

Alleviation of temperature stress by nutrient management in crop plants: a review

E.A. Waraich^{1,2,*}, R. Ahmad², A. Halim² and T. Aziz^{3,4}

¹*School of Earth and Environmental Sciences, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009.* ²*Department of Crop Physiology, University of Agriculture, Faisalabad. Pakistan.* ³*Institute of Soil and Environmental Sciences, University of Agriculture, Faisalabad. Pakistan.* ⁴*School of Plant Biology, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009. (Present address).* *Corresponding author. Tel: +61 4 6900 9687, + 92 336 6553081; E-mail uaf_ewarraich@yahoo.com (Ejaz Ahmad Waraich). Fax no.92-041-9200764 (Attn. Ejaz Ahmad Waraich, Crop Physiology)

Abstract

The burgeoning population of world is expected to reach about 9-10 billion by the end of year 2050. Due to this rapidly increasing population, food productivity is decreasing. Temperature induced stress is an important environmental factor that influences the growth and development of plants. Both low and high temperatures affect plant growth and development at whole plant level, tissue and cell level and even at sub-cellular level. Temperature variation may affect morphology, anatomy, phenology and plant biochemistry at all levels of organization. Direct injuries due to high temperatures in plants include protein denaturation and aggregation, and increased fluidity of membrane lipids. Indirect or slower high temperature injuries include inactivation of enzymes in chloroplast and mitochondria, inhibition of protein synthesis, protein degradation and loss of membrane integrity. Low temperature stress during reproductive development induces flower abscission, pollen sterility, pollen tube distortion, ovule abortion and reduced fruit set, which ultimately lowers yield. A number of approaches are being used to alleviate the effect of temperature stress in crop plants. Proper plant nutrition is one of the good strategies to alleviate the temperature stress and in crop plants. Plant nutrients play a greater role in improving the temperature stress tolerance. In this paper we discuss the possible effective techniques to alleviate the temperature stress and the role of some macronutrients (nitrogen, potassium, calcium and magnesium) micronutrients (boron, manganese, and selenium) and salicylic acid in detail as how these nutrients play their role in alleviation of temperature stress in crop plant.

Keywords: Macronutrients; Mechanisms; Micronutrients; Temperature stress.

1. Introduction

World's population is increasing at an alarming rate and is expected to reach about nine to ten billion by the end of year 2050. The growing population will result in considerable additional demand for food (Waraich *et al.*, 2011) and it will also contribute towards changing climate, which is an alarming issue to the world's food safety. Due to the effect of various abiotic stresses the food productivity is decreasing and to minimize these losses is a major concern for all nations to cope with the increasing food requirements (Mahajan and Tuteja, 2005). Temperature stresses (high and low temperature) are the major environmental factors affecting plant growth, development and also induce morphological, physiological and biochemical changes in plants. According to a report of the Intergovernmental Panel on Climatic Change (IPCC) (IPCC Expert Meeting Report, 2007) the global mean temperature will rise 0.2 °C per decade in the coming years. This change in global temperature may alter the geographical distribution and growing season of agricultural crops (Porter, 2005). High temperature stress induces the rapid production and accumulation of reactive oxygen species (ROS) (Mittler, 2002; Almeselmani *et al.*, 2006; Xu *et al.* 2008). These high levels of ROS are harmful to all cellular compounds and negatively influence cellular metabolic processes (Breusegem *et al.*, 2001). The detoxification of these ROS is very important and plants have evolved complex strategies to deal with them (Asthir *et al.*, 2009). The plant cells typically respond to increases in ROS levels by increasing the expression and activity of ROS-scavenging enzymes and increasing their production of antioxidants in order to maintain redox homeostasis.

The plant life cycle both vegetative and reproductive phases are affected by the low temperature stress

(Nishiyama, 1995). During reproductive development low temperature stress induces flower abscission, pollen sterility, pollen tube distortion, ovule abortion and reduced fruit set, which ultimately lowers yield. During the reproductive phase cold stress has important economic and social consequences because the reproductive phase products are the key components of economic yield and are the principle source of food for entire humanity (Thakur *et al.*, 2010). The reproductive phase begins with transformation of the meristem into inflorescence and flower and, in annuals, ends upon seed reaching maturity. The reproductive phase consists of flower initiation, differentiation of male and female floral parts, micro- and mega-sporogenesis, development of male and female gametophytes (pollen grain and embryo sac), pollination, micro- and mega-gametogenesis, fertilization and seed development. All these stages respond differently to cold stress (Staggenborg and Vanderlip, 1996; Verheul *et al.*, 1996) but collectively all responses are negative and reduce net yield.

In response to these temperature stresses various approaches are being used, which can mitigate the effect of stress and lead to the adjustment of the cellular milieu and plant tolerance. In nature stress does not generally come in isolation and many stresses act hand in hand with each other. In response to these stress signals that cross talk with each other, plants naturally have developed diverse mechanisms for combating and tolerating them. In this review we have first emphasized high temperature stress followed by cold temperature stress and the injurious effects of these stresses on plants. Various mechanisms involved in cold and hot acclimation and their role towards membrane stabilization have also been discussed. The physiological and biochemical mechanisms pertain-

ing to each stress, and the role of nitrogen, potassium, calcium and magnesium, boron, manganese, and selenium have also been discussed in detail as how these nutrients play their role in alleviation of temperature stress in crop plant.

2. High temperature stress

2.1 Effects of high temperature stress on plants

High temperature stress induces morphological and (Giaveno and Ferrero, 2003), anatomical (Zhang *et al.*, 2005) as well as physiological and biochemical changes in plants. It induces the changes in water relations (Simoes-Araujo *et al.*, 2003; Morales *et al.*, 2003; Cabañero *et al.*, 2004), accumulation of compatible osmolytes (Hare *et al.*, 1998; Sakamoto and Murata, 2002), decrease in photosynthesis (Sharkova, 2001; Wise *et al.*, 2004), hormonal changes (Maestri *et al.*, 2002) and cell membrane thermostability (Martineau *et al.*, 1979; Somerville and Browse, 1991).

High temperatures stress ($\leq 40^{\circ}\text{C}$) can cause 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 in plants (Guilioni *et al.*, 1997; Ismail and Hall, 1999; Vollenweider and Gunthardt-Goerg, 2005). In melon, superoptimal temperatures can cause various damages like inhibition of seed germination and seedling growth (Kadota, 1959), depression of female flower expression (Kamiya and Tamura, 1965), failure of fertilization, reduction of fruit growth and sugar accumulation (Suzuki and Masuda, 1961). Hall (1992) reported that high

temperature stress in sugarcane causes a severe reduction in the first internode length resulting in premature death of plants. Sugarcane plants grown under high temperatures exhibited smaller internodes, increased tillering, early senescence, and reduced total biomass (Ebrahim *et al.*, 1998). In rice, anthesis and fertilization and to a some extent microsporogenesis (booting), are the most susceptible stages to high temperature stress (Satake and Yoshida, 1978; Farrell *et al.*, 2006). High temperature stress-induced spikelet sterility is linked to decreased anther dehiscence, poor shedding of pollen, poor germination of pollen grains on the stigma and decreased elongation of pollen tubes in rice (Prasad *et al.*, 2006).

Environmental stresses in plants have been associated with production of activated forms of oxygen (Figure 1), including hydrogen peroxide (H_2O_2), singlet oxygen, superoxide, and the hydroxyl radical (Anderson, 2002). Reactive oxygen species (ROS) are produced continuously as byproducts of different metabolic pathways which are located in different cellular compartments such as chloroplast, mitochondria and peroxisomes (Rio *et al.*, 2006; Navrot *et al.*, 2007). Through a variety of reactions, O_2^{\bullet} leads to the formation of H_2O_2 , OH^{\bullet} and other ROS. The ROS comprising O_2^{\bullet} , H_2O_2 , $^1\text{O}_2$, HO_2^{\bullet} , OH^{\bullet} , ROOH , ROO^+ and RO^+ are highly reactive and toxic and causes damage to proteins, lipids, carbohydrates and DNA which ultimately results in cell death. Accumulation of ROS as a result of high temperature stress is a major cause of loss of crop productivity worldwide. (Mittler, 2002; Apel and Hirt, 2004; Mahajan and Tuteja, 2005; Tuteja, 2007; Tuteja, 2010; Khan and Singh, 2008; Gill *et al.*, 2010.)

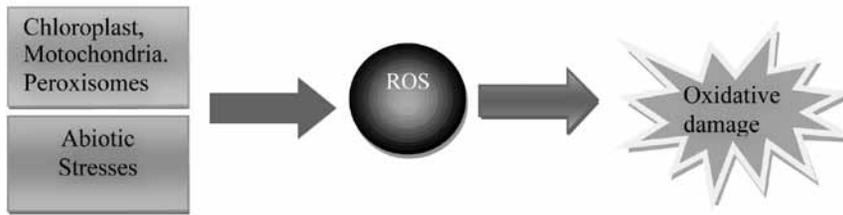


Figure 1. Schematic representation of Reactive Oxygen Species (ROS) generation in chloroplasts, Mitochondria and Peroxisomes causing oxidative damage due to abiotic stresses

In wheat (*Triticum aestivum* L.) high temperature stress during reproductive development is a primary constraint to its production. Formation of ROS is related to ethylene production and lipid peroxidation and results in membrane fluidity (Weckx *et al.*, 1989). Increased ethylene has been shown in mature wheat plants, to shorten the grain filling period, decrease 1000 kernel weight, hasten maturity and trigger premature senescence (Beltrano *et al.*, 1999). Ethylene overproduction has also been found during or after recovery from water stress (Beltrano *et al.*, 1999 ; Morgan *et al.*, 1990; Narayana *et al.*, 1991; Beltrano *et al.*, 1997).

Don *et al.* (2005) reported that high temperature effects the high molecular weight fraction of gluten protein in wheat. They reported significant effects of prolonged exposure to high temperatures (up to 40°C) on gluten in macropolymer (GMP) and its constituting gluten in particles and concluded that changes in dough mixing requirements were directly related to changes in gluten in macropolymer. Similar reductions were observed in starch, protein and oil contents of the maize kernel (Wilhelm *et al.*, 1999) and grain quality in other cereals under high temperature stress (Maestri *et al.*, 2002)

2.2. Approaches to induce high temperature stress tolerance

Among the various methods to induce high temperature stress in plant, foliar application of, or pre-sowing seed treatment with, low concentrations of inorganic salts, osmoprotectants, signalling molecules (e.g., growth hormones) and oxidants (e.g., H₂O₂) as well as preconditioning of plants are common approaches (Wahid *et al.*; 2007)

In black spruce high-temperature preconditioning has been shown to reduce the heat-induced damage to seedlings (Colclough *et al.*, 1990). Tomato plants exhibited good osmotic adjustment by maintaining the osmotic potential and stomatal conductance, and better growth in preconditioned plants as compare to control or non-preconditioned plants (Morales *et al.*, 2003). Similarly, turfgrass leaves manifested higher thermostability, lower lipid peroxidation product malondialdehyde (MDA) and lower damage to chloroplast upon exposure to high temperature stress in heat-acclimated as compared to non-acclimated plants (Xu *et al.*, 2006). Pre-sowing hardening of the seed at high temperature (42 °C) resulted in plants tolerance to overheating and dehydration and showing higher

levels of water-soluble proteins and lower amounts of amide-N in leaves compared to non-hardened plants in pearl millet (Tikhomirova, 1985). Kolupaev *et al* (2005) reported that exogenous application of Ca^{2+} promotes plant's heat tolerance. Calcium application in the form of CaCl_2 prior to the stress treatment has been shown to increase the malondialdehyde (MDA) content (lipid peroxidation product), and stimulated the activities of guaiacol peroxidase, SOD and catalase, which could be the reasons for the induction of heat tolerance.

Glycinebetaine and polyamines are the low molecular weight organic compounds have been successfully applied to induce heat tolerance in various plant species. Wahid and Shabbir (2005) reported that barley seeds pre-treated with glycinebetaine led to plants with lower membrane damage, better photosynthetic rate, improved leaf water potential and greater shoot dry mass, compared to untreated seeds. While in tomato exogenous application of 4mM spermidine improved heat resistance by improving chlorophyll fluorescence properties, hardening and higher resistance to thermal damage of the pigment-protein complexes structure, and the activity of PSII during linear increase in temperature (Murkowski, 2001). Under heat stress, Ca^{2+} is required for maintenance of

antioxidant activity and not for osmotic adjustment in some cool season grasses (Jiang and Haung, 2001). Under heat stress, Ca^{2+} requirement for growth is high to mitigate adverse effects of the stress (Kleinhenz and Palta, 2002).

The mechanisms through which the plants can cope with high temperature stress are described in Fig.2. The plants can cope with the high temperature stress by physiological, morpho-anatomical and biochemical alterations. Under high temperature stress the plants accumulate the compatible osmolytes which helps to increase the retention of water in plants for better stomatal regulation and increased photosynthetic rate (Figure 2). The plants also exhibit some morpho-anatomical alterations to cope with high temperature stress which includes reduction in cell size, closure of stomata, increased stomatal and trichomes densities and greater xylem vessels (Figure 2). The third mechanism to cope with the high temperature is the biochemical alterations. The plants increased the stress related proteins which enhance the activities of antioxidants like superoxide dismutase (SOD); Catalase (CAT) and peroxidase (POD) in the plant cells. These antioxidants scavenge the ROS and reduce the photo-oxidation and maintain the integrity of chloroplast membrane and increase the photosynthetic rate (Figure 2).

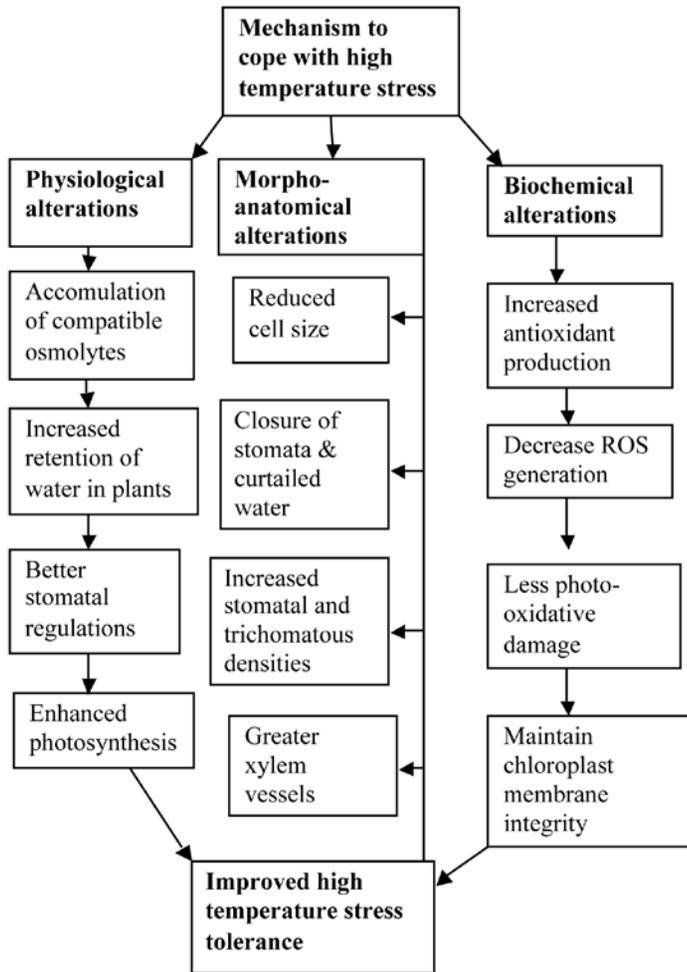


Figure 2. Schematic representation of morphological, Physiological and biochemical alteration of plants to cope with high temperature stress.

3. Low Temperature Stress

3.1 Effects of low temperature stress on plants

Rate of metabolic processes (biochemical processes) decreases gradually with a decrease in temperature and may cease under severe stresses (Taize and Zieger, 2001). Cold temperature stress (0 to -10°C) has broad spectrum effects on cellular components and meta-

bolic processes of plants. Cold temperature extremes impose stresses of variable severity that depending on the intensity and duration of the stress. Several studies indicate that the membrane systems of the cell are the primary site of freezing injury in plants (Levitt, 1980; Steponkus, 1984) and freeze-induced membrane damage results primarily from the severe dehydration associated with freezing (Steponkus, 1984; Steponkus et al. 1993). As temperatures drop below 0°C, ice

formation is generally initiated in the intercellular spaces in the extracellular fluid having a higher freezing point (lower solute concentration) than the intracellular fluid (Jan *et al.*; 2009). Because the chemical potential of ice is less than that of liquid water at a given temperature, the formation of extracellular ice results in a drop in water potential outside the cell. Consequently, there is movement of unfrozen water down the chemical potential gradient from inside the cell to the intercellular spaces. At 10°C, more than 90% of the osmotically active water typically moves out of the cells, and the osmotic potential of the remaining unfrozen intracellular and intercellular fluid is greater than 5 osmolar. Multiple forms of membrane damage can occur as a consequence of freeze induced cellular dehydration including expansion-induced-lysis, lamellar-to-hexagonal- II phase transitions, and fracture jump lesions (Steponkus *et al.*, 1993).

Low temperature induced change in membrane fluidity is one of the immediate consequences in plants during low temperature stress and might represent a potential site of perception and/or injury (Horváth *et al.* 1998; Orvar *et al.* 2000). It is well documented that freeze-induced production of reactive oxygen species contributes to membrane damage and that intercellular ice can form adhesions with cell walls and membranes and cause cell rupture (Olien and Smith, 1977). There is also an evidence that protein denaturation occurs in plants at low temperature (Guy *et al.* 1998) which could potentially result in cellular damage.

3.2 Approaches to induce low temperature stress tolerance

The importance of proper membrane fluidity in low temperature tolerance has been delineated by mutation analysis, transgenic and physiological studies. At low temperature, greater membrane lipid unsaturation appears to be crucial for optimum membrane function.

The plants have several mechanisms or approaches to cope with low temperature stress (Steponkus *et al.* 1993). Cold acclimation is a key approach to stabilize membranes against freezing injury. It prevents expansion-induced-lyses and the formation of hexagonal II phase lipids in rye and other plants (Steponkus *et al.* 1993). Multiple mechanisms appear to be involved in this stabilization. The best documented are changes in lipid composition (Steponkus *et al.* 1993). Similarly, the accumulation of sucrose and other simple sugars that typically occurs with cold acclimation also seems likely to contribute to the stabilization of membranes as these molecules can protect membranes against freeze-induced damage *in vitro* (Strauss and Hauser, 1986; Anchordoguy *et al.* 1987). In addition, there is emerging evidence that certain novel hydrophilic and late embryogenesis abundant (LEA) proteins also participate in the stabilization of membranes against freeze-induced injury (Erand *et al.*, 1995). These hydrophilic and LEA proteins are predicted to contain regions capable of forming amphipathic α -helices which are shown to have strong effect on intrinsic curvature of monolayers and their propensity to form hexagonal II phase. They are said to defer their formation at lower temperatures (Erand *et al.* 1995). Another mechanism through which plants can cope with the low temperature stress might be the extensive water binding capacity of hydrophilic proteins which provide a protective environment in the proximity of stabilization. Although freezing injury is thought to result primarily from membrane lesions caused by cellular dehydration, additional factors may also contribute to freezing-induced cellular damage (Jan *et al.* 2009).

The enhancement of antioxidative mechanisms (Aroca *et al.* 2003), increased levels of sugars in the apoplastic space (Livingston and Henson, 1998), and the induction of genes encoding molecular chaperones (Guy and Li, 1998), respectively, could have protective effects to reduce the freeze induced cellular damage.

4. Nutrient management approaches to alleviate the temperature stresses

Inadequate and unbalanced supply of mineral nutrients and impaired soil fertility are particular problems, causing decreases in global food production, especially in the developing countries. It is estimated that around 60% of cultivated soils have growth-limiting problems associated with mineral-nutrient deficiencies and toxicities (Cakmak, 2002). Adequate nutrition is essential for the integrity of plant structure and key physiological processes such as nitrogen and magnesium is structural part of chlorophyll needed for photosynthesis, phosphorus is needed for energy production and storage, is a structural part of nucleic acids, potassium is needed for osmotic regulation and activation of enzymes (Waraich *et al.*, 2011).

Therefore, a well-nourished plant is expected to produce more biomass per unit of transpired water than an unwell-nourished one. Radin and Mathews (1989) also found that N and P deficient plants strongly reduced the hydraulic conductivity of the root cortical cells. Our recent work suggested that plants nutrients are not only required for better plant growth and development, but also helpful to improve agricultural WUE (Waraich *et al.*, 2011). A number of reports are available indicating the role of nutrients in alleviating various abiotic stresses such as Si has beneficial effects on increased salinity tolerance in wheat (Tahir *et al.*, 2011), K for increased salinity tolerance (Munns, 2005). According to Byrnes and Bumb (1998), in the next 20 years fertilizer consumption has to increase by around 2-fold to achieve the needed increases in food production. It seems that in the coming decades plant-nutrition-related research will be a high-priority research area contributing to crop production and sustaining soil fertility. Survival and productivity of crop plants exposed to environmental stresses are dependent on their ability to develop adaptive mechanisms to avoid or tolerate stress. Accumulating evidence

suggests that the mineral nutritional status of plants greatly affects their ability to adapt to adverse environmental conditions. This review is an effort to highlight the role of essential mineral nutrients in improving the temperature stress tolerance in crop plants.

4.1 Macronutrients

Nitrogen

Nitrogen plays a very crucial role in temperature stress tolerance. At higher temperatures, the intensity of light is also very high. So high light intensity, as a function of high temperature, affects mineral nutrient uptake in plants and affect plant growth negatively. Of the mineral nutrients, nitrogen plays a major role in utilization of absorbed light energy and photosynthetic carbon metabolism (Kato *et al.*, 2003; Huang *et al.*, 2004). An excess of non-utilized light energy can be expected to occur in N-deficient leaves, where it leads to a high risk of photo-oxidative damage. In rice plants under high light intensity, N deficiency is associated with enhanced lipid peroxidation (Huang *et al.*, 2004). Kato *et al.* (2003) reported that plants grown under high-intensity light with a high N supply had greater tolerance to photo-oxidative damage and higher photosynthesis capacity than those grown under similar high light with a low N supply. Utilization of the absorbed light energy in electron transport was also much higher in N-adequate than in N-deficient plants. These results indicate that N-adequate plants are able to tolerate excess light by maintaining photosynthesis at high rates and developing protective mechanisms. To avoid the occurrence of photo-oxidative damage in response to excess light energy, the thylakoid membranes have a protective mechanism by which excess energy is dissipated as heat. Dissipation of excess light energy is associated with enhanced formation of the xanthophyll pigment zeaxanthin.

xanthin, which is synthesized from violaxanthin in the light-dependent xanthophyll cycle (Demmig-Adams and Adams, 1992, 1996). On the other hand, in plants suffering from N deficiency, the conversion of xanthophyll cycle pigments and formation of zeaxanthin were enhanced, and caused the chlorophyll bleaching, particularly under high light intensity (Verhoeven *et al.*, 1997; Kato *et al.*, 2003). In spinach, N-deficient plants dissipate a greater fraction of the absorbed light energy than N-adequate ones: up to 64% and only 36%, respectively. This difference was associated with corresponding changes in xanthophyll cycle pigments: about 65% of the total xanthophyll pigments were present as zeaxanthin and antheraxanthin in N-deficient plants compared with 18% in the N-adequate plants (Verhoeven *et al.*, 1997). These results indicate impaired use of the absorbed light energy in photosynthetic fixation of CO₂, with consequently enhanced demand for protection against excess light energy, in N-deficient plants. Certainly, the reduction in the utilization of light energy and the consequently elevated need for protection against photo-oxidative damage in N-deficient plants can be more marked when the N deficiency stress is combined with an environmental stress. Bendixen *et al.* (2001) reported that the form of N in which it is supplied affects plant tolerance to damage caused by temperature stress. e.g. light-induced conversion of violaxanthin to zeaxanthin, as a means to dissipate excess light energy was found to be stronger in bean leaves supplied with nitrate than in those supplied with ammonium. Similar results have been reported by Zhu *et al.* (2000), they demonstrated that nitrate-grown bean plants had higher tolerance to photodamage than ammonium-grown ones. Under very high light intensity ammonium-grown plants had, therefore, higher levels of lipid peroxidation and higher contents of antioxidative enzymes.

Nitrogen fertilization has been reported to mitigate the adverse effects of abiotic stresses (Waraich

et al., 2011). Nitrogen in the form of nitric oxide (NO) is a highly reactive, membrane-permeant free radical with a broad spectrum of regulatory functions in many physiological processes, such as seed germination, leaf expansion, cell senescence, ethylene emission, stomatal closure and programmed cell death, and a signal molecular mediating responses to abiotic and biotic stresses such as drought stress, salinity, UV-B-radiation and heat stress (Zhao *et al.*, 2007; Yang *et al.*, 2006; Crawford and Guo, 2005 and Zhang *et al.*, 2006). NO may protect plant against stress by acting as an antioxidant directly scavenging the reactive oxygen species (ROS) generated under high or low temperature stress. (Wendehenne *et al.*, 2001). Some earlier reports revealed that NO act as a signal in inducement of thermotolerance in plant by activating active oxygen scavenging enzymes (Song *et al.*, 2006). In addition, Uchida *et al.* (2002) reported that northern blot analysis demonstrated that NO protected the chloroplast against oxidative damage under heat stress by inducing expression of gene encoding small heat shock protein 26 (HSP26).

Potassium

Mineral nutrition of plants plays a critical role in increasing plant resistance to environmental stresses (Marschner, 1995). Among the mineral nutrients, Potassium (K) plays a crucial role in survival of crop plants under environmental stress conditions. K is essential for many physiological processes, such as photosynthesis, translocation of photosynthates into sink organs, maintenance of turgidity and activation of enzymes under stress conditions (Marschner, 1995; Mengel and Kirkby, 2001). Potassium deficiency causes severe reduction in photosynthetic CO₂ fixation and impairment in partitioning and utilization of photosynthates. Such disturbances result in excess of photosynthetically produced electrons and thus stimulation of ROS produc-

tion by intensified transfer of electrons to O₂ (Waraich *et al.*, 2011). K deficiency also caused an increase in NADPH dependent O₂ generation in root cells which indicates that increased ROS production during both

photosynthetic electron transport and NADPH-oxidizing enzyme reactions may be involved in membrane damage and chlorophyll degradation in K deficient plant (Waraich *et al.*, 2011)

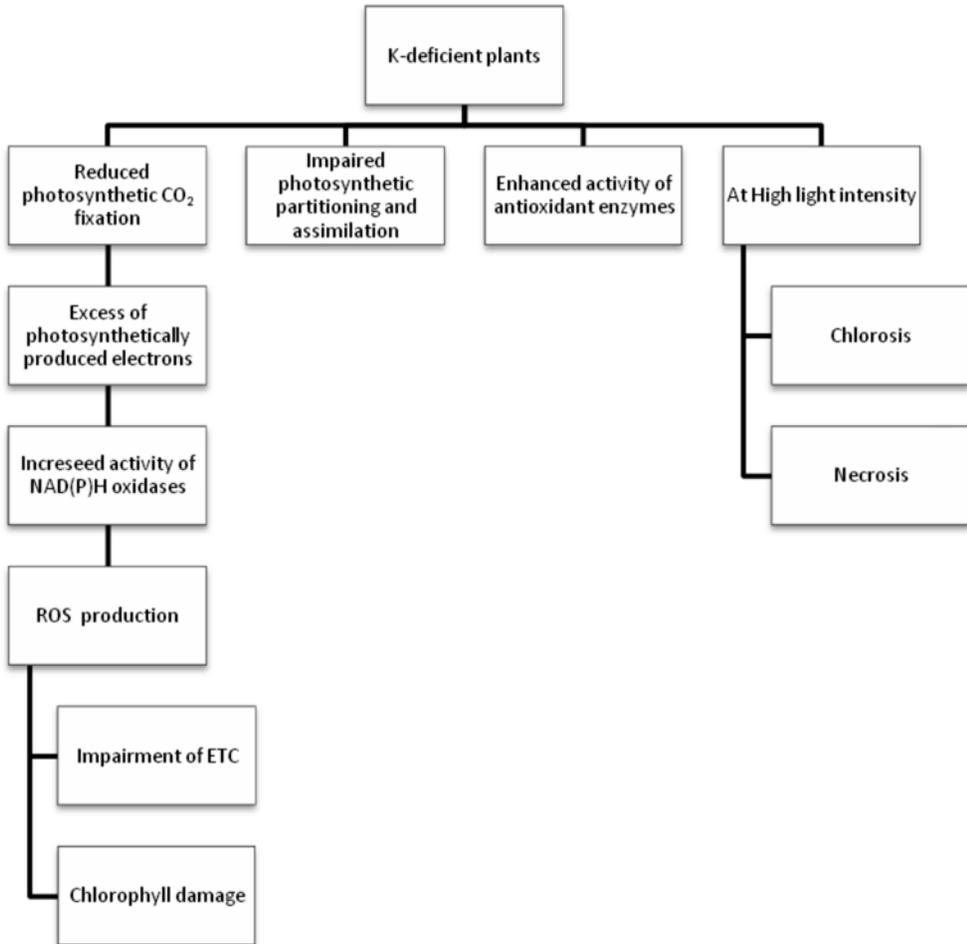


Figure 3. Schematic representation of potassium deficiency resulting in ROS production in plants.

Plants have developed a wide range of adaptive/resistance mechanisms to maintain productivity and ensure survival under a variety of environmental stresses like drought, chilling, frost stresses and high temperature stress. Low temperature stress affects the fluidity of

membrane lipids thus may alters membrane structure (Marschner, 1995). Low temperature also affects photosynthetic electron transport, stomatal conductance, rubisco activity, and CO₂ fixation in plants due to conversion of O₂ to ROS (Huner *et al.*, 1998; Foyer

et al., 2002). Under low supply of K, chilling- or frost induced photo-oxidative damage can be exacerbated causing more decreases in plant growth and yield. Potassium supply in high amounts can provide protection against oxidative damage caused by chilling or frost.

Kafkafi (1990) reported that increasing K concentration in irrigation water provided important protection against stem damage from low night temperatures in carnation plants. Similarly, Grewal and Singh (1980) reported that in potato plants, decreases in yield and increases in leaf damage induced by frost under field conditions could be alleviated by high application of K fertilizer. Similar results have also been reported by Hakerlerler *et al* (1997). They observed that K supply enhanced total plant yield by 2.4-fold, 1.9-fold, and 1.7-fold in tomato, pepper, and eggplant, respectively depending on source of potassium fertilizer.

Calcium

Calcium plays a vital role in regulating a number of physiological processes in plants at tissue, cellular and molecular levels that influence both growth and responses to environmental stresses (Waraich *et al*, 2011). Generally, plant genotypes that tolerate low temperature stress are able to maintain high leaf water potential by closing their stomata and preventing transpirational water loss (Wilkinson *et al.*, 2001). Calcium has been shown to be an essential requirement for chilling induced stomatal closure in chilling tolerant genotypes. Increasing the Ca²⁺ supply induces stomatal closure, and this effect is most distinct in plants grown at low temperatures. It is also believed that ABA induced stomatal closure is partially mediated by Ca²⁺ released from internal guard cell stores or the apoplast (Wilkinson *et al.*, 2001), and this function seems to make Ca²⁺ a major contributing factor to chilling tolerance and protection of leaves from dehydration.

Calcium is considered to play a role in mediating stress response during cold injury, recovery from injury, and acclimation to cold stress (Palta, 2000). It has been suggested that Ca is necessary for recovery from low temperature stress by activating the plasma membrane enzyme ATPase which is required to pump back the nutrients that were lost in cell damage (Palta, 2000). Since dehydration is the common denominator, Ca also has a role to play in freeze injury tolerance. Calcium has a very prominent role in the maintenance of cell structure. Its activates the plasma membrane enzyme ATPase which pumps back the nutrients lost during cell membrane damage due to Ca deficiency and recover the plant from cold injury. Calcium also plays a role as calmodulin which controls the plant metabolic activities and enhances the plant growth under low temperature stress condition (Waraich *et al.*, 2011)

Magnesium

Magnesium (Mg) is involved in numerous physiological and biochemical processes in plants affecting growth and development (Waraich *et al*, 2011). It plays an essential role in photosynthesis and many other metabolic processes. Many key chloroplast enzymes are strongly affected by small variations in Mg levels (Shaul, 2002). Both Mg deficiency and Mg excess have detrimental effects on plant photosynthesis (Shabala and Hariadi, 2005). There are several reports that photosynthesis rate is significantly declined in leaves of Mg deficient plants (Fischer, 1997; Sun and Payn, 1999; Ridolfi and Garrec, 2000; Hermans and Verbruggen, 2005). Due to temperature stress the reactive oxygen species (ROS) are produced continuously as byproducts of different metabolic pathways which are located in different cellular compartments such as chloroplast, mitochondria and peroxisomes (Rio *et al.*, 2006; Navrot *et al.*, 2007). The ROS are

highly toxic and cause damage to proteins, lipids, carbohydrates and DNA which ultimately results in cell death. Accumulation of ROS as a result of high temperature stress is a major cause of loss of crop productivity worldwide. (Tuteja, 2007; Tuteja, 2010; Khan and Singh, 2008; Gill *et al.*, 2010).

It is well documented that Mg plays an important function in the electron transport chain of the chloroplast. Mg plays role to transfer energy from photosystem II to nicotinamide adenine dinucleotide phosphate (NADP⁺) and protect thylakoid membrane which inturn reduce accumulation of excitation energy and oxidative damage (Halliwell, 1987). Yu *et al* (1999) reported that oxidative stress is one of the components of mineral nutrient deficiency stress. Mg increased the activities of antioxidative enzymes and the concentration of antioxidant molecules in bean (Cakmak and Marschner, 1992; Cakmak, 1994), *Mentha pulegium* (Candan and Tarhan, 2003), maize (Tewari *et al.*, 2004), pepper (Anza *et al.*, 2005), and mulberry (Tewari *et al.*, 2006). Moreover, Mg deficient plants have also shown to accumulate significantly higher amount of malondialdehyde (MDA), a general indicator of lipid peroxidation (Candan and Tarhan, 2003; Tewari *et al.*, 2004).

Magnesium increases the root growth and root surface area which helps to increase uptake of water and nutrients by root. Mg being a constituent of chlorophyll increases the amount of sucrose and enhances the transport of sucrose from leaves to roots (Waraich *et al*, 2011). Magnesium improves carbohydrates translocation by increasing phloem export and reduces ROS generation and photo-oxidative damage to chloroplast under temperature stress (high or low) conditions. Maintenance of chloroplast structure by improving Mg nutrition enhances the photosynthetic rate under temperature stress which in turn improves the productivity (Waraich *et al*, 2011).

4.2 Micronutrients

Boron

Boron is directly or indirectly involved in several physiological and biochemical processes during plant growth such as cell elongation, cell division, cell wall biosynthesis, membrane function, nitrogen (N) metabolism, leaf photosynthesis, and uracil synthesis (Marschner, 1995; Zhao and Oosterhuis, 2002). Low temperature stress inhibits the growth and development of plants (Xu *et al.*, 2008). Temperature stress (high or low) induces the production of reactive oxygen species (ROS) such as superoxide radical (O₂⁻) and hydrogen peroxide (H₂O₂) (Xu *et al.*, 2008). The accumulation of ROS damages membrane lipids and can lead to the death of plant cells (Molassiotis *et al.*, 2006). Plants possess enzymatic and non-enzymatic antioxidants in order to scavenge ROS. The enzyme antioxidants are superoxide dismutase (SOD), catalase (CAT), guaiacol peroxidase (GPX), glutathione peroxidase (GSH-Px), ascorbate peroxidase (APX), glutathione reductase (GR), dehydroascorbate reductase (DHAR) and monodehydroascorbate reductase (MDHAR), while non-enzymatic antioxidants include reduced glutathione (GSH) and ascorbate (AsA) (Asada, 1992).

Boron can increase the antioxidant activities of plants and thereby alleviate ROS damage induced by temperature stress. Boron nutrition improves sugar transport in the plant body which helps to improve seed germination and seed grain formation. This in turn improves the yield by improving the temperature stress (Waraich *et al.*, 2011). B application also improves the CHO metabolism and decreases the phenolic compounds in leaves. This inturn reduces the production of ROS species and enhances the photosynthetic rate and reduces the cell damage (Waraich *et al.*, 2011).

Manganese (Mn)

Manganese is necessary in photosynthesis, nitrogen metabolism and to form other compounds required for plant metabolism. Temperature stress (high and low) reduces the nutrient uptake and induces many morphological and physiological disorders in plants. Interveinal chlorosis, brown necrotic spots and delayed maturity are the characteristics of Mn deficiency. Manganese has no direct role in temperature stress alleviation. It can reduce the adverse effects of temperature stress indirectly by enhancing the photosynthetic rate, and nitrogen metabolism in the plant body. Manganese nutrition reduces the interveinal chlorosis, brown necrotic spots on leaves and reduces premature leaf drop. Manganese (Mn) is also reported to involve in the activation of many enzymes in plant systems, mostly in oxidation–reduction, decarboxylation and hydrolytic reactions (Marschner, 1995) hence may play a role in detoxification of ROS.

Recently, it has been reported that Mn has a crucial role in diminution the production of oxygen free-radicals and increase the anti-oxidative compounds and enzymatic activities (Aktas *et al.*, 2005; Turhan *et al.*, 2006; Aloni *et al.*, 2008) under temperature stress.

Selenium

Selenium was recognized as an essential trace element with a relatively low concentration range (Schwartz and Foltz, 1957) and its physiological role was established when it was shown to be one of the glutathione peroxidase (GPx) components (Rotruck *et al.*, 1973). This enzyme is termed a selenoprotein since it contains l-selenomethionine and l-selenocysteine residues (Low and Berry, 1996). Selenium deficiency is usually associated with increased lipid peroxidation which alters the integrity of cell membranes and

consequently, affects cell functions (Stadtman, 1990; Valko *et al.*, 2005).

Recent studies have shown that Se at low concentrations can protect plants from several types of abiotic stresses (Hawrylak-Nowak *et al.*, 2010 ; Valadabadi *et al.*, 2010). Temperature stress (high temperature) can cause premature leaf senescence which leads to loss of chlorophyll, increased membrane damage and progressive decline in photosynthetic capacity (Djanaguiraman *et al.*, 2009). High temperature stress directly damages the photosynthetic apparatus and decreases both photosynthetic rate and duration of the assimilate supply (Prasad *et al.*, 2008; 2009). Temperature stress (high and low) can promote accumulation of reactive oxygen species (ROS) in the chloroplasts and decrease the antioxidant activity. A decrease in antioxidant enzyme activity is noticed during leaf senescence (Srivalli and Khanna-Chopra, 2004). Selenium (Se) can prevent oxidative damage to body tissues (Lobanov *et al.*, 2008) because of its structural role in synthesis of glutathione peroxidase enzyme. Se can also increase tolerance of plants exposed to low temperature (Hawrylak-Nowak *et al.*, 2010), drought stress (Valadabadi *et al.*, 2010) and aluminum toxicity (Cartes *et al.*, 2010). Djanaguiraman *et al.* (2005) reported that foliar spray of Se can increase antioxidant enzyme activity and decrease membrane damage and ROS content in soybean [*Glycine max* (L.) Merr.]. Similarly, Freeman *et al.* (2010) reported that molecular mechanism responsible for Se accumulation in *Stanleya pinnata* revealed higher expression of genes involved in sulfur assimilation, antioxidant activities and defense genes of jasmonic acid and salicylic acid pathway. They further reported Se can delay leaf senescence and increase the carbon supply to developing grain under high temperature stress mainly because of its antioxidative and defense gene expression role.

Recent findings on lettuce (*Lactuca sativa* L.) and ryegrass (*Lolium perenne* L.) show that although Se is toxic at high concentrations, it can exert beneficial effects on plants at low concentrations. Selenium can increase the tolerance of plants to UV-induced oxidative stress as well as delay senescence and promote the growth of aging seedlings (Hartikainen *et al.*, 2000; Xue *et al.*, 2001). Xue *et al.* (2001) reported that plants grown under high temperature stress showed less senescence related oxidative stress and maintained green leaf color for a longer period when treated with selenium. They further reported that Se-treated plants showed an anti-aging affect that was related to decrease lipid peroxidation and enhanced glutathione peroxidase (GPX) activity.

Others

High temperature stress can cause serious perturbations in plant growth and development which may be due to membrane disruptions, metabolic alterations and generation of oxidative stress (Mittler, 2002; Posmyk and Janas, 2007). Salicylic acid plays a key role in providing tolerance against high temperature stress. Dat *et al.* (1998) reported that foliar spray of lower concentrations of salicylic acid in mustard increased the H₂O₂ level and also reduced the Catalase (CAT) activity when accompanied with hardening (45°C for 1 h) thereby increasing the potential of plants to withstand the heat stress. Larkindale and Huang (2004) reported that the pre-treatment with salicylic acid in *Agrostis stolonifera* had no effect on POX activity, whereas, the CAT activity declined, compared to control. They further reported that SA treatment enhanced the activity of enzyme ascorbate peroxidase. A similar response was observed in potato plantlets, raised from the cultures, supplemented with lower concentrations of acetyl salicylic acid (Lopez-Delgado *et al.*, 1998).

Besides providing tolerance to the plants against high temperature stress, exogenous application of SA also induces resistance against the low temperature stress (chilling or cold stress). An enhanced cold tolerance in maize plants, grown in hydroponic solutions, supplemented with 0.5mM of salicylic acid was observed by Janda *et al.* (1997, 1999). SA application reduced electrolyte leakage and CAT activity with a concomitant enhancement in the activities of glutathione reductase and guaiacol peroxidase. SA may exert deleterious effects on plants under normal growth conditions. Janda *et al.* (1998, 2000) observed a decline in net photosynthetic rate, stomatal conductance and transpiration rate in maize plants after 1 day of SA treatment under normal growth conditions. Kang and Saltveit (2002) reported that electrolyte leakage due to low temperature stress in the leaves of maize, cucumber and rice plants can be significantly reduced by the application of lower concentrations of salicylic acid. Similar reports also indicate that exogenous salicylic acid application alleviates the damaging effects of low temperatures in rice and wheat (Szalai *et al.*, 2002; Tasgin *et al.*, 2003), bean (Senaratna *et al.*, 2000) and banana (Kang *et al.*, 2003a) by activating various antioxidant enzymes in maize (Janda *et al.*, 1999, 2000) and banana (Kang *et al.*, 2003b).

5. Conclusions

Temperature stress (high and low) is one of the important environmental factors that may affect morphology, anatomy, phenology and plant biochemistry at all levels of organization. Direct injuries due to high temperatures in plants include protein denaturation and aggregation, and increased fluidity of membrane lipids. Indirect or slower high temperature injuries include inactivation of enzymes in chloroplast and mitochondria, inhibition of protein synthesis, protein

degradation and loss of membrane integrity. Low temperature stress during reproductive development induces flower abscission, pollen sterility, pollen tube distortion, ovule abortion and reduced fruit set, which ultimately lowers yield. Due to these risks, it is necessary to minimise the detrimental effects of temperature stress in plants below permissible limits. The management of plant nutrients is very helpful to develop plant tolerance to temperature stress. Better plant nutrition can effectively alleviate the adverse effects of temperature stress by a number of mechanisms. Temperature stress (high and low) results in increased generation of the reactive oxygen species (ROS) due to energy accumulation in stressed plants which increases the photo-oxidative effect and damage the chloroplast membrane. Application of nutrients like N, K, Ca and Mg reduce the toxicity of ROS by increasing the concentration of antioxidants like superoxide dismutase (SOD); Catalase (CAT) and peroxidase (POD) in the plant cells. These antioxidants scavenge the ROS and reduce the photo-oxidation and maintain the integrity of chloroplast membrane and increase the photosynthetic rate in the crop plants. Nutrients like K and Ca improve intake of water which helps in stomatal regulation and enhances the temperature stress tolerance by maintaining the plant body temperature. Application of K and Ca helps in osmotic adjustment. These nutrients help to maintain high tissue water potential under temperature stress condition. The micronutrients like B, Mn and Se alleviate the adverse effects of temperature stress by activating the physiological, biochemical and metabolic processes in the plants. Selenium (Se) and Salicylic acid (SA) application can increase the temperature stress tolerance by increasing antioxidant enzyme activity and decrease membrane damage by ROS. The literature available on this aspect is insufficient to fully understand the role of Se and SA to minimise detrimental effects of temperature stress. Therefore, more future research is required for

better understanding of interactions between temperature stress and Se in soil-plant systems.

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