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A Review Report: Low Temperature Stress for Crop Production

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ABSTRACT

Temperature is a key abiotic signal that regulates plant function throughout development. Alterations in growth temperature act as a stimulus to initiate metabolic changes and promote developmental switches. In the first sight a simple question arises. How do plants sense change in temperature or more specifically how is lower than optimum temperature sensed by plants? Do they have a single thermo-sensor or multiple thermo-sensing mechanisms? The answer lies in the fact that plants are having special temperature preceptor organs, which are highly sensitive to sense a slight negative or positive change in its environment. These receptors not only sense the change in temperature but also inform the cellular headquarters (the nucleus) about the temperature-change condition. Low Temperature Stress in Crop Plants: The fundamental mechanisms involved in the temperature response of crop plants. It examines the hypotheses related to the primary temperature sensor in crop plants and the mechanisms of low temperature injury. It also explores the genetic potential for cold resistance. Special topics related to the utilization of Arrhenius plots of the temperature response of plants are also discussed. The Chilling and freezing 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. Response of plants to low temperature exposure is associated with a change in the rate of gene transcription of a number of low molecular weight proteins. According to this concept, there were distinguished possible ways to improve cold tolerance, which were combined into several groups: the thermal effect, chemical and the use of gene and cell engineering.

Key words: *Temperature, Stress, Chilling injury, Water regimes*

INTRODUCTION

Stress: - every plant has some requirement of some physical factors *viz*; light temperature air, water etc. and for some chemical factors for example inorganic nutrients, organic nutrients in optimum amount and in available form at a right time as its nutritional for its proper growth and development. Any deviation from this optimum condition of any factor essential for its growth will lead to aberrant change in physiological processes and due to this plant body will experience tension and this state can be referred as plant under stress.

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When this condition prevail for some time stress cause injury with or without producing visible symptom which can referred as strain. Injury occurs as result of aberrant metabolism and may be expressed as reduction in growth, value, or death of two plants.

Zero stress: - in concept that level of exposure to an environment factor that leads to injury nor to reduction in growth, yield, or value.

Temperature stress: Temperature on earth changes along attitudinal and attitudinal clines and also with season, most plants are specially adopted to grow over a limited range of temperatures[131]. Extremes of temperatures .com limit plant survival and its reproduction and therefore temperature is required as are of the strongest determinants of plants growth and metabolism[131]. The extremes of temperatures either very high or very low both cause severe per duration in the plant metabolism machinery. Both these conditions are stressful for the growth and disturb the plants physiology and biochemical process[28].

Type of temperature stress: - All plant species perform their metabolic arthritis and complete the life cycle under on optimum temperature range. Among the various climatic factors, vital for the growth of autotrophic plants, temperature is the crucial one, besides light, water, atmospheric CO_2, Minerals and oxygen. Temperature a true sense dictates the rate at which metabolism's activity proceeds in plants and it must be present at a certain level of warmth in plants for productive metabolism[172]

Any change in temperature affect plants greatly so stress imposed by temperature have important implication for agriculture for example, it has been conjectured that a 1^0C decrease in the world mean temperature.

Temperature these can be categorized in to two

1. Low temperature
2. High temperature

Low Temperature stress: - The temperatures considerably lower than the optimal growth temperatures result in two temperature stress in plant. In majorly of plants this temperature is usually below 10° C the low temperature i.e. lower than 10° C can be further subdivided in to two main categories.

This is decided by the fact whether these is formation of ice within the tissues or nat. Both these condition also cause water deficit inside the plant[111].

Low temperature and frost have a negative effect on the metabolism with a corresponding reduction in crop quality and quantity. Chilling resistance and freeing resistance are complex phenomenon, as most plants are capable of hardening to cold i.e. acquisition of increased resistance upon exposure to low temperature. These results in irreversible and proper honor loss of cell proteins and disturbed plasma membrane integrity Tropical plants are more susceptible to chilling than those growing in cold regions. When exposed to temperature higher than 12-13^0C.

An altered $N0_3$- uptake and its metabolism are observed under low temperature. There becomes reduced N uptake[19], decreased N partitioning in young shoots induced remobilization of N from older to younger leaves and inhibition in N assimilation process at low temperatures. Low temperature treatment modulates the effect of hyper-osmoticum stress on photosynthesis and respiration, and result in increased participating of alternative pathway[28].

The crown of the plant, consisting of shoot apex and young leaves, is much colder hardy and can tolerate low temperatures than the more mature older parts.

Low temperature stress also manifests increased oxidative damage in plants. There is enhancement of antioxidant defense mechanism of the plant under low temperature stress. A major response of the plant under low temperature stress inviters enhanced activities and content of each of the as scavenging enzyme and ran enzymatic antioxidant[124,140]. As chilling and freezing temperature cause water deficit inside the cells the compatible solute manital, which alleviates water stress has been shown to protect chloroplastic, phosphokinase from hydroxyl redical of damage under stressfully condition[127].

Effect of low temperature many tropical and sub-tropical plants under go certain adoptive charges which are commonly referred to as cold acclimation, freezing tolerance or winter hardening. Several genes are activated during cold acclimation of plants[54]. Among the series of changes that occurs during low temperature and cold acclimation of plants the important ques are the

i. Alterations in membrane lipids.
ii. Accumulation of osmolyte.
iii. Synthesis of antifreeze protein. (AFP'S)
iv. Synthesis of proteins which protect membranes and macro-molecules against dehydrative damage, etc[135]. (Srivastava, 2002)

(i):-Nitrogen assimilation & low temperature stress –

Plant accumulates certain compatible nitrogenous compound specific to a particular stress. These compound help to combat that particular stress condition[20,122,123].

The most common nitrogenous compound which accumulate upon chilling injury are proline and glycine betaine[11]. In barley and radish substantial amount of proline and amino acids, serine, glysine and alkaline accumulate on exposure to low temperatures[103]. Low temperature caused reduced $N0_3$ uptake by the roots[25]. Soyabean plants when exposed to 15^0C for 4 days showed about 52-61% decrease in N partitioning in the young shoots compared to plant grown at 25^0C. It is suggested that tolerance to low temperature can be increased by increasing N supply to young shoots. An enhancement in the level of soluble protein during the cold hardening was accompanied with increased activity of enzyme of nitrate reduction, nitrate reeducates (NR) and glutamine synthetase (GS) in many plant species including Wheat, Barley, Sugar beet, Rose, Sunflower, etc[44]. the prime enzyme of nitrate reduction, nitrate reductase shows vary behaviour depending on the plant species when plant is exposed to low temperature[25]. Low temperature stress along with low soil pH influenced nitrate reduction by strongly decreasing NR actively in growing plants[44] as NR is a substrate inducible enzyme; its activity is depending on the level of $N0_3$ in the active pool. Reduced $N0_3$ uptake under low temperature would thus lead to decrease in NR activity.

(ii):-Low temperatures and photosynthesis.

Change in membrane fluidity has been well documented upon exposure of plant to low temperatures. Chloroplast membranes are also susceptible to these changes. a reduction in chloroplast membrane content and its disorganization has been reported in spinach leaves under chilling Swelling of chloroplast and accumulation of starch grains within the chloroplast has also been reported in plants upon exposure to low temperature Low temperature enhanced the distribution of excitation energy of PSI and altered the amount transferred from Chub to Chi a in maize. The most commonly accumulated sugar in plant exposed to low temperature is sucrose. Its gets accumulated to about 10 fold in spinach leaves with an increase in sucrose phosphate syntheses activity upon exposure to cold temperature[47]. In winter wheat, activity of enzyme of sucrose biosynthesis sucrose phosphate temperature[135] Over all photosynthetic CO_2 assimilation CO_2 assimilation decrease to 50% indications a significant inhabitation of RSD at 10 ^{0}C[104].

(iii):-Low temperature and oxidative stress

Low temperature leads to production of reactive oxygen species become the light harvesting reaction continue to function[9]. low temperature stress responses include oxidative stress responses which are also observed under water deficit conditions in higher plants[13]. Increased SOD activity in response to stresses has been shown to confer increased protection form oxidative damage[5,124]. It is attributed to inhibitions of enzyme sub units under low temperature.

(iv): -Synthesis of Cold related proteins.

These proteins have given names after the inducing agent e.q. early dehydration inducible ERD, low temperature induced (LTI) low temperature responsive or cold responsive (Thomahow.1998). These compound exhibit ability to arrest growth of plant pathogen and levels of certain LTP have been shown to increase in winter barley fallowing exposure to low, above freezing hardening temperature (2^0C) both in the field and under controlled environment condition[34,111].

(v):-Low temperature and membrane fluidity

Membrane fluidity is important to ensure selective permeability, transport of ions and membrane associated electron transport. Zeng and Cowerker[168], have discussed the comparison of the change of membrane protective system in rice during enhancement of chilling resistance by different stress pretreatment like cold and heat shock.

Classification Low Temperature

Chilling sensitive plants: Seriously injured by temperature above 0^0C, below 15^0C

Chilling resistant Plants:

(i) Able to tolerate low temperature

(ii) Seriously injured when ice start to form in tissues

Frost Resistant Plants: tolerate exposure to very low temperatures (-50^0C to -100^0C) even when immersed in liquid N_2.

Chilling injury

- Occurs at Low temperature but nonfreezing temperatures
- Chilling injury occurs in
  - Tropical and subtropical plants at10^0C to 25^0C
  - Temperate plants at 0 to 15^0C
- Chilling Effect is manifested by physiological and cytological changes
- Cytological changes may be reversible or irreversible depending upon time of exposure to low temperature

Symptoms of chilling injury include

1. **Cellular changes:** Changes in membrane structure and composition, decreased protoplasmic streaming, electrolyte leakage and plasmolysis.
2. **Altered metabolism:** Increased or reduced respiration, depending on severity of stress, production of abnormal metabolites due to anaerobic condition.

Common Symptoms

- Reduced plant growth and death
- Surface lesions on leaves and fruits
- Abnormal curling, lobbing and crinkling of leaves
- Water soaking of tissues
- Cracking, splitting and dieback of stems
- Internal discolouration (vascular browning)
- Increased susceptibility to decay
- Failure to ripen normally
- Loss of vigour (potato lose the ability to sprout if chilled)

Some of the more common symptoms of chilling stress are rapid wilting followed by water soaked patches which develop into sunken pits that reflect cells tissue collapse. Following warming, the sunken pits usually dry up, leaving necrotic patches of tissues on the leaf surface.

Chilling symptoms in fruits vary and include

- Sunken pits in cucumber
- Browning of sp skins and degradation of pulp tissue in banana
- Blackheart of pine apple

Cellular Membranes

- The first symptom of chilling injury is the phase transition from liquid crytalline phase to solid gel state
- Increase in permeability of plasmalemma results in leakage of organic and inorganic substances
- Plasmolysis: Plasmolemma- pressed against the tonoplast and deleted into the vacuole as sac like intrusions
- deposits in root cells, epidermal, mesophyll and vascular cells of leaves - leading to tonoplast disruption.Formation of crystalline
- Tonoplast injury is irrevesible
- During hardening at low or above zero temp the lipid bodies accumulate in cytoplasm in close association with plasmalemma.

Chilling Injury:-Chilling injury is damage to plant parts caused by temperatures above the freezing point (32°F, 0°C). Plants of tropical or subtropical origin are most susceptible. Chilling-injured leaves may become purple or reddish and in some cases wilt. Both flowers and fruit of sensitive species can be injured.

Chilling injury refers to an injury that is caused by a temperature drop to below 15°C but above the freezing point. The symptoms of chilling injury are usually a rapid wilting of the leaves and the development of water soaked patches that go on to form sunken pits due to cell collapse. Warming will lead to these damaged areas becoming brown and necrotic while continued chilling will eventually lead to the death of the plant.

Plants may develop physiological disorders when exposed to low but non-freezing temperatures. The German plant physiologist Molisch suggested the term 'chilling injury' as long ago as 1897 to describe this phenomenon. Symptoms of chilling injury can differ widely between species, but usually develop rapidly in plants native to tropical and subtropical climates and almost imperceptibly slowly in plants originating in cool temperate climates. Within the range of chilling temperatures, that is, from the temperature of the freezing point of the plant tissue up to about 13°C, the rate at which chilling injury develops intensifies with decreasing temperature and increasing duration.

Chilling-sensitive foliage plants such as *Episcia* spp. which are native to the Amazon basin are killed within 30 min of being exposed to 1°C. Survival of such highly sensitive plants necessitated year-round protection from cold. This requirement was met by the invention of the heated glasshouse in the 1880s. Modeled on the famous Palm House at Kew Gardens, London, the Palm House in the Adelaide Botanical Gardens is an example of the type of glasshouse that was constructed in this period. Only when the extent of the climate change for introduced species is less severe can plants be held cultivated. In modern-day agriculture, many plants are often cultivated outside their customary microclimate. For example, avocado (*Persea americana* Mill.) was taken from tropical highlands in Mexico and is now grown in the temperate North Island of New Zealand and in inland Australia where nights are cold. When the new location has temperature minima below those of the region in which the plant evolved, problems of chilling injury can arise. With annual crops, the time of greatest risk is likely to be early in a growth season, and especially during seedling establishment. Chilling injury to seedlings can show up as necrotic lesions on the young roots and shoots, with slowed growth and increased susceptibility to disease attack, and even death. Crops adversely affected by low temperatures during the establishment period take longer to mature and this in turn may mean that they are at risk to chilling temperatures towards the end of the growing season.

- Occurs at low temperature but nonfreezing temperature chilling injury in tropical and subtropical plant at 10^0C to 25^0C.
- Temperate plant at 0^0C to 15^0C.
- Chilling effect is manifested by physiological and cytological changes
- Cytological changes may be reversible or irreversible depending upon time of exposure to low temperature.

Direct effect of injury:-

- Necrosis
- Discoloration
- Tissue breakdown and browning
- Reduced growth
- Failure to germinate in the case of seeds

Indirect effect of injury:-

- Reduced grain set.
- Delay harvest
- Reduced photosynthesis
- Reduced water absorption

The ability to withstand low temperatures most of these species are damaged during storage at temperatures above the freezing point of tissues, but lower than 15°C (chilling temperatures). This damage is called chilling injury[81]. Thus, chilling injury is damage to chilling-sensitive plant species during storage at temperatures above the freezing point of tissues, but lower than 15°C. Chilling-sensitive plants are the plants sensitive to chilling and damaged at chilling temperatures. The ability of plants in a vegetative state to survive the action of chilling temperatures without harm to the future growth and development is called cold resistance. In turn, chilling-sensitive plants are sensitive to chilling and after prolonged storage in these temperatures external symptoms of injury are developed and death of the organism occurs (Table). Plants, which have the visual injuries at temperatures above 15°C, are called “very sensitive to chilling”. A number of tropical or subtropical plants, such as rice, maize, tomato, cucumber, cotton, soybeans, etc., introduced in the higher latitudes have not acquired substantial resistance to chilling, despite the long history of cultivation in temperate regions (Wilson,1985). Chilling temperatures effects on plants in temperate climates 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. For example, chilling damage to young cotton plants in U.S. in 1980 resulted in the loss of 60 million dollars. In South and South-East Asia, high-yielding varieties of rice are not grown in areas of more than 7 million hectares, where they may be exposed to chilling temperatures. Obviously, the problem of plant resistance to chilling temperatures, which often occur in spring and autumn in many countries, is important for practical plant breeding.

Table: (1) The list of chilling sensitive crop and their symptoms

Crop	Lowest safe temperature °C	Chilling injury symptoms
Asparagus	0–2	Dull , gray-green, limp tips
Bean(snap)	7	Pitting and russeting
Cucumber	7	Pitting , water-soaked lesions, decay
Eggplant	7	Surface scald, *Alternaria* rot, seed blackening
Okra	7	Discoloration , water-soaked areas, pitting, decay
Pepper	7	Pitting , *Alternaria* rot, seed blackening
Potato	2	Mahogany browning, sweetening
Pumpkin	10	Decay , especially *Alternaria* rot
Squash	10	Decay , especially *Alternaria* rot
Sweet potato	10	Decay, pitting, internal discoloration
Tomato (ripe)	7–10	Water-soaking, softening, decay
Tomat0(mature-green)	13	Poor colour when ripe, *Alternaria* rot

Table: (2) - common symptoms of chilling injury

Visible symptoms leaves	Wilting, necrotic lesions, chlorophyll loss, increased susceptible to pathogens
Fruit and vegetable	Surface pitting and necrotic lesions, Surface dulling and discoloration, Internal tissue breakdown and browning, Inhibition of ripening Increased attacks by pathogen.
Physiological symptoms	Cessation of protoplasmic streaming, Decrease in photo synthetic activity, Loss of membrane semi permeability, Leakage of ions, Decreases in activity of a number of enzymes, Increases in metabolic (Alanine, Ethenol, Acetaldehyde, Keto acids), inhibition of Chlorophyll synthesis, Post chilling increase in respiratory rate, Abnormal patterns of ethylene production in fruit, Inhibition of starch conversion in fruit, Inhibition of development of flavor components in fruit.

The most noticeable visual symptoms of chilling injury in herbaceous plants are leaf and hypocotyls wilting[31,100], which often precedes the appearance of infiltration (water saturated areas)[97,125], the appearance of surface pits and large cavities[17,23,31], discoloration of leaves and internal tissues[125,146,163], accelerated aging and rupture of chilled tissues, slow, incomplete or uneven ripening[23], accompanied by a deterioration of the structure and flavor[51,150]; increased susceptibility to decay[17], drying of the edges or tips of leaf blades[48] and in the case of prolonged chilling – leaf necrosis and plant death[18,31,100]. According to Skog[128], potential symptoms of chilling injury are surface lesions, water soaking of tissues, water loss, desiccation or shriveling, internal discoloration, tissue breakdown, failure of fruit to ripen, or uneven or slow ripening, accelerated senescence and ethylene production, shortened storage or shelf life, compositional changes, loss of growth or sprouting capability, wilting and increased decay due to leakage of plant metabolites, which encourage growth of microorganisms, especially fungi. Seeds of chilling-sensitive plants do not germinate at temperatures below 10–15°C[57], and by this parameter can be divided into two main groups. The seeds of the first group (representatives – *Solanaceae* and pumpkin) are not damaged during imbibitions at chilling temperatures. With temperature increase they grow normally, but initiation of root growth leads to underdeveloped root tip tissue, tissue necrosis after the root tip, damage to the cortex or stele[12,61]. The second group includes plants whose seeds are particularly sensitive to low temperatures during imbibitions and may not germinate at low temperatures: beans, soybeans, chickpeas, corn, and cotton[38,167]. There, plant damage is increased by soil pathogens, although it is a secondary factor. A characteristic effect of chilling temperature son chilling-sensitive plants is growth slowing, more pronounced in susceptible species and varieties in comparison with the tolerant species[116,145,149]. In addition, there is a delayed development and lengthening of the growing season[130]. At the same time apical cone differentiation is delayed, reducing the number of newly formed plant organs and the rate of their occurrence, the structure of roots is changed, and flowering rate, fruit and seed filling are reduced[75,116,130].

Changes during the chilling-

(i) Cytophysiological changes caused by chilling in the chilling-sensitive plants

Chilling temperatures cause multiple disorganizations of the cells ultra-structure in sensitive plants[77]. The damaging effect of chilling is often revealed in the destruction of the cells membrane systems, leading to loss of cell compartmentation[45]. It was shown the swelling and rupture of the plasmalemma[143], destruction of the endoplasmic reticulum and vesiculation of its membranes[94], and changes of the Golgi apparatus. Upon chilling, the most noticeable changes were shown in the structure of mitochondria, namely their swelling and degeneration[45], matrix enlightenment, cristae shortening and a decrease in their number, which should lead to a reducing of oxidative phosphorylation[21,162]. Chilling temperatures disturbed the formation of prolamellar plastids caused swelling and structural changes in chloroplasts, namely destruction of chloroplasts membranes, disintegration of grains, reduction of ribosome number sickles of envelope) and the accumulation of lipid bodies, and the disappearance of starch grains[45,77]. The sharp decrease in the number of dividing cells during chilling decreased the mitotic index in apexes and in the basal part of young leaves. The relationship between the cell cycle phases was changed too[120]. Significant reduction of cell growth in root elongation zone at low temperature was shown[55]. Chilling temperatures cause accelerated cell differentiation. So, in chilled root apexes of maize the progressing differentiation of some cell lines was observed. Inhibition of cell growth leads to significant changes in growth of the plant and its organs[116,120,137]. Colloid-chemical properties of the cytoplasm are affected by chilling to. So, cytoplasm viscosity decreases at a slight chilling due to the increase of colloids dispersion and decay of structural formations, but it grows at a strong and long-term chilling due to coagulation of structural proteins[169]. The content of soluble proteins was decreased in chilling-sensitive plants at low temperatures, and this led to a reduction in the isoelectric zone of the cytoplasm Chilling of sensitive plants leads to a shift of intracellular pH[67,164,166] and an increase in cell membranes permeability[90,95]. A very sensitive indicator of the cell is a cytoplasmic streaming, which was stopped for several minutes after chilling of sensitive plants (tomato, tobacco, and pumpkin) to 10°C. Other studies found a gradual deceleration of the cytoplasmic streaming in the trichomes of tomato, watermelon, spiderwort and digitalis when the temperature dropped below 5°C, and the streaming rate correlated with resistance of plants to chilling temperature. The changes in cyclosis response to chilling were associated with changes in the cytoplasm viscosity, ATP (adenosine-5'-triphosphate) level, sensitivity to chilling of enzyme systems responsible for the use of ATP for the streaming, with damaging of the cytoskeleton.

- Swelling of plastid membranes and mitochondrial membranes
- Swelling of chloroplast thylakoids
- Decrease in size and no. of starch grains
- Grana disintegration and increase in size and number of plastoglobules
- Mitochondria with reduced cristae and transparent matrix
- Mitochondria – double the volume
- Extensive dilation and vesiculation of smooth ER cisternae
- Rough ER completely disappears *ie*.,Ribosomes are lost from the membrane
- Dilated Vesicular ER cisternae – Accumulation of cryoprotective substances
- Transformation of rough ER into vacuolated smooth ER-represents early stage of chilling
- Since ER-most dynamic structure-full reversibility of ER ultra-structure is possible
- Swelling of dictyosomes
- Longer exposure to chilling-disintegration of dictyosomes

(ii)-Effect of chilling on the physiological processes in chilling-sensitive plants

Incubation of chilling-sensitive plants at low temperatures induces disturbances in physiological processes: water regime, mineral nutrition, photosynthesis, respiration and total metabolism[81].

(a):- Water Regime:-

Chilling of sensitive plants affects all components of water regime and causes loss of water, resulting in strong wilting[7,8,151]. It is based on the two main factors:

(i) rapid decline in the ability of roots to absorb water and transport it to the shoots[10] and reduced ability to close stomata in response to subsequent water deficit[7,109,158].

(ii) Insufficient water supply provokes rapid drop in water potential of leaves during the first hours of cooling[8,18,159]. The degree of chilling damage of plants can be reduced by means of preventing the disturbance of the water regime[8,60,109,151,159].

(b):-Mineral nutrition

Low temperatures have an effect on mineral nutrition of plants. Absorption of ions by roots is difficult, as well as their movement in the aboveground parts of plants. The distribution of nutrients between the plant organs is disrupted, with general decrease in the nutrient content in the plant. Chilling of plants leads to a decrease in the activity of nitrate reductase, reduction in the nitrogen incorporation in the amino acids and proteins, and a drop in the proportion of organic phosphorus and an increase in inorganic P content[171], which is a consequence of a breach of phosphorylation and enhanced decomposition of organic P compounds. Mechanisms to reduce the absorption of nutrients by chilling temperatures include depression of respiration and/or oxidative phosphorylation, impair enzymatic transport systems associated with conformational proteins changes in membranes, changes in membrane potential, reducing the supply of ATP to H+-transporting ATPase, as well as lowering the permeability coefficients for ions.

(c):-Respiratory rate

The consequence of keeping plants at chilling temperatures is a change in respiratory rate. There is evidence of its decline, occurring as a result of destruction of the mitochondria structure, the general lowering of kinetic energy, and the inhibition of some enzymes[78,101,112]. 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[136,160]. The mechanism of stimulation is unknown, but it is possible to assume that it was the result of uncoupling of oxidative phosphorylation. It is also possible that the increased respiration reflects a reaction to the transfer of plants from chilling temperatures to the higher temperatures[165]. As a result of decreased respiration and increased consumption of energy-rich phosphates at chilling temperatures is a reduction of ATP levels[78,142]. Cold-tolerant crop species have greater temperature homeostasis of leaf respiration than cold-sensitive species[161]. Chilling reduces the cytochrome path of the electron transport in seedlings[112,118] and enhances alternative respiratory pathways[37,108,115]. Perhaps these alternative pathways play an important role in plant adaptation to chilling[136]. They are triggered at the chilling period and increase with decreasing temperature[108]. These alternative pathways induced by chilling caused a decrease in superoxide generated in mitochondria[53,115].

(d):-Rate of photosynthesis.

During and after chilling, the rate of photosynthesis in the leaves of chilling sensitive plants decreased and this is more related to decreasing temperature and lengthening of chilling period and persisted for a long time after transfer of chilled plants in the heat[4,8,35,58,83,133,137,147]. The physiological reasons for the suppression of photosynthesis are the inhibition of phloem transport of carbohydrates from the leaves, stomata limitation, destruction of the photosynthetic apparatus, damage to water- splitting complex of photo system I, inhibiting electron transport, and uncoupling of electron transfer and energy storage, changes in the activity and inhibition of synthesis of key enzymes of the Calvin cycle and C4-way[33,35,70,97,104,131,144,147,149,163]. Cold-sensitive crop species have smaller temperature homeostasis of leaf photosynthesis than cold-tolerant species[161]. Chilling of sensitive plants in light had much stronger effects on the photosynthetic apparatus than chilling in the dark[3,141]. It is considered that a disturbance of photosynthesis due to the light chilling is largely a result of photo inhibition and photo oxidation occurring in the chilling-sensitive plants (but not cold-resistant), as a result of the excess energy of excitation obtained by photosynthetic apparatus. Photo inhibition of photosynthesis is the lowering of photosynthetic activity under excessive illumination during chilling[104,155]. It increases with decreasing temperature and increasing light intensity[41,59]. Primary site photo inhibition is the photo system II. However, it was discovered that photo inhibition occurs at relatively low light and low temperature, and the main site of damage is photo system I[132,134]. Decrease of photosynthesis at chilling temperatures may be a consequence of photo oxidative damage to the photo systems in the membranes of chloroplasts, which is manifested by increased lipid per oxidation, degradation of chlorophyll, carotene, and xanthophylls[32,69]. It was caused by activated oxygen species and was associated with reduced antioxidant activity of tissues[3,79,80,144].

The inactivation of metabolism is a complex function of both temperature value and duration of its effects[14]. It is difficult to distinguish between metabolic changes in chilled plants, occurring as a result of chilling damage or preceding it. So, protein content in tissues of chilling-sensitive plants is usually reduced with chilling, mainly due to a sharp decrease in synthesis[81,98]. As a result of inhibition of protein synthesis is the increase in the level of free amino acids[64], especially proline[27,62], accumulation of which is considered as the element of the mechanism of cold hardening. Low temperatures reduce the activity of many enzymes[46]. The reasons for this may be the dissociation of multimeric enzymes, protein-lipid and hydrophobic interactions disorders, reversible changes in kinetic properties of enzymes and allosteric regulation[39,96]. Keeping the chilling-sensitive plants at low temperature the concentration of soluble sugars increased and starch content decreased significantly in all organs[62]. Changes in the level of carbohydrates caused by the chilling are associated with impaired respiration, photosynthesis, and the activity of enzymes of carbohydrate metabolism[29]. Various physiological functions are not equally sensitive to cooling. Physiological dysfunction induced by low temperatures, can be converted (or function restored) if the tissue is returned to normal temperature before the appearance of damage. Thus, temperatures below critical trigger the disturbances of physiological functions, but these disturbances do not lead to visible manifestations of injury or to changes in the rate of growth and development, since disturbances of the physiological processes are reversible until they become stable. Irreversible damage arising from prolonged chilling may be caused by the accumulation of toxic metabolites[39].

(ii):-Molecular-genetic changes

During growth, plants are exposed to various abiotic stresses such as low temperature, salt, drought, flooding, heat, heavy metal toxicity, etc. Plants must be able to respond appropriately to the stress. In nature, many stresses affect plants together. Due to the complex nature of stress, multiple sensors are more likely to be responsible for perception of the stress. After the initial recognition of the stress, a signal transduction cascade is invoked. Secondary messengers relay the signal, ultimately activating stress-responsive genes generating the initial stress response[26,42,93,107]. Now it is known that drought and salt stresses were found to induce many of the same genes as did drought stress and ABA application or response to both cold and salinity stresses is regulated by genes of calcium-signaling and nucleic acid pathways[42,93]. Apparently, that chilling sensitivity is generically determined, and the species and varietal differences of chilling resistance are connected to definite genes[42,112,121,138]. There were identified 634 chilling responsive genes in the chilling-lethal mutants of *Arabidopsis*. This gene list includes genes related to lipid metabolism, chloroplast function, carbohydrate metabolism, free radical detoxification[114]. In sweet potato there was examined transcriptional regulation of expansingenes in response to various chilling temperatures[106]. 90% of the 108 cDNA clones of low temperature-grown sunflower plants expressed at various temperatures were to be down-regulated and involved in the metabolism of carbohydrate, protein synthesis, signal transduction and transport function[52]. Response of plants to low temperature is associated with a change in the rate of gene transcription of low molecular weight proteins. Even very brief plant exposures to chilling temperature are sufficient for the appearance of stress proteins. Cooling several chilling sensitive plants (corn, rice, waving, tomato, cucumber, peanuts, cotton, sunflower, etc.) induced the synthesis of more than 20 polypeptides with molecular masses of 14 to 94 kDa, which were similar to HSP, induced by heating, or different from them[48,82,110]. Cold acclimation of chilling sensitive plants is also accompanied by the changes in synthesis of several proteins[6,16,46,48]. Chilling leads to differential expression (down-regulated and up-regulated) of genes encoding different proteins[120,147,155].

(iii):-Cell membrane changes

Low temperatures alter the physical properties of cell membranes. Chilling of sensitive plants leads to multiple changes in their membranes, namely reduce the membrane elasticity, decreasing their compliance and preventing lipid inclusion in their composition, lower lipid fluidity, thereby reducing the activity of several membrane-bound enzymes, including H+-ATPase, increase the lateral diffusion of phospholipids, sterols and proteins in the plasma membrane[66,67,76]. The phase transition of cell membranes occurs at chilling temperatures in chilling-sensitive plants (but not cold-resistant), and membranes from flexible liquid-crystal turn into solid-gel structure, leading to changes in the properties of membranes and membrane-bound enzyme activity. It is believed that the phase transitions of even small fractions of membrane lipids result in the formation of solid domains that cause cell membrane and cell damage. The phase separation of the membrane components is linked with phase transition. This phase separation is characterized by the appearance of gel-like sites in the plane of the bilayer lipid. These sites are partially or completely free of proteins. When the cells were not damaged, the formation of these micro domains was of a temporary nature. The disturbances became irreversible with long-term chilling, and coincided with the appearance of visual symptoms of damage. A number of species of tropical origin have the lateral phase separation temperature some higher (15°C) than in plants from temperate zones (6–8°C) suggesting that plants reduce the freezing point of membranes with the distance from zone of tropical origin. The lipid components of membranes are considered the most important for the membranes functioning at low temperatures[105,119]. Chilling of sensitive plants causes degradation of galactic- and phospholipids, resulting in increased free fatty acids. Chilling of plants and fruits changed the molar ratio of sterols and increased the ratio of sterols/phospholipids, which may be one reason for lowering the membrane fluidity when cooled[154,157]. Chilling sensitive plants growing at lower hardening temperature show an increase in unsaturated fatty acids, phospholipids accumulation in the tissues, lower levels of sterols and their esters, which reduced the ratio of sterol/PL[65,66,73]. Exposure of chilling-sensitive plants to low temperature changes protein components in their membranes. These changes include: disorders of protein structure, the release of non-protein components of enzymes, changes in allosteric control of activity and kinetic parameters. At the same time the protein-lipid interactions in the membrane have a significant role in the low-temperature inactivation of enzymes. Changes in the state of membranes may lead to secondary or irreversible reactions, depending on temperature, exposure duration and sensitivity of the species. After a prolonged chilling, these changes will cause loss of membrane integrity and compartmentation, the leakage of solutes, decrease of oxidative activity of mitochondria, increase of the activation energy of membrane-bound enzymes, reduce the rate of photosynthesis, cause disruption and imbalance of metabolism, the accumulation of toxic substances and the symptoms of chilling injury[81].

The theory of chilling injury: - The influence of low temperatures on chilling-sensitive plants was widespread theory Sachs about the death of plants due to disorders of water regime. However, subsequent studies have shown one-sided interpretation of these data. Changes in water regime were likely due to disturbances of other processes. It was found that the wilting of the aerial organs is not due to excessive transpiration over slow supply of water by roots, but is the result of lowering water-holding capacity due to disorganization of the cytoplasm structure and metabolic decomposition .Based on observations of changes in protoplasmic viscosity at low temperatures, it has been suggested that this cell property plays a key role in the damage The less tolerant plants to cold, the higher temperature at which cytoplasm gelling occurs and the faster increases the viscosity of the cytoplasm. At considerable increase in viscosity the rate of biochemical reactions in the cytoplasm is decreased, the metabolism is disturbed, which leads to dysfunction of physiological processes. At the same time, it is noteworthy that the low un saturation of membranous phospholipids, which is generically determined, gives sensitivity to cold temperatures to chilling-sensitive plants[170]. The data about the introduction of genes of fatty acid de saturases in a genome of chilling-sensitive plants confirms that this gives sensitive plants more pronounced chilling resistance[24,49,56,72,102]. In recent years, special attention of researchers has been drawn to two hypotheses to explain the induction of chilling damage to a rapid increase in the concentration of free cytosolic Ca2+ ([Ca2+] cyt) and the occurrence of oxidative stress upon chilling of chilling-sensitive plants[50,113]. In recent years, the calcium hypothesis has been further developed in view of oxidative stress that occurs when cooling the chilling-sensitive plants. Oxidative stress that occurs during cooling of chilling-sensitive plants plays a leading role in the transduction of chilling injury[53,85]. The reason why production of free radicals and reactive oxygen species (ROS) increased is singlet oxygen, superoxide anion, hydroxyl radical, hydrogen peroxide[139]. Summarized scheme of the initiation and development of chilling injury in the cells of chilling-sensitive plants is shown in Figure. This scheme includes all physiological and biochemical events which are known as chilling damage of susceptible plants.

Ways to improve chilling tolerance of chilling-sensitive plants

At the present time, to improve the chilling tolerance of sensitive plants various techniques are used, which can be divided into several groups: the thermal effect, chemical treatment, the use of cellular and genetic engineering.

Thermal effects include low-temperature hardening, thermal conditioning, intermediate warming, and the effect of heat stress. The basis of seed and seedling hardening of chilling-sensitive plants to cold, which has long been used in practical plant breeding, is the adaptation of the organism in the early stages of development, accompanied by the emergence of specific structural and functional rearrangements. Low-temperature hardening process is associated with the protein-synthesizing system and is accompanied by a rearrangement of the hormonal system of plants. Similar to the hardening is the thermal conditioning ("preconditioning"), associated with changes in plant response to chilling connected with growth temperature in the preceding period. Growing plants at lower temperatures leads to acclimation, which increases their resistance to chilling[68,79,80,104], as well as exposure of chilling-sensitive plants or their tissue for some period of time (from 2 to 14 days) to a relatively reduced temperature (10...18°C)[2]. Such conditioning gives the plants a greater degree of chilling tolerance for some time[6,10,16,152,153,154]. Conditioning causes changes in physiological and biochemical processes in plants, changes operation of protein-synthesizing system, leads to the synthesis of new proteins, possibly involved in protection against chilling shock[6,16,94,112]. The thermal conditioning is dependent on temperature and light in this period[43].

Intermediate warming is another way of thermal regulation of chilling injury. Transfer of the chilled plants in the warm afternoon prevented the appearance of visible symptoms of damage, impaired inhibition of photosynthesis and transpiration, reduced leaf osmotic potential[74,75,129]. Intermediate warming is often used for storage of chilling-sensitive plants' fruits[152]. It is assumed that the temporary placement in heat allows the chilled tissues to metabolize toxic substances that accumulate during the chilling process, or helps to restore the compounds in tissues that are depleted during chilling. High-temperature conditioning (heating for several minutes) of seeds and seedlings induced increased chilling- resistance in plants[117] So, in tissues exposed to heat stress there is observed the appearance of new mRNAs and proteins that are maintained and even increased after chilling, but quickly disappear at the optimum temperature[1,63,121].

Chemical treatments of chilling-sensitive plants lead to increased chilling tolerance. The effects of trace elements, synthetic growth regulators, and antioxidants were most studied. One group of compounds, the most promising in terms of increasing the chilling resistance of chillingsensitive plants is synthetic analogues of phytohormones and other plant growth regulators. The efficacy, which induced an increased resistance to chilling, was shown for all groups of phytohormones. Cytokinins and ABA were most effective of all plant growth regulators[6,88,91,100,110]. Non-hormonal growth regulators are used also in order to improve the chilling tolerance of cultivated plants. These include paklobutrazol, chlorocholinchloride, mefluidid, unikonazol and other triazoles[30,92]. The treatment by antioxidants and free radicals quenching (ethoxyquin, sodium benzoate, glutathione, tyrone, formate, ascorbate, diphenylamine, α-tocopherol, propyl gallate) can slow down the degradation of unsaturated fatty acids and reduce chilling damage in chilling-sensitive plants, leaves and fruits[70,84,89,99]. Increasing the chilling resistance of chilling-sensitive plants is also shown for compounds of different nature: choline, proline, polyamines, glycine betaine, alcohols, anesthetics, etc.[22,31,126,152,156]. The mechanisms of their action are different. They increase the fluidity of membranes, protecting them from free radical peroxidation, alter the ratio of lipid as well as protein conformation, thereby alter activity of membrane enzymes, influence hormones synthesis, water regime, etc.

Cellular and genetic engineering is a new trend, which allows fundamental changes in the chilling resistancen of chilling-sensitive plants. They are based on a large genetic variability in components, controlling sensitivity, on the one hand, and on the development of gene transfer technology, transformation and selection markers, on the other hand[40]. So, screening the surviving cells during chilling of callus and suspension cultures and subsequent plant regeneration yielded plants with increased epigenetic resistance to chilling temperatures[86,87]. Somatic hybridization may be a convenient way for the introduction of germplasm, associated with resistance to chilling, in new lines of tomato[15,148]. The increased chilling tolerance observed in transgenic tobacco plants with introduced chloroplast ω-3 fatty acid desaturase from *Arabidopsis thaliana* or Δ9-desaturase from the cyanobacterium *Anacystis nidulans* with increased levels of polyunsaturated fatty acids in membrane lipids[49,56,72,102].

Freezing Injury -At O° c there is a phase transition in water from solid to liquid or from liquid to solid. Dilute solution, such as are pound in plant cell, undergo meeting or freezing at different temperatures. As the phase separation occurs, both liquid and solid coexist. The melting points of the solution are lowered to below O° c. The solution usually super cool before actual freezing occurs and the magnitude of the super cooling varies with the in plural of a number of factories.

Freezing may be triggered by ice nucleators, which are materials that occurs crystallization one started, may proceed readily until a impercooled solution is completely frozen. Usually ice elevation of water occurs between 0 and - 10° C but, if water occurs in small droplets of less than 10 mm diameter, the water may super cool to – 38.1˚C, which is the super cool homogenous nucleation temperature.

Many plants can avoid freezing injury, because they allow deep super cooling –

1. In plants the temperature of water will drop below its freezing temperature and will still remain liquid- super cooling.
2. The liquid in the intercellular space never makes the transition to prolix phase, so ice crystal does not form.
3. Some can super cool down to - 350˚C
4. At - 40˚C ice crystal formation begins spontaneously.
5. Occurs in hardwoods and some fruit trees.
6. When the ice crystals formed are very small due to rapid freezing, there crystal & melt before they reach a harmful size.

What are the events that occur as parts of plants freeze?

If one starts with temperature decreasing below the freezing point of water then-

1. Later are the cells and in the intercellular space super cools.
2. Ice forms extracellular because the solute concentration present.
3. Intracellular hydration is prevented by the plasma lemma.
4. Since there is no contact of ice with intracellular water, a vapor pressure gradient is formed from inside to outside.
5. Equilibrium is established either by the water evaporating out the cell to the extra cellular ice or by the formation of intracellular ice.
6. Some liquid water or solution not foyer.
7. Injury becomes apparent only upon thawing and some of the injury may be the result of the thanking process.

Freezing injury to membranes - In freezing injury to membranes research involves the change in the cellular membranes when cell volume contracts because of dehydration caused by the freezing process. If a membrane can be envisioned as a mono or belayed of liquid, when the surface is reduced there is a tangent ion of pressure included within the interface.

The potential energy stored in this fashion eventually exceeds the hydrophobic forces holding the layer together and liquid is lost to the environment. This suggests that the point at which tangential pressure causes irreversible loss of membrane materials coincide with the limit of reversible psalmody. In tolerant plants the liquid is stored in the cytoplasm and then restored to the membrane upon remigration of the cell when they are thawed.

Infect cellular membranes act as affective barrier to the propagation of ice. This depends upon temperature and cold hardening. Cellular membranes are none susceptible to freeing damage than soluble enzymes. Plasma lemma is the mayor site of lethal injury. Leakage of irons from thawed tires occurs due to protoplasmic swelling and alteration in permeability to K+ ions.

Freezing injury in plants can be from two sources:

1. Freezing of soil water.
2. Freezing of the fluids within the plant

The soil water that is available to plants is found in the porous regions between soil particles. It freezes at about -2°C, depriving the plant of its source of water. The freezing of the fluids within the plants is a more serious threat, as it can cause disruption of structure and function of cells and tissues. Freezing stress occurs primarily due to the formation of ice crystals. Which damage cell structure when the temperature falls below 0^0C.

- Ice usually forms first in the cell walls and intercellular spaces
- Damage occurs when ice crystals grow and puncture into the cytoplasm

Physics of ice formation

- For the transition to solid phase to take place, need ice nucleation points
- When becoming solid, ice gives off heat, so the temperature rises
- When all of the water in the cell wall has frozen, then the temperature begins to drop again

Two types of freezing occur in plant cells and tissues

- **Vitrification :** Solidification of the cellular content into non-crystalline state (amorphous state) .It occurs by rapid freezing of cells (decrease in temperature by more than 30C/ min) to a very low temp.C
- **Crystallisation / ice formation** : Crystallization of ice occur either extracellularly or intracellularly (gradual cooling /drop in temperature)

Formation of ice intracellularly may be due to

- By internal nucleation (certain large polysaccharides /proteins serve as nucleating agents to form ice)
- By penetration of external ice crystals into the cells
- Intracellular ice formation is very lethal which causes immediate disruption of cells.

Many plants can avoid freezing injury, because they allow deep super cooling

- In plants, the temperature of water will drop below its freezing temperature and will still remain liquid - supercooling
- The liquid in the intercellular space never makes the transition to solid phase, so ice crystals don't form
- Some can supercool down to -350C
- At -40C, ice crystal formation begins spontaneously
- Occurs in hardwoods and some fruit trees
- When the ice crystals formed are very small due to rapid freezing, these crystals melt before they reach a harmful size.

Intracellular Ice Formation

- Spreads from cell to cell through plasmadesmata
- Formed in the cellwall adjacent to the intercellular spaces
- Originates spontaneously from centres of nucleation in the cytoplasm.

Membrane changes

Intact cellular membranes act as effective barrier to the propagation of ice. This depends upon temperature and cold hardening .Cellular Membranes are more susceptible to freezing damage than soluble enzymes. Plasmalemma is the major site of lethal injury. Leakage of ions from thawed tissues occurs due to protoplasmic swelling and alteration in permeability to K+ions.

The lower region of annual bluegrass crowns is more susceptible to freezing stress injury than the upper region.

Turf injury or loss results from

1. Freezing stress
2. Chilling stress
3. Desiccation
4. Frost heaving
5. Ice encasement
6. Winter diseases

Freezing stress

Mechanisms of freezing protection

1. Freezing point depression by solutes
2. Deep supercooling - used to protect critical meristematic tissues of woody species
3. Most important and common mechanism is intercellular ice formation. Water leaves the cells and crystallizes is intercellular spaces

Cold Adaptation:- Plants that live in Arctic or temperate regions where temperatures are likely to fall as low as -40°C during the winter, any vegetative structures that are subjected to these temperatures must deal with the potential for internal freezing. They will also have to survive the extended drought that is imposed by soil freezing. The small flowering plants are able to solve both problems by spending the winter as seeds. The vegetative growth renews itself annually and dies off in the autumn. The seeds have a low water content and are able to avoid extremes in temperature by laying on the ground under the insulated snow-cover. Environmental freezing in plants is usually extracellular. As there are no efficient nucleators within most plants, ice is usually transferred through the epidermis from frost that forms on the outer surface. Bacteria with ice nucleating proteins in their cell walls are often the sites of frost growth on the plants. Once ice growth occurs within the plant, the normal osmotic and chemical effects will result in cellular injury.

Freeze Avoidance: - One strategy for avoiding ice formation within the plant is to exist in a super cooled state. This is not an overwintering strategy for most small plants as they can only super cool to about 4-6°C below the freezing point, sufficient only to avoid a few early frosts. In woody plants, the cells of the xylem tissue remain super cooled throughout the winter although extracellular freezing occurs in other tissues. There is a waterproof barrier that prevents ice growth into the xylem rays (and also prevents ice-driven dehydration of the xylem). Several apocryphal accounts of exploding trees exist, initiated by an axe cut at very low temperatures (below -40°C). In some conifers, the vegetative buds also super cool.

Freeze Tolerance: - Plants that have a freeze tolerance will harden as winter approaches, undergoing changes that are necessary for surviving ice growth within the tissues. These changes must occur before the temperature gets too low so that the metabolic demands of tissue remodeling can be met. The alterations that commonly occur consist of an increase in cytoplasmic solutes both to act as a cryoprotectant as well as to buffer any freeze-concentration of other solutes that could be toxic in high concentrations, as well as membrane alterations that increase the fluidity of membranes at low temperatures and increase the stability of the membranes to low water contents.

CONCLUSION

The Chilling and freezing 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. Response of plants to low temperature exposure is associated with a change in the rate of gene transcription of a number of low molecular weight proteins. Based on the authors' own research and the literature data, the concept of cold damage was proposed, which highlighted the leading role of oxidative stress in the induction of stress response. According to this concept, there were distinguished possible ways to improve cold tolerance, which were combined into several groups: the thermal effect, chemical and the use of gene and cell engineering.

REFERENCES

1. Adnan S., Lurie S., We N.D., Isolation and characterization of a heat induced gene, *Hcit2*, encoding a novel 16.5 Kda protein. Expression coincides with heat-induced tolerance to chilling stress. *Plant Molecular Biology*, **36(6):** 935–939 (1998).
2. Ahn, S.J., Im, Y.J., Chung, G.C. and Cho, B.H., Inducible expression of plasma-membrane H+-ATPase in the roots of fig leaf gourd plants under chilling root temperature. *Physiologia Plantarum*., **106(1):** 35–40 (1999).
3. Alam, B. and Jacob, J., Overproduction of photosynthetic electrons is associated with chilling injury in green leaves, *Photosynthetica*., **40(1):** 91–95 (2002).
4. Allen, D.J. and Ort, D.R., Impacts of chilling temperatures on photosynthesis in warm-climate plants, *Trends in Plant Science*., **6(1):** 36–42 (2001).
5. Allen, R.D., Webb, R.P. and Schake, S.A., Use of transgenic plants to study antioxidant defenses.*Free Rad.Boil.Med.*, **23:** 472-479 (1997).
6. Anderson, M.D., Prasad, T.K., Martin, B.A. and Stewart, C.R., Differential gene expression in chilling-acclimated maize seedlings and ISSN 1392-3196

Zemdirbyste Agriculture **99(2):** 119 evidence for the involvement of abscisic acid in chilling tolerance, *Plant Physiology*., **105(1):** 331–339 (1994).

7. Bloom, A.J., Zwieniecki, M.A., Passioura, J.B., Randall, L.B., Holbrook, N.M., Clair, D. A. St., Water relations under root chilling in a sensitive and tolerant tomato species, *Plant, Cell and Environment*, **27(8):** 971–979 (2004).
8. Boese, S.R., Wolfem, D.W., Melkonian, J.J., Elevated CO2 mitigates chilling-induced water stress and photosynthetic reduction during chilling. *Plant, Cell and Environment*, **20(5):** 625–632 (1997).
9. Bohnert, H.J., Nelson, D.E., and Jensen R.G., Adaptations of environmental stress, *Plant Cell*, **7:** 1099-1111 (1995).
10. Bolger, T.P., Upchurch, D.R. and Mcmichael, B.L., Temperature effects on cotton root hydraulic conductance, *Environmental and Experimental Botany*, **32(1):** 49–54 (1992).
11. Borsani, O., Diaz, P. and Monza, J., Proline is involved in water stress. (1999).
12. Bradow, J.M., Chilling sensitivity of photosynthetic oil-seedlings. 2. Cucurbitaceae, *Journal of Experimental Botany*, **41(233):** 1595–1600 (1990).
13. Bray, E.A., Molecular response of water deficit., *Plant physiology*, **103:** 1035-1040 (1993).
14. Breidenbach, R.W., Rank, D.R., Fontana, A.J., Hansen, L.D. and Criddle, R.S., Calorimetric determination of tissue responses to thermal extremes as a function of time and temperature, Thermochimica Acta., **172:** 179–186 (1990).
15. Bruggemann, W., Wenner, A., Sakata, Y., Long-term chilling of young tomato plants under low light. 7. Increasing chilling tolerance of photosynthesis in *Lycopersicon esculentum* by somatic hybridization with *Lycopersicon peruvianum*, Plant Science, **108(1):** 23–30 (1995).
16. Cabane, M., Calvet, P., Vincens, P. and Boudet, A.M., Characterization of chilling acclimation-related proteins in soybean and identification of one as a member of the heat-shock protein (HSP-70) family, *Planta*., **190(3):** 346–353 (1993).
17. Cabrera, R.M., Saltveit, M.E., Owens, K., Cucumber cultivars differ in their response to chilling temperatures, *Journal of the American Society for Horticultural Science*, **117(5):** 802–807 (1992).
18. Capell, B. And Dörffling, K., Genotype-specific differences in chilling tolerance of maize in relation to chilling-induced changes in water status and abscisic acid accumulation, *Physiologia Plantarum*., **88(4):** 638–646 (1993).
19. Chandra, R. and Pareak, R.P., Influence the soil temperature on nodulation, nitrogen fixation and compactitiveness of chickpea(*Cicer arietinum* L) rhizobium spp.*Leg.Res*., **13:** 95-99 (1990).
20. Choudhary, A. and Singh, R.P., Cadmium induced change in diamine oxidase activity and polyamine levels in *Vigna radiate* Wilcrez seedling. *J.Plant Physiology*., **1:** 87-97 (2000).
21. Desantis, A., Landi, P. and Genchi, G., 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, *Plant Physiology*, **119(2):** 743–754 (1999).
22. Ding, Z.-S., Tian, S.-P., Zheng, X.-L., Zhou, Z.-W. and Xu, Y., Responses of reactive oxygen metabolism and quality in mango fruit to exogenous oxalic acid or salicylic acid under chilling temperature stress, *Physiologia Plantarum*., **130(1):** 112–121 (2007).
23. Dodds, G.T. and Ludford, P.M., Surface topology of chilling injury of tomato fruit, HortScience., **25(11):** 1416–1419 (1990).
24. Domínguez, T., Hernández, M.L., Pennycooke, J.C., Jiménez, P., Martínez-Rivas, J.M., Sanz, C., Stockinger, E.J., Sánchez-Serrano, J.J. and Sanmartín, M., Increasing omega-3 desaturase expression in tomato results in altered aroma profile and enhanced resistance to cold stress, *Plant Physiology*, 1**53(2):** 655–665 (2010).
25. Dubey, R.S. and Pessarakli, M., Physiological mechanisms of nitrogen absorption and assimilation in plants under stressful conditions. In *Handbook of plant and crop physiology*. Marcel Dekkar Inc.N.Y.2[nd] edition .pp.637-656 (2002).
26. Duchovskis, P., Brazaitytė, A., Juknys, R., Januškaitienė, I., Sliesaravičius, A., Ramaškevičienė, A., Burbulis, N., Sikšnianienė, J.B., Baranauskis, K.,

Duchovskienė, L., Stanys, V. and Bobinas, Č., Changes of physiological and genetic indices of *Lycopersicon esculentum* Mill. by cadmium under different acidicity and nutrition, *Polish Journal of Environmental Studies*, **15(2):** 235–242 (2006).

27. Duncan, D.R. and Widholm, J.M., Proline is not me primary determination of chilling tolerance induced by mannitol or abscisic acid in regenerable maize callus cultures, *Plant Physiology*, **95(4):** 1284–1287 (1991).
28. Dwivedi, P. and Raghvendra, A.S., Modulation of osmatic stress effects on photosynthesis and respiration by temperature in mesophyll protoplast of pea. *Ind.J Exptl.Biol*, **42:** 1208-1211 (2004).
29. Ebrahim, M.K.H., Vogg, G., Osman, M.N.E.H. and Komor, E., Photosynthetic performance and adaptation of sugarcane at suboptimal temperatures. *Journal of Plant Physiology*, **153(5–6):** 587–592 (1998).
30. Feng, Z., Guo, A. and Feng, Z. Amelioration of chilling stress by triadimefon in cucumber seedlings, *Plant Growth Regulation Journal*, **39(3):** 277–283 (2003).
31. Frenkel, C. and Erez, A., Induction of chilling tolerance in cucumber (*Cucumis sativus*) seedlings by endogenous and applied ethanol, *Physiologia Plantarum*, **96(4):** 593–600 (1996).
32. Fryer, M.J., Andrews, J.R., Oxborough, K., Blowers, D.A. Baker, N.R., Relationship between CO2 assimilation, photosynthetic electron transport, and active O2 metabolism in leaves of maize in the field during periods of low temperature, *Plant Physiology*, **116(2):** 571–580 (1998).
33. Garstka, M., Venema, J.H., Runiak, I., Gieczewska, K., Rosiak, M., Koziol-Lipinska, J., Kierdaszuk, B., Vredenberg, W.J. and Mostowska, A., Contrasting effect of dark-chilling on chloroplast structure and arrangement of chlorophyll-protein complexes in pea and tomato: plants with a different susceptibility to non-freezing temperature, Plant., **226(5):** 1165–1181 (2007).
34. Gaudet, D., Loroche, A., Frick, M., Huel, R.and Puchelski, B., Cold induced expression of plant defensin and lipid transfer protein transcript in winter wheat.*Physiology Plant*., **117:** 195-205 (2003).
35. Gesch, R.W. and Heilman, J.L., Chilling-induced photoinhibition and recovery in rice. *Plant Physiology*, **111(2(suppl.):** 70 (1996).
36. Gesch R.W. and Heilman J.L., Responses of photosynthesis and phosphorylation of the light-harvesting complex of photosystem II to chilling temperature in ecologically divergent cultivars of rice, *Environmental and Experimental Botany*, **41(3):** 257–266 (1999).
37. Gonzalez-Meler, M.A., Ribascarbo, M., Giles, L. and Siedow, J.N., The effect of growth and measurement temperature on the activity of the alternative respiratory pathway, *Plant Physiology*, **120(3):** 765–772 (1999).
38. Gorecki, R.J., Fordonski, G., Bieniaszewski, T. and Jacunski, K., Comparative studies on chilling sensitivity in some legume seeds, *Act Physiologiae Plantarum*, **12(2):** 149–158 (1990).
39. Graham, D. and Patterson, B.D., Responses of plants to low, non-freezing temperatures:proteins, metabolism, and acclimation, *Annual Review of Plant Physiology*, **33:** 347–372 (1982).
40. Greaves, J.A., Improving suboptimal temperature tolerance in maize: the search for variation, *Journal of Experimental Botany*, **47(296):** 307–323 (1996).
41. Greer, D.H., Effect of daily photon receipt on the susceptibility of dwarf bean (*Phaseolus vulgaris* L.) leaves to photoinhibition of photosynthesis, *Planta*., **197(1):** 31–38 (1995).
42. Grennan, A.K., Abiotic stress in rice. An “omic” approach, *Plant Physiology*, **140(4):** 1139–1141 (2006).
43. Grishenkova, N.N., Lukatkin, A.S., Stanys, V.A. and Duchovskis, P.V., Light effects on chilling adaptation of maize seedlings, *Russian Agricultural Sciences*, **10:** 1–3 (2006).
44. Gusta, L.V.,O’Connor, B.J. and Lafond, G.L., Phosphorus and nitrogen effect on the freezing tolerance of norstar winter wheat. *Con.J.Plant Sci.*,**79:** 191-195 (1999).
45. Gutierrez, M., Sola, M.D., Pascual, L., Rodriguez-Garcia, M.I. and Vargas, A.M., Ultrastructural changes in cherimoya fruit injured by chilling, *Food Structure*, **11(4):** 323–332 (1992).

46. Guy, C.L., Cold acclimation and freezing stress tolerance: role of protein metabolism, *Annual Review of Plant Physiology and Plant Molecular Biology*, **41:** 187–223 (1990).
47. Guy, C.L., Haskel, D., Neven, L., Klein, P and Smelser, C., Hydration state responsive proteins link cold and drought stress in spinch. *Planta*, **188:** 265-270 (1992).
48. Hahn, M. and Walbot, V., Effect of cold-treatment on protein synthesis and mRNA levels in rice leaves, *Plant Physiology*, **91(3):** 930–938 (1989).
49. Hamada, T., Kodama, H., Takeshita, K., Utsumi, H. and Iba, K., Characterization of transgenic tobacco with an increased α-linolenic acid level, *Plant Physiology*, **118(2):** 591–598 (1998).
50. Hariyadi, P. and Parkin, K.L. Chilling-induced oxidative stress in cucumber (*Cucumis sativus* L. cv. Calypso) seedlings, *Journal of Plant Physiology*, **141:** 733–738 (1993).
51. Harker, F.R. and Maindonald, J.H., Ripening of nectarine fruit. Changes in the cell wall, vacuole, and membranes detected using electrical impedance measurements, *Plant Physiology*, **106(l):** 165–171 (1994).
52. Hewezi, T., Leger, M., El Kayal, W. and Gentzbittel, L., Transcriptional profiling of sunflower plants growing under low temperatures reveals an extensive down-regulation of gene expression associated with chilling sensitivity, *Journal of Experimental Botany*, **57:** 3109–3122 (2006).
53. Hu, W.H., Song, X.S., Shi, K., Xia, X.J., Zhou, Y.H. and Yu, J.Q., 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 (2008).
54. Hughes, M.A. and Dunn, A., The molecular biology of plant acclimation to low temperature, *J.Exp.Bot.*, **47:** 291-305 (1996).
55. Ikeda, T., Nonami, H., Fukuyama, T. and Hashimoto, Y., Hydraulic contribution in cell elongation of tissue-cultured plants. Growth retardation induced by osmotic and temperature stresses and addition of 2,4-dichlorophenoxyacetic acid and benzyl amino purine, *Plant, Cell and Environment*, **22(8):** 899–912 (1999).
56. Ishizaki-Nishizawa, O., Fujii, T., Azuma, M., Sekiguchi, K., Murata, N., Ohtani, T. and Toguri, T., Low temperature resistance of higher plants is significantly enhanced by a nonspecific cyano-bacterial desaturase, *Nature Biotechnology*, **14(8):** 1003–1006 (1996).
57. Ismail, A.M., Hall, A.E. and Close, T.J., Chilling tolerance during emergence of cowpea associated with a dehydrin and slow electrolyte leakage, *Crop Science*, **37(4):** 1270–1277 (1997).
58. Janda, T., Szalai, G., Kissimon, J., Paldi, E., Marton, C. and Szigeti, Z., Role of irradiance in the chilling injury of young maize plants studied by chlorophyll fluorescence induction measurements, *Photosynthetica*, **30(2):** 293–299 (1994).
59. Janda, T., Szalai, G., Tari, I. and Paldi, E., Hydroponic treatment with salicylic acid decreased the effect of chilling injury in maize (*Zea mays* L.) plants. *Planta*., **208(2):** 175–180 (1999).
60. Janowiak, F. and Dörffling, K., Chilling of maize seedlings: changes in water status and abscisic acid content in 10 genotypes differing in chilling tolerance Journal of Plant Physiology, **147(5):** 582–588 (1996).
61. Jennings, P. and Saltveit, M.E., Temperature effects on imbibition and germination of cucumber (*Cucumis sativus*) seeds, *Journal of the American Society for Horticultural Science*, **119(3):** 464 (1994).
62. Jouve, L., Engelmann, F., Noirot, M. and Charrier, A., Evaluation of biochemical markers (sugar, proline, malonedialdehyde and ethylene) for cold sensitivity in microcuttings of two coffee species, *Plant Science*, **91(1):** 109–116 (1993).
63. Kadyrzhanova, D.K., Vlachonasios, K.E., Ververidis, P. and Dilley, D.R., Molecular-cloning of a novel heat-induced chilling tolerance related cDNA in tomato fruit by use of messenger RNA differential display. *Plant Molecular Biology*, **36(6):** 885–895 (1998).
64. Kanda, H.O., Studies on nucleic acid and protein metabolism in root relating to low temperature-tolerant elongation ability of fig leaf gourd for root stock, *Bulletin of the Akita Prefectural College of Agriculture*, (24): 29–62 (1998).

65. Kaniuga, Z., Saczynska, V., Miskiewicz, E. and Garstka, M., The fatty acid composition of phosphatidylglycerol and sulfoquinovosyldiacylglycerol of *Zea mays* genotypes differing in chilling susceptibility, Journal of Plant Physiology. –vol. 154, No. 2,p. 256–263 (1999).
66. Kasamo, K., Kagita, F., Yamanishi, H. and Sakaki, T., Low temperature induced changes in the thermo tropic properties and fatty acid composition of the plasma membrane and tonoplast of cultured rice (*Oryza sativa* L.) cells, *Plant and Cell Physiology*, **33(5):** 609–616 (1992).
67. Kasamo, K., Yamaguchi, M. and Nakamura, Y., Mechanism of the chilling-induced decrease in proton pumping across the tonoplast of rice cells, Plant and Cell Physiology, **41(7):** 840–849 (2000).
68. Kato-Noguchi, H., Low temperature acclimation to chilling tolerance in rice roots, *Plant Growth Regulation*, **51(2):** 171–175 (2007).
69. Kingston-Smith, A.H. and Foyer, C.H., Bundle-sheath proteins are more sensitive to oxidative damage than those of the mesophyll in maize leaves exposed to paraquat or low temperatures, *Journal of Experimental Botany*, **51**(**342):** 123–130 (2000).
70. Kingston-Smith, A.H., Harbinson, J. and Foyer, C.H., Acclimation of photosynthesis, H_2O_2 content and antioxidants in maize (*Zea mays*) grown at suboptimal temperatures. *Plant, Cell and Environment*, **22(9):** 1071–1083 (1999).
71. Kocsy, G., Toth, B., Berzy, T., Szalai, G., Jednakovits, A. and Galiba, G., Glutathione-reductase activity and chilling tolerance are induced by a hydroxylamine derivative Brx-156 in maize and soybean, *Plant Science*, **160(5):** 943–950 (2001).
72. Kodama, H., Hamada, T., Horiguchi, G., Nishimura, M. and Iba, K., Genetic enhancement of cold tolerance by expression of a gene for chloroplast ω-3-fatty-acid desaturase in transgenic tobacco, *Plant Physiology*, **105(2):** 601–605 (1994).
73. Kojima, M., Suzuki, H., Ohnishi, M. and Ito, S., Effects of growth temperature on lipids of adzuki bean cells, *Phytochemistry*, **47(8):** 1483–1487 (1998).
74. Koscielniak, J. and Biesaga-Koscielniak, J., The effect of short warm breaks during chilling on water status, intensity of photosynthesis of maize seedlings and final grain yield, *Journal of Agronomy and Crop Science*, **184(1):** 1–12 (2000).
75. Koscielniak, J., Markowski, A., Skrudlik, G. and Filek, M., Effects of some periods of variable daily exposure to temperatures of 5 and 20°C on photosynthesis and water relations in maize seedlings, *Photosynthetica*, **32(1):** 53–61 (1996).
76. Koster, K.L., Tengbe, M.A., Furtula, V. and Nothnagel, E.A., Effects of low temperature on lateral diffusion in plasma membranes on maize (*Zea mays* L.) root cortex protoplasts. Relevance to chilling sensitivity, *Plant, Cell and Environment*, **17(12):** 1285–1294 (1994).
77. Kratsch, H.A. and Wise, R.R., The ultrastructure of chilling stress , Plant, Cell and Environment, **23(4):** 337–350 (2000).
78. Lawrence, C. and Holaday, A.S., Effects of mild night chilling on respiration of expanding cotton leaves, *Plant Science*, **157(2):** 233–244 (2000).
79. Leipner, J., Basilides, A., Stamp, P. and Fracheboud, Y., Hardly increased oxidative stress after exposure to low temperature in chillingacclimated and non-acclimated maize leaves, *Plant Biology*, **2(2):** 243–251 (2000).
80. Leipner, J., Fracheboud, Y. and Stamp, P., Acclimation by suboptimal growth temperature diminishes photooxidative damage in ISSN 1392-3196 Zemdirbyste agriculture Vol. 99, No. 2 121 maize leaves, Plant, Cell and Environment, **20(3):** 366–372 (2012).
81. Levitt, J., Responses of plants to environmental stresses. Vol. 1. Chilling, freezing and high temperatures stresses. – New York, 426 p. (1980).
82. Li, Q.B., Haskell, D.W. and Guy, C.L., Coordinate and non-coordinate expression of the stress 70 family and other molecular chaperones at high and low temperature in spinach and tomato, *Plant Molecular Biology*, **39(1):** 21–34 (1999).
83. Li, X.-G., Wang, X.-M., Meng, Q.-W. and Zou, Q., Factors limiting photosynthetic recovery in sweet pepper leaves after short-term chilling stress under low irradiance, *Photosynthetica*, **42(2):** 257–262 (2004).
84. Lukatkin, A.S., The use of cucumber callus cultures to study cold damage, Biology Bulletin / Izvestiya Rossiiskoi

Akademii Nauk, Seriya Biologicheskaya, **26(3):** 242–246 (1999).

85. Lukatkin, A.S., Contribution of oxidative stress to the development of cold-induced damage to leaves of chilling-sensitive plants: 2. The activity of antioxidant enzymes during plant chilling , *Russian Journal of Plant Physiology*, **49(6):** 782–788 (2002b).
86. Lukatkin, A.S., Use of maize callus cultures for assessing chilling stress resistance, *Russian Agricultural Sciences*, **36(5):** 331–333 (2010).
87. Lukatkin, A.S., Bashmakov, D.I. and Kipaikina, N.V., Protective role of thidiazuron treatment on cucumber seedlings exposed to heavy metals and chilling , *Russian Journal of Plant Physiology*, **50(3):** 305–307 (2003).
88. Lukatkin, A.S. and Geras'kina, A.V., Screening for the improved cold resistance of the cucumber cell cultures, *Biotechnology in Russia*, **(3):** 64–72 (2003).
89. Lukatkin, A.S. and Isaikina, E.E., Calcium status and chilling injury in maize seedlings , *Russian Journal of Plant Physiology*, **44(3):** 339–342 (1997).
90. Lukatkin, A.S., Sharkaeva, E.Sh. and Zauralov, O.A., Exosmosis of electrolytes from maize leaves under chilling stresses, *Russian Journal of Plant Physiology*, **40(5):** 770–775 (1993).
91. Lukatkin, A.S. and Zauralov ,O.A., Exogenous growth regulators as a means of increasing the cold resistance of chilling-sensitive plants, *Russian Agricultural Sciences*, **35(6):** 384–386 (2009).
92. Lurie, S., Ronen, R., Lipsker, Z. and Aloni, B., Effects of paclobutrazol and chilling temperatures on lipids, antioxidants and ATPase activity of plasma-membrane isolated from green bell pepper fruits , *Physiologia Plantarum*, **91(4):** 593–598 (1994).
93. Mahajan, S. and Tuteja, N., Cold, salinity and drought stresses: an overview, *Archives of Biochemistry and Biophysics*, **444:** 139–158 (2005).
94. Marangoni, A.G., Butuner, Z., Smith, J.L. and Stanley, D.W., Physical and biochemical changes in the microsomal membranes of tomato fruit associated with acclimation to chilling, *Journal of Plant Physiology*, **135(6):** 653–661 (1990).
95. Markowski, A., Augustyniak, G. and Janowiak, F., Sensitivity of different species of field crops to chilling temperature. III. ATP content and electrolyte leakage from seedlings leaves, *Acta Physiologiae Plantarum*, **12(2):** 167–173 (1990).
96. Matsuo, T., Graham, D., Patterson, B.D. and Hockley, D.B., An electrophoretic method to detect cold-induced dissociation of proteins in crude extracts of higher plants, *Analytical Biochemistry*, **223(2):** 181–184 (1994).
97. McMahon, M.J., Permit, A.J. and Arnold, J.E., Effects of chilling on *Episcia* and *Dieffenbachia* , *Journal of the American Society for Horticultural Science*, **119(1):** 80–83 (1994).
98. Mercado, J.A., Reid, M.S., Valpuesta, V. and Quesada, M.A., Metabolic changes and susceptibility to chilling stress in *Capsicum annuum* plants grown at suboptimal temperature, *Australian Journal of Plant Physiology*, **24(6):** 759–767 (1997).
99. Michaeli, R., Riov, J., Philosophhadas, S. and Meir, S., Chilling-induced leaf abscission of *Ixora coccinea* plants. II. Alteration of auxin economy by oxidative stress, *Physiologia Plantarum*, **107(2):** 174–180 (1999).
100. Mitchell, D.E. and Madore, M.A., Patterns of assimilates production and translocation in muskmelon (*Cucumis melo* L.). 2. Low temperature affects, *Plant Physiology*., **99(3):** 966–971 (1992).
101. Munro, K.D., Hodges, D.M., DeLong, J.M., Forney, C.F. and Kristie, D.N., Low temperature effects on ubiquinone content, respiration rates and lipid peroxidation levels of etiolated seedlings of two differentially chilling-sensitive species, *Physiologia Plantarum*., **121(3):** 488–497 (2004).
102. Murata, N. and Tasaka, Y., Glycerol-3-phosphate acyltransferase in plants, *Biochimica et Biophysica Acta*., **1348(1–2):** 10–16 (1997).
103. Nandwal, A.S., Godara. M., Sheokhand, S., Kamboj, D.V., Kundu, B.S., Kushad, M.S., Kumar, B. and Sharma, S.K., Salinity induced change in plant water status, nodule functioning and ionic distribution in phonotypically differing ecotype of *Vigna radiata* L *Plant physiology*, **156:** 350-359 (2000).

104. Nie, G.Y., Long, S.P. and Baker, N.R., The effects of development at suboptimal growth temperatures on photosynthetic capacity and susceptibility to chilling-dependent photo inhibition in *Zea mays* , *Physiologia Plantarum*., **85(3):** 554–560 (1992).
105. Nishida, I. and Murata, N., Chilling sensitivity in plants and cyanobacteria. The crucial contribution of membrane lipids, *Annual Review of Plant Physiology and Plant Molecular Biology*, **47:** 541–568 (1996).
106. Noh, S.A., Park, S.H., Huh, G.H., Paek, K.H., Shin, J.S. and Bae, J.M., Growth retardation and differential regulation of expansin genes in chilling-stressed sweet potato, *Plant Biotechnology Report*, **3:** 75–85 (2009).
107. Oktem, H.A., Eyidogan, F., Selcuk, F., Oz, M.T., da Silva, J.A.T. and Yucel, M., Revealing response of plants to biotic and abiotic stresses with microarray technology, Genes, Genomes and Genomics. –p. 15–48 122 *Chilling injury in chilling-sensitive plants: a review* (2008).
108. Ordentlich, A., Linzer, R.A. and Raskin, I., Alternative respiration and heat evolution in plants, *Plant Physiology*, **97(4):** 1545–1550 (1991).
109. Pardossi, A., Vernieri, P. and Tognoni, F., Involvement of abscisic acid in regulating water status in *Phaseolus vulgaris* L. during chilling, *Plant Physiology*, **100(3):** 1243–1250 (1992).
110. Pareek, A., Singla, S.L. and Grover, A., Proteins alterations associated with salinity, desiccation, high and low-temperature stresses and abscisic acid application in seedlings of Pusa 169, a highyielding rice (*Oryza sativa* L.) cultivar, *Current Science*, **75(10):** 1023–1035 (1997).
111. Pearce, R.S., Molecular analysis of acclimation to cold. *Plant Grow regul.*, **29:** 47-76 (1999).
112. Prasad, T.K., Anderson, M.D., Martin, B.A. and Stewart, C.R., Evidence for chilling-induced oxidative stress in maize seedlings and a regulatore role for hydrogen peroxide, *Plant Cell*, **6:** 65–74 (1994a).
113. Prasad, T.K., Anderson, M.D. and Stewart, C.R., Acclimation, hydrogenperoxide, and abscisic acid protect mitochondria against irreversible chilling injury in maize seedlings, *Plant Physiology*, **105(2):** 619–627 (1994b).
114. Provart, N.J., Gil, P., Chen, W., Han, B., Chang, H.S., Wang, X. and Zhu, T., Gene expression phenotypes of *Arabidopsis* associated with sensitivity to low temperatures, *Plant Physiology*, **132:** 893–906 (2003).
115. Purvis, A.C. and Shewfelt, R.L., Does the alternative pathway ameliorate chilling injury in sensitive plant tissues? *Physiologia Plantarum.*, **88(4):** 712–718 (1993).
116. Rab, A. and Saltveit, M.E., Differential chilling sensitivity in cucumber (*Cucumis sativus*) seedlings, *Physiologia Plantarum*, **96(3):** 375–382 (1996a).
117. Rab, A. and Saltveit, M.E., Sensitivity of seedling radicles to chilling and heat shock-induced chilling tolerance, *Journal of the American Society for Horticultural Science*, **121(4):** 711–715 (1996b).
118. Reyes, L. and Jennings, P.H., Effects of chilling on respiration and induction of cyanide- resistant respiration in seedling roots of cucumber, *Journal of the American Society for Horticultural Science*, **122(2):** 190–194 (1997).
119. Routaboul, J.M., Fisher, S.F. and Browse, J., Trienoic fatty acids are required to maintain chloroplast function at low temperatures, *Plant Physiology*, **124(4):** 1697–1705 (2000).
120. Rymen, B., Fiorani, F., Kartal, F., Vandepoele, K., Inze, D., Beemster, G.T.S., Cold nights impair leaf growth and cell cycle progression in maize through transcriptional changes of cell cycle genes, *Plant Physiology*, **143(3):** 1429–1438 (2007).
121. Sabehat, A., Lurie, S. and We, N.D., Expression of small heat-shock proteins at low-temperatures. A possible role in protecting against chilling injuries, *Plant Physiology*, **117(2):** 651–658 (1998).
122. Sakamoto, A. and Murata, N., Genetic engineering of glycinebetaine synthesis in plants: Currents status and implication for enhancementof stress tolerance. *J.Exp.Bot.*, **51:** 81-88 (2000).
123. Sakamoto, A. and Murata, N., The use of bacterial choline oxidase, a glycinebetaine synthesizing enzyme to

create stress resistant transgenic plants, plant physiology, **125:** 180-188 (2001).

124. Shah, K., Kumar, R.G., Verma, S. and Dubey, R.S., Effect of cadmium on lipid peroxidation. Superoxide anion generation and activity of antioxidant enzyme in growing rice seedlings. *Plant Sci.*, **161:** 1135-1144 (2001).

125. Sharom, M., Willemot, C. and Thompson, J.E., Chilling injury induces lipid phase changes in membranes of tomato fruit, *Plant Physiology,* **105(1):** 305–308 (1994).

126. Shen, W., Nada, K. and Tachibana, S., Involvement of polyamines in the chilling tolerance of cucumber cultivars, *Plant Physiology*, **124(1):** 431–439 (2000).

127. Shen, B., Jenesen, R.G. and Bohnert, H.J., Mannitol protects against oxidation by hydroxyl radicals. *Plant Physiology.*, **115:** 527-532 (1997).

128. Skog, L.J., Chilling injury of horticultural crops. Ontario Ministry of Agriculture, Food and Rural Affairs Fact sheet.http:,www.omafra.gov.on.ca/english/crops/facts/98–021 (1998).

129. Skrudlik, G., Baczek-Kwinta, R. and Koscielniak, J., The effect of short warm breaks during chilling on photosynthesis and of antioxidant enzymes in plants sensitive to chilling, *Journal of Agronomy and Crop Science*, **184(4):** 233–240 (2000).

130. Skrudlik, G. and Koscielniak, J., Effects of low-temperature treatment at seedling stage on soybean growth, development and final yield, *Journal of Agronomy and Crop Science*, **176(2):** 111–117 (1996).

131. Smith, B.N., Jones, A.R., Hanson, L.D. and Criddle, R.S., Growth, respiration rate, and efficiency response to temperature. *Handbook of plant and crop stress.*2nd edition, Marcel Dekker, New York, 417-440 (1999).

132. Sonoike, K., Photo inhibition of photo system I – its physiological significance in the chilling sensitivity of plants, *Plant and Cell Physiology*, **37(3):** 239–247 (1996).

133. Sonoike, K., Various aspects of inhibition of photosynthesis under light/chilling stress. Photoinhibition at chilling temperatures versus chilling damage in the light, *Journal of Plant Research*, **111(1101):** 121–129 (1998).

134. Sonoike, K., The different roles of chilling temperatures in the photo inhibition of photo system I and photo system II, *Journal of Photochemistry and Photobiology B: Biology*, **48(2–3):** 136–141 (1999).

135. Srivastava, L.M., Abscesic acid and stress tolerance in plant. In *Plant growth development and environment.* Academic press New York, pp 381-408 (2002).

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

137. Strauss, A.J., Kruger, G.H.J., Strasser, R.J. and van Heerden, P.D.R., The role of low soil temperature in the inhibition of growth and PSII function during dark chilling in soybean genotypes of contrasting tolerance, *Physiologia Plantarum*, **131(1):** 89–105 (2007).

138. Su, Ch.-F., Wang, Y.-Ch., Hsieh, T.-H., Lu, Ch.-A., Tseng, T.-H. and Yu, S.-M. A novel MYBS3-dependent pathway confers cold tolerance in rice, *Plant Physiology*, **153(4):** 145–158 (2010).

139. Suzuki, N. and Mittler, R., Reactive oxygen species and temperature stresses: a delicate balance between signaling and destruction, *Physiologia Plantarum*, **126(1):** 45–51 (2006).

140. Sylvie, F.M., Murchie, E. Hirel, B., Galteir, N., Quick, W.P. and Fayer, C.H., Manipulation of pathways of sucrose biosynthesis and nitrogen assimilation in transformed plants to improve photosynthesis and productivity. In *A molecular approach to primary metabolismin higher plants.*Taylar and Francis Ltd.,U.K.pp,125-153 (1997).

141. Szalai, G., Janda, T., Bartok, T. And Paldi, E., Role of light in changes in free amino-acid and polyamine contents at chilling temperature in maize (Zea *mays*) *Physiologia Plantarum,* **101(2):** 434–438 (1997).

142. Takeda, Y., Ogawa, T., Nakamura, Y., Kasamo, K., Sakata, M. and Ohta, E., 31P-NMR study of the physiological conditions in intact root cells of mung bean seedlings under low temperature stress, *Plant and Cell Physiology*, **36(5):** 865–871 (1995).

143. Tao, Z., Zou, Q. and Cheng, B., Effect of low temperature during imbibitions on ultrastructure in hypocotyls, *Acta Botanica Sinica*, **33(7):** 511–515 (1991).
144. Terashima, I., Noguchi, K., Itohnemoto, T., Park, Y.M., Kubo, A. and Tanaka, K., The cause of PSI photoinhibition at low temperatures in leaves of *Cucumis sativus*, a chilling-sensitive plant, *Physiologia Plantarum*, **103(3):** 295–303 (1998).
145. Ting, C.S., Owens, T.G. and Wolfe, D.W., Seedling growth and chilling stress effect on photosynthesis in chilling-sensitive and chilling ISSN 1392-3196 *Zemdirbyste Agriculture*, **99(2):** (2012).
146. Tsuda, H., Niimura, Y. and Katoh, T., Chill injury in Saintpaulia leaf with special reference to leaf spot formation, *Journal of Agricultural Science*. – Tokyo Nogyo Daigaku., **47(4):** 283–289 (2003).
147. Van Heerden, P.D.R., Kruger, G.H.J., Loveland, J.E., Parry, M.A.J., Foyer, C.H., Dark chilling imposes metabolic restrictions on photosynthesis in soybean, Plant, *Cell and Environment*, **26(2):** 323–337 (2003).
148. Venema, J.H., Eekhof, M., van Hasselt, P.R., Analysis of low-temperature tolerance of a tomato (*Lycopersicon esculentum*) cybrid with chloroplasts from a more chilling-tolerant *L. hirsutum* accession, *Annals of Botany*, **85(6):** 799–807 (2000).
149. Venema, J.H., Posthumus, F., de Vries, M. and van Hasselt, P.R., Differential response of domestic and wild *Lycopersicon* species to chilling under low light: growth, carbohydrate content, photosynthesis and the xanthophyll cycle, *Physiologia Plantarum*, **105(1):** 81–88 (1999).
150. Ventura, Y. and Mendlinger, S., Effects of suboptimal low temperature on yield, fruit appearance and quality in muskmelon (*Cucumis melo* L.) cultivars, *The Journal of Horticultural Science and Biotechnology*, **74(5):** 602–607 (1999).
151. Vernieri, P., Pardossi, A. and Tognoni, F., Influence of chilling and drought on water relations and abscisic acid accumulation in bean, *Australian Journal of Plant Physiology*, **18(1):** 25–35 (1991).
152. Wang, C.Y., Approaches to reduce chilling injury of fruit and vegetables, Horticulture Review, **15:** 63–95 (1993).
153. Wang, C.Y., Temperature preconditioning affects glutathione content and glutathione reductase activity in chilled zucchini squash, Journal of Plant Physiology, **145(1–2):** 148–152 (1995).
154. Wang, C.Y., Kramer, G.F., Whitaker, B.D. and Lusby, W.R., Temperature preconditioning increases tolerance to chilling injury and alters lipid composition in zucchini squash, *Journal of Plant Physiology*, **140(2):** 229–235 (1992).
155. Wang, C., Ma, X.L., Hui, Z. and Wang, W., Glycine betaine improves thylakoid membrane function of tobacco leaves under low temperature stress, *Photo synthetic*, **46(3):** 400–409 (2008b).
156. Wang, N., Fang, W., Han, H., Sui, N., Li, B. and Meng, Q.W., Overexpression of zeaxanthin epoxidase gene enhances the sensitivity of tomato PSII photoinhibition to high fight and chilling stress, *Physiologia Plantarum*, **132(3):** 384–396 (2008a).
157. Whitaker, B.D., Lipid changes in microsomes and crude plastid fractions during storage of tomato fruits at chilling and non-chilling temperatures, *Phyto chemistry*, **32(2):** 265–271 (1993).
158. Wilkinson, S., Clephan, A.L. and Davies, W.J., Rapid low temperature induced stomatal closure occurs in cold-tolerant *Commelina communis* leaves but not in cold-sensitive tobacco-leaves, via a mechanism that involves apoplastic calcium but not abscisic acid, *Plant Physiology*, **126(4):** 1566–1578 (2001).
159. Wolfe, D.W., Low-temperature effects on early vegetative growth, leaf gas-exchange and water potential of chilling-sensitive and chilling-tolerant crop species, *Annals of Botany*, **67(3):** 205–212 (1991).
160. Yadegari, L.Z., Heidari, R. and Carapetian, J., Chilling pretreatment causes some changes in respiration, membrane permeability and some other factors in soybean seedlings, *Research Journal of Biological Sciences*, **3(9):**1054–1059 (2008).
161. Yamori, W., Noguchi, K., Hikosaka, K. and Terashima, I., Cold-tolerant crop species have greater temperature homeostasis of leaf respiration and photosynthesis than cold-sensitive species, *Plant and Cell Physiology*, **50(2):** 203–215 (2009).

162. Yin, G., Sun, H., Xin, X., Qin, G., Liang, Z. and Jing, X., Mitochondrial damage in the soybean seed axis during imbibition at chilling temperatures, *Plant and Cell Physiology*, **50(7):** 1305–1318 (2009).
163. Yoshida, R., Kanno, A., Sato, T. and Kameya, T., Cool temperature-induced chlorosis in rice plants. 1. Relationship between the induction and a disturbance of etioplast development, *Plant Physiology*, **110(3):** 997–1005 (1996).
164. Yoshida, S., Low temperature-induced cytoplasmic acidosis in cultured mung bean (*Vigna radiata* L. Wilczek) cells, *Plant Physiology*, **104(4):** 1131–1138 (1994).
165. Zauralov, O.A. and Lukatkin, A.S., Aftereffect of low temperatures on the respiration of heat-loving plants, *Russian Journal of Plant Physiology*, **44(5):** 640–644 (1997).
166. Zauralov, O.A., Lukatkin, A.S. and Sharkaeva, E. Sh., Intracellular pH of maize leaf tissues upon different degrees of chilling, *Biology Bulletin*, **24(1):** 82–84 (1997).
167. Zemetra, R.S. and Cuany, R.L., Variation among inbreds for seed response to low temperatures in maize (*Zea mays* L.), *Maydica*., **36(1):** 17–23 (1991).
168. Zeng, S.,Wang,Y. and Meiru, L., Comparision of the changes of membrane protective system in rice seedling during enhancement of chilling resistance by different stress pretreatment. *Xieu Xuebao*, **39(4):** 308-314 (1997).
169. Zhang, J.X., Cui, S.P., Li, J.M., Wei, J.K. and Kirkham, M.B., Protoplasmic factors, antioxidant responses, and chilling resistance in maize, *Plant Physiology and Biochemistry*, **33(5):** 567–575 (1995).
170. Zhu, S.-Q., Zhao, H., Liang, J.-S., Ji, B.-H. and Jiao, D.-M., Relationships between phosphatidylglycerol molecular species of thylakoid membrane lipids and sensitivities to chilling-induced photoinhibition in rice, *Journal of Integrative Plant Biology*, **50(2):** 194–202 (2008).
171. Zia, M.S., Salim, M., Aslam, M. and Gill, M.A., Rahmatullah. Effect of low temperature of irrigation water on rice growth and nutrient uptake, *The Journal of Agricultural Science*, **173(1):** 22–31 (1994).
172. Ziegler, P., Environmental stress and stress responses plants. In *the Co- Action between living system and the planet.*(University of Genava, Switzerland, pp 67-100 (1998).