ISSN NO. 2320-5407

Journal homepage: http://www.journalijar.com

INTERNATIONAL JOURNAL OF ADVANCED RESEARCH

RESEARCH ARTICLE

PHYSIOLOGICAL RESPONSES AND TOLERANCE MECHANISMS OF LOW TEMPERATURE STRESS IN PLANTS

Madhu Dhingra
Department of Botany Punjab Agricultural University Ludhiana-141004

Manuscript Info

Manuscript History:

Received: 15 December 2014
Final Accepted: 15 January 2015
Published Online: February 2015

Key words:

Low temperature stress, physiological response, tolerance mechanisms, osmolytes, antioxidant enzymes.

Corresponding Author

Madhu Dhingra

Abstract

Among various environmental stresses, low temperature is one of the most important factors limiting the productivity and quality of economically important crops. Many food crops such as maize, sorghum, tomato, soybean and rice are adversely affected by temperature below the optimum required for their normal growth and development. Exposure to sub-optimum temperature is a major challenge to plant growth and development. The literature review shows that the exposure of chilling-sensitive plants to low temperatures causes disturbances in all physiological processes – membrane alterations, photosynthesis, respiration, water regime, mineral nutrition, and metabolism. Inactivation of metabolism, observed at low temperature is a complex function of both temperature and duration of exposure. Low temperature tolerance involves several mechanisms- alterations in fatty acid composition of membranes, enhanced efficiency of antioxidant enzyme system, accumulation of low molecular weight osmolytes, induction of molecular chaperones and expression of specific genes encoding products that confer increased cold tolerance. Understanding of various physiological responses and tolerance mechanisms of plants to low temperature stress can form the basis for management of this stress by different approaches like plant growth regulators application, development and selection of chilling-tolerant genotypes, exogenous application of growth hormones and osmoprotectants.

INTRODUCTION

Among various environmental stresses, low temperature is one of the most important factors limiting the productivity and quality of economically important crops. Many food crops such as maize, sorghum, tomato, soybean and rice are adversely affected by temperature below the optimum required for their normal growth and development. Exposure to sub-optimum temperature is a major challenge to plant growth and development. Cold injury is a physiological damage caused by temperatures between 0ºC and 16ºC (Lyons 1973). Chilling sensitivity is manifested by susceptible plants whose germination, growth, development of reproductive organs and post-harvest longevity are restricted within a range of chilling temperatures. Chilling temperatures effects on plants lead to a reduction or complete crop failure due to either direct damage or delayed maturation. Even a small drop in temperature, causing no visible damage to chilling-sensitive plants, caused to up to 50% reduction in their productivity (Jouyban 2013). Plants can grow only in species-specific temperature range. Cold stress has strong limiting effect with regard to geographical distribution, agronomic yield and product quality (Bracale and Corragio 2003) of a crop species. However, chilling temperatures may differ for different species. For instance, temperate plants may be more chilling tolerant than the tropical plants.

Cold stress adversely affects plant growth and development throughout the ontogeny of the plant (Foolad 2000). Seeds are often the first to encounter stress during a plant’s life cycle. Seedlings appear to be more susceptible to chilling than plants at advanced stages of development (Lyons 1973). Under field conditions, low soil temperatures lead to poor seedling establishment with consequences for both crop survival and yield. At later stages, cold stress results in reduced plant growth and development, poor flower development and fruit set, and substantial reduction in fruit yield.

Chilling stress is known to induce several abnormalities at various organisational levels of cells. There is no unique or characteristic symptom associated with chilling injury. Instead, the symptoms of chilling injury in a plant or species, varies depending on the temperature, duration of exposure, stage of development and tissue, the time of day and other environmental conditions such as light, wind, water and nutrients (Saltveit and Morris 1990). Symptoms of chilling stress include reductions in plant growth rate and leaf elongation (Sowinski et al 2005), mineral and water uptake (Aroca et al 2003), stomatal conductance (Aroca et al 2003), photosynthesis (Foyer et al 2002, Aroca et al 2003), increased production of reactive oxygen species (ROS) (Foyer et al 2002) and activities of antioxidants (Foyer et al 2002, Aroca et al 2003), and changes in membrane properties (Farooq et al 2009).

The term 'chilling tolerance' describes beneficial reactions of plants to low temperatures in order to cope with unfavourable environmental conditions. This includes survival during and after severe chilling stress, and maintenance of growth processes under mild chilling stress at ~10–15°C (Stamp 1984). Exposure of plants to temperature stress leads to the modification of metabolism in two ways. First, plants try to adjust their cellular metabolism that altered due to falling of temperatures. Temperature stress changes the structure, catalytic properties and function of enzymes (Kubien et al 2003) and membrane metabolite transporters. Interestingly, regulatory mechanisms of plants become active and function to restore normal metabolite levels, and most importantly, metabolic fluxes (Schwender et al 2004, Fernie et al 2005). Secondly, the modifications of metabolism in response to temperature stress are mainly linked to enhanced tolerance mechanisms.

Physiological responses to low temperature stress

Steponkus (1984) suggested that membrane systems of the cell are primary sites of chilling injury in plants. Lipids in the plasma membrane are made up of two kinds of fatty acids: unsaturated and saturated fatty acids. The relative proportion of these two types of fatty acids in the lipids of the plasma membrane determines the fluidity of the membrane (Steponkus et al 1993). Physical transition of membranes from a liquid-crystalline phase to a solid-gel phase was first suggested to be the primary response of chilling sensitive plants subjected to low temperature stress (Lyons and Raison 1970). At the transition temperature, a membrane changes from a semi-fluid state into a semi-crystalline state. Cold-sensitive plants usually have a higher proportion of saturated fatty acids in their plasma membrane. Therefore, cold-sensitive plants have a higher transition temperature. On the contrary, cold-resistant plants have a higher proportion of unsaturated fatty acids and hence a lower transition temperature. Pereira da Cruz (2010) observed higher linolenic acid and palmitic acid contents in cold tolerant genotypes than in the cold sensitive genotypes. The presence of a gel phase domain in the membrane bilayer prevents proper functioning of integral membrane proteins and does not maintain an effective permeability barrier. As membranes become less fluid, their protein components can no longer function normally, causing water and soluble materials to leak out into the intercellular spaces where water is lost through evaporation, which is the primary cause of wilting (Wright 1974). Under extensive cold events, loss of water through membranes leads to an irreversible damage.

Phase transition could result in conformational changes in membrane bound enzymes and account for the discontinuities in the function of many enzyme systems. Chilling temperatures have been reported to lower expression and activity of cytochrome oxidase in the mitochondrial inner membrane of a chilling susceptible genotype of maize (Prasad *et al* 1994b). Through the primary effect on membrane lipids, chilling stress causes a cascade of secondary events including loss of turgor, leakage of cytoplasmic solutes, lack of energy metabolism, disruption of photosystems, cell autolysis and cell death (Lyons and Raison 1970). Increase in permeability and leakage of cell solutes is one of the responses which can occur at an early or late stage of the chilling exposures. Jatimliansky *et al* (2004) showed that electrolyte leakage was higher in chilled than control maize plants.

Inhibition of photosynthesis is an early response to low temperature. The response of photosynthesis to chilling includes changes in pigment composition (Haldimann 1998), decreased quantum efficiency (Fryer *et al* 1995), modified thylakoid membranes, and impaired chloroplastic development (Nie et al 1995). Photosynthetic rate and chlorophyll content decreased significantly under low temperature in grafted squash seedlings (Chen et al 2000). In maize, a reduction in chloroplast development (Moseki 2004b) and photosynthetic yield (Moseki 2004a) has been observed when subjected to low growth temperatures. Inhibition of photosynthesis occurs *via* inhibition of electron transport chain. Leipner *et al* (2000) reported that leaves of maize respond to chilling stress by down-regulation of PSII. Guo-li and Zhen-fei (2005) found dramatic decline in photosynthetic rates during chilling, and in cold tolerant as well as cold sensitive cultivar of rice. Chlorophyll fluorescence measurements showed that relatively higher *q*P and *q*NP in cold tolerant cultivar were maintained to dissipate the redundant excitation energy and protect the reaction centers from chill injury; accordingly, redundant excitation energy accumulated less in the reaction centers, and antenna systems were less injured by chilling in cold tolerant cultivar. Thus, chilling damages the reaction centers and antenna systems leading to the lower photosynthetic rate.

Low temperature slows all the metabolic reactions, but in terms of photosynthesis, those involved in CO_2 fixation, and regulation of stomatal aperture are particularly sensitive. CO_2 assimilation by leaves is reduced mainly due to membrane damage, photoinhibition, and disturbed activity of various enzymes (Farooq et al 2009). Chilling affects both the maximal catalytic activities and the activation states of photosynthetic enzymes. Inhibition of activity of some photosynthetic enzymes, e.g. ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) or fructose-1,6-bisphosphatase (FBP), is observed at low temperatures (Kingston-Smith et al 1997), resulting in slowing down of carbon assimilation.

Under low temperature, demand for chemical energy is automatically reduced and the ability of stomata to regulate water stress and CO_2 is impeded. Stomatal aperture is generally reduced at low temperatures, partly because water conductivity is decreased through the root plasma membrane (McWilliam et al 1982). A gradual temperature fall disturbs the water balance in tissues and consequently, a series of the metabolic reactions. Water stress is the primary basis for the changes caused by chilling and other abiotic stresses (Bohnert et al 1995). Chilling of sensitive plants affects all components of water regime and causes loss of water, resulting in strong wilting (Bloom et al 2004). It is based on the two main factors: rapid decline in the ability of roots to absorb water and transport it to the shoots (Bolger et al 1992) and reduced ability to close stomata in response to subsequent water deficit (Bloom et al., 2004). Chilling of maize seedlings to 5.5ºC for 24 h resulted in decreased root hydraulic conductance (Melkonian *et al* 2004). This decrease was attributed to increased water viscosity and factors intrinsic to the roots.

Roots reduce their growth and capacity for water and mineral uptake under mild cold stress (Stamp et al 1997), resulting in subsequent nutritional influences on plant growth (Blum 1988). Uptake of potassium (K) and phosphorus (P) by maize roots is strongly dependent on temperature (Bravo-F and Uribe 1981). Shoot growth of maize seedlings at suboptimal root-zone temperatures was limited by reduced supply of nutrients through the roots and by the direct influence of temperature on shoot meristems (Hund et al 2007). Low root-zone temperatures reduced nutrient acquisition by decreasing root growth (Pritchard et al 1990) and uptake rates of mineral nutrients (Bravo-F and Uribe 1981). Chilling treatments greatly inhibited sorghum growth and N uptake during chilling exposure (Ercoli 2004).

Chilling, in general, impairs respiratory activity, the cytochrome pathway of electron transport and ATPase activity. In maize, populations with high germination levels have higher fluidity of mitochondrial membranes and higher activity of cytochrome C oxidase relative to populations with low germination levels (Santis et al 1999). Other authors have observed that an increase in respiratory activity during chilling and prolonged elevation of the respiration rate after cold exposure may indicate irreversible metabolic dysfunction and accumulation of incompletely oxidized intermediates (Yadegari et al 2008). The mechanism of stimulation is unknown, but it is possible to assume that it was the result of uncoupling of oxidative phosphorylation (Wang 1982). It is also possible that the increased respiration reflects a reaction to the transfer of plants from chilling temperatures to the higher temperatures (Lukatkin 2012). As a result of decreased respiration and increased consumption of energy-rich phosphates at chilling temperatures is a reduction of ATP levels. Cold-tolerant crop species have greater temperature homeostasis of leaf respiration than cold-sensitive species (Yamori et al 2009). Chilling reduces the cytochrome path of the electron transport in seedlings (Prasad et al 1994b) and enhances alternative respiratory pathways (Ribascarbo et al 2000). Perhaps these alternative pathways play an important role in plant adaptation to chilling (Steward et al 1990). These alternative pathways induced by chilling caused a decrease in superoxide generated in mitochondria (Hu et al 2008).

Low temperature is known to induce oxidative stress in tissues leading to generation of reactive oxygen species (ROS) including superoxide radicals, hydrogen peroxide and hydroxyl radicals. ROS are believed to be responsible for cold injury in plants (Prasad *et al* 1994a). Injury caused by ROS to macromolecules under chilling stress is one of the major deterrents to growth. Most sub-cellular compartments are potential sites of ROS production and they include chloroplasts, mitochondria, peroxisomes, plasma membranes, endoplasmic reticulum (Srivalli et al 2003). ROS cause damage to lipids, proteins and DNA. The harmful effects of ROS are due to their ability to initiate a variety of auto-oxidative chain reactions on unsaturated fatty acids (Smirnoff 1993). ROS induced cell death can result from oxidative processes such as membrane lipid peroxidation, protein oxidation, enzyme inhibition and DNA and RNA damages (Mittler 2002). In maize seedlings, lipid peroxidation was increased by about two-fold in non-acclimated seedlings compared to control or acclimated during 4ºC stress and recovery (Prasad 1996).

Mechanisms of chilling tolerance:

Chilling resistance or tolerance can be defined as the ability of the chilling sensitive plant to withstand the strain of the low temperature stress. Acclimation or hardening may be defined as changes that occur in a plant in response to chilling temperatures which confer subsequent tolerance to the cold injury (Huner 1985). Plants resort to many adaptive strategies in response to different abiotic stresses such as high salt, dehydration, cold, heat and excessive osmotic pressure which ultimately affect the plant growth and productivity (Yancey et al 1982). Against these stresses, plants adapt themselves by different mechanisms including change in morphological and developmental pattern as well as physiological and biochemical processes (Bohnert et al 1995). It is the ability of the plants to undergo such changes that account for major differences in chilling susceptibilities between species and protect against irreversible chilling induced injury.

The contribution of membrane lipids, particularly the level of unsaturation of fatty acids, to chilling sensitivity of plants has been intensively discussed for many years. Chilling sensitivity or tolerance was linked with the extent of lipid unsaturation in some plant species (Riken et al 1993). A downward shift in the temperature generally increases the degree of unsaturation of membrane lipids which compensates for the decrease in the fluidity of membrane lipids. The increase in the degree of unsaturation of membrane lipids is also correlated with the sustained activity of membrane bound enzymes at lower temperature. Leaves of transgenic tobacco plants with decreased levels of fatty acid unsaturation in phosphatidylglycerol (PG) exhibited a slightly lower level of the steady state oxidation of the photosystem I (PSI) than wild-type plants at low temperature (Ivanov 2012).

Another mechanism involves cellular defense against membrane lipid peroxidation caused by chill-induced increase in the generation of ROS (Prasad et al 1994b). These ROS are kept under control by various antioxidants (α-tocopherol, ascorbate etc.) and antioxidant enzymes (superoxide dismutase, catalase, peroxidase, glutathione reductase etc.) (Bowler et al 1992). Lower concentrations of antioxidant compounds (ascorbate, glutathione, and β-carotene) were found in chilling sensitive lines than chilling tolerant lines in maize (Hodges et al 1996). In rice also, activities of antioxidant enzymes *viz.*, superoxide dismutase, catalase, ascorbate peroxidase and glutathione reductase were higher in chilling tolerant cultivar than in chilling sensitive (Huang and Guo 2005). These results indicated that higher activities of defense enzymes and higher contents of antioxidants under stress were associated with tolerance to chilling. ROS production in mitochondria and chloroplast can be decreased by the alternative channeling of group of enzymes called alternative oxidases (AOXs). AOXs decrease ROS production by two mechanisms: they prevent electrons from reducing O_2 into superoxide radical and they reduce the overall level of $O_{2,}$ the substrate for ROS production in the organelles. In the mitochondria of pre-emergent maize seedlings, the cytochrome pathway was induced in both acclimated and non-acclimated mitochondria at the end if the 4ºC stress period (Prasad 2000). The increase in the alternative oxidase activity has been shown to be due to an increase in protein synthesis (Steward et al 1990).

Another mechanism of chilling tolerance involves the induction of molecular chaperones by low temperature. Molecular chaperones induced by low temperature presumably protect the proteins from chilling induced protein denaturation (Neven *et al* 1990). This induction of molecular chaperones in response to low temperature suggests that protein protection from low temperature damage is likely a part of the tolerance mechanism in plant cells (Prasad 2000).

In response to cold and other osmotic stresses, plants accumulate a range of compatible solutes including carbohydrates- sucrose, raffinose, sorbitol and trehalose glucosides, raffinose, arbinoxylans, and amino acids such as glutamic acid, alanine, glycine, proline, and serine, polyamines and betaines (Theocharis 2012). These different molecules, which are often degraded once the stress has passed, are referred to as osmolytes, osmoprotectants or compatible solutes. Sugars play multiple roles in low temperature tolerance. As typical compatible osmolytes, they contribute to the preservation of water within plant cells (Ruelland et al. 2009). Sugars might protect plant cell membranes during cold-induced dehydration, replacing water molecules in establishing hydrogen bonds with lipid molecules (Ruelland et al. 2009). The most abundantly accumulated free sugar in response to low temperature is sucrose (Kaurin et al 1981). During cold acclimation, levels of soluble sugars increased in both genotypes of *Arabidopsis*, but raffinose accumulation discriminated the more tolerant one (Klotke et al 2004).

Paldi et al (2002) suggested the role of some N-containing compounds (glycinebetaine, agmatine, putrescine, and proline) in chilling tolerance of maize. Proline content increased significantly in sunflower under moisture stress (Deshmukh and Srivastava 1982), in barley under salinity stress (El-Tayeb 2005) and in maize under chilling stress (Chen and Li 2002). Proline has been shown to protect plants against free-radical induced damage (Matysik et al 2002). Low temperature increased spermidine and spermine but not putrescine levels in watermelon (Kwon et al 2003) Low temperature stress has been reported to cause significant increases in the levels of the soluble non-enzymatic antioxidants ascorbate and glutathione (Airaki et al. 2011).

Low temperature induces ABA accumulation providing a mechanism for chilling resistance. Higher ABA levels were accumulated and maintained in tolerant cultivars of rice (Liu et al 2003). Likewise in maize, under field conditions, chilling tolerant genotypes accumulated higher amounts of ABA during chilling periods than chilling sensitive genotypes (Janowiak et al 2003). The results suggest that exogenous application of ABA can induce chilling tolerance in the plants. Exogenous application of ABA improved germination (Basra et al 1989), increased protein content (Stupnikova et al 2001) and decreased leaf water deficit (Aroca et al 2003) in maize.

Plant acclimation to low temperature depends on changes in the expression of specific genes encoding products that confer increased cold tolerance (Doherty et al 2009). The process involves modifying preexisting proteins and up- or down-regulating gene expression and protein synthesis. Several studies have suggested that activity of cold/chilling-induced genes may facilitate the metabolic changes that confer low temperature tolerance (Doherty et al 2009). They may also be involved in the signal transduction of the stress-response (Thomashow 2010). Yakovlev and Borovsky

(2003) suggested the accumulation of proteins named as cold shock proteins (CSPs) during low temperature stress. Several antioxidant enzymes and proteins of unknown function have been reported to increase during low temperature (Guy 1990). In *Arabidopsis*, cold acclimation induced the accumulation of four major mRNAs which code for highly hydrophobic proteins similar to cryoprotectant proteins in spinach. Several cold regulated genes whose expression was changed during freezing acclimation (Thomashow 2010) have also been isolated and characterized. Hiilovaara-Teijo (1999) suggested the accumulation of antifreeze proteins in winter rye plants during cold acclimation. Some genes expressed differentially during chilling acclimation, designated as chilling acclimation responsive genes, have been isolated from various plants, including maize (Anderson et al 1994).

Conclusion

The literature review shows that the exposure of chilling-sensitive plants to low temperatures leads to disturbances in all physiological processes – water regime, mineral nutrition, photosynthesis, respiration and metabolism. Inactivation of metabolism, observed at chilling of chilling-sensitive plants is a complex function of both temperature and duration of exposure. Tolerance mechanisms involve alterations in fatty acid composition of membranes, enhanced efficiency of antioxidant enzyme system, accumulation of low molecular weight osmolytes, induction of molecular chaperons and expression of specific genes encoding products that confer increased cold tolerance. Understanding of various physiological responses and tolerance mechanisms of plants to low temperature stress can form the basis for management of this stress by different approaches like plant growth regulators application, development and selection of chilling-tolerant genotypes, exogenous application of growth hormones and osmoprotectants.

References:

Airaki, M., Leterrier, M., Mateos, R. M., Valderrama, R, Chaki, M., Barroso, J. B., Del Rio, L. A., Palma, J. M. and Corpas, F. J. (2011) Metabolism of reactive oxygen species and reactive nitrogen species in pepper (*Capsicum annuum* L.) plants under low temperature stress. Plant Cell Environ. 35:281–295

Anderson, M. D., Prasad, T. K., Martin, B. A. and Stewart, C. R. (1994) Differential gene expression in chilling-acclimated maize seedlings and evidence for the involvement of abscisic acid in chilling tolerance. Pl. Physiol. 105: 331-39.

Arin, L., and Kiyak, Y.(2003). The effect of pre-sowing on emergence and seedling growth of tomato seed (Lycopersicon esculentum Mill.) under several stress conditions. Pakistan J. Biol. Sci. 6(11): 990-994.

Aroca R, Vernieri P, Irigoyen JJ, Sancher-Diaz M, Tognoni F, Pardossi A (2003) Involvement of abscisic acid in leaf and root of maize (*Zea mays* L.) in avoiding chilling-induced water stress. Plant Science.165: 671–679.

Basra, A. S., Dhillon, R. and Malik, C. P. (1989) Influence of seed pre-treatments with plant growth regulators on metabolic alterations of germinating maize embryos under stressing temperature regimes. Annals Bot. 64 : 37-41.

Bloom A. J., Zwieniecki M. A., Passioura J. B., Randall L. B., Holbrook N. M., Clair D. A. St. (2004) Water relations under root chilling in a sensitive and tolerant tomato species. Plant Cell Environ. 27(8): 971–979

Blum, A. (1988) Plant breeding for stress environments. (CRC Press Inc.: Boca Raton, FL)

Bohnert. H. J., Nelson, D. E. and Jensen, R. G. (1995) Adaptations to environmental stresses. The Plant Cell. 7 : 1099-111.

Bolger, T. P., Upchurch D. R. and Mcmichael, B. L. (1992) Temperature effects on cotton root hydraulic conductance. Env. Exp. Bot.32 (1): 49–54

Bowler, C., Van Montagu, M. and Inze, D. (1992) Superoxide dismutase and stress tolerance. Ann. Rev. Pl. Physiol. Mol. Biol. 43: 83-116.

Bracale, M. and Corragio, I. (2003) Chilling and freezing stresses in plants: cellular responses and molecular strategies for adaptation. In Sanita di Toppi L. and Pawlik-Skowronska B. (eds)

Bravo, F. P. and Uribe, E. G. (1981) Temperature dependence of the concentration kinetics of absorption of phosphate and potassium in corn roots. Pl. Physiol. 67: 815–819.

Chen, G. L., Nie, L. C., Li, J. W. and Xiao, K. (2000) Effect of low temperature stress on photosynthetic characteristics of grafted squash seedlings. Acta Agriculturae Shanghai. 16: 42-45.

Chen, W. P. and Li, P. H. (2002) Membrane stabilization by abscisic acid under cold aids proline in alleviating chilling injury in maize (*Zea mays* L.) cultured cells. Plant Cell Environ. 25 : 955-62

Deshmukh, P. S, and Srivastava, G. C. (1982) Variation in proline accumulation in sunflower genotypes under moisture stress conditions. Indian J. Pl. Physiol. 25 : 396-99.

Doherty, C. J., Van Buskirk, H. A., Myers, S. J., Thomashow, M. F. (2009) Roles for Arabidopsis CAMTA transcription factors in coldregulated gene expression and freezing tolerance. Plant Cell. 21: 972–984

El-Tayeb, M. A. (2005) Salicylic acid-induced adaptive response to copper stress in sunflower (*Helianthus annuus* L.). Pl. Growth Reg. 50 : 191-99

Ercolia, L., Mariottib, M., Masonib, A. and Arduinic, I. (2004) Growth responses of sorghum plants to chilling temperature and duration of exposure. Europ. J. Agronomy. 21 : 93–103

Farooq, M., Aziz, T., Wahid, A., Lee, D. and Siddique, K. H. M. (2009) Chilling tolerance in maize: agronomic and physiological approaches. Crop & Pasture Science. 60: 501–516

Fernie, A. R., Geigenberger, P. and Stitt, M. (2005) Flux an important, but neglected, component of functional genomics, Curr. Opin. Plant Biol. 8:174–182.

Foolad, M. R. and Lin, G. Y. (2000) Relationship between Cold Tolerance during Seed Germination and Vegetative Growth in Tomato: Germplasm Evaluation. J. Amer. Soc. Hort. Sci. 125(6):679–683. 2000.

Foyer, C. H., Descourvieres, P. and Kunert, K. J. (1994) Protection against oxygen radicals an important defense mechanism studied in transgenic plants. Plant Cell Environ.17: 507-23.

Foyer, C. H., Vanacker, H., Gomez, L. D. and Harbinson, J. (2002) Regulation of photosynthesis and antioxidant metabolism in maize leaves at optimal and chilling temperatures. Plant Physiol. & Biochem. 40: 659–668.

Fryer, M. J., Oxborough, K., Martin, B., Ort, D. R. and Baker, N. R. (1995) Factors associated with depression of photosynthetic quantum efficiency in maize at low growth temperature. Pl. Physiol. 108: 761–767.

Guo-li, W. and Zhen-fei, G. (2005) Effects of Chilling Stress on Photosynthetic Rate and chlorophyll Fluorescence Parameter in Seedlings of Two Rice Cultivars Differing in Cold Tolerance. Rice Science 12(3): 187-191

Guy, C. L. (1990) Cold acclimation and freezing stress tolerance: role of protein metabolism. Ann. Rev. Pl. Physiol. Mol. Biol. 41: 187-223.

Haldimann, P. (1998) Low growth temperature-induced changes to pigment composition and photosynthesis in *Zea mays* L. genotypes differing in chilling sensitivity. Plant Cell Environ. 21: 200–208.

Hiilovaara-Teijo, M., Hannukkala, A., Griffith, M., Yu, X. M., Pihakaski, M. K. (1999) Snow-mold induced apoplastic proteins in winter rye leaves lack antifreeze activity. Pl. Physiol. 121 : 665-73.

Hodges, D. M., Andrews C, J., Johnson, D. A. and Hamilton, R. I. (1996) Antioxidant compound responses to chilling stress in differentially sensitive inbred maize lines. Physiol. Plant. 98 : 685-92.

Huang, M. and Guo, Z. (2005) Responses of antioxidative system to chilling stress in two rice cultivars differing in sensitivity. Biol. Plant. 49 : 81-84.

Hund, A., Richner, W., Soldati, A., Fracheboud, Y. and Stamp, P. (2007) Root morphology and photosynthetic performance of maize inbred lines at low temperature. Eur. J. Agron. 27: 52–61.

Hu, W. H., Song, X. S., Shi, K., Xia, X. J., Zhou, Y. H. and Yu, J. Q. (2008) Changes in electron transport, superoxide dismutase and ascorbate peroxidase isoenzymes in chloroplasts and mitochondria of cucumber leaves as influenced by chilling. Photosynthetica. 46(4): 581–588.

Huner, N. P. A. (1985) Morphological, anatomical and molecular consequences of growth and development at low temperature in *Secale cereale* L. cv puma. Am. J. Bot. 72 : 1290-1306.

Ivanov, A.G., Allakhverdiev, S. I,. Huner, N. P. A. and Murata, N. (2012) Genetic decrease in fatty acid unsaturation of phosphatidylglycerol increased photoinhibition of photosystem I at low temperature in tobacco leaves. Biochimica et Biophysica Acta. 1817(8): 1374–1379

Janowiak, F., Luck, E. and Dorffling, K. (2003) Chilling tolerance of maize seedlings in the field during cold periods in spring is related to chilling-induced increase in abscisic acid level. J. Agron. Crop. Sci. 189 : 156-61.

Jatimliansky, J. R., Garcia, M. D. and Molina, M. C. (2004) Response to chilling of *Zea mays*, *Tripsacum dactyloides* and their hybrid. Biol. Plant. 48 : 561-67.

Jouyban. Z., Hasanzade, R. and Sharafi, S. (2013) Chilling stress in plants. Intl. J. Agri. Crop. Sci. 5 (24): 2961-2968.

Kang, Ho-Min, and Saltveit, M. E. (2002) Chilling tolerance of maize, cucumber and rice seedling leaves and roots are differentially affected by salicylic acid. Physiol. Plant. 115: 571–576.

Kaurin, A., Juntilla, O. and Hansen, J. (1981) Seasonal changes in frost hardiness in cloudberry (*Rubus chamacmorus*) in relation to carbohydrate content with special reference to sucrose. Physiol. Plant. 52 : 310-14.

Kingston-Smith, A. H., Harbinson, J., Williams, J. and Foyer, C. H. (1997) Effect of chilling on carbon assimilation, enzyme activation, and photosynthetic electron transport in the absence of photoinhibition in maize leaves. Pl. Physiol. 114:1039–1046.

Klotke, J., Kopka, J., Gatzke, N. and Heyer, A. G. (2004) Impact of soluble sugar concentrations on the acquisition of freezing tolerance in accessions of *Arabidopsis thaliana* with contrasting cold acclimation. Plant Cell Environ. 27 : 1395-1404.

Kubien, D. S., von Caemmerer, S., Furbank, R.T. and Sage, R.F. (2003) C4 photosynthesis at low temperature. A study using transgenic plants with reduced amounts of rubisco, Pl. Physiol. 132: 1577–1585.

Kwon, S. W., Ko, B. R. and Bai, D. G. (2003) Changes in antioxidant enzymes and polyamines in response to low temperature chilling in watermelon plants. Acta Horticulturae 620 : 111-17.

Leipner, J., Basilides, A., Stamp, P. and Fracheboud, Y. (2000) Hardly increased oxidative stress after exposure to low temperature in chilling acclimated and non-acclimated maize leaves. Plant Biology. 2 : 243-51.

Liu, C. L., Chen, H. P., Liu, E. E, Peg, X. X., Lu, S. Y. and Guo, Z. F. (2003) Multiple tolerance of rice to abiotic stresses and its relationship with ABA accumulation. Acta Agronomica Sinica 29 : 725-29.

Lukatkin, A. S., Brazaitytė, A., Bobinas, Č. and Duchovskis, P (2012) Chilling injury in chilling-sensitive plants: a review. Žemdirbystė=Agriculture. 99(2): 111–124.

Lyons, J. M. (1973) Chilling injury in plants. Ann. Rev. Pl. Physiol. 24 : 445-66.

Lyons, J. M. and Raison, J. K. (1970) Oxidative activity of mitochondria isolated from plant tissues sensitive and resistant to chilling injury. Pl. Physiol. 45 : 386-89.

Matysik, J., Alia, Bhalu, B. and Mohanty, P. (2002) Molecular mechanisms of quenching reactive species by proline under stress in plants. Curr. Sci. 82 : 525-32.

McWilliam, J. R., Kramer, P. J. and Musser, R. L. (1982) Temperature induced water stress in chilling sensitive plants. Aust. J. Plant Physiol. 9:343-52.

Melkonian, J., Yu, L. X. and Setter, T. L. (2004) Chilling responses of maize (*Zea mays*L.) seedlings: root hydraulic conductance, abscisic acid and stomatal conductance. J. Exp. Bot. 55: 1751-60.

Mittler, R .(2002) Oxidative stress, antioxidants and stress tolerance. Trends Pl. Sci .7 : 405-10.

Moseki, B. (2004a) Characterization of low temperature stress effects on photosynthetic performance of maize cultivars using chlorophyll fluorescence. South African J. Bot. 70 : 730-33.

Moseki, B. (2004b) Effects of low temperature stress on chloroplast development in a range of *Zea mays* cultivars. South African J. Bot. 70 : 726-29.

Neven, L. G., Haskel, D. and Guy, C. L. (1990) A heat shock cognates comes out in the cold. Cryobiology. 27 : 661-68.

Nie, G.Y., Robertson, E. J., Fryer, M. J., Leech, R. M. and Bake, N. R. (1995) Response of the photosynthetic apparatus in maize leaves grown at low temperature on transfer to normal temperature. Pl. Cell Env. 18: 1–12.

Paldi, E., Szalai, G., Marton, C. L., Pal, M. and Janda, T. (2002) Role of some N-containing compounds in chilling tolerance of maize. Acta. Biol. Szeged. 46 : 99-100.

Pereira da Cruz, R., Golombieski, J. I., Bazana M. T., Cabreira C., Silveira T. F. and Picolli da Silva, L. (2010) Alterations in fatty acid composition due to cold exposure at the vegetative stage in rice. Braz. J. Plant Physiol. 22(3):199-207.

Prasad, T. K. (1996) Mechanisms of chilling-induced oxidative stress injury and tolerance: changes in antioxidant system, oxidation of proteins and lipids and protease activities. Plant J. 10 : 1017-26.

Prasad, T. K. (2000) The role of oxidative stress in mediating the mechanisms of chilling injury and tolerance in maize. In Basra A S (ed)

Prasad, T. K., Anderson, M. D. and Stewart, C. R. (1994b) Acclimation, hydrogen peroxide and abscisic acid protect mitochondria against irreversible chilling injury in maize seedlings. Pl. Physiol. 105 : 619-27.

Prasad, T. K., Anderson, M. D. and Stewart, C. R. (1994a) Evidence for chilling induced oxidative stress in maize seedlings and a regulatory role for hydrogen peroxide. Pl. Cell. 6: 65-74.

Pritchard, J., Barlow, P. W., Adams, J. S. and Tomos AD (1990) Biophysics of the inhibition of the growth of maize roots by lowered temperature. Pl. Physiol. 93: 222–230.

Ribascarbo, M., Aroca, R., Gonzalez-Meler, M. A., Irigoyen, J. J. and Sanchezdiaz, M. (2000) The electron partitioning between the cytochrome and alternative respiratory pathways during chilling recovery in 2 cultivars of maize differing in chilling sensitivity. Pl. Physiol. 122(1):199–204.

Riken, A., Dilwith, J. W. and Bergman, D. K. (1993) Correlation between the circadian rhythm of resistance to extreme temperatures and changes in fatty acid composition in cotton seedlings. Pl. Physiol. 101 : 31-36.

Ruelland, E., Vaultier, M. N., Zachowski, A., Hurry, V., Kader J. C. and Delseny, M. (2009) Cold signalling and cold acclimation in plants. Adv. Bot. Res. 49:35–150

Saltveit, M. E. and Morris, L. L. (1990) Overview of chilling injury of horticultural crops. In Wang C Y (ed)

Santis, A de., Landi, P. and Genchi, G. (1999) Changes of mitochondrial properties in maize seedlings associated with selection for germination at low temperature, fatty acid composition, cytochrome C oxidase and adenine nucleotide translocase activities. Pl. Physiol. 119 : 743-54.

Schwender, J., Ohlrogge, J. and Shachar-Hill, Y. (2004) Understanding flux in plant metabolic networks, Curr. Opin. Plant Biol. 7: 309–317.

Smirnoff, N. (1993) The role of active oxygen species in the response of plants to water deficit and desiccation. New Phytol. 125 : 27-58.

Sowinski, P., Rudzinska-Langwald, A., Adamczyk, J., Kubica, I. and Fronk, J. (2005) Recovery of maize seedling growth, development and photosynthetic efficiency after initial growth at low temperature. J. Pl. Physiol. 162:67–80.

Srivalli, B., Chinnusamy, V. and Khanna-Chopra, R .(2003) Antioxidant defense response to abiotic stresses in plants. J. Plant Biol. 30: 121-39.

Stamp, P. (1984) Chilling tolerance of young plants demonstrated on the example of maize (*Zea mays* L.). In Geisler G. (ed)

Stamp, P., Feil, B., Schortemeyer, M. and Richner,W.(1997) Responses of roots to low temperatures and nitrogen forms. In Anderson H. M. (ed)

Steponkus, P. L. (1984) Role of plasma membrane in freezing injury and cold acclimation. Ann. Rev. Pl. Physiol. 35 : 543-84.

Steponkus, P.L., Uemura, M. and Webb, M.S. (1993) A contrast of the cryostability of the plasma membrane of winter rye and spring oat-two species that widely differ in their freezing tolerance and plasma membrane lipid composition, In Steponkus P. L. (ed)

Steward, C. R., Martin, B. A., Reding, L. and Cerwick, S. (1990) Respiration and alternative oxidase in corn seedling tissues during germination at different temperatures. Pl. Physiol. 92(3): 755–760.

Stupnikova, I. V., Borovskii, G. B. and Voinikov, V. K. (2001) ABA-induction of cold hardy state and heat stable COR proteins in maize seedlings and other cereals. Maize Genetics Cooperation Newsletter. 75 : 29-30.

Theocharis, A., Cle´ment C. and Ait Barka, E. (2012) Physiological and molecular changes in plants grown at low temperatures. Planta. 235:1091–1105

Thomashow, M. F. (2010) Molecular basis of plant cold acclimation: insights gained from studying the CBF cold response pathway. Pl. Physiol. 154:571–577

Wang, C. Y. (1982) Physiological and biochemical responses of plants to chilling stress. Hort. Sci. 17(2):173–186

Wright, M. (1974) The effect of chilling on ethylene production, membrane permeability and water loss of leaves of *Phaseolus vulgaris*. Planta 120 : 63-69.

Yadegari, L. Z., Heidari, R. and Carapetian J. (2008) Chilling pretreatment causes some changes in respiration, membrane permeability and some other factors in soybean seedlings. Res. J. Biol. Sci. 3(9): 1054–1059

Yakovlev, A. Yu, and Borovsky, G. V. (2003) Low- temperature protective proteins of fungi and plants. Mikologiya-i-Fitopatologiya 37 : 87-93.

Yamori, W., Noguchi, K., Hikosaka, K. and Terashima, I. (2009) Cold-tolerant crop species have greater temperature homeostasis of leaf respiration and photosynthesis than cold-sensitive species. Pl. & Cell Physiol. 50(2): 203–215

Yancey, P. H., Clark, M. E., Hand, S. C., Bowlis, R. D. and Somero, G. N. (1982) Living with water stress: evolution of osmolyte system. Science 17 : 1214-22.