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Review Article

Coping Up With Heat Stress in Crops: A Review

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ABSTRACT

High temperature can adversely affect the plant growth and development resulting in a severe threat to crop production. Although all the growth stages of plant are sensitive to high temperature, the reproductive phase is the most sensitive one as it affects both grain setting and grain filling. Heat stress can alter biochemical, physiological, and morpho-anatomical behavior in various crops which in turn affects its growth and development causing a reduction in pollen viability, duration of grain filling, and starch synthesis in the endosperm. At flowering, temperature above optimum results in seed sterility, while post-anthesis heat stress causes a reduction in starch synthesis and alters the grain composition. Cereal crops have evolved an appropriate mechanism such as escape, avoidance or to stay green to cope with heat stress. In addition, foliar sprays of antioxidants and osmoprotectants at anthesis/post anthesis stage may protect the plant against heat induced oxidative damage.

Keywords: *Crop production, Development, Heat stress, Plant growth.*

INTRODUCTION

High temperature is the major environmental stress affecting plant growth, development and also induce morpho-physiological and biochemical alterations in affected plants. High temperatures stress (≤ 40ºC) can cause shoot and root growth inhibition and damage and reduced yield in plants, scorching of leaves and twigs, sunburns on leaves, branches and stems, leaf senescence and abscission, fruit discoloration.

International Heat Stress Genotype Experiment (IHSGE) involves the evaluation of physiological potential techniques screening by observing genetic diversity for trait and their association with heat tolerance. Canopy temperature depression, flag leaf stomatal conductance, as well as photosynthetic rate are highly correlated with field performance at various locations worldwide (Reynolds et al., 1994). The apparent sensitivity of metabolic processes to heat stress in the field (Reynolds et al., 2000), coupled with the decreased viability at high temperature determines total plant biomass and ultimately grain yield in hot environments.

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The crop yield in such conditions could be improved by modifying the crop micro-climate through some cultural practices and their optimum use such as time of sowing, mulching, frequent irrigation, ethylene inhibitors, osmoprotectants and nutrients (Dupont et al., 2006). In many crop species, the effects of high temperature stress are more prominent on reproductive development than on vegetative growth and the sudden decline in the yield with temperature is mainly associated with pollen infertility (Young et al., 2004).

Chemicals like cobalt chloride, potassium nitrate and calcium chloride have a role in heat stress management in cereals (Sarlach et al., 2013). Foliar spray of thiourea induced both salinity and heat tolerance by improving net photosynthesis and grain yield in wheat (Anjum et al., 2008). Foliar spray of sodium benzoate inhibited the ethylene synthesis and results in longer grain filling period which increased grain weight and protein content (Beltrano et al., 1999). Ascorbic acid and α-tocopherol sprayed plants postponed the senescence by antioxidant system which is involved in scavenging the reactive oxygen species (ROS) produced during cell death.

Heat stress and its effect on plant physiology and biochemistry

Heat stress induces the rapid production and accumulation of reactive oxygen species (ROS) (Xu et al., 2008). The detoxification of these ROS is very important and plants have evolved complex strategies to deal with them (Asthir et al., 2009). The cellular metabolism of plants typically changes with increase in ROS levels by increasing the expression and activity of ROS-scavenging enzymes and increasing production of antioxidants in order to maintain redox balance in a cell. Plants possess both enzymatic antioxidants which includes superoxide dismutase, catalase, guaiacol peroxidase, glutathione peroxidase, ascorbate peroxidase, glutathione reductase, dehydro-ascorbate reductase and monodehydroascorbate reductase, while non-enzymatic antioxidants include reduced glutathione and ascorbate (Asada, 1992). Formation of ROS is also related to ethylene production and lipid peroxidation which causes membrane damage. Increased ethylene content in plants can shorten the grain filling period, decrease 1000 kernel weight and trigger premature senescence (Beltrano et al., 1999). Don et al., (2005) found that the heat stress effects the high molecular weight fraction of gluten protein in wheat. They reported that the significant effect of prolonged exposure to high temperatures on gluten and its constituting gluten particles and they reported changes in dough mixing requirements were directly related to changes in gluten.

Activities of numerous antioxidative enzymes are temperature sensitive and their activation occurs at different temperature ranges. Their activities also differ according to tolerance/susceptibility of different crop genotypes to certain environmental factors. Secondary metabolites like ascorbic acid, tocopherol and carotene also protect plants against oxidative damage (Sairam et al., 2000). The enzymes *viz.*, glutathione *S*-transferase, peroxidase and catalase were more enhanced in the cultivar of barley which showed better tolerance to heat stress and provides protection against ROS generation. Almeselmani et al., (2006) concluded that various antioxidant enzymes showed positive correlation with chlorophyll content and negative with membrane injury index at different developmental stages in the four maize genotypes. Hence, it can be concluded that the antioxidant defense mechanism plays an important role in the heat stress tolerance. The activity of antioxidative enzymes increased significantly at different developmental growth stages in heat tolerant cultivars in response to heat stress treatment, while susceptible cultivar showed a significant reduction in catalase and peroxidase activity during heat stress.

Heat stress affects photosynthetic apparatus of crops, reduces pollen tube development and leads to pollen mortality (Hays et al., 2007) and causes oxidative damage to the plastids resulting in lesser grain yield and abortion (Farooq et al., 2011).

Reactions in the thylakoid membranes of higher plant chloroplasts are most sensitive to high-temperature damage, with consequent effects on the efficiency of photosynthesis. Exposure of plants to abiotic stresses such as drought and temperature extremes usually increases the susceptibility of these plants to attack by insects and plant diseases. It is also reported that the cool period for cereal crops in India is shrinking, while the threat of high temperature is expanding (Joshi et al., 2007).

Heat stress and its effects on plant productivity

Heat tolerance is a multi-genic character, numerous biochemical and metabolic traits are also involved in the development and maintenance of thermo-tolerance: antioxidant activity, membrane lipid un-saturation, gene expression and translation, protein stability, and accumulation of compatible solutes

Sexual reproduction and flowering in particular plants have been recognized as extremely sensitive process to heat stress which results in reduced crop productivity (Hedhly et al., 2009). Studies carried out under glass chambers suggest that heat stress is most injurious at the stage of flowering (Nava et al., 2009). However, many cereals show a high sensitivity to heat stress during harvesting and shows severe reductions in fruit set and minerals transportation (Frank et al., 2009).

Heat stress can occur at any developmental stage such as reproduction and this becomes one of the major constraints of plant adaptation to a changing environment. High temperature during reproductive phase hastened the decline in photosynthesis and leaf area, decreased shoot and grain mass as well as weight and sugar content of developing kernels.

Nevertheless, plant responses to high temperatures clearly depend on genotypic parameters, as certain genotypes are more tolerant (Challinor et al., 2007). Nawaz et al. (2013) found that heat stress negatively influences the chlorophyll and grain filling processes. Heat stress at all the stages drastically reduced the performance of all tested wheat cultivars; severity being at booting and heading stages than anthesis and grain filling stages. Physiological evidence indicates that loss of chlorophyll during grain filling is associated with reduced grain yield.

Morpho-physiological attributes as affected under heat stress

Days to anthesis

Tewolde et al. (2006) reported that early-heading varieties performed better than later-heading varieties because they produced fewer leaves per tiller and retained more green leaves, had longer grain-filling periods, and completed grain filling earlier in the season when air temperatures were lower. Application of heat event immediately before anthesis or during anthesis induced a significant reduction in the measured growth parameters (Wollenweber et al., 2003) and grain yield (Russel & Wilson 1994).

Heat stress reduces sugar accumulation in developing pollen grains and in the stigmatic surface by altering assimilate partitioning and changing the balance between symplastic and apoplastic pathways. Heat stress down-regulates the activity of sucrose synthase and cell wall degrading enzymes and invertases in the developing grains; as consequence, sucrose and starch turnover are disrupted (Sato et al., 2006). A high night temperature during growth, flower initiation and reproductive phase in cowpea from June-September during summer season in North-West India remains around 24°C which adversely affects the flowering and seed setting in cowpea thereby reducing its yield and quality.

Yield contributing attributes as affected under heat stress

Various physiological injuries have been observed under elevated temperatures, such as scorching of leaves and stems, leaf abscission and senescence, shoot and root growth inhibition or fruit damage, which consequently lead to a decreased plant productivity (Vollenweider & Günthardt-Goerg, 2005). High temperatures reduce plant growth by affecting the shoot net assimilation rates and thus the total dry weight of the plant (Wahid et al., 2007).

Grain development is also hindered by heat stress because assimilate translocation and grain-filling duration are influenced by changes in surrounding temperature.

Elevated temperatures can also cause grain shrinkage throughultra-structural changes in the aleurone layer and endospermcells as observed by Dias et al. (2008). Heat stress hastens the rate of grain filling whereas grainfilling duration is shortened (Dias & Lidon, 2009).

Number of spikelets per spike of wheat

Heat stress speeds up development of the spike reducing spikelet number and thus, the number of grains per spike. An inverse relationship between duration of heat stress and grain number per spike has been observed during this time. The reason for this sensitivity is because spikelet begin to form in the tissue between ridges of undifferentiated leaf primordia which is also called as double ridge stage. The reduction in the duration of emergence to double ridge to anthesis stage reduces the spikelet number per spike and grain number per spikelet (McMaster, 1997).

Number of grains per spike of wheat

In many temperate cereal crops, both grain weight and grain number appear to be impacted by heat stress, with a decline in grain number directly proportional with increasing temperatures during flowering and grain filling (Calderini et al., 1999). Influence of temperature on each of these components of grain yield depends on the developmental phase at which the elevated temperature occurs. For instance, between spike initiation and anthesis, temperatures above 20 ^{o}C may substantially reduce grain number per spike. Heat stress effects during pre-anthesis, particularly during meiosis and growth of the ovaries which may impose an upper limit for potential grain weight, are also associated with reduced grain numbers (Calderini et al., 1999).

Thousand grain weight of wheat

Both grain number and weight are sensitive to elevated temperature (Ferris *et al* 1998). Elevated temperatures reduce the duration between anthesis and physiological maturity which is associated with a reduction in grain weight (Warrington et al., 1977). Maintaining grain weight under heat stress during grain filling is a measure of heat tolerance. In this regard, Dias and Lidon (2009) proposed that high grain-filling rate and high potential grain weight can be useful selection criteria for improving heat tolerance.

Role of osmo-protectants

Accumulation of osmo-protectants is an important adaptive mechanism in plants subjected to high temperatures, as production of these primary metabolites is directly involved in the osmotic adjustment. Sarlach et al. (2013) found promising chemicals like cobalt chloride, potassium nitrate and calcium chloride in heat stress management in maize becausedaily high temperature appears to have greater impact on rice production as grain yield is more strongly positively correlated with increasing temperatures above optimum range.

Role of salicylic acid

Salicylic acid commonly known as “Aspirin” obtained from bark of willow tree is a plant growth regulator and is extensively used in agriculture for improving crop yield (Bera et al., 2008). Salicylic acid is a commonly plant produced phenolic compound that can function as a plant growth regulator (Arfan et al., 2007). Salicylic acid is involved in many physiological processes *viz.*, photosynthesis, transpiration, nutrient uptake, chlorophyll and protein synthesis. It is also involved in endogenous signaling, mediating in plant defense mechanisms against various stresses. It helps in protection of nucleic acid and preventions of protein degradation. The salicylic acid also known to induce many genes coding for pathogenesis-related proteins in response to biotic and abiotic stresses (Enyedi et al., 1992). Jeyakumar et al. (2008) reported that application of salicylic acid @ 125 mg/Lincreased the dry matter production of 21.6 g per plant and seed yield of 855 kg ha^{-1} in black gram. The salicylic acid also effected the seed quality of black gram resulting in highest protein content of seed i.e. 24.5 per cent. Salicylic acid is an endogenous growth regulator having phenolic nature which regulates several physiological processes in soybean such as stomatal closure, ion uptake, inhibition of ethylene biosynthesis and transpiration. Chandra et al. (2007) observed that application of salicylic acid increased the total soluble sugar and soluble protein of cowpea plants. Bekheta and Talaat (2009) conducted a pot experiment to study the physiological response of a mung bean plants to plant growth regulators and reported that foliar application of salicylic acid @ 15 mg L^{-1} significantly increased the plant height, number of branches per plant, fresh and dry weight of leaves and branches as well as seed yield. They also observed that the nutritional quality like total carbohydrates, total protein and mineral ions content of produced seeds were increased with salicylic acid at the same level.

Kothule et al. (2003) studied the effect of salicylic acid @ 100 or 200 ppm was applied as foliar spray at 35 DAS on various characteristics of soybean and observed that salicylic acid @ 100 ppm recorded effective in increasing plant height, number of branches, leaf area and total dry matter of plants as well as increasing the number of pods per plant, seeds per pod, weight of grain per pod, 100-seed weight, seed yield per plant and harvest index. Bera et al. (2008) observed the impact of foliar application of two sprays of salicylic acid at pre-flowering (30 DAS) and at flowering stage (40 DAS) on vegetative growth, flowering, pod setting and yield of green gram. The salicylic acid showed its effect by increasing flower production, number of pods set and yield of green gram. Kumar et al. (2014) recorded increase in seed yield in chickpea by foliar application of salicylic acid at both stages i.e. vegetative and reproductive stages and also in quality attributes viz. proteins, methionine and carbohydrates though favorable metabolism translated in yield enhancement (Mandavia et al., 2010). Kamal et al. (1995) observed that 150 ppm of salicylic acid as a foliar application gave the highest number of pods, pod setting and green pod yield of snap bean.

A field experiment on productivity of barley was conducted by Dhikwal et al. 2012 and reported that foliar spray of salicylic acid @ 100 ppm significantly improved the plant height, dry matter accumulation, effective tillers per meter row length, and spike length grains per spike and test weight of barley. Foliar application of salicylic acid exerted a significant effect on plant growth regulating substance when applied at physiological concentration, and thus acted as one of the plant growth regulating substance (Kalarani et al., 2002).

Khan et al. (2003) observed that foliar application of salicylic acid enhanced the photosynthetic rate, stomatal conductance and transpiration rate in Soybean.

Kumar et al. (2014) conducted field experiment for two consecutive years to investigate the effect of foliar application of bioregulators applied at different concentrations *viz.* salicylic acid @ 50 and 100 µg ml^{-1} on grain yield and quality of two forage cowpea cultivars CL 367 and Cowpea 88. Three foliar sprays of each bioregulator were applied at weekly interval with the onset of flower initiation. The highest grain yield and crude protein was recorded with foliar application of 50 µg ml^{-1} salicylic acid. The grain produced with 50 µg ml^{-1} salicylic acid had better quality in term of N, P, K, Zn, Fe and organic matter content than control. Increased seed yield and quality of cowpea with growth regulators certainly will improve livestock health and milk production thereby increasing the income of farmers. Kumar et al. (2013) concluded that foliar application of salicylic acid @ 50 mg L^{-1} and 100 mg L^{-1} at pre-flowering stage is known to induce more flowering and increase seed production of berseem (Egyptian clover). Significant increase in yield parameters and seed yield of Egyptian clover was observed with salicylic acid starting at flowering initiation stage, at weekly interval. Foliar application of salicylic acid at 50 mg L^{-1} recorded maximum heads per square metre, seeds per head, 1000-seed weight, seed yield and seed quality which were significantly higher. Salicylic acid at 50 mg L^{-1}

showed maximum increase in seed germination (13 per cent), shoot length (20.9 per cent), root length (26.3 per cent) and seedling vigour index (37.0 per cent) as compared to the control. Ali and Mahmoud (2013) conducted field experiment to investigate the effect of salicylic acid @ 0, 50, 100 and 150 ppm and observed that foliar application of salicylic acid @ 150 ppm enhanced significantly plant height, number of branches per plant, number of pods per plant, number of seeds per pod, 1000-seed weight, seed weight per plant and seed yield.

Devi et al. (2011) conducted three-year study and reported that salicylic acid @ 50 ppm at flower initiation stage, pod initiation stage and flower + pod initiation stages resulted in number of pods per plant (52), seeds per pod (2.45), 100-seed weight (11.7 g) and seed yield (1.51 t ha^{-1}) as compared to control. Chandrasekher and Bangarusamy (2003) reported that combination of 100 ppm salicylic acid, 2 per cent DAP, 1 per cent potassium chloride and 40 ppm naphthalene acetic acid were influenced the total dry matter production and yield components in moong bean.

Kumar et al. (2013) also found that foliar application of salicylic acid at 50 mg L^{-1} and KNO_3 at 2% recorded the maximum heads per meter square, seeds per head, thousand seed weight, seed yield and seed quality in berseem, which were significantly higher than the control. They also found that sodium benzoate showed minimum effect on seed yields but was significantly better than control.

Role of KNO_3

Farshad et al. (2011) found that the foliar spray of KNO_3 during (0.5%) at 50% flowering stage, 1.0 percent KNO_3 during anthesis stage, 2.5 mM of arginine, extra irrigation water during grain filling stage, use of potassium fertilizers with municipal waste water could alleviate the adverse impact of high temperature on wheat.

Role of $ZnSO_4.7H_2O$

Zinc has been found useful in improving yield and yield components of wheat (Cakmak et al., 1996) and adequately applied zinc has been shown to improve the water use efficiency of wheat plants (Bagci et al., 2007). High temperature during maturation and ripening is a major stress in many wheat production areas (Gibson & Paulsen, 1999) and zinc can help provide thermo-tolerance to the photosynthetic apparatus of wheat (Graham & McDonald, 2001).

Role of ascorbic acid

Heat stress triggers the production and accumulation of ROS (Sairam et al., 2000, Mittler, 2002 and Almeselmani et al., 2009). Hence their detoxification by antioxidant systems is important for protecting plants against heat stress. Vitamin C is a very important water-soluble vitamin taken up directly by the cells as L-ascorbic acid (AA) via high affinity/low capacity Na^+-dependent transporters (Tsukaguchi et al., 2003). Farouk (2011) reported that ascorbic acid and α-tocopherol sprayed plants postponed the leaf senescence by peroxide/ phenolic/ ascorbate system which is involved in scavenging the reactive oxygen species (ROS) produced during leaf senescence (Dwivedi et al., 2012).

Previous studies reported that an increase in chlorophyll content in strawberry under heat stress (Gulen & Eris, 2003). Similarly, in their study, the chlorophyll content of cultivars was increased with high temperature in AA non-applied plants in contrast to AA applied plants. This situation could explain that AA may protects the plants to heat stress as an antioxidant. Endogenous AA can be increased by exogenous application of AA through the rooting medium, as a foliar spray and as seed priming (Ebrahimian & Bybordi, 2012). Ascorbate helps scavenge hydrogen peroxide for the ascorbate-peroxidase-mediated reactions, while guaiacol scavenges ROS for GPX mediated reactions (Goyal & Asthir, 2010). Likewise, protection of cereal crops from heat-induced oxidative damage during the reproductive phase has also been correlated with non-enzymic antioxidants, such as ascorbate (Sairam et al., 2000).

CONCLUSIONS AND FUTURE PROSPECTS

In order to improve the yield plateau under heat stress, identification of the genetic elements associated with resistance/tolerance to high temperature is a novel approach in plant breeding and further utilization to develop resistant/tolerant varieties along with high yield performance. Hence, this review briefly explains about the various aspects of heat stress and tolerance through application of antioxidants and osmoprotectants in crops to be used for crop improvement for better mankind.

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