Full Length Research

Adaptations and Mechanisms of Heat Stress Tolerance of Plants

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Heat stress is one of the major abiotic factor limiting production and productivity of crops in several regions round the world. In spite of variation in susceptibility of different stages to heat stress, almost all stages of plant life are affected by heat stress. The developmental stage at which the plant is exposed to the stress may determine the severity of possible damages experienced by the crop. During heat stress modifications in different plant processes takes place in such a way to minimize the effect and develop tolerance to sustain stressful environment. A key adaptive mechanism in many plants grown under heat stress is an accumulation of certain organic compounds of low molecular mass, generally referred to as compatible osmolytes. Osmolytes help in heat stress tolerance. The heat stress response is characterized by inhibition of normal transcription and translation, an enhanced expression of heat shock proteins (HSPs) and induction of thermo tolerance. Expression of heat shock proteins (HSPs) is known to be an important adaptive strategy. Secondary metabolites, antioxidants as well as antioxidant enzymes play crucial role in heat stress tolerance. Their expression varies in different species as well as in different cultivars of same species. Plant genetic resources having maximum yield in normal condition and performing better in heat stress condition are suitable for cultivation in heat stress condition.

Keywords: Heat stress, osmolytes, secondary metabolites, antioxidants, photosynthesis, tolerance

INTRODUCTION

Heat stress is defined as where temperature is hot enough for sufficient time that it can cause an *irreversible* damage to plant development or functions. In addition, high temperature can increase the rate of reproductive development, which shortens the time for photosynthesis to contribute to seed or fruit production. The extent to which heat stress occurs in specific climatic zones is a complex issue. Plants can be damaged in different ways by either high day or high night temperature and by either high air or high soil temperatures. There is no consensus on the effect of day and night temperature on plants. Some researchers believe that night temperature is the major limiting factor while others consider that day and night temperatures do not affect the plant independently. According to second group diurnal mean temperature is a better predictor of plant response to high temperature with day temperature having a secondary role (Peet and Willits, 1998). Also, crop species and cultivars differ in their sensitivity to high temperature. Cool season annual species are more sensitive to hot weather than warm

season annuals. High day temperatures can have direct damaging effects associated with hot tissue temperature or indirect effects associated with the plant water deficits that can arise due to high evaporative demands. Evaporative demand exhibits near exponential increase with increase in day time temperatures and can result in high transpiration rate and low plant water potential. At very high temperature, severe cellular injury and even cell death may occur within minutes, which could be attributed to a ruinous collapse of cellular organization (Schöffl et al., 1999). Globally, in different regions heat stress due to high ambient temperature is a major constraint in successful crop production worldwide (Hall, 2001). Due to drastic reduction in yield of crops, researchers are predicting the expected effects of heat stress on agriculture in near future through different types of models. As per report of the Intergovernmental Panel on Climatic Change (IPCC), global mean temperature will rise 0.3 ^{0}C per decade (Jones et al., 1999) reaching to approximately 1 and 3 ^{0}C above the present value by years 2025 and 2100, respectively.

The extent of heat stress that can occur in a specific climatic zone depends on the probability of high temperature occurring in the particular zone and duration of the high temperature during the day or night. Considering the fact that the global climate change is occurring, these probabilities may not be predicted well based only on historical records for specific locations. In fact, heat stress is a complex function of intensity (temperature degrees), duration and rate of increase in temperature. The magnitude of heat stress rapidly increases as temperature increases above a threshold level and complex acclimation effects can occur that depend on temperature and other environmental factors. A threshold temperature refers to a value of daily mean temperature at which a detectable reduction in growth begins. Information of lower and upper threshold temperature for a crop or cultivar is important for successful crop production as well as for further physiological research. Base threshold temperature vary with plant species, but for cool season crops 0 ^{0}C is often the best-predicted base temperature (Miller et al., 2001). Upper threshold temperature also differs for different plant species and genotypes within species. To cope with elevated temperature conditions, three types of adaptations take place in plants viz., morphological, physiological and biochemical (Figure. 1). Consequently, plants develop tolerance to survive in stressful environment but in turn this affects vegetative growth, reproductive development as well as yield and quality of produce through effect on different plant processes.

Impact of heat stress on vegetative growth

During the vegetative stage, high day temperature can

cause damage to components of leaf photosynthesis, decrease in carbon dioxide assimilation rate compared with environments having optimal temperature. Extreme temperature can cause premature death of plants causing complete loss of a crop. Heat stress adversely affects membrane thermo stability which can be evaluated by measuring electrolyte leakage from leaf disks subjected to extreme temperature. More stable membranes exhibit slower electrolyte leakage. Studies comparing responses to heat of contrasting species indicate that photosystem II of the cool season species such as wheat is more sensitive to heat than photosystem II of warm season species such as rice which is adapted to much higher temperature.

Even among cool season or warm season species drastic variability exists for heat stress, for example among the cool season annuals, pea is very sensitive to high day temperature with death of the plants occurring when air temperature exceeds about 35^{0}C for sufficient duration, whereas barley is heat tolerant especially during grain filling stage which is most sensitive stage of the crop for heat stress. Warm season annuals such as cowpea can produce substantial biomass when growing in heat stressed condition although vegetative development may exhibit abnormalities. For monocotyledons, including cool season and warm season annuals, high day time temperature can cause leaf firing which involves necrosis of the leaf tips. High temperature can cause visible morphological changes such as scorching of leaves and twigs, sunburns on leaves, branches and stems, leaf senescence and abscission, shoot and root growth inhibition, fruit discoloration and damage, and reduced yield (Ismail and Hall, 1999; Vollenweider and Gunthardt- Goerg, 2005). Germination of seeds may be delayed. In addition, heat stress may cause loss of vigor, ultimately leading to reduced emergence and seedling establishment. Heat stress causes most damaging effects when flowers are first visible and sensitivity continues for 10–15 days. In heat stress condition cell size decreases, stomatal closure takes place, trichomatous density increases as well as increase in xylem vessels takes place both in root and shoot (A˜non et al., 2004). High temperatures reduces photosynthesis by changing the structural organization of thylakoids (Karim et al., 1997). The specific effects of high temperature on photosynthetic membranes result in the loss of grana stacking or its swelling. The severity of damage depends on the developmental stage of the plant at which it is exposed to stress. Although, severity of the damage vary with developmental stage but all vegetative as well as reproductive stages are affected by heat stress up to some extent.

Heat stress is a major factor affecting the rate of plant development, which may be increasing to a certain limit and decreasing afterwards (Hall, 1992; Marcum, 1998;
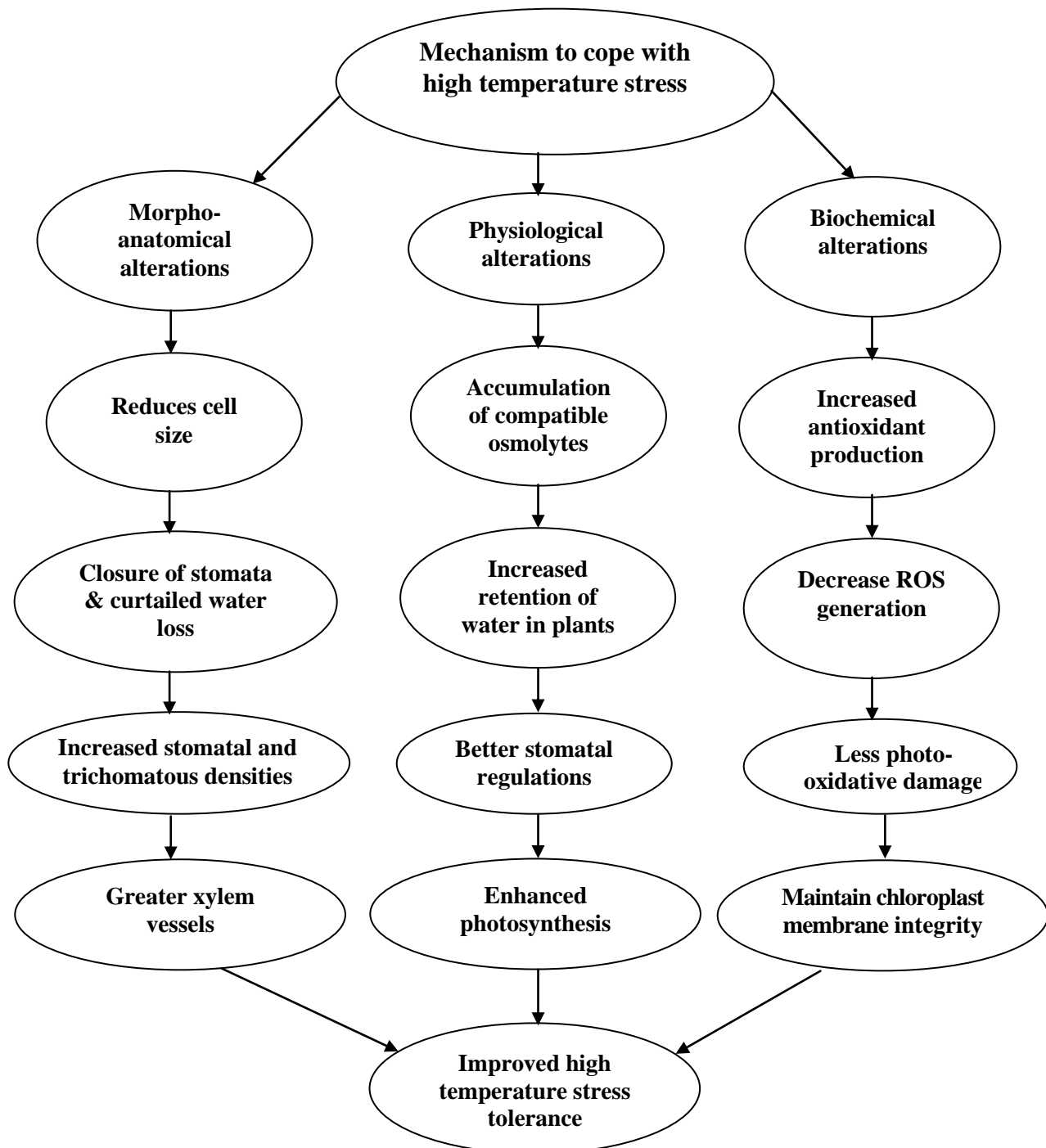
Figure 1. Flow chart of morphological, physiological and biochemical adaptations of plants to deal with heat stress.

Howarth, 2005) due to alteration in hormones. Initial slight decrease in abscisic acid and slight increase in cytokinin takes place as a fast response to stress condition but as stress progresses a gradual decrease in cytokinin and an increase in abscisic acid content occurs to acclimatize the plant to stressful environment (Figure. 2).

FAST RESPONSE   **ACCLIMATION**
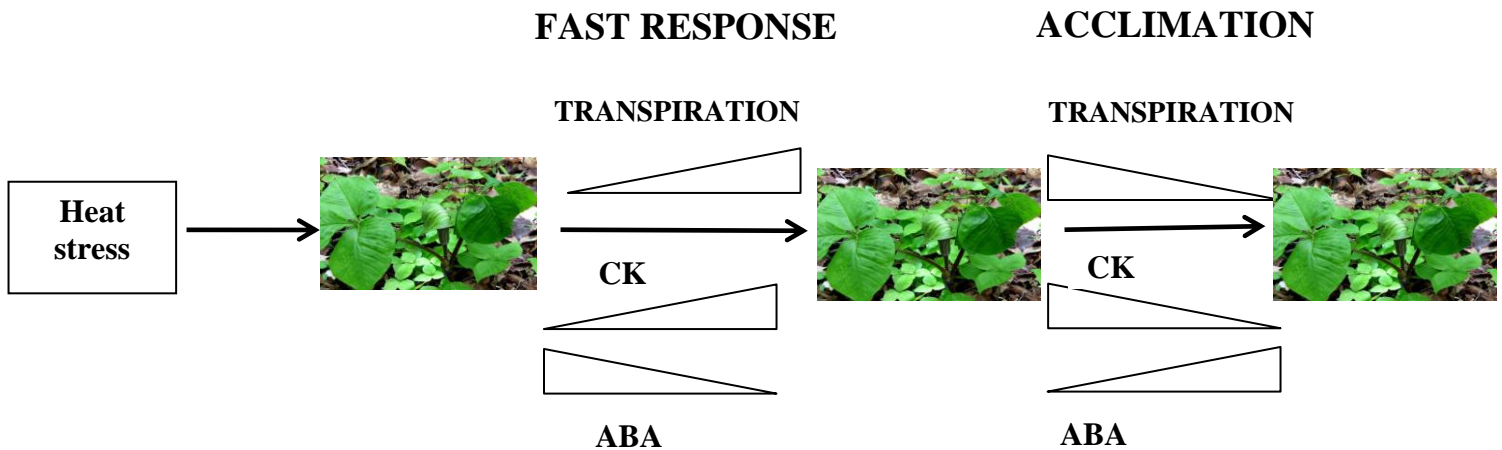
Figure 2. Short term and long term response of plants to heat stress. (ABA denotes abscisic acid and CK denotes cytokinin).

Impact of heat stress on reproductive growth

Reproductive development of many crop species is damaged by heat such that they produce no flowers or if flowers are produced there may be no fruit set or seeds. However, as compared to effect on flowers much hotter day temperature does not damage pod set. Reciprocal artificial pollinations between plants grown under high and optimal night temperature indicate that the reason for low pod set is male sterility. Pistils do not appear to be damaged by high night temperature.

During 24 hour diurnal cycle pollen development is sensitive to high night temperature at distinct period. High temperature during the last six hours of the night causes substantial decrease in pollen viability and pod set, whereas high temperature during the first six hours of a twelve hour night reveals no damage. There is a heat sensitive process in pollen development which is under circadian control, which occurs during late night period. The damaging effect of high night temperature on pod set is greater in long days than in short days and it is a phytochrome mediated response.

Stage of floral development most sensitive to high night temperature occurs 7 to 10 days prior to anthesis, which is after meiosis and coincides with release of pollen microspores from the tetrads. Damage due to high night temperature is associated with premature degeneration of the tapetal layer that provides nutrients to developing pollen. Comparisons of heat sensitive and heat tolerant genotypes show a genotypic association between sensitivity to heat and rapid leakage of electrolytes from leaf discs subjected to heat stress. Damage to pollen development by high night temperature may be associated with a heat induced malfunction of membrane properties. Impairment of pollen and anther development by elevated temperature contributes to decreased fruit set.

Stress induced arrest of male gametophyte development is preceded by disturbances in carbohydrate metabolism and distribution within anthers. The affected pollen grains fail to accumulate starch which is a major constituent of fertile pollen. Failure of viable pollen grain production under high temperature conditions may also be associated with hindered sugar metabolism.

For annual crops two weeks or more of consecutive or interrupted high temperature at night during the first month after germination causes suppression of floral bud development. In extreme cases the floral buds become necrotic and die. Response to red and far red light indicates that the effect is partially consistent with the system mediated by phytochrome. The damaging effect of high night temperature on floral bud development depends on light quality also whereas the damaging effect on seed/ pod set is independent of light quality. The extent to which high temperature causes damage to photosynthesis or reproductive development affects fruit or grain yield, probably depends on the extent to which the photosynthetic source and the reproductive sinks are limiting fruit or grain yield. This may vary among different species as well as among cultivars of the same species. Heat stress causes impairment of pollen and anther development leading to decreased fruit set in many crops at moderate to high temperatures (Sato et al., 2006). Under high temperature conditions, earlier heading is advantageous in the retention of more green leaves at anthesis, leading to a smaller reduction in yield (Tewolde et al., 2006). Furthermore, high temperatures during grain filling affects physico-chemical properties of grain crops like wheat (Perrotta et al., 1998).

Effect of heat stress on plant processes

Water Relations:

Water status of tissues is most crucial factor for survival of plants. Plants tend to maintain stable water status of tissues but high temperature impairs this particularly if water is limiting (Machado and Paulsen, 2001). To enhance stress tolerance, plants accumulate different osmolytes such as sugars and sugar alcohols (polyols), proline, tertiary and quaternary ammonium compounds and tertiary sulphonium compounds (Sairam and Tyagi, 2004). These compounds help to maintain stable water status of tissues by absorbing and retaining water.

Photosynthesis:

Photosynthesis is basic plant process responsible for yield of a crop. Heat stress affects different steps of photosynthetic process including photochemical reaction in thylakoid membrane and carbon metabolism in stroma of chloroplast (Wise et al., 2004). Alterations in photosynthetic attributes under heat stress are good indicators of thermo tolerance of plants as these show correlations with growth. Any constraint in photosynthesis at high temperature may limit plant growth. Sensitivity of photosynthesis to heat may be due to damage to components of photosystem II located in the thylakoid membranes of the chloroplast as well as membrane properties. Photochemical reactions in thylakoid lamellae and carbon metabolism in the stroma of chloroplast are the primary sites of injury at high temperature.

Chlorophyll fluorescence, the ratio of variable fluorescence to maximum fluorescence (Fv/Fm) and the base fluorescence ($F0$) are physiological parameters that have correlation with heat tolerance (Yamada et al., 1996). Increasing leaf temperature and photosynthetic photon flux density influences thermo tolerance adjustments of PSII indicating their potential to optimize photosynthesis under varying environmental conditions as long as the upper thermal limits are not exceeded. An increased chlorophyll $a:b$ ratio and a decreased chlorophyll: carotenoids ratio is also found to be associated with thermo tolerance.

Furthermore, under high temperature degradation of chlorophyll a and b is found to be more pronounced in developed leaves as compared to developing leaves. Such effects on chlorophyll or photosynthetic apparatus have been found to be associated with the production of active oxygen species (AOS). PSII is highly thermo labile in heat stress condition and its activity decreases drastically and some times high temperature stops its activity (Camejo et al., 2005). This is due to the properties of thylakoid membrane where PSII is located

(Mcdonald and Paulsen, 1997). Heat stress may lead to the dissociation of oxygen evolving complex (OEC) resulting in an imbalance between the electron flow from OEC towards the acceptor side of PSII in the direction of PSI reaction center. Furthermore, heat stress causes dissociation of a manganese (Mn) stabilizing 33 kDa protein at PSII reaction center complex followed by the release of Mn atoms. Heat stress may also impair other parts of the reaction center such as D1 and/or the D2 proteins. Following this, *de novo* synthesis of PSII units in the light is found to give a gradual rise to the observed PSII activities. These effects can result from different events including inhibition of electron transport activity and limited generation of reducing powers for metabolic functions. Under high temperature, leaf photosynthesis is found to be functionally limited by photosynthetic electron transport and ribulose-1,5-bisphosphate (RuBP) regeneration capacity. On the other hand, under high temperature, PSI stromal enzymes and chloroplast envelopes are thermo stable. In fact, under such condition PSI driven cyclic electron pathway, capable of contributing to thylakoid proton gradient is activated. Influence of heat stress is more on the photosynthetic capacity of C_3 plants than C_4 plants. It alters the energy distribution and changes the activities of carbon metabolism enzymes. Primarily the activity of Rubisco is affected which alters the rate of RuBP regeneration by the disruption of electron transport and inactivation of the oxygen evolving enzymes of PSII. Heat shock reduces the amount of photosynthetic pigments soluble proteins, Rubisco binding proteins (RBP) and large (LS) as well as small subunits (SS) of rubisco in darkness but increases them in light indicating their roles as chaperones and HSPs. Moreover, under heat stress sucrose or starch synthesis is adversely affected as the activity of sucrose phosphate synthase and ADP glucose pyrophosphorylase and invertase are found to be decreased.

Moreover, the ability to sustain leaf gas exchange under heat stress has a direct relationship with heat tolerance. During the vegetative stage, high day temperature can cause damage to compensated leaf photosynthesis reducing CO_2 assimilation rate. Increased temperature has been observed to limit photosynthesis and increase CO_2 transfer conductance between intercellular spaces and carboxylation sites. Stomatal conductance (gs) and net photosynthesis (Pn) are inhibited by moderate heat stress in many plant species due to a decrease in the activation state of Rubisco. With an increase in temperature Rubisco catalytic activity increases, a low affinity of the enzyme for CO_2 and its dual nature as an oxygenase limits the possible increases in Pn.

Heat stress induces imbalance in photosynthesis and respiration. In general, the rate of photosynthesis decreases while dark and photo respiration rates

increases significantly under high temperature. As the temperature increases rate of biochemical reactions decreases and enzyme inactivation as well as denaturation takes place leading to severely reduced photosynthesis. The magnitude of such alterations in response to heat stress varies with species as well as among genotypes of the same species. In addition, the photosynthetic CO_2 assimilation rate in developing leaves is less affected by heat stress than in completely developed leaves. In heat stress condition, the duration of developmental phases decreases leading to reduced light perception and carbon assimilation processes as well as smaller organs.

Assimilate partitioning:

Besides gross and net photosynthesis, partitioning of photosynthates is important for crop production. Under heat stress condition reductions in growth, economic yield and harvest index is common in almost all crops.

Thermo stability of cell membrane:

Heat stress causes loss of integrity and functions of biological membranes due to alteration in the tertiary and quaternary structures of membrane proteins. Such alterations enhance the permeability of membranes and cause increased leakage of solutes. It is an indication of decreased cell membrane thermo stability (CMT). CMT has been used as an indirect measure of heat stress tolerance in different plant species such as cotton (Ashraf et al., 1994), barley (Wahid and Shabbir, 2005) and wheat (Blum et al., 2001).

Secondary metabolites:

Heat stress induces production of phenolic compounds such as flavonoids and phenylpropanoids. Phenylalanine ammonia lyase (PAL) is considered to be the principal enzyme of the phenylpropanoid pathway. Increased activity of PAL in response to thermal stress is considered as the main acclimatory response of cells to heat stress. Thermal stress induces the biosynthesis of phenolics and suppresses their oxidation, which is considered to trigger the acclimation to heat stress. Moreover, under heat stress condition carotenoids protect cellular structures of plants. When plants are exposed to harmful environmental conditions, like heat stress, xanthophylls including violaxanthin, antheraxanthin and zeaxanthin partition between the light-harvesting complexes and the lipid phase of the thylakoid membranes. The interaction of the xanthophylls molecules and the membrane lipids brings about a decreased fluidity (thermo stability) of membrane and a lowered susceptibility to lipid peroxidation under high temperature (Havaux, 1998). Phenolic compounds such as flavonoids, anthocyanins, lignins, etc., are important class of secondary metabolites in plants which play diverse roles in abiotic stresses tolerance (Wahid and Ghazanfar, 2006; Wahid, 2007). Although, anthocyanins play important roles as UV screen but they have significant contribution in decreasing leaf osmotic potential, which is linked to increased uptake and reduced transpirational loss of water under environmental stresses including high temperature (Chalker-Scott, 2002). In addition isoprenoids are important low molecular weight secondary plant products synthesized via mevalonate pathway (Taiz and Zeiger, 2006). These are volatile in nature; their emission from leaves has been reported to confer heat-stress tolerance to photosynthetic apparatus in plants (Loreto et al., 1998).

Involvement of oxidative stress, antioxidants in heat stress tolerance:

Oxidative stress is a key stress involved in almost all stresses. Activated oxygen species (AOS) including singlet oxygen ($^1O_2$), superoxide radical ($O_2^{.-}$), hydrogen peroxide (H_2O_2) and hydroxyl radical ($OH^.$) are involved in the cellular injury due to high temperature (Liu and Huang, 2000). AOS cause the autocatalytic peroxidation of membrane lipids and pigments thus leading to the loss of membrane semi-permeability and modifying its functions (Xu et al., 2006).

Stress proteins:

During heat stress, synthesis and accumulation of specific proteins known as heat shock proteins (HSP) takes place. Increased production of HSPs occurs when plants experience either abrupt or gradual increase in temperature (Nakamoto and Hiyama, 1999). There are considerable variations in patterns of HSP production in different species and even among genotypes within species (Wood et al., 1998). This may be attributed to the variation in thermo tolerance of different genotypes within a species. In addition to HSPs, other plant proteins, such as ubiquitin (Sun and Callis, 1997), cytosolic Cu/Zn-SOD (Herouart and Inz´e, 1994) and Mn-POD (Brown et al., 1993) are also stimulated upon heat stress. Moreover, other proteins such as Pir proteins (Yun et al., 1997) and late embryogenesis abundant (LEA) proteins (Goyal et al., 2005) are also directly or indirectly involved in heat tolerance.

Even though the presence of a plant thermometer has not been established, but changing membrane fluidity plays a central role in sensing and influencing gene

expression under heat stress condition. Hence it may be speculated that sensors are located in microdomains of membranes, which are capable of detecting physical phase transition, eventually leading to conformational changes and/or phosphorylation/dephosphorylation cycles due to change in temperature (Plieth, 1999).

Effect of heat stress on gene expression in plants:

The heat stress responses are characterized by inhibition of normal transcription and translation, higher expression of heat shock proteins (HSPs) and induction of thermo tolerance. In severe heat stress condition, signaling pathways leading to apoptotic cell death are activated. As molecular chaperones, HSPs provide protection to cells against the damaging effects of heat stress and enhance survival. The enhanced expression of HSPs is regulated by heat shock transcription factors (HSFs). Recent advances in molecular genetic approaches have provided new insights into the plant heat stress response. Plants contain highly complex multigene families encoding HSFs and HSPs.

Moreover, cyclophilins (Cyp) are ubiquitous proteins with peptidyl-prolyl *cis-trans* isomerase activity that catalyses rotation of X-Pro peptide bonds and facilitate the folding of proteins. These enzymes are believed to play an important role in *in vivo* protein folding. During development of normal annual plants, Cyp transcripts are first detected three days after beginning of germination and these are present in all the plant tissues. Higher amounts of Cyp mRNAs are found in developing tissues. In response to heat shock, Cyp mRNA significantly accumulates. Members of the cyclophilin (Cyp) family are known to function as co-chaperones, interacting with chaperones such as heat shock protein 90 and perform important functions in the protein folding under high temperature stress.

Under control conditions, SsCyP is distributed throughout the plant in an organ specific manner. Highest protein levels are available in transporting organs and in tubers and substantial amounts have been observed in open flowers and in stamens. The SsCyP abundance in leaves strongly decreases with age. The organ-dependent SsCyP protein distribution and abundance are not modified by cold, drought, salinity and photo oxidative treatments. In contrast, the protein abundance substantially decreases in all organs of plants subjected to heat shock. Plants have various metabolic and developmental processes which are regulated by cross-talk between reactive oxygen species (ROS) and hormones (Kocsy et al., 2013). The redox state of the cell may be affected by plant hormones through transcriptional stimulation of genes coding for molecules involved in redox system (Laskowski et al., 2002).

Impact of heat stress on seed/ kernel growth:

Mature seed/ kernel dry weight is determined by the product of the rate and duration of grain growth, both of which are influenced by temperature. Generally, in lower temperature ranges ($\approx$10–25°C) cereals respond to increasing temperature with an increase in the rate of grain filling per unit of time. At temperature greater than a critical maximum ($\approx$25–35°C), the gain in the rate of grain filling begins to diminish and at supra optimal temperature ($\approx$40–45°C), the grain filling rate drops sharply. Rising temperature also causes a progressive decline in grain filling duration. Hence, at high temperature, yield losses are the result of loss in both grain filling rate as well as duration.

Grain filling duration may be determined by a number of factors including sucrose availability to the seed/ kernel and activity levels of enzymes involved in the sugar and starch metabolism in the kernel. Similarly, the rate of grain filling may be affected by sucrose concentration in the kernel and activity levels of enzymes in the pathway of starch biosynthesis. The effects of temperature on starch biosynthesis in the kernel have received much attention of the researchers as starch accounts for most of the dry weight in cereal grains. In wheat grains, losses in starch accumulation caused by heat stress are believed to be linked to a reduction in the activity of soluble starch synthase (SSS). Out of 13 enzymes of sugar and starch metabolism in kernels grown *in vitro* and exposed to a range of chronic heat stress, the activities of ADP glucose pyrophosphorylase (AGPase) and SSS have been found to be reduced most and their activities are found to be prematurely terminated compared with other enzymes. Reductions in starch synthesis under heat stress are closely tied to the duration of the activity of these enzymes. The activity of SSS has been found to be reduced most by high temperature and reaches a maximal rate at 25°C. Activities of other enzymes (with the exception of branching enzyme) increase up to a temperature of 45°C. Reduction in the rate of SSS is similar to the loss in the rate of starch synthesis caused by heat stress. In wheat, high temperature stress at the grain filling stage (10 days after anthesis to physiological maturity) leads to yield loss because it adversely affects physiological traits and individual grain weight (IGW) (Pradhan and Prasad, 2015).

CONCLUSION

Although heat stress affects almost all plant processes but impact on some processes is more as compared to others. Photosynthesis is considered as the physiological process most sensitive to high temperature and that the rising atmospheric CO_2 content will drive temperature increase in many already stressful environments.
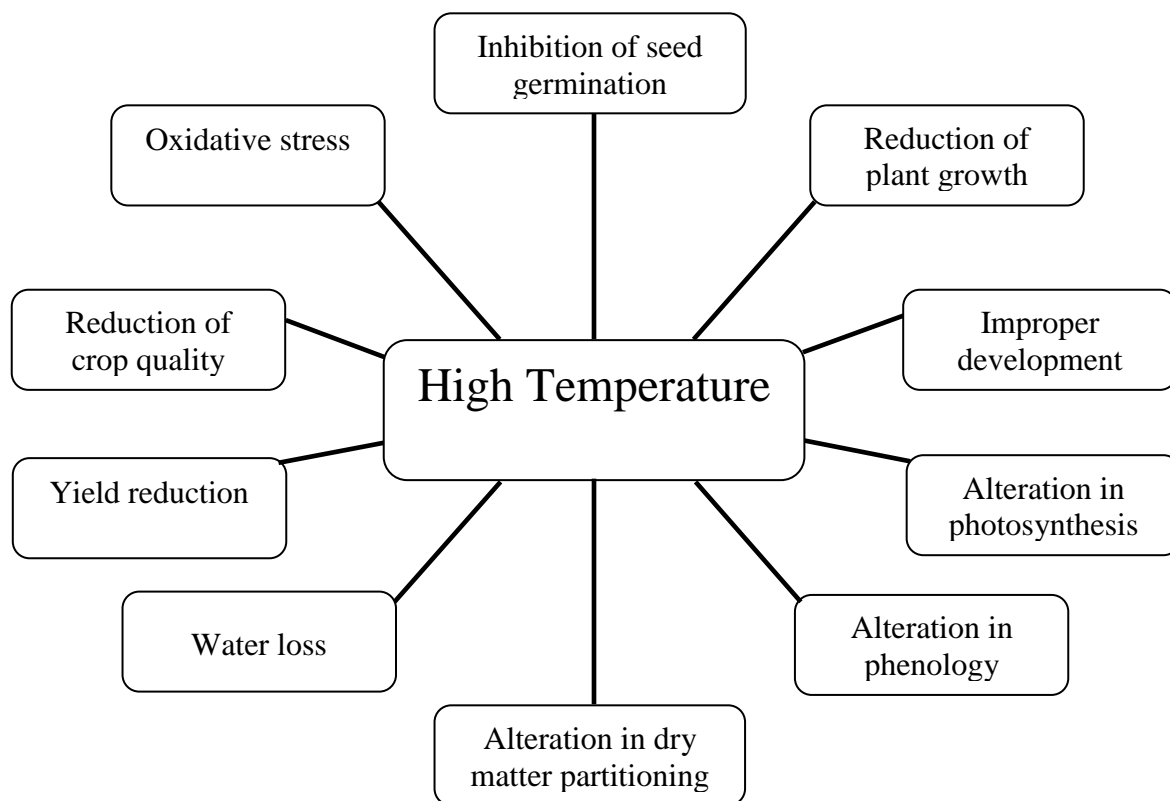
Figure 3. Effects of heat stress on plants.

The CO_2 induced increase in plant high temperature tolerance may have a substantial impact on both the productivity and distribution of many crop species in the near future.

Identification of genetic resources with heat tolerance attributes is an important approach to stabilize or maintain food production in heat stress condition. Screening different genotypes of crop wild relatives or wild accessions for growth under heat stress, distinction must be made between heat tolerance and growth potential. Usually plants with higher growth potential perform better regardless of the growing conditions.

During screening and breeding for heat stress tolerance, it is needed to opt for a two pronged strategy i.e., available genetic resources be able to produce maximum yield under normal condition and reduction in yield must be minimum under heat stress condition (Figure 3).

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