Review Article

Alterations in carbohydrate metabolism and modulation of thermo-tolerance in tomato under heat stress.

Abstract: Heat stress affects the source and sink activities, growth and development, economic yield and harvest index of plants negatively. Heat stress has got severe effects on the biochemical reactions of photosynthesis which included irreversible damages of RuBisCO, oxygen evolving complexes, PSII reaction centres and disruptions of chloroplast ultrastructure and thylakoid membrane. Sugars are products of photosynthesis in plants which serve as substrates for energy metabolism and are required for synthesis of cellulose and starch polysaccharides. Glucose, fructose, sucrose, mannose, trehalose, maltose etc. are the sugars present in plants. Abiotic stresses like temperature, drought, flood and salinity causes crucial differences in the carbohydrate metabolism. Sugars acts as primary signaling molecules and regulate signals that control the expression of many genes and enzymes involved in carbohydrate metabolism**.** Decrease in crop productivity under heat stress is chiefly associated with alterations in carbohydrate accumulation and resulting defects in assimilation partitioning from source to sink. It is essential to understand the responses and acclimatization processes to extreme temperatures in plants, such that the mechanisms underlying can be used for developing heat-tolerant varieties. Sugars such as glucose, sucrose, fructan, raffinose and trehalose not only acts structural component and metabolic resources also regulate genes associated with heat stress tolerance and reduce the chances of crop loss. The external application of compounds like osmoregulators, phytohormones, signaling molecules, etc., have exhibited positive responses in stress tolerance due to its growth promoting and antioxidant activities.

Keywords: Carbohydrate metabolism, heat stress, tomato, reproductive development, sugar signalling, thermotolerance, management

Introduction

Global warming and changing climate change associated heat stress is a major threat for crop growth and productivity worldwide [1]. The climate change model by Intergovernmental Panel on Climate Change (IPCC) globally forecast a hike of 2°C daily mean surface temperature during the year 2046 to 2065 and a further hike forecast of 3.7°C by 2100 [2]. Heat stress can be defined as the rise in temperature beyond a threshold level for a period of time sufficient to cause irreversible damage to plant growth and development. The vegetables are very much sensitive to abiotic stresses and nearly 50% yield loss are recorded under abiotic stress.

Tomato is the second most consumed vegetable in the world. Major tomato producers are from Asia, which constitute 60.3 per cent of the total tomato production. With regard to the area and production of tomato, India stands third [3]. Major tomato producing agro-climatic zones of India as well as the world are facing the problems of temperature hike in all tomato growing seasons throughout the year [4].

The growth stages of tomato can be divided into five stages (fig 1), such as germination and early growth for 25 to 35 days, vegetative growth for 20 to 25 days, flowering stage for 20 to 30 days, early fruiting stage with 20 to 30 days, and mature fruiting for 15 to 20 days which differ based on environmental conditions like temperature, light, water, soil conditions and nutrient availability [5]. During heat stress, plants undergo metabolic reprogramming to adapt to the unfavorable conditions. One of the prominent changes observed is an increased accumulation of soluble sugars, such as sucrose, glucose, and fructose. These sugars serve as osmoprotectants and antioxidants, helping to maintain cellular turgor and scavenge reactive oxygen species (ROS) generated under heat stress. The accumulation of soluble sugars also enhances the stability of membranes and proteins, protecting cellular structures from damage caused by heat-induced denaturation.

Heat stress also affects the partitioning and metabolism of starch, the major carbohydrate storage form in plants. Starch breakdown is accelerated under heat stress, leading to increased levels of soluble sugars. This shift in carbohydrate partitioning is thought to provide an immediate energy source for maintaining essential cellular functions under heat stress conditions [6].

Furthermore, altered carbohydrate metabolism influences various signaling pathways involved in plant thermotolerance. Heat stress triggers the activation of specific genes and proteins involved in heat shock responses and heat stress signaling pathways. Carbohydrates, particularly sugars, have been implicated in regulating the expression of these heat stress-responsive genes. They act as signaling molecules, mediating the crosstalk between metabolic and stress signaling pathways [7].

Understanding the intricate relationship between carbohydrate metabolism and heat stress responses in tomatoes can provide valuable insights into developing strategies to improve thermotolerance in this economically important crop. Manipulating carbohydrate metabolism through genetic and physiological approaches offers potential avenues for breeding or engineering heat-tolerant tomato varieties. By enhancing the plant's ability to accumulate and utilize carbohydrates efficiently, it may be possible to mitigate the negative effects of heat stress and ensure sustainable tomato production under changing climatic conditions.

In conclusion, alterations in carbohydrate metabolism play a crucial role in modulating the thermotolerance of tomato plants under heat stress. The accumulation of soluble sugars, changes in starch metabolism, and their involvement in signaling pathways contribute to the plant's ability to withstand high temperatures. Further research in this field will help unravel the molecular mechanisms underlying these processes, paving the way for the development of heat-tolerant crop varieties to ensure food security in a changing climate.

Impact of heat stress on seed germination and plant growth:

Tomato cultivation above the optimum growth temperature has got severe negative effect on plant physiological processes like assimilate partitioning, growth and development [8]. Under mild heat stress situation, reduction in source and sink related activities leading to reduced economic yield and harvest index. Giri *et al.* [9], studied that the tomato plants under temperature > 35^0C resulted in reduced shoot dry weight, root dry weight, total dry mass and root to shoot ratio. Plants when grown at different day and night heat conditions for six days, wherein different stress set-up are prevailed 25 ^{O}C /20^{O}C – control temperature, 35^{O}C / 30^{O}C – moderate temperature and 42^{O}C / 37^{O}C - heat stress. The plants later are transferred to control conditions for next seven days as recovery period. Decreased nutrient uptake levels and lower activity of assimilation proteins are possible effects of stress conditions. Heat stress has a significant impact on seed germination and subsequent plant growth, particularly concerning carbohydrate metabolism. Carbohydrates are essential energy sources and signaling molecules during seed germination and early seedling growth. Heat stress disrupts the balance of carbohydrate metabolism, leading to altered germination rates, impaired seedling establishment, and reduced growth [8, 10]. Here's a closer look at the impact of heat stress on seed germination and growth in relation to carbohydrates:

a. Delayed or Reduced Seed Germination: Heat stress can delay or inhibit seed germination. Elevated temperatures can disrupt the mobilization of stored carbohydrates in seeds, affecting the activation of enzymes involved in the breakdown of complex carbohydrates into simple sugars needed for germination. This disruption can lead to reduced availability of energy for germination processes, resulting in delayed or failed seed germination [11].

b. Impaired Reserve Mobilization: During germination, stored carbohydrates, such as starch, are mobilized to provide energy for seedling growth. Heat stress can interfere with the enzymatic breakdown of starch into soluble sugars required for energy production. As a result, the availability of energy substrates becomes limited, negatively impacting seedling vigor and growth [12].

c. Reduced Photosynthesis: Heat stress often leads to a decline in photosynthetic efficiency due to damage to the photosynthetic apparatus, such as chlorophyll degradation and impaired electron transport. Photosynthesis is a crucial process for carbohydrate production in plants. Reduced photosynthetic rates under heat stress conditions limit the synthesis of new carbohydrates, which are essential for sustaining seedling growth [13].

d. Altered Carbohydrate Partitioning: Heat stress can alter the partitioning of carbohydrates within the plant. It often leads to an accumulation of soluble sugars, such as sucrose, glucose, and fructose, in different plant tissues. This shift in carbohydrate partitioning is believed to be a protective mechanism against heat-induced oxidative stress. However, excessive accumulation of soluble sugars can disrupt osmotic balance and affect seedling growth [14].

e. Impaired Root Development: Heat stress can negatively affect root growth and development. Roots are responsible for nutrient and water uptake, which are crucial for carbohydrate metabolism. Under heat stress, root growth may be restricted, leading to reduced nutrient and water absorption. This limitation can further hamper carbohydrate synthesis and utilization, affecting overall plant growth and development [15].

f. Altered Hormone Balance: Heat stress can disrupt the hormonal balance in plants, including the levels of growth-promoting hormones such as gibberellins and auxins. Carbohydrates play a role in regulating hormone synthesis, transport, and signaling pathways. Heat stress-induced alterations in carbohydrate metabolism can disrupt hormonal regulation, affecting seed germination, root elongation, and shoot growth [16].

g. Overall, heat stress-induced disruptions in carbohydrate metabolism have profound implications for seed germination and subsequent plant growth. The limited availability of energy substrates, altered carbohydrate partitioning, impaired photosynthesis, and hormonal imbalances contribute to reduced seed germination rates, poor seedling establishment, and stunted growth under heat stress conditions. Understanding the underlying mechanisms of carbohydrate metabolism and developing strategies to enhance thermotolerance can help mitigate the negative effects of heat stress on seedling growth and improve overall plant performance under high-temperature environments [17].

To study the effects of temperature on germination process in case of tomato Nafees *et al.* [18] conducted an experiment. Seeds were grown under two temperature conditions of 10^{o}C and 40^{o}C, the germination rate at 40^{O}C was negligible than those at 10^{o}C. To improve the germination under 40^{o}C, seed priming was given as an effective treatment. T_0 - non-primed control, T_1 - hydro-primed, T_2, T_3 and T_4 are 5, 7.5 and 10 mM concentration of $Mg(NO_3)_2$ solution respectively. Increase in the superoxide dismutase (SOD) activity, starch, sugar content and protein content for treatment with 7.5 mM showed better stress tolerance capacity in this experiment as seen in fig 2. [18].

Impact of heat stress on photosynthesis:

Energy allocation to the photosystems changes as a result of structural changes in plant cells subjected to high temperatures [19, 20]. The capacity for photosynthetic activity is more affected by high temperature stress, notably in C3 plants as opposed to C4 plants [21]. Reduced Calvin cycle enzyme activity, namely ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) [22], may be the cause of decreased photosynthetic efficiency. Decline in assimilation rate with every single degree temperature increase when temperature is 30^{0} C and more [23]. With increasing temperature, photosynthetic rate as well as the respiratory rate falls off and the photosynthetic rate declines at a faster rate than the respiratory rate (Fig 3). The biochemical reactions involved for photosynthesis process are affected by heat stress, by irreversibly disrupting RuBisCO, oxygen complexes, chloroplast ultrastructure, thylakoid membrane and PSII apparatus thereby assimilation rate declines.

Chloroplast structure:

Exposure of tomato varieties under heat stress condition causes damage to the microstructure of leaf and chloroplast ultrastructure. Zhou *et al.* [24] observed that under heat stress the chloroplast ultrastructure and grana arrangement get completely damaged in susceptible genotypes along with swollen chloroplast and decomposition of starch (Fig 1). The loss of ordered grana stacking as well as chloroplast lamella, increase in the number of plastoglobuli, swelling of grana are the major ultrastructural changes in chloroplast under heat stress [25, 26].

Photosynthetic apparatus:

Photosystem II, photosynthetic apparatus forms very susceptible element under stress and damage to the PSII and its inactivity is the first response under heat stress. PSII being thermo-labile the activity is greatly reduced or fully lost under heat stress which is due to the features of location of PS II on thylakoid membranes [27]. Heat stress causes an imbalance in the electron flow from OEC through direction of PSI towards the acceptor side of PSII due to the impairment of oxygen evolving complex (OEC). Damaged PSII reaction centre causes loss of the capacity of oxygen evolution by restricting the electron transport [28]. Hence the electron transport is limited under high temperature which ultimately decreases photosynthesis [20, 29].

Chlorophyll content:

Reduction in photosynthetic rate is related to the loss or degradation of chlorophyll, also the lipid peroxidation in membranes of chloroplast and thylakoid also result in reduction in chlorophyll content. Under stress condition, the enzyme 5-aminolevulinic acid dehydratase (ALAD) or porphobilinogen synthase gets inactivated under stress [30, 31], this enzyme helps formation of the carbon-carbon and the carbon-nitrogen bonds during pyrrole ring formation in porphobilinogen [32].

Stomatal closure:

The water content present in plant and the atmosphere has impacts on transpiration rate, stomatal conductance and intercellular CO_2 concentrations. Heat stress increases Rubisco enzyme catalytic activity by enhancing oxygenase activity and lowering affinity of Rubisco to CO2 thus assimilation rate gets reduced [22]. Since the carboxylase activity is lowered significantly efficiency of photosynthesis is low. Another reason for reduced photosynthesis that impacts the intercellular CO2 concentration is HS-induced stomatal closure [8]. Photosynthesis can also be hampered by the reduction of soluble proteins, Rubisco-binding proteins, big and small Rubisco subunits, etc. [33]. By decreasing the activities of sucrose phosphate synthase (SPS), ADP-glucose pyrophosphorylase, and invertase (INV), high-temperature stress also negatively impacts the synthesis of starch and sucrose [34].

Sugars

As a result of photosynthesis by plants carbohydrates are synthesized among which sugars are significant. Different forms of sugars are glucose, fructose, sucrose, maltose, mannose, trehalose etc. Photosynthates are primarily carried through phloem in the form of sucrose. Sucrose gets broken down into glucose and fructose. Abiotic stresses like drought, temperature, flood and salinity lead to crucial alternations in the carbohydrate metabolism [35]. Regulation of growth activities by coordinated modulation of gene expression and enzyme activities are controlled by light and sugars in source and sink organs. Sucrose and hexoses are main sensing-molecules and they confer sugar responses in both source and sink. Basically sugars are involved in various metabolic processes and regulate different genes regulating photosynthesis, sucrose metabolism, antioxidants and osmoprotectants [36].

Essential roles of sugars are that they acts as substrates in carbon and energy metabolic pathways, basic building blocks involved in starch and cellulose polymer biosynthesis, act as messengers in signal transduction they also critically regulate various genes and its expression [37].

Carbohydrate as Protectives Molecules

Osmolyte – Carbohydrates are primary metabolites involved in maintaining osmotic balance by accumulation of soluble sugars. Along with the role as osmoprotectants, they act as antioxidants, maintain ionic balance, membrane stability and buffer the redox potential. Sorbitol, mannitol are sugar alcohols which act as osmoprotectant. By preserving the cell-water balance, maintaining the stability of the membrane, and buffering the cellular redox potential, carbohydrates defends a number of crucial cellular structures from the stress of elevated temperature [38]. These compounds serve as antioxidants in addition to their osmoprotective functions. According to Wahid and Close [39], the buildup of soluble sugars has significant effects on capacity to withstand heat. Sato *et al.* [40] found that interruption in proline transport and sugar metabolism during pollen development under HS caused problems with fruit set in tomato.

Thermoprotectant – Due to its direct connection to a plant's ability to act photosynthetically under stressful conditions, such as high temperatures, glucose metabolism is important in the tolerance mechanism. Maltose, galactinol, sucrose, myo-inositol, and raffinose, along with cell wall precursors, primarily monosaccharides, are reported to accumulate during HS. According to metabolic profiling, plants that were treated to both drought and HS accumulated sugars such glucose, fructose, sucrose, trehalose, and maltose. These sugars assisted to preserve cell turgor by stabilising cell membranes and halting the breakdown of proteins [41]. The presence of sugars like glucose, fructose, sucrose, trehalose, and maltose in plants, help maintain cell turgidity, stabilize cell membrane structure and maintain protein structure and prevent protein degradation [42]. The plants use starch and fructans as energy sources instead of glucose during adverse stress. Oligosaccharides like raffinose and stachyose are involved in reducing oxidative stress damage.

Carbohydrates as Signaling Molecules - According to research by Li *et al.* [43], the major metabolic and transcriptional factor that determines a plant's vulnerability to abiotic stressors is carbohydrate metabolism. As a result, changes in sugar metabolism brought on by HS have a negative impact on sugar-sensing systems. Sugar sensor proteins specifically senses the sugar level of plant cell. Sugar sensing involves the interaction of the sugar molecule with the sensor protein and then sugar signal gets generated. This signal generated, initiates the signal transduction cascade activity by phosphorylation that result in responses like changes in gene expression and enzymatic activities. Sugars act like hormones and second messengers that control the expression of genes and enzymes needed in sugar metabolism and signaling [44].

Enzyme Activity – When exposed to abiotic challenges, the expression of several genes encoding enzymes involved in cellular metabolism changes, and some of the transcription factors associated with stress are modulated. It has been demonstrated that transcription factors (TFs) can alter stress-related metabolites. High-temperature stress also has a negative impact on the synthesis of sugars by decreasing the activity of enzymes that break down carbohydrates. Heat stress adversely affects the activities of carbohydrate metabolizing enzymes involved in the synthesis of sugars [45].

Sucrose synthase (SS) - main catalytic enzyme for sucrose breakdown. Heat stress reduces the activity of soluble sucrose synthase (SSS). SS is essential for amylopectin biosythesis, is a component of endosperm starch. HS alters SSS activity and blocks starch granule synthesis [46]. When HS is present, SS activity may be decreased in heat-sensitive genotypes, which also influences the overall yield by changing how carbohydrates are partitioned from roots to shoots. The production of amylopectin, a crucial component of starch in the endosperm, is dependent on soluble sucrose synthase (SSS), which is less active under high-temperature stress [47]. It has been proven that changes in ambient temperature have a direct impact on the rate of assimilation, translocation, and length of grain filling, HS during endosperm development is a significant yield-limiting factor [48]. Starch granule production is similarly disrupted and distorted by altered SSS activity under HS [46].

Soluble acid invertase (SAINV) – The enhanced amounts of total soluble sugar may be connected to enhanced INV activity, which is an adaptation for abiotic challenges since sugar works as a signalling molecule, assuming protective roles in the context of HS [49]. The increased levels of soluble sugar is due to enhanced INV activity. HS block the mechanism of sucrose import and INV activity is reduced. Then starch reserves get utilized to meet energy requirements, and hence reduction of hexoses in the reproductive structure occur resulting high rate of pollen abortion [50].

Sucrose phosphate synthase (SPS) - SPS and sucrose-6-phosphate catalyzes sucrose synthesis, while SS and INV are involved in degradation pathway. During HS, SPS activity is significantly altered which results reduced sucrose synthesis [51]. This results in the pollen function impairment, defects in fertilization, and reduce fruit setting rate [52]. SPS genes gets activated and causes increase in the sucrose synthesis and enhances tolerance level of plants under mild HS. The overexpression of SPS in tomato leaves to increase the foliar sucrose concentration but decrease the starch content further demonstrated that SPS is the key control point for the partitioning of photosynthate between sucrose and starch [53]. Due to a slower conversion of sucrose to starch, Wallwork *et al.* [54] discovered that the heat-treated plants stored less starch than the control plants. Stress, according to [55], may prevent pollen from accumulating starch by reducing the availability of assimilates or by compromising the functions of enzymes involved in starch production.

ADP-glucose pyrophosphorylase (AGPase) - It has also been demonstrated that ADP glucose pyrophosphorylase is a crucial enzyme involved in the synthesis of starch. Crop growth and maturation processes are said to be connected to it [56].

Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco)- The Calvin cycle's Rubisco activation during dark reactions of photosynthesis has been identified as a crucial phase that is impeded around 35–40 °C, which leads to a reduction in net CO2 assimilation and the creation of carbohydrates [57]. C3 plants are more sensitive to high temperatures than C4 plants when it comes to their ability to photosynthesize. By disrupting electron transport and inactivating the oxygen evolving enzymes of photosystem II, it modifies energy distribution and modulates the activities of carbon metabolising enzymes, particularly Rubisco, which modifies the rate of RuBP renewal [58].

Galactinol synthase (GolS)- The activation of myo-inositol begins a series of reactions that result in the formation of raffinose, which is the most abundant raffinose family oligosaccharides in plants. Raffinose is synthesized from galactinol by a series of complex modifications that involve enzymes such as myo-inositol-1-phosphate synthase (MIPS) and myo-inositol-3-phosphate synthase (MIPS3). The final step in the raffinose biosynthesis pathway is the action of stachyose synthase (STS), which catalyzes the formation of the final product, stachyose [59]. In addition to raffinose, other compounds such as verbascose and stachyose are also formed by the biosynthesis pathway. Verbascose has been shown to play a role in plant defense and stachyose is believed to play a role in the transport of water and nutrients in plants. The study likely involved comparing plants with normal raffinose accumulation to those with impaired or reduced raffinose accumulation. The researchers subjected both groups of plants to heat and freezing stress and observed their responses. The results of a study conducted by Zuther *et al.* [60] indicated that the plants with impaired raffinose accumulation exhibited a higher sensitivity to heat or freezing stress compared to the plants with normal raffinose accumulation. This suggests that raffinose accumulation plays a protective role in plants, enabling them to better withstand these types of stressors.

Trehalose phosphate synthase (TPS) - Trehalose-6-phosphate synthase (TPS) is an enzyme involved in the synthesis of trehalose-6-phosphate, a sugar molecule that plays important roles in stress responses in plants. Trehalose synthesis is a two-step process. First being the production of synthesize trehalose 6-phosphate (T6P) from UDP-glucose and glucose-6-phosphate with trehalose-6-phosphate synthase (TPS) enzyme followed by action of trehalose-6-phosphate phosphatase (TPP) enzyme here dephosphorylation reaction occur to produce trehalose [61]. Trehalose-6-phosphate has been associated with various stress tolerance mechanisms, including heat stress, in plants. In the context of heat stress in tomatoes, TPS is likely to play a role in the plant's response to elevated temperatures. When tomato plants are exposed to heat stress, TPS activity may be induced to increase the production of trehalose-6-phosphate [62]. Trehalose-6-phosphate is believed to act as a signaling molecule, triggering various stress-related pathways and protective mechanisms within the plant. The accumulation of trehalose-6-phosphate through TPS activity during heat stress can help regulate plant metabolism, maintain cellular integrity, and protect against damage caused by high temperatures. It may also play a role in the activation of heat shock proteins, which assist in protein folding and protect against protein denaturation under heat stress conditions [63].

Major and Minor Carbohydrate Metabolic processes – Under heat stress the genes and enzymes involved in carbon and energy metabolism are negatively affected. Intermediary products of carbon metablic cycles acts as substrates for minor biosynthetic pathways. Many metabolic pathways like carotenoid pathway, flavonoid pathway, polyamine pathway etc. are secondary metabolic pathways whereas, phytohormone metabolism of auxins, gibberelins, ethylene, abscisic acid, jasmonic acid and brassinosteroid also requires the involvement of sugars or carbohydrate in them (Fig 1). The major pathways like glycolysis, N-metabolism and minor pathways of amino acid metabolism, vitamin metabolism are affected. Short-term heat stress causes improper glycolysis and fermentation, photosynthesis, oxidative phosphorylation, tetrapyrrole synthesis, nucleotide metabolism, etc., whereas long-term stress deters the equilibrium of redox potential, phytohormone synthesis, etc. [64].

In an experiment conducted by Zheng *et al.* [65], tomato plants were grown under three temperature regimes, 25/15, 25/9 and 25/6°C conditions for 9 days and then they were transferred to control temperature condition for 9 days as a recovery period. After recovery period, under heat stress the fructose, glucose and sucrose content and starch content were less than that of the control and significant reduction in starch content occurred at 6°C night temperature and there was no significant difference in fructose content.

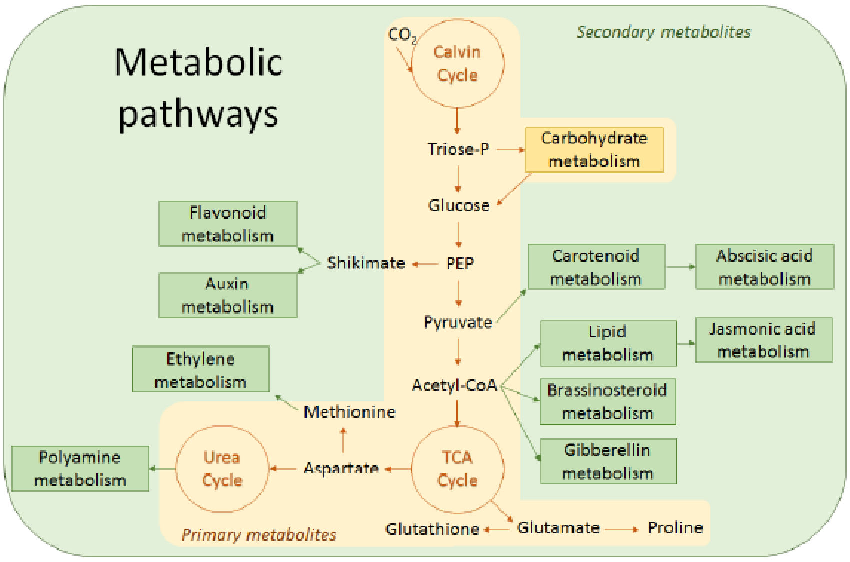

Fig. 1: Major (yellow marked) and minor (green marked) carbohydrate metabolic pathways [64].

Mechanism of sugar signaling in plants:

Glucose and fructose are the main sensing molecules in the plant systems which are sucrose and hexoses.

Generation of Sugar Signals: Sugar signal is generated through different means. Differences in the carbohydrate concentration and other metabolites or due to differences in the ion or assimilate movement or flux variation through sugar specific sensors or transporters [66]. Otherwise the production of sucrose in cells from SPS enzyme activity also generate sugar signal. Differences in the concentration of glucose molecules generated from hexokinase or invertase activity can also generate signal. Trehalose-6-phosphate produced from TPS activity is also possible.

Sensors– Figure 2 shows the major sugar sensors involved in sugar signaling in plants [66]. Figure 3 shows the location of different sugar sensors and the important transcription factors involved in the production and enzymes involved [67]. Figure 4: Major conversions in sugar signaling pathway involving sugar sensing, transduction and responses in a nutshell [72].

Hexokinase, HXK1 acts as conserved glucose sensor. Catalyses the process of phosphorylation of glucose also acts as hexose sensor that transmit signals based on amount and availability of sugar. The best evidence on cellular sugar sensing systems currently comes from hexose kinases, which phosphorylate glucose (hexokinase) and fructose (fructokinase). Hexokinase I from Arabidopsis has been implicated in these early steps [67], and two complementary overview articles in this research topic provide detailed updates on hexokinases and fructokinases in plants [68, 69].

Regulator of G-protein signaling, RGS1 acts as cell surface receptor for sensing extracellular sugar signals.

G-protein-coupled-receptors (GPCRs) - Extracellular glucose and sucrose can be perceived by this type of sensors [70].

Sucrose non-fermenting Related Kinase (SnRK1) - SnRK1 gets activated by stress conditions and limit energy production in the cell caused due to abiotic stresses like hypoxia, flooding. This sensor phosphorylate and inactivate activity of biosynthetic enzymes like nitrate reductase (NR) and Sucrose phosphate synthase (SPS) thus limits energy generation in cell thus imparting survival strategy [71]. The processes positively promoted by TOR are regulated by SnRK1 in an opposite manner. T6P which senses sugar availability is a direct negative regulator of SnRK1 activity. SnRK1 phosphorylates and regulates the activity of transcription factor basic leucine zipper 63 (bZIP63) in order to trigger global adaptation to low energy.

Trehalose-6-phosphate (T6P) - T6P control process like glycolysis and sugar signaling along with interaction with hexokinase sensor. Under stress or carbon starved conditions, the complex formed between trehalose phosphate synthase (TPS) interacts with 14-3-3 proteins dissociates to liberate T6P and this interact with enzymes and proteins [72].

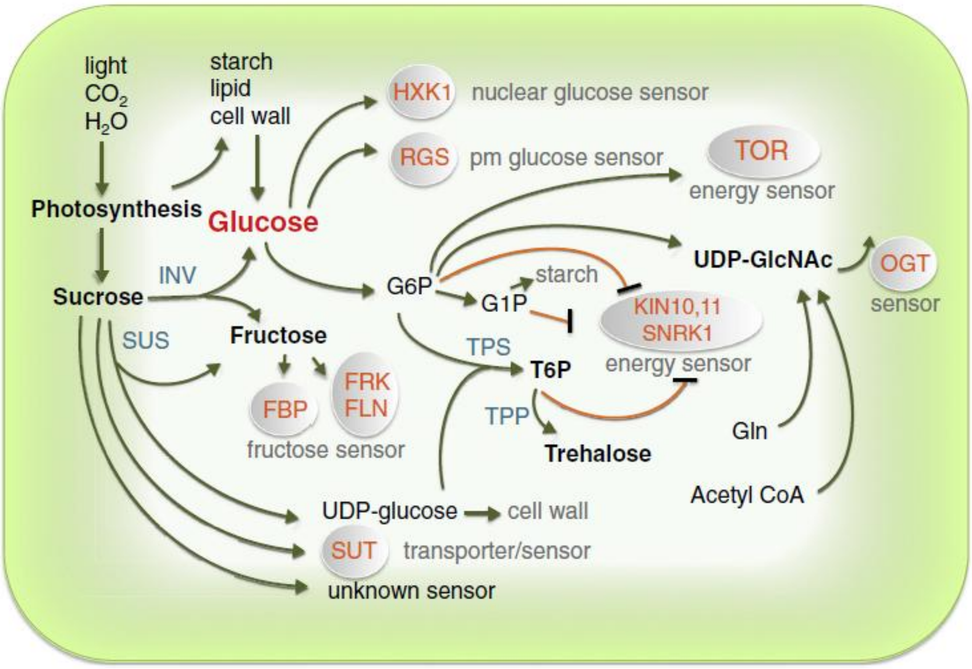

Figure 2: Major sugar sensors involved in sugar signaling in plants [66]

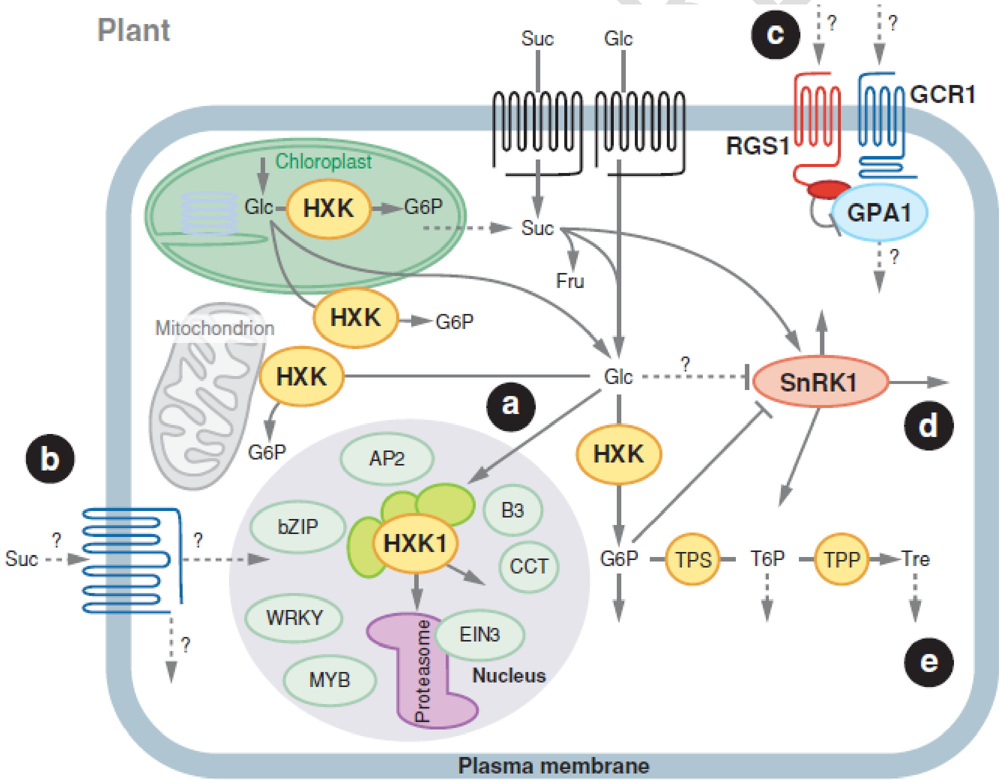

Figure 3: Location of different sugar sensors and the important transcription factors involved in the production and enzymes involved [67].

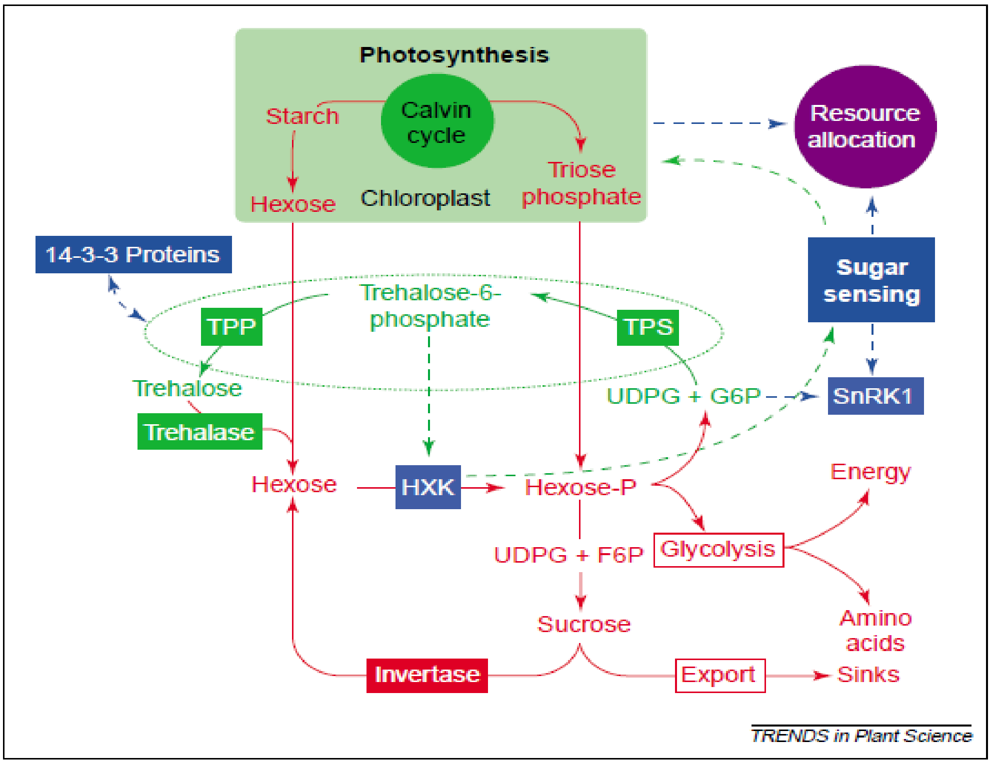

Figure 4: Major conversions in sugar signaling pathway involving sugar sensing, transduction and responses in a nutshell [72].

Signaling cascades - Information from the sensors is transferred down through signaling transduction amplifying the cascades. Responses involve changes in gene expression and altered enzyme activities. The cascade mediate the activity of protein kinases, protein phosphatases, Ca+2, calmodulin and phytohormones. 14-3-3 proteins bind generally to phosphorylated substrates (27) and hereby, they control phosphorylation and dephosphorylation, enzyme activities, and protein-protein interactions required for signal transduction pathways [73, 74]. Table 1 shows the data on genes which are up-regulated and down- regulated in carbohydrate metabolism and sugar signaling pathway.

Other mechanisms involving sugar signaling: Sugars cross-talk with phytohormone signaling networks to modulate critical growth processes such as embryo establishment, seed germination, and seedling and tuber growth. Sugars regulate genes that control meristem maintenance and identity. It was observed that spatio temporal expression of carbohydrate metabolic genes in the tomato shoot apical meristem (SAM) and developing leaf primordia are also controlled by sugar signaling. Sugar signaling interacts with hormone, light and stress signaling by regulating the expression of diverse pathway components and transcription factors. Circadian clock allows plants to anticipate daily changes. This is achieved by the actual sensing of quality and quantity of light and especially sugars ensures an appropriate response of metabolism to specific situations. Photosynthesis is controlled at the molecular level by sugars and nitrogen signals through changes in the whole plant carbon-nitrogen balance. This overides the control of photosynthesis by other mechanisms. Microbial pathogens can synthesize and release trehalose to the plant cell. This interferes with the host sugar-sensing pathways, therby manipulating host metabolism in their favour.

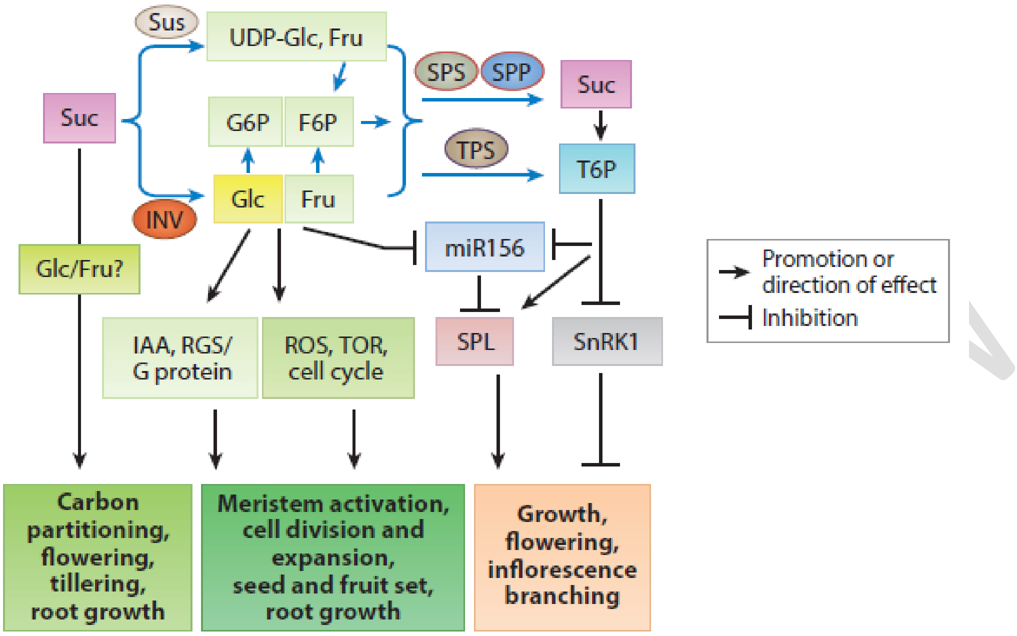

Figure 5: An overview of sugar signaling pathways

Table 1. Genes which are up-regulated and down- regulated involved in carbohydrate metabolism and sugar signaling pathway.

Genes up-regulated	**Genes down-regulated**
Cytosolic glyceraldehyde-3-phosphate dehydrogenase	Phospho ribulokinase (one gene)
Sucrose phosphate synthase	Glyceraldehyde-3-phosphate dehydrogenase (three genes)
Sucrose synthase	Aldolases (two gene)
Phosphoenol pyruvate carboxylase	Fructose bisphosphates (two genes)
Lipoxygenase	B-glucosidase (three genes)
Protein kinase	
Glutathione-S-transferase	
Cytosolic ascorbate peroxidase	
Cytosolic copper zinc superoxide dismutase	

Mechanism involved in thermo-tolerance:

Sugars have a key role in seed germination, growth, and protection from abiotic stressors by acting as a signalling molecule. Under abiotic stressors, sugars act as a main messenger to govern signals that affect the expression of numerous genes involved in glucose metabolism. Sugars the products of plant photosynthesis serve as base substance for energy metabolism and precursors of polysaccharides such as starch and cellulose. Under abiotic stress conditions, sugars acts as primary signal molecule and regulate signals that control the various gene expression and enzymes involved in carbohydrate metabolism. The protective roles or activity of sugars during stress like osmoprotectants, role of antioxidants, maintain the ionic equilibrium, membrane stability, prevent protein degradation and cellular redox potential balance [75]. Under mild heat stress conditions, due to inhibition of SS and INV, accumulation of sugars occur, while at high heat stress sugar content get depleted and result in stress induced photosynthetic rate reduction and photoassimilate scarcity [76].

Glucose and HS tolerance – Glucose is a primary source of energy and a key regulator of plant metabolism. It is involved in various physiological processes, including photosynthesis, respiration, and the synthesis of macromolecules. Glucose also acts as a signaling molecule, influencing plant growth, development, and stress responses. Studies have shown that glucose levels affect tomato plant growth and development. High glucose concentrations can lead to increased plant height, leaf size, and biomass production [77]. However, excessive glucose can also result in adverse effects, such as reduced photosynthetic efficiency, altered root development, and increased susceptibility to diseases. Production and accumulation of glucose and fructose provide heat tolerance in plants. Chandrakar and Keshavkant [78] reported that under HS conditions, pretreatment of plants using glucose decreases the damages of oxidative stress by reducing the severity of lipid peroxidation, regulating photosynthesis and antioxidant production thereby impart heat stress tolerance. Heat-tolerant species maintain a lower respiration rate and hence minimize the toxic damages of stress.

Management Strategies: To improve glucose and heat stress tolerance in tomato plants, several management strategies can be employed:

a. Genetic Selection: Breeding programs can focus on selecting tomato varieties that exhibit enhanced glucose and heat stress tolerance traits. This can involve screening for genes associated with stress tolerance and incorporating them into new cultivars.

b. Cultural Practices: Providing optimal growing conditions, such as appropriate irrigation, shading, and mulching, can help mitigate heat stress in tomato plants. These practices maintain soil moisture, reduce temperature extremes, and minimize water stress.

c. Foliar Application: Foliar application of glucose or glucose-containing compounds can enhance heat stress tolerance in tomato plants. This can be done by spraying a glucose solution on the leaves, which facilitates the uptake of glucose and its utilization in stress tolerance mechanisms.

d. Stress Priming: Pre-exposing tomato plants to mild heat stress or glucose treatment before severe heat stress can induce a priming effect. This priming enhances the plant's defense mechanisms, making it more resilient to subsequent stress events.

It is important to note that while glucose can contribute to heat stress tolerance, excessive glucose levels can have detrimental effects on tomato plants. Therefore, it is crucial to maintain a balance and provide optimal glucose concentrations for promoting stress tolerance without causing negative impacts.

Sucrose and HS tolerance - The transcriptional analysis revealed that the increased SS gene expression due to increased sucrose or carbon demand and under such mild stress conditions plants uses other metabolites to meet the energy requirements. But under heat stress, sucrose synthase enzyme is denatured or inactivated completely or partially and thereby carbon metabolism is interrupted [79].

Managing sucrose and high salinity (HS) tolerance in tomatoes involves several strategies aimed at optimizing the plant's ability to cope with these stress factors. Here are some approaches commonly used in tomato cultivation:

a. Genetic selection and breeding: Genetic improvement programs focus on selecting and breeding tomato varieties that exhibit enhanced tolerance to sucrose and high salinity. This involves identifying and selecting plants with desirable traits, such as improved osmotic adjustment, ion homeostasis, and efficient sugar metabolism.

b. Osmotic adjustment: High sucrose levels and HS can cause water deficit stress in tomato plants. Osmotic adjustment involves maintaining cellular hydration by accumulating compatible solutes, such as proline, glycine betaine, and sugars, in the cytoplasm. This helps regulate cell turgor and minimizes water loss. Cultivating tomato varieties with a higher capacity for osmotic adjustment can improve their tolerance to sucrose and HS.

c. Nutrient management: High salinity can disrupt nutrient uptake and imbalance nutrient concentrations within the plant. Optimizing nutrient management, particularly the levels of essential elements like potassium, calcium, and magnesium, can improve tomato plant tolerance to HS. Adequate nutrient availability helps maintain ion homeostasis and supports various physiological processes, enhancing the plant's ability to withstand sucrose and salinity stress.

d. Irrigation management: Proper irrigation practices are crucial for managing both sucrose and high salinity stress. Controlled irrigation techniques, such as drip irrigation or precision irrigation, allow for better water and nutrient management, reducing the risk of waterlogging and salinity buildup. Adjusting irrigation schedules and volumes according to the plant's needs can help maintain soil moisture levels and minimize the impact of sucrose and HS stress.

e. Soil amendments: Incorporating organic matter, such as compost or well-decomposed manure, into the soil can enhance its structure, water-holding capacity, and nutrient availability. This promotes root development and nutrient uptake, improving the plant's resilience to sucrose and high salinity.

f. Exogenous application of osmoprotectants: Foliar application of osmoprotectants, such as glycine betaine or proline, can enhance tomato plant tolerance to sucrose and HS stress. These compounds act as compatible solutes, maintaining cellular water balance and protecting cellular structures from damage caused by osmotic and oxidative stress.

g. Hormone application: The application of growth-promoting hormones, such as abscisic acid (ABA), can help regulate stomatal closure and reduce water loss in tomato plants under sucrose and high salinity stress. ABA application can improve water use efficiency and enhance the plant's ability to withstand water stress conditions (Yuan *et al.,* 2017).

It's important to note that the effectiveness of these management strategies may vary depending on the specific tomato variety, environmental conditions, and the severity of sucrose and high salinity stress. Implementing a combination of these approaches and adapting them to local conditions can help improve sucrose and HS tolerance in tomato crops.

Fructan and HS response – Tonoplast vesicles store fructan in vacuole and are transported to the apoplast under stress. Fructan play a role in HS adaptation, because of the high water solubility and its ability to maintain membrane permeability, and contribute to osmotic adjustments. Fructans act as osmoprotectants, helping to maintain cell turgor and protect cellular structures from damage caused by HS [64]. Here are some management strategies to consider for fructan and HS response in tomatoes:

a. Variety selection: Choose tomato varieties that have been bred or selected for their tolerance to HS stress and their ability to accumulate fructans. Some tomato cultivars are naturally more resilient to HS and exhibit higher fructan accumulation, which can aid in osmotic adjustment and enhance plant tolerance.

b. Soil preparation and amendment: Prior to planting, prepare the soil by incorporating organic matter, such as compost or well-rotted manure. This helps improve soil structure, water retention capacity, and nutrient availability. Well-drained soils with good water-holding capacity are essential for managing HS stress. Soil amendments like gypsum can also help reduce the negative impact of soil salinity on tomato plants.

c. Irrigation management: Develop an irrigation strategy that balances the water requirements of tomato plants with the need to prevent excessive salt accumulation. Irrigate tomato plants adequately to maintain optimal soil moisture levels and avoid both water stress and waterlogging. Techniques such as drip irrigation or subsurface drip irrigation can be beneficial as they deliver water directly to the root zone, minimizing salt buildup in the soil.

d. Salinity management: Implement salt management practices to minimize salt accumulation in the root zone. This includes leaching excess salts from the soil by applying water in amounts greater than the crop's water requirement. Controlled drainage systems can also be employed to remove excess salts from the field.

e. Nutrient management: HS stress can affect nutrient uptake and nutrient balance in tomato plants. Monitor and manage the nutrient levels carefully, paying particular attention to essential elements like potassium, calcium, and magnesium. Adequate nutrition can help maintain the balance of ions within the plant, reducing the negative effects of HS stress.

f. Foliar application of osmoprotectants: To enhance the fructan accumulation and osmotic adjustment in tomato plants, foliar application of osmoprotectants such as sucrose or mannitol can be considered. These compounds can improve the plant's ability to cope with osmotic stress caused by HS.

g. Crop rotation and intercropping: Implement crop rotation practices to break the cycle of soil salinity and reduce the risk of HS stress. Additionally, intercropping with salt-tolerant companion plants can help alleviate the impact of HS stress on tomatoes by reducing soil salinity and competition for resources.

It's important to note that the effectiveness of these strategies may vary depending on the specific tomato variety, local conditions, and severity of HS stress. Monitoring the plants closely, adapting management practices to the specific situation, and seeking local agricultural expertise can further optimize fructan and HS response in tomato cultivation.

Trehalose and HS response - Up-regulation of genes involved in the trehalose metabolism that contributes to abiotic stress tolerance. The precursor of trehalose is T6P and they are involved in glycolytic flux regulation of carbohydrate metabolism [80]. The disruption of *TPS* gene causes scarcity of trehalose carbon source and increases the oxidative stress damage and chances in loss of pollen viability increase. Trehalose stabilizes biological membrane structure by replacing water and form hydrogen bonding with the polar heads of lipids and proteins, thereby stabilizing membranes.

Management of HS stress in tomatoes involves both pre-emptive measures and post-stress recovery strategies. Here are some approaches that can help manage HS stress in tomato plants:

a. Cultivar selection: Choose tomato cultivars that exhibit better HS tolerance. Some varieties are naturally more resistant to HS stress than others.

b. Irrigation management: Optimize irrigation practices to provide adequate water to plants while avoiding waterlogging. Proper irrigation scheduling can help maintain soil moisture levels and mitigate the effects of HS stress.

c. Mulching: Apply organic or plastic mulch around tomato plants to conserve soil moisture, reduce weed competition, and moderate soil temperature.

d. Shade structures: Install shade cloths or structures to partially shade tomato plants and reduce direct exposure to intense sunlight during the hottest parts of the day.

e. Nutrient management: Maintain proper nutrient levels in the soil through regular soil testing and appropriate fertilization. Nutrient deficiencies or imbalances can make plants more susceptible to HS stress.

f. Plant protection: Use physical barriers or shading materials to protect young tomato plants from direct exposure to high temperatures. This can be particularly helpful during the early stages of plant establishment.

g. Post-stress recovery: After HS stress episodes, provide optimal growing conditions, including sufficient water, nutrients, and protection from additional stressors, to help plants recover and resume normal growth.

It's important to note that the effectiveness of these management strategies may vary depending on the severity and duration of HS stress, local climatic conditions, and specific tomato cultivars. Therefore, it's advisable to adapt and tailor these approaches based on the specific needs of your tomato plants and local environmental conditions.

Impact of heat stress on reproductive development:

The limiting factor of fruit production under stress condition is the pollen development stage in case of a plant system.

Impaired meiosis:

The heat sensitive stage of pollen development is from meiosis to mitosis I stage [81]. Microspores exposed to heat stress resulted in microspore abortion, reduction in the number of pollen grain during anthesis, reduction in the number of viable or competent pollen (Fig 6). The nutrition to the pollen is provided by a key tissue called tapetum at the early stage of development further it degenerate and this happens once the microspore start to develop vacuole and form polarized microspore. Once tapetum degenerate, nutrients as well as metabolites are provided to the pollen from the locular fluid. The tapetum layer degenerate prematurely after the release of the tetrad, and causes reduction in pollen viability under high temperature [82]. Several metabolites show a drastic drop in the accumulation rate, which consisted of reduction in fructose, glucose, sucrose and starch content during the developmental stage of microspore. In figure 8, it shows the different developmental stages of pollen development under control conditions and the changes under heat stress conditions. In the figure it is evident that the opening of locule gets severely affected. Anther deformation and distinct locules will no longer be visible under HS. Ultimately the flower abscission or flower drop can be observed under mild heat stress (Fig 7).

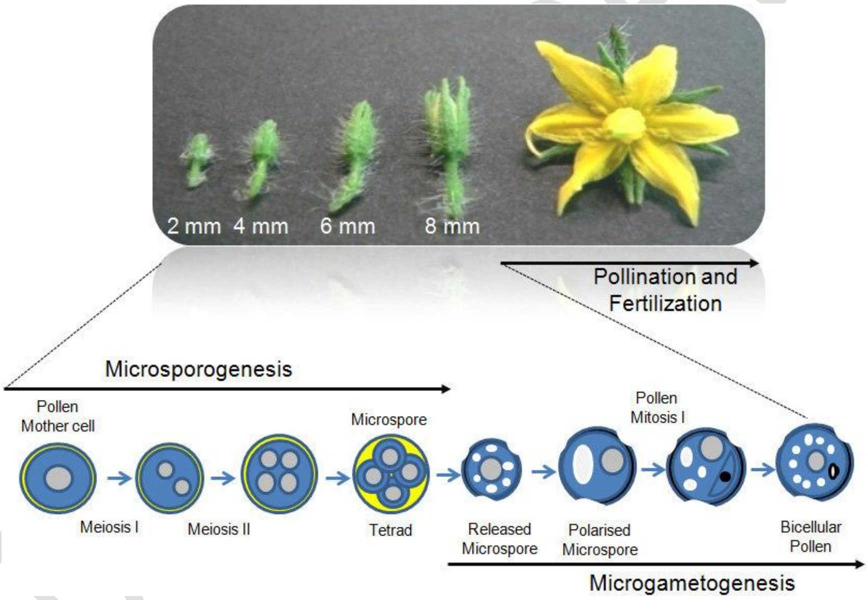

Fig. 6. The different stages of pollen development [81].

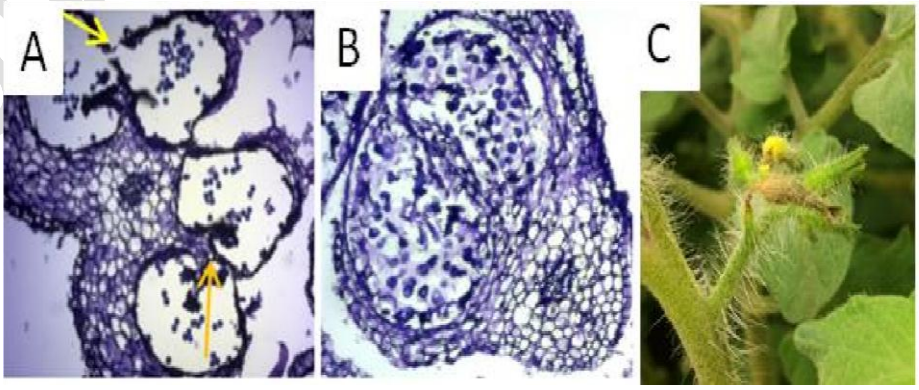

Figure 7. Effect of high temperature on anther [82].

A- Anther at mature stage of pollen development under control conditions, the opening of locule is indicated with an arrow. B - Severe anther deformation and four distinct locules no longer visible. C- Flower abscission under heat stress.

Pollen germination percentage and pollen viability:

Under elevated temperatures and fluctuating relative humidity, the pollen viability of tomato differs greatly, and hence it can be considered as a principle element in selecting a hotset genotype. Pollen maturation, pollen viability, pollen germination and pollen tube growth are reduced significantly under HS [84]. The starch provides energy for the pollen maturation, germination and pollen tube elongation. The reduced assimilation rate under heat stress result in poor germination rate [85]. The sucrose and hexoses also acts as energy sources for the development and germination, and these act as osmolytes also [86].

An experiment conducted by Bita and Gerats [86] proved that the pollen germination and pollen tube growth reduced significantly for plants grown under stress when compared to plants under normal condition. Exposure to mild heat stress resulted in small flower size with malformed anther cones which reduced pollen germination rate and thus significantly reduced pollination effectiveness. Tolerant genotype is less affected by heat stress and tube growth and produce relatively higher fruit yield compared to those of susceptible genotypes.

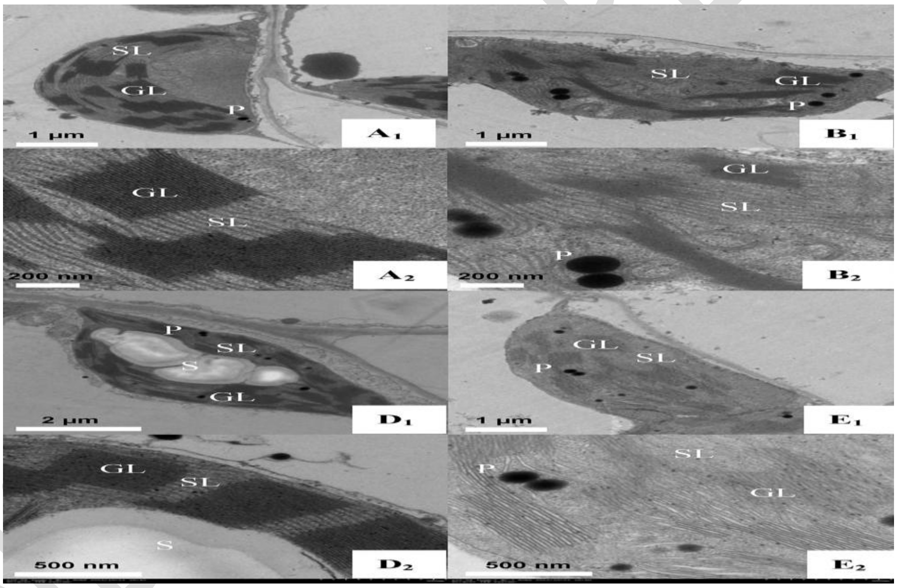

Fig. 8. The chloroplast ultrastructure for tolerant genotype (40x) under both control and under heat stress [86].

(GL- grana lamella; SL- stroma lamella: P- plastoglobulus: S- starch)

Stigma exertion:

The stigma exertion indicates the presence of elongated stigma beyond the anther cone during reproductive development [86]. Stigma exertion resulting from high temperature prevents self-pollination and subsequent pollination efficiency and reduce fruit yield. Elongation of stigma tube and antheridial cone splitting occur in tomato. For genotypes having no stigma exertion at high temperature will be having effective pollination and thus better yield. Plants exposed to temperatures greater than 40° C for a period of 4 hours resulted abortion of flowers and pollen.

Plants grown below 12°C during night time or when day temperature is above 29°C, tacky and nonviable pollens are produced, thus pollination effectiveness and the flowers dry and drop off ultimately. Heat stress reduced pollination rate in flowers of tomato and thus lower fruit setting and lower yields are possible [87].

Cell membrane integrity:

Because of high temperatures change the tertiary and quaternary structures of proteins, they have an adverse effect on the integrity and functionality of biological membranes. Increased membrane permeability brought on by such alterations increases the loss of cellular electrolytes. enhanced Ca2+ inflow, enhanced Ca2+ signalling cascade activation, and cytoskeleton reorganisation are all effects of increased membrane fluidity. Osmolytes and other antioxidants are produced as a result of this signalling pathway in response to high temperatures [86]. An indirect indicator of HS tolerance has been the decreasing solute leakage, which is an indication of increasing cell membrane integrity. Due to the higher permeability of thylakoid membranes, high-temperature stress also decouples electron transport from photophosphorylation [88] According to Los and Murata (2004), the degree of membrane lipid unsaturation is related to membrane fluidity. Mature leaves contain more saturated fatty acids, which raises the plasma membranes' melting point and lowers the plants' ability to withstand heat.

Conclusion

Development of heat tolerant genotypes should be the objective of future tomato breeding and biotechnology with respect to global warming scenario. The reduction in crop productivity under heat stress is chiefly associated with alterations in carbohydrate accumulation and resulting defects in assimilation partitioning from source to sink. It is necessary to understand the responses and acclimatization processes to higher temperatures in plants, such that the mechanisms underlying can be used for developing heat-tolerant varieties. Sugars not only acts structural component and metabolic substrates but also regulate genes associated with heat stress tolerance and reduce chance of crop loss. The external application of compounds having activities of osmoregulators, phytohormones, signaling molecules, etc., have showed positive responses in stress tolerance due to its growth promoting and antioxidant activities.

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