity of sucrose synthesizing and sucrose degrading enzymes enhance under stress conditions. The role of sucrose towards its metabolic pathways to acclimatize with the stress is by increasing its concentrations (Wang *et al*., 2000).

Role of sucrose transporter under drought stress

Plant sucrose transporters regulate the redistribution of sucrose between source and sink under abiotic stress (Durand *et al*., 2016). Sucrose transporter genes such *as AtSWEET11, AtSWEET12* and *AtSUC2* in *A. thaliana* leaves shows upregulated expression during the stress condition, leads to the higher sucrose transport (Durand *et al.,* 2016). Drought stress up-regulated the expression levels of *GmSWEET11/12* and *GmSUC2* in leaves and roots of soybean seedlings and promoted the transport of sucrose from leaves to roots (Du *et al.,* 2020). Mathan *et al.,* (2020) shows the induced expression of *OsSWEET13* and *OsSWEET15* under drought stress condition and higher sucrose content in phloem sap, then, hypothesis the role of apoplasmic transport and sucrose transporters under stress for sucrose distribution. These all are suggested that sucrose distribution and transport are the critical for the survival of plants under stress.

Drought stress increased soluble sugar and starch contents in soybean roots by regulating sugar metabolism and transport. Du *et al.,* (2020) finalize that this seems to be the preferred mechanism for maintaining root growth and metabolism in response to drought stress.

Several studies have shown that the abscisic acid induced genes were highly expressed under drought stress which represents that a relation between ABA signaling and stress response (Nakashima *et al.* 2009. Mathan *et al.,* (2020) identified that *OsSWEET13* and *OsSWEET15* as the main *SWEET* transporters being affected by the drought (Fig 7). They hypothesized that induction of *OsSWEET13* and *OsSWEET15* during drought stress is promoted by the increase in the abscisic acid level,through the ABA-responsive transcription factors, showed binding of an ABA-responsive transcription factor, OsbZIP72, to the promoters of *OsSWEET13* and *OsSWEET15*. Thereby confirmed that *OsbZIP72-OsSWEET* could possibly be a target module for maintaining desirable sucrose dynamics in rice under stress.

Stress responses of reproductive and vegetative tissues mediated by sucrose metabolism

Compared with vegetative stages, reproductive development is more sensitive tostress, particularly during the seed and fruit set phase around fertilization (Kakumanu, 2012). This is overviewed by the phenotypic difference in the severity

Fig 7: Under stress condition, the ABA- mediated induction of *OsSWEET13* and *OsSWEET15* expression. (Mathan *et al.,* (2020).

of their responses: Abiotic stress often inhibits leaf expansion in a reversible manner but causes substantial abortion of ûowers, young seeds and fruitlets and hence irreversible yield loss (Beena, 2005; Muller *et al* .2011; Prince *et al.*, 2015). These are might be advantageous for plants to reserve limited resources during stress. Recent studies have shown that the high sensitivity of reproductive development relates to disruption of sucrose metabolism and reduction of hexose availability, triggering downstream stress responses.

During reproductive stages, drought stress seriously weakened the capacity of sucrose transport from leaves to seeds. Decreased hexose-to-sucrose ratio in seeds, together resulting the loss of seed weight thus disrupted the balance of sucrose metabolism and transport in leaves and seeds at reproductive stages, which seemed to be the main mechanism through which drought caused seed weight to decrease (Du *et al.,* 2020).

Disruption of sucrose metabolism and signaling, causing reproductive failure under drought stress

Water stress blocks sucrose import, represses invertase (INV) and sucrose synthase (Sus) activities and depletes starch reserves. This leads to lowering the concentration of glucose in reproductive organs and ultimately to their abortion (Fig 8). Emerging evidence, largely based on gene expression analyses, suggests that the low glucose may (i) directly inhibit cell cycle gene expression and hence cell division (Ruan *et al.*, 2012) and (ii) reduce the metabolic

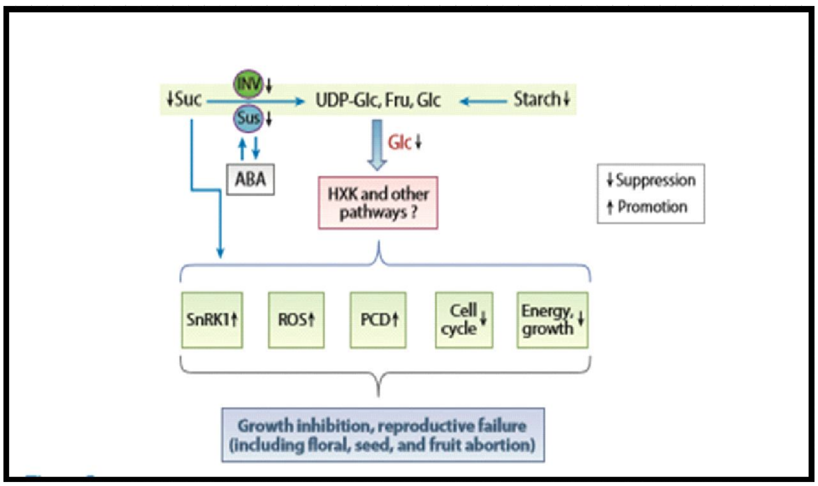

Fig 8: Growth inhibition, reproductive failure in sink organs (Ruan *et al.*, 2012).

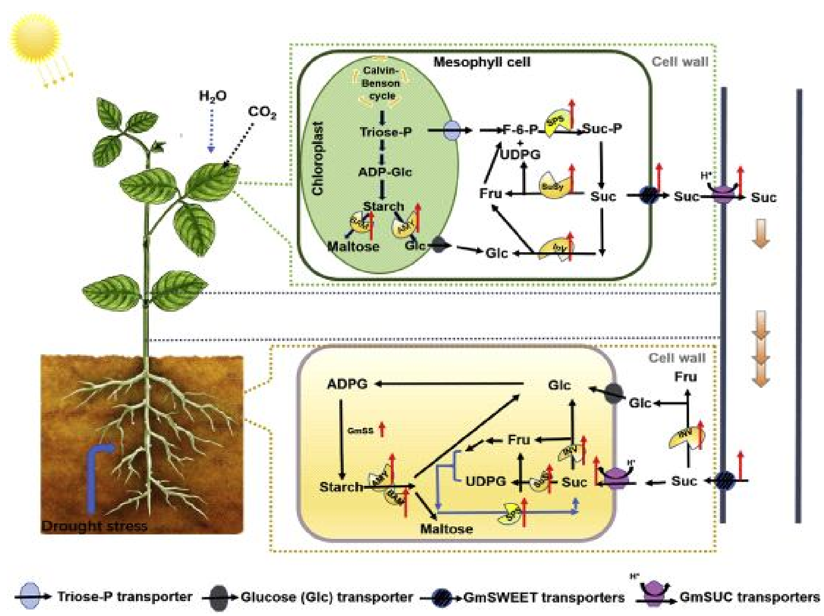

Fig 9: A model of the sugar regulation in soybean seedlings in response to drought stress. Here, drought stress stimulates a sugar mediated tandem reaction, which improves the soybean drought tolerance. Reducing the soil moisture content might alter the expression levels of key regulatory metabolic genes and the activities of sugar metabolism enzymes, which in turn modulates sugar accumulation, activates the transcription of sugar transporters to regulate sugar allocation to adapt to environmental stress. (Du *et al.,* 2020).

activity of hexokinase associated with the mitochondrial outer membrane, hence decreasing ATP use and the regeneration of ADP required for ATP synthesis (Kakumanu, 2012). This may affect the energization status of the electron transport chain, causes the overproduction of reactive oxygen species (ROS) and hence leads to the oxidative damage and even programmed cell death (Foyer and Shigeoka, 2011). In parallel, the low availability of sucrose may activate sucrose non-fermenting related kinase 1 (*SnRK1*) to repress growth (Paul *et al.*, 2008). The low expression of invertase and Sucrose synthase may occur before the rise in abscisic acid level, but, reciprocally, the stress-induced increase in ABA can reduce the expression of invertase and Sucrose synthase.

Response of root to shoot ratio to drought stress

To estimate the relative biomass distribution between roots and shoots, the root to shoot ratio (R/S) and shoot to root ratio are often used (Poorter *et al.*, 2012). Distribution of carbohydrates between shoots and roots may be associated with the change in R/S. Farrar (1996) proposed that sucrose perform a key role in biomass partitioning between shoots and roots. One of the major determinants of plant growth is the sucrose transport across source to sink (Lemoine *et al.*, 2013). The R/S ratio is often observed to increase under adverse conditions such as drought (Xu *et al.*, 2015) which was a result of a greater reduction in above ground biomass rather than an increase in root biomass because the absolute root dry weight under drought stress was not greater than that under well watered condition. It has also been reported that mild water stress restricts shoot growth, while its effect on root growth is little (Lemoine *et al.*, 2013). Mahajan and Tuteja (2005) reviewed that leaf growth is generally more sensitive to stresses than the root growth. The greater proportion of sucrose allocated to roots is responsible for the increase in R/S under drought stress (Xu *et al*, 2015).

Drought stress stimulates a sugar mediated tandem reaction, which improves the soybean drought tolerance (Fig 9). Reducing the soil moisture content might alter the expression levels of key regulatory metabolic genes and the activities of sugar metabolism enzymes, which in turn modulates sugar accumulation, activates the transcription of sugar transporters to regulate sugar allocation to adapt to environmental stress (Du *et al.,* 2020).

CONCLUSION

Plants responses to drought by regulating the sucrose metabolism and its transport from source to sink. Drought stress reduces the production of photosynthetic products, alters the distribution of photosynthetic products and reduces the starch content of leaves ultimately to survive during the stress condition. Drought stress enhanced the utilization efficiency of sucrose by increasing the activity levels of sucrose synthesis and degradation of enzymes and also sucrose transporters. Sucrose synthesis and breakdown are central to the production of food, feed, fiber and fuel and therefore are important for modern agriculture, economies and energy sustainability. Therefore, understanding the underlying mechanisms is essential for improving tolerance to stresses to develop techniques to enhance productivity with limited water and nutrient use.

FUTURE PERSPECTIVE

However, the effect of drought stress on the sucrose metabolism during plant growth and development have been studied, the putative mechanism of sucrose status and efficacy in physiological events during germination, establishment and seedling growth are not well understood and also little aware about the response of sucrose metabolism during stress at the sink site.

Based on available evidence, it is hypothesized that sucrose signaling may operate through hexose signaling in sinks but independently from hexose in source tissues. Further studies are needed to differentiate sucrose signaling from hexose signaling.

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