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REVIEW ARTICLE

Source-Sink Regulation of Photo-Assimilates under High Temperature Conditions

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ABSTRACT
Manipulating crop yield is the ultimate objective of crop research. Serious efforts have been directed towards increasing the accumulation of photo-assimilates in the economic organs of a plant. The major factors that are crucial in this regard are the enzymatic mechanisms active in the source and sink organs as well as the transport of photo-assimilates between them. Carbon partitioning determines the rate of transport and quantity of photo-assimilates that contribute to the increase or decrease of crop yield. However, abiotic and biotic stress conditions pose a serious challenge to maintaining the yield of a plant. It is well known how increased temperatures have serious impact on the molecular, biochemical and physiological functions of a plant. Manipulation of the source-sink factors has been found to ameliorate the effects of high temperature on carbon partitioning. In light of the predicted increase in global atmospheric temperatures, it is essential to review the impact of high temperature on plant growth and development. Understanding the regulation of photo-assimilates under the limiting conditions could provide management options for optimizing the production potential.
Keywords: carbon partitioning, heat stress, sink regulation, enzymatic activity

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INTRODUCTION

Plants require photo-assimilates as a source of carbon for growth and development. This is achieved through the process of photosynthesis which occurs in the source organs such as leaves. Source organs are the factories where carbon is produced in the form of sugars and are the exporters of energy for the rest of the plant[1]. The sink organs are the importers of this energy wherein these assimilates are stored. The production of the photo-assimilates as well as their accumulation is of crucial importance as the yield of the plant is the net accumulation of these photosynthates. Several factors come into play while determining the the storage capacity of a sink organ[2]. The capacity of the source organs in their rate of production of photo-assimilates, the rate and quantity at which these sugars are transported to the sink organs, and the size and capacity to store these resources in the sink organs all play a major role in this regard. Apart from these, several enzymes such as the invertases, sucrose and starch synthases etc.[3][4] are critical as the activators of conversion of the storage compounds into transportable as well as accumulating forms.

High temperatures have a deleterious effect on plant growth and development. Predicted rise in temperatures due to global warming [5] is a major concern for researchers as maintaining the yield potential under increased temperatures is a challenge. The current review explores the effect of high temperature on the source-sink regulation, the factors involved and the ways in which their effects can be mitigated.

EFFECT OF HEAT STRESS

High temperature stress causes damage to proteins, disturbs protein synthesis, inactivates major enzymes, damages membranes, impairs cell division and causes oxidative damage.

1) Effect on water uptake – There is negative impact on the root conductance. Rapid reduction in leaf tissue water content was observed in sugarcane inspite of sufficient availability of soil water [6]. Increased rate of transpiration leads to loss of water impairing certain important physiological processes in plants. The growth of the roots is affected by heat stress leading to a reduction in the number and mass which leads to a limitation the supply of water and nutrients.

2) Effect on nutrient relations of crops - Activity of the major enzymes like nitrate reductase involved in the nutrient metabolism is significantly reduced under high temperature stress [7]. Reduced root mass and nutrient uptake per unit root areaaffects nutrient cycling, uptake and availability to plants by hampering the physiological functions of plants.Nitrogen limitation affects photosynthetic components rich in nitrogen such as chlorophyll, light-harvesting complex and Rubisco. Phosphorus limitation affects photosynthesis through changes in the activity of Calvin-cycle enzymes, RuBP regeneration and/or Rubisco activity and is also part of ATP and NADPH/NADP+

3)Effect on photosynthesis - Reduction in chlorophyll biosynthesis is due to deactivation of enzymes [8]. Increased temperature of the leaf and photon flux density effects the thermo-tolerance adjustment of the PSII[9]. Damage to oxygen evolving complex results in imbalanced flow of electrons to the acceptor site of PSII[10]. Activity of 5-aminolevulinatedehydratase, an important enzyme in the pyrrole biosynthesis pathway, decreased significantly in wheat under heat stress [11]. Higher temperatures caused a reduction in biosynthesis of the protochlorophyllide by 70%. Heat stress caused more accelerated degradation of chlorophyll a and b in developed leaves[12]. Net photosynthesis in many plant species is inhibited due to reduction in the activation state of the CO_2 binding enzyme, Rubisco[9]. On the whole, the reduction in photosynthesis under high temperature is due to damage to chlorophyll pigments, decline in leaf nitrogen contents, blockage of PSII reaction center and electron flow, decreased quantum efficiency (Fv/Fm) and down-regulation of PSII photochemistry [13].

4) Oxidative damage - Oxidative damage in the cells is caused by excessive production of reactive oxygen species (ROS). ROS affect cell functioning by damaging lipids and proteins. Antioxidant defense mechanisms are of two types - enzymatic and non-enzymatic. Enzymatic mechanisms involve superoxide dismutase (SOD), glutathione reductase (GR), peroxidase (POD) and catalase (CAT) while non-enzymatic enzymes include certain carotenoids and glutathione. Oxidative damage can be overcome by maintaining higher levels of the anti-oxidants. Phyto-hormones can be used which act as natural defense molecules. Exogenous application of calcium induces heat stress resistance in plants by inducing higher antioxidant activity [14]. Treatment of barley seeds with glycine betaine resulted in improved membrane stability, photosynthetic rate and leaf water status [15].

5) Effect on Reproductive Physiology - A number of physiological processes that occur during anthesis, such as pollination, pollen germination and fertilization, are highly sensitive to extremes of temperature. High temperature reduces the cell wall invertase (CWI) activity which is required for mediating sucrose hydrolysis in anthers and microspores. This leads to altered carbohydrate metabolism leading to starch deficiency in pollen resulting in male sterility [16].

EFFECT OF HIGH NIGHT TEMPERATURE (HNT)

High night temperature also plays a critical role in crop productivity. There is significant reduction in grain weight and quality under high night temperature. This is due to reduced phloem unloading to sink tissue (lower CWI), slower cell expansion (lower VI) and limited substrate supply for starch synthesis (lower SuSy) [17]. Significant decline in spikelet SuSy activity under HNT limits sucrose breakdown and substrate (UDP glucose/ADP glucose) supply for starch synthesis in the grain. This results in poor sink strength. Significant increase in intermediates of TCA cycle compounds like isocitrate and fumarate were recorded in rice leaves exposed to HNT, likely reflecting an increase in respiration [18].

Reduced assimilate production is observed during later grain filling phase in rice. This results in higher Rn/Pn ratio. Therefore, higher respiratory carbon losses under HNT during post-flowering phase could contribute to loss in biomass and grain weight [17]. Under high night temperature auxin, cytokinin and gibberellins were down-regulated while ethylene and abscisic acid were upregulated [19]. In Tascosa, a tolerant wheat cultivar, an increase in methionine due to the conversion of S-Adenosyl methionine back to methionine lowered ethylene production thereby countering HNT induced early senescence [20].

For developing improved cultivars with HNT tolerance the following characters should be selected for: Lower maintenance respiration (Rn) during post-flowering phase, sustained supply of photo-assimilates. The genetic regulation of key sink enzymes such as cell wall invertase (CWI), vacuolar invertase (VI) and sucrose synthase (SuSy) can be explored and utilised in advanced breeding and molecular approaches, increased production of osmolytes such as maltose and simple sugars.

CARBON PARTITIONING

Photosynthesis determines the amount of substrate available for plant growth. Carbon partitioning determines both the efficiency with which substrate is used and the extent of its productive investment. Sucrose is the primary product of source and is the substrate of sink. It is the most abundant compound transported in the plants. The transport of assimilates occurs from photosynthetically active source tissues such as mature leaves to non-photosynthetic sink tissues such as fruits or reproductive organs, tubers, meristems or roots. Assimilates are converted into sucrose in the cytosol. Alternately, transitory starch is synthesized in the plastids, which is in turn degraded into glucose and maltose at night during respiration. There are three key factors that regulate carbon partitioning – i) Production of photo-assimilates (source capacity) ii) Transport of photo-assimilates iii) Utilization of photo-assimilates in sink organs.

i) Source Capacity - Carbon partitioning in source organs depends on the efficiency of photosynthetic activity. It is also controlled by the metabolism of photo-assimilates and the rate of transport to sink tissues. Reduced fruit set and decreased growth rate was reported in transgenic tomatoes which expressed reduced sucrose synthase (SuSy) activity [21].Fructose-2,6-bisphosphate, a signal metabolite caused accumulation of phosphorylated intermediates resulting in activation of ADP-glucose pyrophosphorylase (AGPase) which led to feedback inhibition of sucrose synthesis [22]. These studies show how the control of assimilates at the sink determines the carbon allocation at the source.

ii) Transport of photo-assimilates - All the photo-assimilates that are not required for the support of leaf function are converted into sucrose or amino acids and loaded into the phloem for translocation to the sink organs. Various transporters are required for efficient movement of sucrose across plasma membranes. Rapid phloem loading in source leaves and phloem unloading in sink organs is possible through the apoplastic pathway. The efficient export into cell wall spaces is mediated by sucrose facilitators such as AtSWEET11 and 12 [23]. Uptake of sucrose in cells as mediated by Suc/H^+symporters[24]. Sucrose is loaded from the cytosol into storage vacuoles by hexose/Suc/H^+antiporters[25]. The transporters fine-tune sucrose/hexose flux to maintain homoeostasis as well as regulate intra-organellarsignaling.

iii) Sink Unloading - Photosynthesis and sink utilization of carbohydrates are tightly coordinated. When the active sink organs are removed or if a deficiency in a particular nutrient is caused, it leads to decreased sink activity. This causes the accumulation of carbohydrates in the leaves resulting in the inhibition of photosynthesis [26]. The remaining sink capacity and the restricted transport capacity determine the degree of phloem unloading. Both, development as well as fruit growth is limited by sucrose available from phloem unloading [27]. Sucrose is broken down into glucose and fructose by cell wall invertase resulting in increased apoplasmic levels of hexoses. This causes a gradient of translocation from source-to-sink and hence the net import into the fruit.

ROLE OF ENZYMES

The enzymes that play an important role in the grain filling are starch synthase, sucrose synthase, starch branching enzyme and ADP glucose pyrophosphorylase [28]. Invertases (INV) and sucrose synthase (SuSy) are considered as key enzymes that determine sink strength. They maintain the sucrose gradient from source to sink tissue by cleaving sucrose into hexoses. Abortion of kernel growth by high temperature is mainly due to impairing the process of sucrose unloading in the pedicel by indirectly inhibiting cytoplasmic invertase (CI) activity, which may prevent starch synthesis in the endosperm [29]. Cell wall invertases (CWI) are insoluble proteins ionically bound to cell wall and plays key role in phloem unloading by cleaving sucrose in the apoplast [30][31]. As symplastic connection is absent between developing grain and maternal tissue, low CWI activity hampers sucrose unloading. Vacuolar invertase (VI) is a key player of sink initiation and expansion by supporting cell division during pre-storage phase in the grain. It regulates overall sucrose pool in the cytosol and its availability for export from the source tissue. Lower VI affects early grain development. It reduces cell expansion with lower hexose-based turgor pressure required for normal cell expansion.

Sucrose synthase (SUSy) is a key enzyme regulating phloem loading of sucrose. It provides substrate (UDP glucose/ADP glucose) for starch synthesis in developing grain. It catalyses the first step for sucrose to starch conversion in grain [32]. ADP-glucose pyrophosphorylase (AGP) catalyses the formation of ADP-glucose, which is a direct substrate for starch synthesis synthesized from glucose-1-phosphate and ATP. Granule Bound Starch Synthase (GBSSI) is responsible for amylose synthase while Branching Enzyme IIb (BEIIb) generates short chains of amylopectin. The down-regulation of GBSSI and BEIIb alters the fine structure of amylose and amylopectin, leading to changes in starch characteristics that degrade the cooking and eating properties of rice [33].

SINK FACTORS

The export of assimilates from source to sink generally depends on the rate of photosynthesis and sucrose concentration in leaves. Carbohydrates supporting grain growth during the grain filling stage are derived from the current photo-assimilate as well as the stored carbohydrate reserves in vegetative organs [34]. High temperature accelerated the remobilization of stored reserves from the leaf sheaths. The starch and dry matter content in the grains increased significantly faster under high temperature than in the control [35]. The important factors affecting grain filling are the shortening of the grain filling duration, loss of activity of source or sink and the panicle contribution to the grain weight [36].

Early termination of grain filling in temperate rice was not due to lack of assimilate because of leaf senescence but due to loss of sink activity owing to the earlier senescence of panicle. Dry matter partitioning to the leaf sheath and culm continued even after termination of grain filling. This indicates that leaves were still maintaining photosynthetic capacity and supplying assimilates into the other plant tissues [37]. Sink senescence leads to reduction of translocation ability and loss of activity of starch synthesis-related enzymes. Slower panicle senescence allows grains to accumulate more assimilates. There was no source limitation as photosynthesis-related proteins [Rubisco, RCA and oxygen evolving enhancer protein (OEEP)] were sufficiently upregulated. Activity of soluble starch synthase was reduced which could have imposed a sink limitation effect [38].

Sink capacity can be increased by enhancing the activities of starch synthesis-related enzymes which cause enhanced starch biosynthesis. Transgenic wheat plants overexpressing the rice starch synthase 1 (OsSSI) gene altered source–sink relationships and extended grain-filling period [39]. Improvements of ovary or endosperm cell development results in larger cells with greater potential for assimilate storage [40]. The number and size of the cells formed and the capacity of endosperm cells determines the yield in wheat. Interaction of phyto-hormones such as cytokinins and hormonal regulation is an important means to improve sink capacity in this regard [41].

ADAPTATION MECHANISMS

Preconditioning of plants - Preconditioned tomato plants showed better performance under the heat stress by making better osmotic and stomatal adjustments [42]ii) Application of hormones - Exogenous application of brassinosteroid on *L. chinensis* improves the stress tolerance by improving the plant growth, synthesis of photosynthetic pigments and antioxidant enzymes activity [43] iii) Partial removal of sink organs - When rice panicles were partly clipped to about 30%, it increased assimilate supply to the remaining grains. This is attributed to upregulation of expression of OsSUT1 and starch synthesis-related genes [35] iv) Pre-anthesis heat treatment - Enhanced carbohydrate remobilization from stems to grains led to less changed starch content and starch granule size through enhancing the fructancatalyzing enzyme (i.e. SST and FFT) activities [44]

Apart from agronomic measures, the best way to combat high temperature stress is to breed for tolerant varieties. In this regard, the following approaches can be followed –

1) Conventional Breeding – The varieties being bred should be selected for the following characters: improved morpho-physiological traits, minimal damage to photosynthetic machinery, increased biosynthesis of the protective compounds, higher membrane thermo-stability, higher fruit setting rate, increased grain filling duration and grain weight.

2) Modern Breeding - Identifying QTLs related to different traits involved in heat tolerance can be useful in incorporating them in breeding programmes. Simple sequence repeat markers linked with different heat tolerance characters were used in marker assisted selection among 25 wheat genotypes for heat tolerance [45].

3) Transgenic approaches - Transgenic approaches involve modifications in the qualitative as well as the quantitative traits through transfer of desired genes. Genes which encode growth regulators, compatible solutes and antioxidants involved in stress tolerance are important targets in this technique. Genetic manipulations for over-expression of SOD under heat stress have been proven to be successful [46]. A transgenic tobacco plant showing a better photosynthetic activity under heat stress has been produced by alteration of the chloroplast membranes (Murakami *et al*., 2000) [47]. HSFs and DREB2A genes have been identified to engineer heat tolerant transgenic plants [48].

4) Metabolomic approaches - Metabolomics could be a useful selection tool to identify associations between genotype and phenotype. It could lead to a better understanding of the genetic basis of plant responses to stresses. Some of the metabolites can be used as stress markers and utilised in breeding [49]. Identifying the rate limiting step/enzyme in the metabolite pathway would be useful in developing gene based markers targeting the specific enzyme. Li *et al*.[50] integrated metabolomic and transcriptomic analyses of heat-tolerant (N22) and heat-sensitive (Moroberekan) rice. They found that

sugar metabolism was the crucial metabolic and transcriptional component that differentiated floral organ susceptibility or tolerance to stress.

CONCLUSION

In view of the rising global warming in the current climate change scenario, we can expect that the temperatures in the coming decades are going to rise steeply. Therefore, in order to adapt crop production to the changing scenario, understanding the regulation of photo-assimilates under high temperature conditions is critical to develop new varieties or solutions to overcome the deleterious effects. Marker assisted selection (MAS) or transgenic interventions would play an important role in this regard. Spraying of phyto-hormones or chemicals to ameliorate the damaging effects would also be crucial.

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Source-Sink Regulation of Photo-Assimilates under High Temperature Conditions

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ABSTRACT
Manipulating crop yield is the ultimate objective of crop research. Serious efforts have been directed towards increasing the accumulation of photo-assimilates in the economic organs of a plant. The major factors that are crucial in this regard are the enzymatic mechanisms active in the source and sink organs as well as the transport of photo-assimilates between them. Carbon partitioning determines the rate of transport and quantity of photo-assimilates that contribute to the increase or decrease of crop yield. However, abiotic and biotic stress conditions pose a serious challenge to maintaining the yield of a plant. It is well known how increased temperatures have serious impact on the molecular, biochemical and physiological functions of a plant. Manipulation of the source-sink factors has been found to ameliorate the effects of high temperature on carbon partitioning. In light of the predicted increase in global atmospheric temperatures, it is essential to review the impact of high temperature on plant growth and development. Understanding the regulation of photo-assimilates under the limiting conditions could provide management options for optimizing the production potential.
Keywords: carbon partitioning, heat stress, sink regulation, enzymatic activity

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INTRODUCTION

Plants require photo-assimilates as a source of carbon for growth and development. This is achieved through the process of photosynthesis which occurs in the source organs such as leaves. Source organs are the factories where carbon is produced in the form of sugars and are the exporters of energy for the rest of the plant[1]. The sink organs are the importers of this energy wherein these assimilates are stored. The production of the photo-assimilates as well as their accumulation is of crucial importance as the yield of the plant is the net accumulation of these photosynthates. Several factors come into play while determining the the storage capacity of a sink organ[2]. The capacity of the source organs in their rate of production of photo-assimilates, the rate and quantity at which these sugars are transported to the sink organs, and the size and capacity to store these resources in the sink organs all play a major role in this regard. Apart from these, several enzymes such as the invertases, sucrose and starch synthases etc.[3][4] are critical as the activators of conversion of the storage compounds into transportable as well as accumulating forms.

High temperatures have a deleterious effect on plant growth and development. Predicted rise in temperatures due to global warming [5] is a major concern for researchers as maintaining the yield potential under increased temperatures is a challenge. The current review explores the effect of high temperature on the source-sink regulation, the factors involved and the ways in which their effects can be mitigated.

EFFECT OF HEAT STRESS

High temperature stress causes damage to proteins, disturbs protein synthesis, inactivates major enzymes, damages membranes, impairs cell division and causes oxidative damage.

1) Effect on water uptake – There is negative impact on the root conductance. Rapid reduction in leaf tissue water content was observed in sugarcane inspite of sufficient availability of soil water [6]. Increased rate of transpiration leads to loss of water impairing certain important physiological processes in plants. The growth of the roots is affected by heat stress leading to a reduction in the number and mass which leads to a limitation the supply of water and nutrients.

2) Effect on nutrient relations of crops - Activity of the major enzymes like nitrate reductase involved in the nutrient metabolism is significantly reduced under high temperature stress [7]. Reduced root mass and nutrient uptake per unit root areaaffects nutrient cycling, uptake and availability to plants by hampering the physiological functions of plants.Nitrogen limitation affects photosynthetic components rich in nitrogen such as chlorophyll, light-harvesting complex and Rubisco. Phosphorus limitation affects photosynthesis through changes in the activity of Calvin-cycle enzymes, RuBP regeneration and/or Rubisco activity and is also part of ATP and NADPH/NADP+

3)Effect on photosynthesis - Reduction in chlorophyll biosynthesis is due to deactivation of enzymes [8]. Increased temperature of the leaf and photon flux density effects the thermo-tolerance adjustment of the PSII[9]. Damage to oxygen evolving complex results in imbalanced flow of electrons to the acceptor site of PSII[10]. Activity of 5-aminolevulinatedehydratase, an important enzyme in the pyrrole biosynthesis pathway, decreased significantly in wheat under heat stress [11]. Higher temperatures caused a reduction in biosynthesis of the protochlorophyllide by 70%. Heat stress caused more accelerated degradation of chlorophyll a and b in developed leaves[12]. Net photosynthesis in many plant species is inhibited due to reduction in the activation state of the CO_2 binding enzyme, Rubisco[9]. On the whole, the reduction in photosynthesis under high temperature is due to damage to chlorophyll pigments, decline in leaf nitrogen contents, blockage of PSII reaction center and electron flow, decreased quantum efficiency (Fv/Fm) and down-regulation of PSII photochemistry [13].

4) Oxidative damage - Oxidative damage in the cells is caused by excessive production of reactive oxygen species (ROS). ROS affect cell functioning by damaging lipids and proteins. Antioxidant defense mechanisms are of two types - enzymatic and non-enzymatic. Enzymatic mechanisms involve superoxide dismutase (SOD), glutathione reductase (GR), peroxidase (POD) and catalase (CAT) while non-enzymatic enzymes include certain carotenoids and glutathione. Oxidative damage can be overcome by maintaining higher levels of the anti-oxidants. Phyto-hormones can be used which act as natural defense molecules. Exogenous application of calcium induces heat stress resistance in plants by inducing higher antioxidant activity [14]. Treatment of barley seeds with glycine betaine resulted in improved membrane stability, photosynthetic rate and leaf water status [15].

5) Effect on Reproductive Physiology - A number of physiological processes that occur during anthesis, such as pollination, pollen germination and fertilization, are highly sensitive to extremes of temperature. High temperature reduces the cell wall invertase (CWI) activity which is required for mediating sucrose hydrolysis in anthers and microspores. This leads to altered carbohydrate metabolism leading to starch deficiency in pollen resulting in male sterility [16].

EFFECT OF HIGH NIGHT TEMPERATURE (HNT)

High night temperature also plays a critical role in crop productivity. There is significant reduction in grain weight and quality under high night temperature. This is due to reduced phloem unloading to sink tissue (lower CWI), slower cell expansion (lower VI) and limited substrate supply for starch synthesis (lower SuSy) [17]. Significant decline in spikelet SuSy activity under HNT limits sucrose breakdown and substrate (UDP glucose/ADP glucose) supply for starch synthesis in the grain. This results in poor sink strength. Significant increase in intermediates of TCA cycle compounds like isocitrate and fumarate were recorded in rice leaves exposed to HNT, likely reflecting an increase in respiration [18].

Reduced assimilate production is observed during later grain filling phase in rice. This results in higher Rn/Pn ratio. Therefore, higher respiratory carbon losses under HNT during post-flowering phase could contribute to loss in biomass and grain weight [17]. Under high night temperature auxin, cytokinin and gibberellins were down-regulated while ethylene and abscisic acid were upregulated [19]. In Tascosa, a tolerant wheat cultivar, an increase in methionine due to the conversion of S-Adenosyl methionine back to methionine lowered ethylene production thereby countering HNT induced early senescence [20].

For developing improved cultivars with HNT tolerance the following characters should be selected for: Lower maintenance respiration (Rn) during post-flowering phase, sustained supply of photo-assimilates. The genetic regulation of key sink enzymes such as cell wall invertase (CWI), vacuolar invertase (VI) and sucrose synthase (SuSy) can be explored and utilised in advanced breeding and molecular approaches, increased production of osmolytes such as maltose and simple sugars.

CARBON PARTITIONING

Photosynthesis determines the amount of substrate available for plant growth. Carbon partitioning determines both the efficiency with which substrate is used and the extent of its productive investment. Sucrose is the primary product of source and is the substrate of sink. It is the most abundant compound transported in the plants. The transport of assimilates occurs from photosynthetically active source tissues such as mature leaves to non-photosynthetic sink tissues such as fruits or reproductive organs, tubers, meristems or roots. Assimilates are converted into sucrose in the cytosol. Alternately, transitory starch is synthesized in the plastids, which is in turn degraded into glucose and maltose at night during respiration. There are three key factors that regulate carbon partitioning – i) Production of photo-assimilates (source capacity) ii) Transport of photo-assimilates iii) Utilization of photo-assimilates in sink organs.

i) Source Capacity - Carbon partitioning in source organs depends on the efficiency of photosynthetic activity. It is also controlled by the metabolism of photo-assimilates and the rate of transport to sink tissues. Reduced fruit set and decreased growth rate was reported in transgenic tomatoes which expressed reduced sucrose synthase (SuSy) activity [21].Fructose-2,6-bisphosphate, a signal metabolite caused accumulation of phosphorylated intermediates resulting in activation of ADP-glucose pyrophosphorylase (AGPase) which led to feedback inhibition of sucrose synthesis [22]. These studies show how the control of assimilates at the sink determines the carbon allocation at the source.

ii) Transport of photo-assimilates - All the photo-assimilates that are not required for the support of leaf function are converted into sucrose or amino acids and loaded into the phloem for translocation to the sink organs. Various transporters are required for efficient movement of sucrose across plasma membranes. Rapid phloem loading in source leaves and phloem unloading in sink organs is possible through the apoplastic pathway. The efficient export into cell wall spaces is mediated by sucrose facilitators such as AtSWEET11 and 12 [23]. Uptake of sucrose in cells as mediated by Suc/H^+symporters[24]. Sucrose is loaded from the cytosol into storage vacuoles by hexose/Suc/H^+antiporters[25]. The transporters fine-tune sucrose/hexose flux to maintain homoeostasis as well as regulate intra-organellarsignaling.

iii) Sink Unloading - Photosynthesis and sink utilization of carbohydrates are tightly coordinated. When the active sink organs are removed or if a deficiency in a particular nutrient is caused, it leads to decreased sink activity. This causes the accumulation of carbohydrates in the leaves resulting in the inhibition of photosynthesis [26]. The remaining sink capacity and the restricted transport capacity determine the degree of phloem unloading. Both, development as well as fruit growth is limited by sucrose available from phloem unloading [27]. Sucrose is broken down into glucose and fructose by cell wall invertase resulting in increased apoplasmic levels of hexoses. This causes a gradient of translocation from source-to-sink and hence the net import into the fruit.

ROLE OF ENZYMES

The enzymes that play an important role in the grain filling are starch synthase, sucrose synthase, starch branching enzyme and ADP glucose pyrophosphorylase [28]. Invertases (INV) and sucrose synthase (SuSy) are considered as key enzymes that determine sink strength. They maintain the sucrose gradient from source to sink tissue by cleaving sucrose into hexoses. Abortion of kernel growth by high temperature is mainly due to impairing the process of sucrose unloading in the pedicel by indirectly inhibiting cytoplasmic invertase (CI) activity, which may prevent starch synthesis in the endosperm [29]. Cell wall invertases (CWI) are insoluble proteins ionically bound to cell wall and plays key role in phloem unloading by cleaving sucrose in the apoplast [30][31]. As symplastic connection is absent between developing grain and maternal tissue, low CWI activity hampers sucrose unloading. Vacuolar invertase (VI) is a key player of sink initiation and expansion by supporting cell division during pre-storage phase in the grain. It regulates overall sucrose pool in the cytosol and its availability for export from the source tissue. Lower VI affects early grain development. It reduces cell expansion with lower hexose-based turgor pressure required for normal cell expansion.

Sucrose synthase (SUSy) is a key enzyme regulating phloem loading of sucrose. It provides substrate (UDP glucose/ADP glucose) for starch synthesis in developing grain. It catalyses the first step for sucrose to starch conversion in grain [32]. ADP-glucose pyrophosphorylase (AGP) catalyses the formation of ADP-glucose, which is a direct substrate for starch synthesis synthesized from glucose-1-phosphate and ATP. Granule Bound Starch Synthase (GBSSI) is responsible for amylose synthase while Branching Enzyme IIb (BEIIb) generates short chains of amylopectin. The down-regulation of GBSSI and BEIIb alters the fine structure of amylose and amylopectin, leading to changes in starch characteristics that degrade the cooking and eating properties of rice [33].

SINK FACTORS

The export of assimilates from source to sink generally depends on the rate of photosynthesis and sucrose concentration in leaves. Carbohydrates supporting grain growth during the grain filling stage are derived from the current photo-assimilate as well as the stored carbohydrate reserves in vegetative organs [34]. High temperature accelerated the remobilization of stored reserves from the leaf sheaths. The starch and dry matter content in the grains increased significantly faster under high temperature than in the control [35]. The important factors affecting grain filling are the shortening of the grain filling duration, loss of activity of source or sink and the panicle contribution to the grain weight [36].

Early termination of grain filling in temperate rice was not due to lack of assimilate because of leaf senescence but due to loss of sink activity owing to the earlier senescence of panicle. Dry matter partitioning to the leaf sheath and culm continued even after termination of grain filling. This indicates that leaves were still maintaining photosynthetic capacity and supplying assimilates into the other plant tissues [37]. Sink senescence leads to reduction of translocation ability and loss of activity of starch synthesis-related enzymes. Slower panicle senescence allows grains to accumulate more assimilates. There was no source limitation as photosynthesis-related proteins [Rubisco, RCA and oxygen evolving enhancer protein (OEEP)] were sufficiently upregulated. Activity of soluble starch synthase was reduced which could have imposed a sink limitation effect [38].

Sink capacity can be increased by enhancing the activities of starch synthesis-related enzymes which cause enhanced starch biosynthesis. Transgenic wheat plants overexpressing the rice starch synthase 1 (OsSSI) gene altered source–sink relationships and extended grain-filling period [39]. Improvements of ovary or endosperm cell development results in larger cells with greater potential for assimilate storage [40]. The number and size of the cells formed and the capacity of endosperm cells determines the yield in wheat. Interaction of phyto-hormones such as cytokinins and hormonal regulation is an important means to improve sink capacity in this regard [41].

ADAPTATION MECHANISMS

Preconditioning of plants - Preconditioned tomato plants showed better performance under the heat stress by making better osmotic and stomatal adjustments [42]ii) Application of hormones - Exogenous application of brassinosteroid on *L. chinensis* improves the stress tolerance by improving the plant growth, synthesis of photosynthetic pigments and antioxidant enzymes activity [43] iii) Partial removal of sink organs - When rice panicles were partly clipped to about 30%, it increased assimilate supply to the remaining grains. This is attributed to upregulation of expression of OsSUT1 and starch synthesis-related genes [35] iv) Pre-anthesis heat treatment - Enhanced carbohydrate remobilization from stems to grains led to less changed starch content and starch granule size through enhancing the fructancatalyzing enzyme (i.e. SST and FFT) activities [44]

Apart from agronomic measures, the best way to combat high temperature stress is to breed for tolerant varieties. In this regard, the following approaches can be followed –

1) Conventional Breeding – The varieties being bred should be selected for the following characters: improved morpho-physiological traits, minimal damage to photosynthetic machinery, increased biosynthesis of the protective compounds, higher membrane thermo-stability, higher fruit setting rate, increased grain filling duration and grain weight.

2) Modern Breeding - Identifying QTLs related to different traits involved in heat tolerance can be useful in incorporating them in breeding programmes. Simple sequence repeat markers linked with different heat tolerance characters were used in marker assisted selection among 25 wheat genotypes for heat tolerance [45].

3) Transgenic approaches - Transgenic approaches involve modifications in the qualitative as well as the quantitative traits through transfer of desired genes. Genes which encode growth regulators, compatible solutes and antioxidants involved in stress tolerance are important targets in this technique. Genetic manipulations for over-expression of SOD under heat stress have been proven to be successful [46]. A transgenic tobacco plant showing a better photosynthetic activity under heat stress has been produced by alteration of the chloroplast membranes (Murakami *et al*., 2000) [47]. HSFs and DREB2A genes have been identified to engineer heat tolerant transgenic plants [48].

4) Metabolomic approaches - Metabolomics could be a useful selection tool to identify associations between genotype and phenotype. It could lead to a better understanding of the genetic basis of plant responses to stresses. Some of the metabolites can be used as stress markers and utilised in breeding [49]. Identifying the rate limiting step/enzyme in the metabolite pathway would be useful in developing gene based markers targeting the specific enzyme. Li *et al*.[50] integrated metabolomic and transcriptomic analyses of heat-tolerant (N22) and heat-sensitive (Moroberekan) rice. They found that

sugar metabolism was the crucial metabolic and transcriptional component that differentiated floral organ susceptibility or tolerance to stress.

CONCLUSION

In view of the rising global warming in the current climate change scenario, we can expect that the temperatures in the coming decades are going to rise steeply. Therefore, in order to adapt crop production to the changing scenario, understanding the regulation of photo-assimilates under high temperature conditions is critical to develop new varieties or solutions to overcome the deleterious effects. Marker assisted selection (MAS) or transgenic interventions would play an important role in this regard. Spraying of phyto-hormones or chemicals to ameliorate the damaging effects would also be crucial.

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