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Review Article

Mitigating Terminal Heat Stress in Wheat

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Abstract

Increasing severity of high temperature worldwide presents an alarming threat to wheat in India as late planting of wheat is very common due to the wide spread intensive rice-wheat cropping system particularly in north-west India. As a result, wheat crop has to face the problem of terminal heat stress. It causes a series of morpho-anatomical, physiological and biochemical changes, which affect plant growth and development and results in reduced yield. However, there are various strategies for yield improvement under high temperature stress after anthesis in wheat. Recently, emphasis has been placed on exploiting prompt and inexpensive means of obtaining satisfactory yields from heat stressed lands. One of the pragmatic approaches is the exogenous use of stress alleviating compounds either as seed or foliar application. In this respect, many nitrogenous compounds, inorganic salts, natural and synthetic plant growth regulators and stress signaling molecules have been used based on their specific properties and roles to improve photosynthesis and other physiological functions in wheat. Several osmoprotectants have been reported for alleviating abiotic stresses in wheat. In this literature review, there is an emphasis on the adverse effect of heat stress during reproductive stage of wheat and efficacy of different bio-regulators on grain yield and quality. It also investigates recent advances in research on all these aspects and focuses on osmoprotectants as an effective tool to improve terminal heat tolerance in wheat.

1. Introduction

The environment within which agricultural crops and agronomic practices developed over the past 10,000 years is rapidly changing due to human-induced climate change (IPCC, 2007) and extreme climate events, such as heat waves and droughts are also more common as a result of climate change (IPCC, 2012). Agricultural production, and thus global food security is directly affected by global warming (Ainsworth and Ort, 2010). Temperature controls the rate of plant metabolic processes that ultimately influence the production of biomass, fruits and grains (Hay and Walker, 1989). High temperature stress is a major environmental stress that limits crop growth, metabolism and productivity worldwide. Global climate models predict an increase in mean ambient temperatures between 1.8 and 5.8 °C by the end of this century (IPCC, 2007). Previous global food assessments have shown that these negative effects are particularly exacerbated in tropical regions (Fischer et al., 2005). Presently, Indian lowlands are the source of approximately 15% of global wheat production but it is anticipated that climate change will transform these into a heat stressed, short season production environment (Beta and Gerats, 2013). The PRECIS 9 providing regional climate for impact studies model for Indian arid region predicted for an increase in annual rainfall by 10-15% in the eastern fringe and 20-40% in the south, but the North West will experience up to 30% reduction in the rainfall (Buttar et al., 2012). Thus, in the changing climatic scenarios, there is a need to reinvent the research strategies i.e. adaptations of resource conservation technologies, judicious use of available water resources, enhance value-added weather management services and also to moderate the stresses due to biotic and abiotic factors to mitigate the deleterious effects of climate change (Buttar et al., 2012). It was further suggested to find out new strategies for ameliorating high temperatures stress in wheat in South East Asia and Southern Africa.

High temperature stress during reproductive development termed as terminal heat stress. Studies suggest that optimal temperature for grain set and grain filling is between 19 °C and 22 °C in wheat (Porter and Gawith, 1999). The threshold temperature i.e. the value of daily mean temperature at which a detectable reduction in growth begins, as 26 °C for wheat at post an thesis stage (Stone and Nicolas, 1994). During the grain filling period, heat stress can accelerate leaf senescence and affect final grain weight by shortening the grain filling duration (Dias and Lidon, 2009). Lobell et al. (2005) reported that wheat yield in Mexico decreased by 10% for every 1 °C increase in night time temperature and grain yield showed a strong negative correlation with increasing minimum temperature. Studies of heat stress on wheat have been focusing on the period of grain filling (Corbellini et al., 1997 and Stone and Nicolas, 1995) and have shown that two typical heat stresses are common during wheat grain filling. "Heat shock" is characterized by sudden, extreme high temperatures (>32 °C) for a short duration (3-5 days), while "chronic heat stress" consists of moderately high maximum temperatures (20-30 °C) for a longer duration. High temperature during wheat reproductive development hastened the decline in photosynthesis and leaf area, decreased shoot and grain mass as well as weight and sugar content of kernels, while also reducing water-use efficiency (Shah and Paulsen, 2003). In this review an attempt is made to outline the effect of terminal heat stress on growth, reproduction and various physiological processes affecting grain yield of wheat and the mitigation strategies.

2. Impact of Terminal Heat Stress on Plant System

Environmental stresses lead to the generation of reactive oxygen species (ROS). Heat stress can induce oxidative stress along with tissue dehydration. Generation and reactions of ROS, that is, singlet oxygen, superoxide radical (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radical (•OH), are common events during cellular injury by high temperature (Liu and Huang, 2000) and drought (Farooq et al., 2009). Autocatalytic peroxidation of membrane lipids and pigments by ROS leads to loss of membrane semi-permeability (Xu et al., 2006). The hydroxyl radical OH^- can damage chlorophyll, protein, DNA, lipids, and other important macromolecules, thus fatally affecting plant metabolism and limiting growth and yield (Sairam and Tyagi, 2004).

Photosynthesis is the most sensitive physiological process to high temperature (Wahid et al., 2007). It has been suggested that photosynthesis II (PSII) was inhibited during heat stress, which is the most thermally liable component of the electron transport chain (Ciaffi et al., 1996) Also, heat stress resulted in disruption in the structure and function of chloroplasts and reduction in chlorophyll content. The early effects of thermal stress comprise of structural alterations in chloroplast protein complexes and reduced activity of enzymes (Ahmad et al., 2010). The photochemical modifications in the carbon flux of the chloroplast stroma and those of the thylakoid membrane system are considered the primary sites of heat injury (Wise et al., 2004), as photosynthesis and the enzymes of the Calvin–Benson cycle, including ribulose 1, 5-bisphosphate carboxylase (Rubisco) and Rubisco activase are very sensitive to increased temperature and are severely inhibited even at low levels of heat stress. A specific effect of high temperatures on photosynthetic membranes includes the swelling of grana stacks and an aberrant stacking. Such structural changes are accompanied by ion-leakage from leaf cells exposed to heat and changes in energy allocation to the photosystems (Wahid and Shabbir, 2005). The detrimental effects of heat on chlorophyll and the photosynthetic apparatus are also associated with the production of injurious reactive oxygen species (Camejo et al., 2006).

Leaf senescence is the progressive loss of green leaf area that occurs during reproductive development of a crop (Nooden, 1988). The reduction in the optimum growth period caused by elevated temperature leads to early leaf senescence resulting in photosynthesis rate that is too low to meet plant economy (Sharma-Natu et al., 2010). Shortage of assimilate during grain filling further reduces number of grains spike^{-1} and grain weight (Ugarte et al., 2007).

Relative water content is useful indicator of the water balance of a plant. Sairam et al. (2000) reported that relative water contents were substantially reduced by increased temperature. Also, high temperature after tillering significantly reduced water potential in 2 wheat genotypes at anthesis and 7 and 15 days after anthesis (Amenselman et al., 2009). Leaf water potential is a reliable parameter for quantifying plant water stress, which is often associated with heat stress. Kramer and Boyer. (1995) reported positive correlation between leaf water potential with photosynthesis rate. As heat stress causes reduced photosynthesis; it also, thus lowers leaf water potential. Balla et al. (2013) investigated change in transpiration (E), the values for plants under heat stress were found more than the value of control plants as the stressed plants attempted to combat the effect of high temperature by increasing their transpiration. Also, the value of stomata conductance demonstration the extent is which stomata remain open. In the same experiment, it was reported that wheat plants showed decrease stomata conductance to that of control.

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 (Mahmood et al., 2010). For example, increase of just 1 °C temperature above 15–20 °C at grain filling stage can reduce grain weight by 1.5 mg per day (Streck, 2005). Although elevated temperatures promote the growth, it reduces the phenological duration of various crop stages, which is not compensated by the enhanced growth rate. Limited grain yield due to heat stress at reproductive stages may be attributed to minimum time duration for resource capture (Wheeler et al., 1996). Heat stress shortens the grain filling duration but accelerates the grain filling rate (Dias and Lidon, 2009). For instance, an increase of 5 °C in temperature above 20 °C shortened the grain filling duration by twelve days in wheat with increase in grain filling rate (Yin et al., 2009). It was reported that high temperature significantly shortened the grain filling period in all the genotypes with an average of about 16%. It was revealed that high temperature stress speeds up spike development (Porter and Gawith, 1999) reducing spikelet number of grains spike^{-1} (Saini and Aspinall, 1982).

Male sterility as a consequence of heat stress can be widely observed among many crop plants and the impairment of pollen and development has been the main factor involved in reduced yield under heat stress (Wassmann et al., 2009). For example, in barley anthers developing under high temperature (30-35 °C), cell-proliferation is arrested, vacuoles are distended, chloroplast development is altered, and mitochondrial abnormalities occur (Sakata et al., 2010). Heat stress also reduces carbohydrate accumulation in pollen grains and in the stigmatic tissue by altering assimilate partitioning and changing the balance between symplastic and apoplastic loading of the phloem (Taiz and Zeiger, 2006).

Extreme temperatures during grain filling have been identified as a major source of variation in wheat quality characteristics. For example, a reduction in the duration of the filling period due to high temperature stress demonstrated a shortened duration of glutenin synthesis, which in turn reduced dough strength (Ciaffi et al., 1996; Corbellini et al., 1997). Stone and Nicolas, (1995) found that the synthesis of the intermediates of SDS soluble polymers (mostly LMW glutenin subunits) continued unimpeded during heat stress, while the synthesis of the intermediates of the SDS insoluble polymers (mostly HMW glutenin subunits) was reduced, resulting in a reduction in the percentage of SDS insoluble polymers in the total polymers. Blumenthal et al. (1991) observed a decrease in the size of glutenin polymers in the mature grain in response to a heat stress treatment, and suggested that this may be due to the heat sensitivity of the enzymes involved in the formation of the disulfide isomerase. Therefore, high temperatures restrict the formation of the complex protein aggregates responsible for superior dough mixing properties (Corbellini et al., 1997). Sato et al. (2006) also reported that elevated temperature impairs pollen and another development leading to decreased yield. For example, high temperature during wheat reproductive development hastens the decline in photosynthesis and leaf area, decreases shoot and grain mass as well as weight and sugar content of kernels, and also reduces water-use efficiency (Shah and Paulsen, 2003). As a consequence, heat stress results in an altered nutritional flour quality (Hedhly et al., 2009).

3. Studies on Mitigation Strategies for Terminal Heat Stress

Terminal heat stress in wheat can be managed by applying bio regulators which may be organic or inorganic in nature. These osmoprotectants are nontoxic, highly soluble, compactable solutes occulting in all organisms from archaebacteria to higher plants. Exogenous application of these osmoprotectants, thus plays important roles in the adaption of calls to adverse effects of heat stress (Yancy, 1994). They also stimulated photosynthesis machinery (Rasheed et al., 2011) and hence improved yield and quality of crops. Wahid et al. (2007) reported that it has the potential to increase food production and quality much more quickly than plant breeding techniques. All available sources of osmoprotectants are now discussed in this paper.

3.1. Ascorbic acid

Ascorbic acid (Vitamin C) is water soluble and acts as a modulator of plant development through hormone signaling and as coenzyme in reactions by which carbohydrates and proteins are metabolized. They catch the free radicals or the reactive oxygen species produced during altered photosynthesis and respiration process under heat stress. They also regulate photosynthesis flowering and senescence (Barth et al., 2006) under elevated temperature. Tocopherol (Vitamin E) is a lipophylic antioxidant which establishes membranes, scavenges various ROS (Maeda and Dellapenna, 2007) and preserves PS II photo inactivation and membrane lipids from photo oxidation.

3.2. Cytokinins

Cytokinins are important group of plant bioregualators which play important role in greater partitioning of photosynthates towards reproductive sink thereby improving the harvest index (Sharma et al., 2008). They protect membranes against degradation by preventing oxidation of unsaturated fatty acids and hence increase drought tolerance in plants. Further, cytokinins inhibit formation and speed up break down of free radicals such as superoxide (O_2^-) and hydroxyl radical (OH^-) that otherwise oxidizes membrane lipids (Werner and Schmulling, 2009). Similarly, Criado et al. (2009) reported that the exogenous cytokinin application increased cell membrane stability in wheat cultivars under drought stress. Delayed chlorophyll degradation on account of cytokinin treatment has been reported by Goyal and Asthir. (2010). Gupta et al. (2003) reported that exogenous application of benzyl adenosine increased grain weight in all genotypes under post and thesis. Husain et al. (2008) also observed higher grain weight spraying benzyl adenine on ears at physiologist maturity Exogenous application of Maringa leaf extract, rich in cytokinin, ascorbic acid, phenol, K and Cs leads to an increase in wheat grain yield, more stable cell membrane and longer seasonal leaf area duration (Yashmeen et al., 2011). Brassinosteroids (BRs) are a new type of polyhydroxy steroidal phytohormones with significant growth-promoting influence (Bajguz and Piotrowska-Niczyporuk, 2014). Extensive research over the years' has established stress-impact-mitigating role of BRs and associated compounds in different plants exposed to various abiotic stresses such as high temperature (Janeczko et al., 2011).

3.3. *Nitric oxide*

In 1992, the biological significance of NO was recognized by SCIENCE which named the free radical NO as Molecule of the year and in 1998, Furchgott, Murad and Ignarro were awarded the Nobel Prize, in physiology and medicine. The exogenous applications of nitric oxide donor (NO) confer tolerance to various stresses (Husanuzzaman et al., 2013; Liv et al., 2011). It also leads to higher water retention and less transpiration rate (Gracia Mata and Lamartine, 2011). In wheat, exogenous SNP application accelerated protein synthesis, enhanced photosynthesis rate and maintained higher relative water content in wheat seedlings under drought stress (Tan et al., 2008). In another experimental, Song et al. (2006) found that both SNP and S-nitrose-N acetyl pinci-Hamine, both acting as NO donor dramatically alleviated heat stress induced in package increase, growth suppression and cell viability decrease in callus of reed under heat stress. In a system where toxicity is increased predominantly from ROS, NO may act as a chain breaker and thus limits the damage (Lipton et al., 1993). It is involved in two respiratory electron transport pathways in mitochondria (Zottini et al., 2003) where it medicates the modulation of ROS and enhances antioxidants defense systems in plants expose to various abiotic stresses. It can eliminate the superoxide anion and 0_2 and lipid radical R^- and enhancesthe activity of superoxide dismulase (Shi et al., 2007); Bavita et al. (2011) also reported that exogenous supply of SNP helps in ameliorating High temperature stress by enhancing activities of antioxide treatment in wheat. Kaur et al. (2010) also concluded that increased grain yield in wheat due to foliar application of N during reproductive phase may be due to better distribution and consistent availability of nitrogen to the plant throughout the crop season, which helped the plants to grow better and continuous supply of nitrogen to the grains during its development.

3.4. *Thiols*

Thiols are stress alleviating agents crucial for improving the metabolic imbalances produced in cell during stress. Thiols are also known for maintaining the redox state (-SM/S-S ratio) of the cell and its proper functioning under heat stress (Nathawat et al., 2007). Thiourea has two functional groups 'thiol' sulfur and amino i.e., NH_2 therefore it can provide both sulfur and nitrogen to plants. Thiourea significantly improve growth, yield and water use efficiency of wheat (Misra et al., 1997). Foliar spray of thiourea improved net photosynthesis, chlorophyll content and nitrogen metabolism in drought stressed dusting leading to improvement in seed yield (Garg et al., 2006). In around two thirds of foliar applied urea N was incorporated into plants within four hours of application, and almost 80% of the N applied was recovered in grain at the final harvest (Smith and Coff., 1991).

3.5. *Potassium (K^+)*

Potassium has substantial effect on enzyme activation, protein synthesis, photosynthesis, stomatal movement and water-relation (turgor regulation and osmotic adjustment) in plants (Marschner, 1995). Increased application of K^+ has been shown to enhance photosynthetic rate, plant growth, yield and drought resistance in different crops under abiotic stress conditions (Egilla et al., 2001). As Potassium is essential for enzyme activation, protein synthesis and photosynthesis (Azedo-Silva, 2004), it may act as osmoregulator during stress for increased active update of K^+ by the guard cells and stomatal regulation, exogeneous application of K^+ was required (Premchandra et al., 1993) under stress conditions. Under draught or heat stress, the photosynthesis efficiency of plants is reduced drastically as a consequence of chloroplast dehydration (Berkowtz and Kiroll, 1998). The chloroplasts lose large amount of K^+ with a simultaneous decrease in photosynthesis. Hence, application of K^+ was necessary to maintain photosynthetic ability in wheat during heat stress. Kaur et al. (2011) also concluded that four foliar sprays of 2% potassium nitrate solution starting from flowering at weekly interval are needed to obtain the highest seed cotton yield.

3.6. *Calcium*

Under heat stress, Ca^{2+} is required for maintenance of antioxidant activity in some cool season grasses (Jiang and Haung, 2001). Calcium application in the form of $CaCl_2$increased the malondialdehyde (MDA) content (lipid per oxidation product) and stimulated the activities of SOD and catalase, which could be the reason for the induction of heat tolerance (koluparv et al., 2005). Calcium plays an essential role in processes that preserve the structural and functional integrity of plant membranes, stabilize cell wall structures, regulate ion transport and selectivity, and control ion-exchange behaviour as well as cell wall enzyme activities (Marschner, 1995).

3.7. *Glycinebetaine*

Glycinebetaine and polyamine are the low molecular weight organic compounds have been successfully applied to induce high temperature tolerance in plants. Polyamines are small ubiquitous nitrogenous compounds, which regulate cellular ionic environment, maintenance of membrane integrity, prevention of chlorophyll loss and stimulation of protein synthesis, nuclear acids and protective alkaloids (Kusano et al., 2008) under stress conditions. Stabilization of membranes and minimization of water stress are the physiological effects of polyamines (e.g. putrescine,) in the plant system (Liv et al., 2007; Goyal and Asthir, 2010). In tomato exogenous application of spermidine improved heat resistance by improving chlorophyll fluorescence properties hardening and the activity of PS II during linear increase in temperature (Murkowski, 2001). The protective role of polyamines (putrescine, spermidine and spermine) on plants was associated with an inhibition of ethylene evolution a maize plants (Todorov et al., 1998). Putrescine treatment also directly antagonizes several ethylene medicated responses in many terrestrial plants (Matto and White, 1991) and delayed senescence of wheat seedling (Mansour et al., 2002).

3.8. *Salicylic acid*

Salicylic acid (SA) is a common phenolic compound that promotes photosynthesis under heat stress by influencing various physiological and biochemical process. The ability of salicylic acid to activate the superoxide dismutase (SOD) has been revealed on certain species of plants (Rao et al., 1997) that, jointly with catalase inhibition, can be one of the probable reasons of increase of hydrogen peroxide content in plant tissues (Kolupaev et al., 2010). Salicylic acid can also exert various (both activating and inhibiting) influence on the activity of peroxidase, participating in the regulation of hydrogen peroxide pool and in the generation of superoxide anion radical on the conditions of presence of surplus of reductants. The activating influence of salicylic acid on the alternative oxidase, that changes the intensity of reactive oxygen species formation in mitochondria, is also founded (Pavlova et al., 2009). In another experimental, Khan et al. (2013) found that exogenous application of 0.5 mm salicylic acid alleviated heat stress in wheat by increasing proline production through the increase in y-gletamyl kinase and decrease in proline oxidize activ, resulting in promotion of osmotic potential and water potential necessary for maintaining photosynthetic activity. Also ethylene formation was restricted which resulted in delayed senescence, retention of stay green trait and increased yield.

3.9. *Zinc and silicon*

Zinc is known to have a stabilizing and protective effect on biomembranes against oxidative and peroxidative damage, and loss of plasma membrane integrity, as well as on membrane permeability alteration (Bettger and Odell, 1981). Zinc ions bind to ligands containing sulfur, nitrogen, and to a lesser extent oxygen, and preferentially bind to the membrane proteins. The balance between free radical generation and free radical defense determines the survival of the system. Therefore, Zn may have a role in modulating free radicals and their related damaging effects by enhancing plant's antioxidant systems (Zago and Oteiza, 2001). Silicon under heat or draught stress maintains plant water balance, photosynthetic efficiency and erectness of leaves and structure of xylem vessels under high transpiration rate (Hattori et al., 2005). It increases the number and mass grain production of wheat by stimulating shoot and root biomass (Filho et al., 2005) under water stressed conditions.

3.10. *Microorganisms*

Microorganisms could play an important role in adaptation strategies and increase of tolerance to abiotic stresses in agricultural plants. Plant-growth-promoting rhizobacteria (PGPR) mitigate most effectively the impact of heat stress on plants through the production of exopolysaccharates and biofilm formation. PGPR mitigate the impact of drought on plants through a process so-called *induced systemic tolerance* (IST), which includes: a) bacterial production of cytokinins b) production of antioxidants and c) degradation of the ethylene precursor ACC by bacterial ACC deaminase. Symbiotic fungi (arbuscular mycorrhizal fungi) and dual symbiotic systems (endophytic rhizospheric bacteria and symbiotic fungi) also tend to mitigate the high temperature stress in plants (Milosevic et al., 2012). Some bacterial species and strains affect plant tolerance to high temperature (Grover et al., 2010). The bacterium Burkholderia phytofirmans PSJN colonizes grapevine residues and protects the plant against heat and frost through increases in the levels of starch, and proline and phenols (Milosevic et al., 2012).

4. Conclusion

Heat stress results in the production of reactive oxygen species which causes cellular damage, hinders photosynthesis and altered metabolic activities, result in poor crop yield. In recent decades, exogenous application of osmoprotectants have shown improvement in growth and yield of wheat under terminal heat stress. However, field experiments that combine different biochemical, molecular and agronomic management practices are needed to investigate further their roles in ameliorating adverse effects of high temperature stress on final grain yield of wheat.

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