

ISSN 1392-3196

Žemdirbystė=Agriculture, vol. 99, No. 2 (2012), p. 111–124

UDK 634.1:581.17:576.3

## Chilling injury in chilling-sensitive plants: a review

Alexander S. LUKATKIN<sup>1</sup>, Aušra BRAZAITYTĖ<sup>2</sup>, Česlovas BOBINAS<sup>2</sup>,  
Pavelas DUCHOVSKIS<sup>2</sup>

<sup>1</sup>Mordovian State University  
Bolshevistskaja 68, Saransk, Russia  
E-mail: aslukatkin@yandex.ru

<sup>2</sup>Institute of Horticulture, Lithuanian Research Centre for Agriculture and Forestry  
Kauno 30, Babtai, Kaunas distr., Lithuania  
E-mail: p.duchovskis@lsdi.lt

### Abstract

Chilling temperatures (1–10°C) lead to numerous physiological disturbances in the cells of chilling-sensitive plants and result in chilling injury and death of tropical and subtropical plants, e.g., many vegetable species. The literature review shows that the exposure of chilling-sensitive plants to low temperatures causes 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.

The review analyzes historical aspects in the development of ideas about the nature of chilling damage of chilling-sensitive plants and direction of modern research. 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 how to improve cold tolerance. They were divided into several groups: the thermal effect (low-temperature hardening, thermal conditioning, intermediate warming and the effect of heat stress), chemical treatment (trace elements, synthetic growth regulators, antioxidants) and the use of gene and cell engineering.

Key words: antioxidants, cell, chilling-sensitive plants, chilling injury, physiological processes, oxidative stress.

### Introduction

More than half of the 350 000 plant species on Earth are grown in the tropics and subtropics. In the course of evolution, they could not develop the ability to withstand low temperatures (Лукаткин, 2002). 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 as opposed to damage during freezing (freezing injury) (Levitt, 1980; Raison, Lyons, 1986). 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 (Генкель, Кушниренко, 1966; Коровин, 1969). 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” (Raison, Lyons, 1986). 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 (Коровин, 1969). 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 (Wilson, 1985). 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.** The list of the vegetables, sensitive to chilling temperatures, the lowest safe storage/handling temperature and the symptoms of chilling injury (DeEll, 2004)

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, <i>Alternaria</i> rot, seed blackening
Okra	7	discoloration, water-soaked areas, pitting, decay
Pepper	7	pitting, <i>Alternaria</i> rot, seed blackening
Potato	2	mahogany browning, sweetening
Pumpkin	10	decay, especially <i>Alternaria</i> rot
Squash	10	decay, especially <i>Alternaria</i> rot
Sweet potato	10	decay, pitting, internal discoloration
Tomato (ripe)	7–10	water-soaking, softening, decay
Tomato (mature-green)	13	poor colour when ripe, <i>Alternaria</i> rot

The most noticeable visual symptoms of chilling injury in herbaceous plants are leaf and hypocotyl wilting (Mitchell, Madore, 1992; Frenkel, Erez, 1996), which often precedes the appearance of infiltration (water saturated areas) (McMahon et al., 1994; Sharom et al., 1994), the appearance of surface pits and large cavities (Dodds, Ludford, 1990; Cabrera et al., 1992; Frenkel, Erez, 1996), discoloration of leaves and internal tissues (Sharom et al., 1994; Yoshida et al., 1996; Tsuda et al., 2003), accelerated aging and rupture of chilled tissues, slow, incomplete or uneven ripening (Dodds, Ludford, 1990), accompanied by a deterioration of the structure and flavor (Harker, Maindonald, 1994; Ventura, Mendlinger, 1999); increased susceptibility to decay (Cabrera et al., 1992), drying of the edges or tips of leaf blades (Жолкевич, 1955; Hahn, Walbot, 1989) and in the case of prolonged chilling – leaf necrosis and plant death (Mitchell, Madore, 1992; Capell, Dörffling, 1993; Frenkel, Erez, 1996). According to Skog (1998), potential symptoms of chilling injury are surface lesions, water-soaking of tissues, water loss, desiccation or shrivelling, 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 (Wolk, Herner, 1982; Ismail et al., 1997), and by this parameter can be divided into two main groups (Markowski, 1988). 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 (Bradow, 1990; Jennings, Saltveit, 1994). 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 (Gorecki

et al., 1990; Zemetra, Cuany, 1991). There, plant damage is increased by soil pathogens, although it is a secondary factor (Wolk, Herner, 1982).

A characteristic effect of chilling temperatures on chilling-sensitive plants is growth slowing, more pronounced in susceptible species and varieties in comparison with the tolerant species (Ting et al., 1991; Rab, Saltveit, 1996 a; Venema et al., 1999). In addition, there is a delayed development and lengthening of the growing season (Skrudlik, Koscielniak, 1996). 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 (Buis et al., 1988, Barlow, Adam, 1989; Rab, Saltveit, 1996 b, Skrudlik, Koscielniak, 1996; Lejeune, Bernier, 1996).

### Cytophysiological changes caused by chilling in the chilling-sensitive plants

Chilling temperatures cause multiple disorganizations of the cells ultrastructure in sensitive plants (Kratsch, Wise, 2000). The damaging effect of chilling is often revealed in the destruction of the cells membrane systems, leading to loss of cell compartmentation (Gutierrez et al., 1992). It was shown the swelling and rupture of the plasmalemma (Tao et al., 1991), destruction of the endoplasmic reticulum and vesiculation of its membranes (Marangoni et al., 1990), and changes of the Golgi apparatus (Yoshida et al., 1989). Upon chilling, the most noticeable changes were shown in the structure of mitochondria, namely their swelling and degeneration (Gutierrez et al., 1992), matrix enlightenment, cristae shortening and a decrease in their number, which should lead to a reducing of oxidative phosphorylation (Desantis et al., 1999; Yin et al., 2009). Chilling temperatures disturbed the formation of prolamellar plastids (Ikeda, Toyama, 1987), caused swelling and structural changes in chloroplasts, namely destruction of chloroplasts membranes, disintegration of grains, reduction of ribosome number,

induced the formation of peripheral reticulum (small vesicles of envelope) and the accumulation of lipid bodies, and the disappearance of starch grains (Gutierrez et al., 1992; Kratsch, Wise, 2000).

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 (Зуралов, 1993; Лукаткин и др., 2010). The relationship between the cell cycle phases was changed too (Francis, Barlow, 1988; Rymen et al., 2007). Significant reduction of cell growth in root elongation zone at low temperature was shown (Ikeda et al., 1999). Chilling temperatures cause accelerated cell differentiation. So, in chilled root apexes of maize the progressing differentiation of some cell lines was observed (Zavala, Lin, 1989). Inhibition of cell growth leads to significant changes in growth of the plant and its organs (Rab, Saltveit, 1996 a; Rymen et al., 2007; Strauss et al., 2007).

Colloid-chemical properties of the cytoplasm are affected by chilling too (Генкель, Кушниренко, 1966; Wang, 1982; Minorski, 1985). 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 (Жолкевич, 1955; Генкель, Кушниренко, 1966; Zhang et al., 1995). 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 (Дроздов и др., 1977). Chilling of sensitive plants leads to a shift of intracellular pH (Yoshida, 1994; Zauralov et al., 1997; Kasamo et al., 2000) and an increase in cell membranes permeability (Markowski et al., 1990; Lukatkin et al., 1993, Лукаткин и др., 2007). 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 (Lewis, 1961). 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 (Patterson et al., 1979), 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 (Patterson et al., 1979; Wang, 1982; Woods et al., 1984 b; Minorsky, 1985).

### **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 (Жолкевич, 1955; Генкель, Кушниренко, 1966; Levitt, 1980; Wang, 1982; Graham, Patterson, 1982).

*Water regime.* Chilling of sensitive plants affects all components of water regime and causes loss of

water, resulting in strong wilting (Vernieri et al., 1991; Boese et al., 1997; Bloom et al., 2004). It is based on the two main factors: rapid decline in the ability of roots to absorb water and transport it to the shoots (Bolger et al., 1992) and reduced ability to close stomata in response to subsequent water deficit (Pardossi et al., 1992; Wilkinson et al., 2001; Bloom et al., 2004). Insufficient water supply provokes rapid drop in water potential of leaves during the first hours of cooling (Wolfe, 1991; Capell, Dörffling, 1993; Boese et al., 1997). The degree of chilling damage of plants can be reduced by means of preventing the disturbance of the water regime (Vernieri et al., 1991; Wolfe, 1991; Pardossi et al., 1992; Janowiak, Dörffling, 1996; Boese et al., 1997).

*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 above-ground parts of plants. The distribution of nutrients between the plant organs is disrupted, with general decrease in the nutrient content in the plant (Лукаткин, 2002). 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 (Holobrada et al., 1981; Zia et al., 1994), 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<sup>+</sup>-transporting ATPase, as well as lowering the permeability coefficients for ions (Clarkson et al., 1988).

*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 (Lyons et al., 1979; Yoshida et al., 1989; Prasad et al., 1994 a; Lawrence, Holaday, 2000; Munro et al., 2004). 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 (Wilson, 1978; Steward et al., 1990; Yadegari et al., 2008). The mechanism of stimulation is unknown, but it is possible to assume that it was the result of uncoupling of oxidative phosphorylation (Wang, 1982). It is also possible that the increased respiration reflects a reaction to the transfer of plants from chilling temperatures to the higher temperatures (Zauralov, Lukatkin, 1997). As a result of decreased respiration and increased consumption of energy-rich phosphates at chilling temperatures is a reduction of ATP levels (Takeda et al., 1995; Lawrence, Holaday, 2000). Cold-tolerant crop species have greater temperature homeostasis of leaf respiration than cold-sensitive species (Yamori et al., 2009). Chilling reduces the cytochrome path of the electron transport in seedlings (Prasad et al.,

1994 a; Reyes, Jennings, 1997) and enhances alternative respiratory pathways (Ordentlich et al., 1991; Purvis, Shewfeld, 1993; Gonzalez-Meier et al., 1999; Ribascarbo et al., 2000). Perhaps these alternative pathways play an important role in plant adaptation to chilling (Steward et al., 1990). They are triggered at the chilling period and increase with decreasing temperature (Ordentlich et al., 1991). These alternative pathways induced by chilling caused a decrease in superoxide generated in mitochondria (Purvis, Shewfelt, 1993; Hu et al., 2008).

*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 (Janda et al., 1994; Boese et al., 1997; Sonoike, 1998; Gesch, Heilman, 1999; Allen, Ort, 2001; Van Heerden et al., 2003; Li et al., 2004; Strauss et al., 2007). The physiological reasons for the suppression of photosynthesis are the inhibition of phloem transport of carbohydrates from the leaves, stomatal limitation, destruction of the photosynthetic apparatus, damage to water-splitting complex of photosystem 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  $C_4$ -way (Yordanov, 1992; Nie et al., 1992; McMahan et al., 1994; Gesch, Heilman, 1996; Yoshida et al., 1996; Terashima et al., 1998; Kingston-Smith et al., 1999; Venema et al., 1999; Van Heerden et al., 2003; Garstka et al., 2007). Cold-sensitive crop species have smaller temperature homeostasis of leaf photosynthesis than cold-tolerant species (Yamori et al., 2009).

Chilling of sensitive plants in light had much stronger effects on the photosynthetic apparatus than chilling in the dark (Szalai et al., 1997; Alam, Jacob, 2002). It is considered that a disturbance of photosynthesis due to the light chilling is largely a result of photoinhibition and photooxidation occurring in the chilling-sensitive plants (but not cold-resistant), as a result of the excess energy of excitation obtained by photosynthetic apparatus. Photoinhibition of photosynthesis is the lowering of photosynthetic activity under excessive illumination during chilling (Nie et al., 1992; Wang et al., 2008 a). It increases with decreasing temperature and increasing light intensity (Janda et al., 1994; Greer, 1995). Primary site photoinhibition is the photosystem II. However, it was discovered that photoinhibition occurs at relatively low light and low temperature, and the main site of damage is photosystem I (Sonoike, 1996; 1999). Decrease of photosynthesis at chilling temperatures may be a consequence of photooxidative damage to the photosystems in the membranes of chloroplasts, which is manifested by increased lipid peroxidation, degradation of chlorophyll, carotene, and xanthophylls (Fryer et al., 1998; Kingston-Smith, Foyer, 2000). It was caused by activated oxygen species and was associated with reduced antioxidant activity of tissues (Leipner et al., 1997; Terashima et al., 1998; Leipner et al., 2000; Alam, Jacob, 2002).

*The inactivation of metabolism* is a complex function of both temperature value and duration of its

effects (Breidenbach et al., 1990). 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 (Levitt, 1980; Mercado et al., 1997). As a result of inhibition of protein synthesis is the increase in the level of free amino acids (Kanda, 1998), especially proline (Duncan, Widholm, 1991; Jouve et al., 1993), accumulation of which is considered as the element of the mechanism of cold hardening. Low temperatures reduce the activity of many enzymes (Guy, 1990). 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 (Graham, Patterson, 1982; Matsuo et al., 1994). Keeping the chilling-sensitive plants at low temperature the concentration of soluble sugars increased and starch content decreased significantly in all organs (Jouve et al., 1993). Changes in the level of carbohydrates caused by the chilling are associated with impaired respiration, photosynthesis, and the activity of enzymes of carbohydrate metabolism (Ebrahim et al., 1998).

Various physiological functions are not equally sensitive to cooling (Wilson, 1978; Yoshida et al., 1989). 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 (Lyons et al., 1979). Irreversible damage arising from prolonged chilling may be caused by the accumulation of toxic metabolites (Lyons, 1973; Graham, Patterson, 1982).

## 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 (Mahajan, Tuteja, 2005; Grennan, 2006; Duchovskis et al., 2006; Oktem et al., 2008). 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 (Mahajan, Tuteja, 2005; Grennan, 2006). Apparently, that chilling sensitivity is generically determined, and the species and varietal differences of chilling resistance are connected to definite genes (Prasad et al., 1994 a; Sabehat et al., 1998; Grennan, 2006; Su et al., 2010). There were identified 634 chilling-respon-

sive genes in the chilling-lethal mutants of *Arabidopsis*. This gene list includes genes related to lipid metabolism, chloroplast function, carbohydrate metabolism, free radical detoxification (Provart et al., 2003). In sweet potato there were examined transcriptional regulation of expansin genes in response to various chilling temperatures (Noh et al., 2009). 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 (Hewezi et al., 2006). 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 (Hahn, Walbot, 1989; Pareek et al., 1997; Li et al., 1999). Cold acclimation of chilling-sensitive plants is also accompanied by the changes in synthesis of several proteins (Hahn, Walbot, 1989; Guy, 1990; Cabane et al., 1993; Anderson et al., 1994). Chilling leads to differential expression (down-regulated and up-regulated) of genes encoding different proteins (Van Heerden et al., 2003; Yamagitchi-Shinozaki, Shinozaki, 2006; Rymen et al., 2007; Wang et al., 2008 a).

### 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<sup>+</sup>-ATPase, increase the lateral diffusion of phospholipids, sterols and proteins in the plasma membrane (Quinn, 1988; Kasamo et al., 1992; Koster et al., 1994; Kasamo et al., 2000). 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 (Raison et al., 1971; Lyons, 1973). 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 (Thompson, 1989). 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 microdomains was of a temporary nature. The disturbances became irreversible with long-term chilling, and coincided with the appearance of visual symptoms of damage (Platt-Aloia, Thomson, 1987). 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 (Terzaghi et al., 1989).

The lipid components of membranes are considered the most important for the membranes functioning at low temperatures (Lyons, 1973; Lyons et al., 1979; Nishida, Murata, 1996; Routaboul et al., 2000). Chilling of sensitive plants causes degradation of galacto- 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 (Wang et al., 1992; Whitaker, 1993). 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 (Kasamo et al., 1992; Kojima et al., 1998; Kaniuga et al., 1999).

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 (Graham, Patterson, 1982).

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 (Lyons, 1973; Levitt, 1980; Quinn, 1988).

### The theory of chilling injury

In the initial period of studying, 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. In the middle of the 20<sup>th</sup> century 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 decompensation (Жолкевич, 1955).

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 (Belehradek, 1935). 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. However, it was shown that cucumber plants decreased viscosity with increasing chilling duration, and the worst after 2.5–4 days, and then increased gradually, reaching viscosity level of non-chilled plant, but shortly before the complete withering away could exceed this level. An increase in viscosity of highly damaged plants also continued after the transfer into heat. “Dying” increase protoplasmic viscosity and is the final stage of death, which has no relation to the first stage of damage, but only deepens it (Жолкевич, 1955).

According to data of some research from the 1950–60s, the main result of chilling-sensitive plants damage during long-term cooling is a metabolic disorder. In this case, the death of plants occurs due to the predominance of the destruction over the synthesis. One of the probable causes of the protoplasm structure disorganization and irreversible changes in the metabolism is the uncoupling between the energy obtaining during respiration and its effective consumption (Жолкевич, 1955). However, metabolic changes occur only after sufficiently long chilling of plants and most of them as well as changes in water regime are not the primary cause of chilling injury. So, shorter duration of chilling does not cause a sharp inhibition of metabolism. Accumulation of toxic products of metabolism as a result of the imbalance that occurs during chilling of sensitive plants and is one of the main reasons of chilling injury (Жолкевич, 1955, Генкель, Кушниренко, 1966), which often occurs after the return of chilled plants to heat, i.e. is the result of secondary dysfunction associated with heating.

Among the hypotheses about the primary events that trigger the occurrence of reaction to lower temperatures, hypothesis of phase change prevailed in the 1970s, according to which the chilling-induced changes in the molecular ordering of membrane lipids may be the cause of chilling injury (Raison et al., 1971). These changes increase the damage by lowering the ATP levels, metabolic imbalances and increasing membrane permeability (Lyons, 1973). However, all these changes do not occur immediately after the start of chilling and are likely to be secondary disorders (Minorsky, 1985). The increase in membrane permeability due to the low-temperature exposure (“membranes leakage”) should be quick, registered in the first few minutes after placing the tissue at chilling temperatures, in accordance with the hypothesis of phase transitions. In reality, this does not happen, and often passive permeability is not increased (Patterson et al., 1979). Moreover, the increase in electrolyte leakage is likely due to chilling-induced water stress, which has been revealed to be considerably weaker in an atmosphere saturated with water (Guinn, 1971). At the same time it is noteworthy that the low unsaturation of membranous phospholipides, which is generically determined, gives sensitivity to cold temperatures to chilling-sensitive plants (Zhu et al., 2008). The data about the introduction of genes of fatty acid desaturases in a genome of chilling-sensitive plants confirms that this gives sensitive plants more pronounced chilling resistance (Kodama et al., 1994; Ishiza-

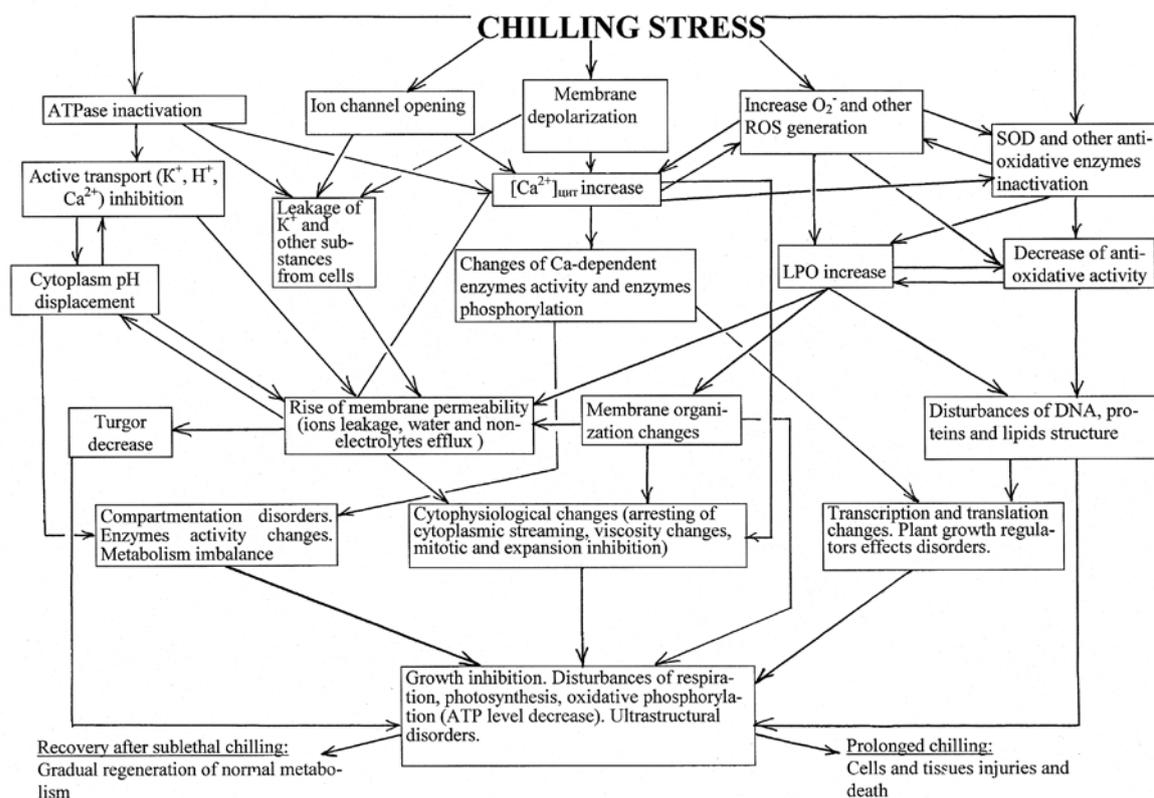
ki-Nishizawa et al., 1996; Hamada et al., 1998; Murata, Tasaka, 1997; Domínguez et al., 2010).

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  $\text{Ca}^{2+}$  ( $[\text{Ca}^{2+}]_{\text{cyt}}$ ) (Minorsky, 1985) and the occurrence of oxidative stress upon chilling of chilling-sensitive plants (Hariyadi, Parkin, 1993; Prasad et al., 1994 b).

Minorsky (1985) proposed a hypothesis to explain most of the secondary effects of chilling shock, which suddenly increases (by 1–2 orders) in the concentration of  $[\text{Ca}^{2+}]_{\text{cyt}}$ . It is assumed that the rapid increase in  $[\text{Ca}^{2+}]_{\text{cyt}}$  due to chilling, may serve as the primary physiological signal of cold exposure. It was shown that changes in intracellular calcium compartmentation in chilled plants, leading to an increase in  $[\text{Ca}^{2+}]_{\text{cyt}}$ , stop cytoplasmic streaming and affect the subcellular structures (Woods et al., 1984 b). There is evidence that input of  $^{45}\text{Ca}^{2+}$  in maize root cells increased by 20–25% at a temperature of 2°C (Zocchi, Hanson, 1982). Changes in  $[\text{Ca}^{2+}]_{\text{cyt}}$  trigger cascade reactions in the cell, which leads to numerous disturbances at all levels of an organization. Our investigation shows that chilling induces abrupt reduction of  $\text{Ca}^{2+}$ -ATPase activity, which pumps out  $\text{Ca}^{2+}$  in apoplast and/or in intracellular depots (Лукаткин, Еремкина, 2002). So, this enhances the  $[\text{Ca}^{2+}]_{\text{cyt}}$  level in cytoplasm. During the growth of maize seedlings on nutrient media with different calcium status more intense chilling injury was observed at reduced or enhanced  $\text{Ca}^{2+}$  doses in comparison with optimal dose (Lukatkin, Isaikina, 1997).

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 (Lukatkin, 2002 a; b; Hu et al., 2008). The reason why production of free radicals and reactive oxygen species (ROS) increased is singlet oxygen, superoxide anion, hydroxyl radical, hydrogen peroxide (Suzuki, Mittler, 2006). These ROS cause considerable damage to membrane lipids and other cellular components (Lukatkin et al., 1995; Lukatkin, 2003; Попов и др., 2010). It was shown that  $[\text{Ca}^{2+}]_{\text{cyt}}$  changes are intimately connected to an oxidative stress. Oxidative stress causes an immediate increase in cytosolic calcium (Price et al., 1994), acting the same as chilling shock (Knight et al., 1996). This reaction is transient, and finishes within 1–2 minutes. In turn,  $[\text{Ca}^{2+}]_{\text{cyt}}$  influences a level of free radicals, inhibiting activity of SOD (Price et al., 1994). So, increasing the concentration of ionized calcium causes increased oxidative stress (Price et al., 1994; Lock, Price, 1994), i.e. is the signal amplification cascade that causes chilling damage.

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.



**Figure.** Scheme of the initiation and development of chilling injury in the cells of chilling-sensitive 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* includes 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 (Генкель, Кушниренко, 1966, Дроздов и др., 1977). Low-temperature hardening process is associated with the protein-synthesizing system (Титов, Шерудило, 1990) and is accompanied by a rearrangement of the hormonal system of plants (Таланова и др., 1991; Волкова и др., 1991).

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 (Nie et al., 1992; Leipner et al., 1997; Kingstom-Smith et al., 1999; Leipner et al., 2000; Kato-Noguchi, 2007; Попов и др., 2010), 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 temperatures (10...18°C) (Wolk, Herner, 1982; Wang, 1982;

Ahn et al., 1999). Such conditioning gives the plants a greater degree of chilling tolerance for some time (Bolger et al., 1992; Cabane et al., 1993; Capell, Dörffling, 1993; Anderson et al., 1994; Wang et al., 1992; Wang, 1993; 1995). 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 (Marangoni et al., 1990; Cabane et al., 1993; Anderson et al., 1994; Prasad et al., 1994 a). The thermal conditioning is dependent on temperature and light in this period (Grishenkova et al., 2006; Лукаткин и др., 2006).

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 (Koscielniak et al., 1996; Koscielniak, Biesaga-Koscielniak, 2000; Skrudlik et al., 2000). Intermediate warming is often used for storage of chilling-sensitive plants' fruits (Wang, 1982; 1993). 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 (Lyons, 1973).

High-temperature conditioning (heating for several minutes) of seeds and seedlings induced increased chilling-resistance in plants (Rab, Saltveit, 1996 b; Mandrich,

Saltveit, 2000). This process involves protein synthesis. 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 (Adnan et al., 1998; Kadyrzhanova et al., 1998; Sabehat et al., 1998).

*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 chilling-sensitive 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 (Генкель, Кушниренко, 1966; Володько, 1983; Зауралов, Лукаткин, 1996).

Cytokinins and ABA were most effective of all plant growth regulators (Duncan, Widholm, 1991; Mitchell, Madore, 1992; Anderson et al., 1994; Pareek et al., 1997; Зауралов и др., 2000; Lukatkin et al., 2003; Lukatkin, Zauralov, 2009; Лукаткин, Овчинникова, 2009). 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 (Lurie et al., 1994; Feng et al., 2003). The treatment by antioxidants and free radicals quenching (ethoxyquin, sodium benzoate, glutathione, tyron, formate, ascorbate, diphenylamine,  $\alpha$ -tocopherol, propyl gallate) can slow down the degradation of unsaturated fatty acids and reduce chilling damage in chilling-sensitive plants, leaves and fruits (Lukatkin, Levina, 1997; Michaeli et al., 1999; Xu et al., 2000; Kocsy et al., 2001). Increasing the chilling resistance of chilling-sensitive plants is also shown for compounds of different nature: choline, proline, polyamines, glycine betaine, alcohols, anesthetics, etc. (Lyons et al., 1979; Wang, 1982; Duncan, Widholm, 1991; Wang, 1993; Frenkel, Erez, 1996; Janda et al., 1999; Shen et al., 2000; Ding et al., 2007; Wang et al., 2008 b). 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 resistance 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 (Greaves, 1996; Лукаткин, Дерябин, 2009). 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 (Dix, 1979; Lukatkin, 1999; Lukatkin, Geras'kina, 2003; Lukatkin, 2010). Somatic hybridization may be a convenient way for the introduction of germplasm, associated with resistance to chilling, in new lines of tomato (Bruggemann et al., 1995; Venema et al., 2000). The increased chilling tolerance observed

in transgenic tobacco plants with introduced chloroplast  $\omega$ -3 fatty acid desaturase from *Arabidopsis thaliana* or  $\Delta$ 9-desaturase from the cyanobacterium *Anacystis nidulans* with increased levels of polyunsaturated fatty acids in membrane lipids (Kodama et al., 1994; Ishizaki-Nishizawa et al., 1996; Hamada et al., 1998; Murata, Tazaka, 1997).

## Conclusion

The literature review shows that the exposure of chilling-sensitive plants to low temperatures leads to disturbances in all physiological processes – water regime, mineral nutrition, photosynthesis, respiration and metabolism. Inactivation of metabolism, observed at chilling of chilling-sensitive plants is a complex function of both temperature and duration of exposure. 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 (low-temperature hardening, thermal conditioning, intermediate warming and the effect of heat stress), chemical treatment (trace elements, synthetic growth regulators, antioxidants) and the use of gene and cell engineering.

## Acknowledgements

This research was supported by the Russian Ministry of Education and Science under the Analytical Departmental Target Program "Development of Scientist Potential of Higher School", Project No. 2.1.1/624.

This work was carried out within the framework of the long term research program "Horticulture: agro-biological basics and technologies implemented by Lithuanian Research Centre for Agriculture and Forestry".

Received 25 11 2011

Accepted 06 02 2012

## References

- 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*. – 1998, vol. 36, No. 6, p. 935–939
- Ahn S. J., Im Y. J., Chung G. C., Cho B. H. Inducible expression of plasma-membrane  $H^+$ -ATPase in the roots of figleaf gourd plants under chilling root temperature // *Physiologia Plantarum*. – 1999, vol. 106, No. 1, p. 35–40
- Alam B., Jacob J. Overproduction of photosynthetic electrons is associated with chilling injury in green leaves // *Photosynthetica*. – 2002, vol. 40, No. 1, p. 91–95
- Allen D. J., Ort D. R. Impacts of chilling temperatures on photosynthesis in warm-climate plants // *Trends in Plant Science*. – 2001, vol. 6, No. 1, p. 36–42
- Anderson M. D., Prasad T. K., Martin B. A., Stewart C. R. Differential gene expression in chilling-acclimated maize seedlings and

- evidence for the involvement of abscisic acid in chilling tolerance // *Plant Physiology*. – 1994, vol. 105, No. 1, p. 331–339
- Barlow P. W., Adam J. S. Anatomical disturbances in primary roots of *Zea mays* following periods of cool temperature // *Environmental and Experimental Botany*. – 1989, vol. 29, No. 3, p. 323–336
- Belehradek H. Temperature and Living Matter // *Protoplasma Monograph*. – 1935, vol. 8, p. 137–162
- 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*. – 2004, vol. 27, No. 8, p. 971–979
- Boese S. R., Wolfe D. W., Melkonian J. J. Elevated CO<sub>2</sub> mitigates chilling-induced water stress and photosynthetic reduction during chilling // *Plant, Cell and Environment*. – 1997, vol. 20, No. 5, p. 625–632
- Bolger T. P., Upchurch D. R., McMichael B. L. Temperature effects on cotton root hydraulic conductance // *Environmental and Experimental Botany*. – 1992, vol. 32, No. 1, p. 49–54
- Bradow J. M. Chilling sensitivity of photosynthetic oil-seedlings. 2. Cucurbitaceae // *Journal of Experimental Botany*. – 1990, vol. 41, No. 233, p. 1595–1600
- Breidenbach R. W., Rank D. R., Fontana A. J., Hansen L. D., Criddle R. S. Calorimetric determination of tissue responses to thermal extremes as a function of time and temperature // *Thermochimica Acta*. – 1990, vol. 172, p. 179–186
- 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*. – 1995, vol. 108, No. 1, p. 23–30
- Buis R., Barthou H., Roux B. Effect of temporary chilling on foliar and caulinary growth and productivity in soybean (*Glycine max*) // *Annals of Botany*. – 1988, vol. 61, No. 6, p. 705–715
- Cabane M., Calvet P., Vincens P., 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*. – 1993, vol. 190, No. 3, p. 346–353
- 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*. – 1992, vol. 117, No. 5, p. 802–807
- Capell B., 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*. – 1993, vol. 88, No. 4, p. 638–646
- Clarkson D. T., Earnshaw M. J., White P. A., Cooper H. D. Temperature dependent factors influencing nutrient uptake: an analysis of responses at different levels of organization // *Plant and Temperature: Symposium of Society for Experimental Biology*. – Cambridge, UK, 1988, p. 281–309
- DeEll J. Symptoms of chilling injury in vegetables // Ontario Ministry of Agriculture, Food and Rural Affairs. – 2004, <<http://www.omafra.gov.on.ca/english/crops/hort/news/hortmatt/2004/18hrt04a5.htm>> [accessed 11 05 2011]
- Desantis A., Landi P., 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*. – 1999, vol. 119, No. 2, p. 743–754
- Ding Z.-S., Tian S.-P., Zheng X.-L., Zhou Z.-W., 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*. – 2007, vol. 130, No. 1, p. 112–121
- Dix P. J. Cell culture manipulations as a potential breeding tool // *Low temperature stress in crop plants*. – New York, USA, 1979, p. 463–472
- Dodds G. T., Ludford P. M. Surface topology of chilling injury of tomato fruit // *HortScience*. – 1990, vol. 25, No. 11, p. 1416–1419
- Domínguez T., Hernández M. L., Pennycooke J. C., Jiménez P., Martínez-Rivas J. M., Sanz C., Stockinger E. J., Sánchez-Serrano J. J., Sanmartín M. Increasing omega-3 desaturase expression in tomato results in altered aroma profile and enhanced resistance to cold stress // *Plant Physiology*. – 2010, vol. 153, No. 2, p. 655–665
- Duchovskis P., Brazaitytė A., Juknys R., Januškaitienė I., Slieravičius A., Ramaškevičienė A., Burbulis N., Šikšnianienė J. B., Baranauskis K., Duchovskienė L., Stanyš V., Bobinas Č. Changes of physiological and genetic indices of *Lycopersicon esculentum* Mill. by cadmium under different acidity and nutrition // *Polish Journal of Environmental Studies*. – 2006, vol. 15, No. 2, p. 235–242
- Duncan D. R., Widholm J. M. Proline is not the primary determination of chilling tolerance induced by mannitol or abscisic acid in regenerable maize callus cultures // *Plant Physiology*. – 1991, vol. 95, No. 4, p. 1284–1287
- Ebrahim M. K. H., Vogt G., Osman M. N. E. H., Komor E. Photosynthetic performance and adaptation of sugarcane at sub-optimal temperatures // *Journal of Plant Physiology*. – 1998, vol. 153, No. 5–6, p. 587–592
- Feng Z., Guo A., Feng Z. Amelioration of chilling stress by triadimefon in cucumber seedlings // *Plant Growth Regulation Journal*. – 2003, vol. 39, No. 3, p. 277–283
- Francis D., Barlow P. W. Temperature and the cell cycle // *Plants and Temperature: Symposium of Society for Experimental Biology*. – Cambridge, UK, 1988, p. 181–201
- Frenkel C., Erez A. Induction of chilling tolerance in cucumber (*Cucumis sativus*) seedlings by endogenous and applied ethanol // *Physiologia Plantarum*. – 1996, vol. 96, No. 4, p. 593–600
- Fryer M. J., Andrews J. R., Oxborough K., Blowers D. A., Baker N. R. Relationship between CO<sub>2</sub> assimilation, photosynthetic electron transport, and active O<sub>2</sub> metabolism in leaves of maize in the field during periods of low temperature // *Plant Physiology*. – 1998, vol. 116, No. 2, p. 571–580
- Garstka M., Venema J. H., Runiak I., Gieczewska K., Rosiak M., Koziol-Lipinska J., Kierdaszuk B., Vredenberg W. J., 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 // *Planta*. – 2007, vol. 226, No. 5, p. 1165–1181
- Gesch R. W., Heilman J. L. Chilling-induced photoinhibition and recovery in rice // *Plant Physiology*. – 1996, vol. 111, No. 2 (suppl.), p. 70
- Gesch R. W., 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*. – 1999, vol. 41, No. 3, p. 257–266
- Gonzalez-Meler M. A., Ribascarbo M., Giles L., Siedow J. N. The effect of growth and measurement temperature on the activity of the alternative respiratory pathway // *Plant Physiology*. – 1999, vol. 120, No. 3, p. 765–772
- Gorecki R. J., Fordonski G., Bieniaszewski T., Jacunski K. Comparative studies on chilling sensitivity in some legume seeds // *Acta Physiologiae Plantarum*. – 1990, vol. 12, No. 2, p. 149–158
- Graham D., Patterson B. D. Responses of plants to low, non-freezing temperatures: proteins, metabolism, and acclimation // *Annual Review of Plant Physiology*. – 1982, vol. 33, p. 347–372
- Greaves J. A. Improving suboptimal temperature tolerance in maize: the search for variation // *Journal of Experimental Botany*. – 1996, vol. 47, No. 296, p. 307–323
- Greer D. H. Effect of daily photon receipt on the susceptibility of dwarf bean (*Phaseolus vulgaris* L.) leaves to photoinhibition of photosynthesis // *Planta*. – 1995, vol. 197, No. 1, p. 31–38
- Grennan A. K. Abiotic stress in rice. An “omic” approach // *Plant Physiology*. – 2006, vol. 140, No. 4, p. 1139–1141
- Grishenkova N. N., Lukatkin A. S., Stanyš V. A., Duchovskis P. V. Light effects on chilling adaptation of maize seedlings // *Russian Agricultural Sciences*. – 2006, No. 10, p. 1–3
- Guinn G. Chilling injury in cotton seedlings: changes in permeability of cotyledons // *Crop Science*. – 1971, vol. 11, p. 101–102

- Gutierrez M., Sola M. D., Pascual L., Rodriguez-Garcia M. I., Vargas A. M. Ultrastructural changes in cherimoya fruit injured by chilling // *Food Structure*. – 1992, vol. 11, No. 4, p. 323–332
- Guy C. L. Cold acclimation and freezing stress tolerance: role of protein metabolism // *Annual Review of Plant Physiology and Plant Molecular Biology*. – 1990, vol. 41, p. 187–223
- Hahn M., Walbot V. Effect of cold-treatment on protein synthesis and mRNA levels in rice leaves // *Plant Physiology*. – 1989, vol. 91, No. 3, p. 930–938
- Hamada T., Kodama H., Takeshita K., Utsumi H., Iba K. Characterization of transgenic tobacco with an increased  $\alpha$ -linolenic acid level // *Plant Physiology*. – 1998, vol. 118, No. 2, p. 591–598
- Hariyadi P., Parkin K. L. Chilling-induced oxidative stress in cucumber (*Cucumis sativus* L. cv. Calypso) seedlings // *Journal of Plant Physiology*. – 1993, vol. 141, p. 733–738
- Harker F. R., Maindonald J. H. Ripening of nectarine fruit. Changes in the cell wall, vacuole, and membranes detected using electrical impedance measurements // *Plant Physiology*. – 1994, vol. 106, No. 1, p. 165–171
- Hewezi T., Leger M., El Kayal W., 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*. – 2006, vol. 57, p. 3109–3122
- Holobrada M., Mistrik J., Kolek J. The effect of temperature on the uptake and loss of anions by seedling roots of *Zea mays* L. // *Biologia Plantarum*. – 1981, vol. 23, No. 4, p. 241–248
- Hu W. H., Song X. S., Shi K., Xia X. J., Zhou Y. H., 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*. – 2008, vol. 46, No. 4, p. 581–588
- Ikeda T., Nonami H., Fukuyama T., 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 benzylaminopurine // *Plant, Cell and Environment*. – 1999, vol. 22, No. 8, p. 899–912
- Ikeda T., Toyama S. Studies on ultrastructure and function of photosynthetic apparatus in rice cells. II. Effect of low temperature on early development of rice plastids // *Japanese Journal of Crop Science*. – 1987, vol. 56, No. 4, p. 632–640
- Ishizaki-Nishizawa O., Fujii T., Azuma M., Sekiguchi K., Murata N., Ohtani T., Toguri T. Low temperature resistance of higher plants is significantly enhanced by a nonspecific cyanobacterial desaturase // *Nature Biotechnology*. – 1996, vol. 14, No. 8, p. 1003–1006
- Ismail A. M., Hall A. E., Close T. J. Chilling tolerance during emergence of cowpea associated with a dehydrin and slow electrolyte leakage // *Crop Science*. – 1997, vol. 37, No. 4, p. 1270–1277
- Janda T., Szalai G., Kissimon J., Paldi E., Marton C., Szigeti Z. Role of irradiance in the chilling injury of young maize plants studied by chlorophyll fluorescence induction measurements // *Photosynthetica*. – 1994, vol. 30, No. 2, p. 293–299
- Janda T., Szalai G., Tari I., Paldi E. Hydroponic treatment with salicylic acid decreased the effect of chilling injury in maize (*Zea mays* L.) plants // *Planta*. – 1999, vol. 208, No. 2, p. 175–180
- Janowiak F., 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*. – 1996, vol. 147, No. 5, p. 582–588
- Jennings P., Saltveit M. E. Temperature effects on imbibition and germination of cucumber (*Cucumis sativus*) seeds // *Journal of the American Society for Horticultural Science*. – 1994, vol. 119, No. 3, p. 464
- Jouve L., Engelmann F., Noirot M., Charrier A. Evaluation of biochemical markers (sugar, proline, malonaldehyde and ethylene) for cold sensitivity in microcuttings of two coffee species // *Plant Science*. – 1993, vol. 91, No. 1, p. 109–116
- Kadyrzhanova D. K., Vlachonassios K. E., Ververidis P., 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*. – 1998, vol. 36, No. 6, p. 885–895
- Kanda H. O. Studies on nucleic acid and protein metabolism in root relating to low temperature-tolerant elongation ability of figleaf gourd for root stock // *Bulletin of the Akita Prefectural College of Agriculture*. – 1998, No. 24, vol. 29–62
- Kaniuga Z., Szczyńska V., Miskiewicz E., Garstka M. The fatty acid composition of phosphatidylglycerol and sulfoquinovosyldiacylglycerol of *Zea mays* genotypes differing in chilling susceptibility // *Journal of Plant Physiology*. – 1999, vol. 154, No. 2, p. 256–263
- Kasamo K., Kagita F., Yamanishi H., Sakaki T. Low temperature-induced changes in the thermotropic properties and fatty acid composition of the plasma membrane and tonoplast of cultured rice (*Oryza sativa* L.) cells // *Plant and Cell Physiology*. – 1992, vol. 33, No. 5, p. 609–616
- Kasamo K., Yamaguchi M., Nakamura Y. Mechanism of the chilling-induced decrease in proton pumping across the tonoplast of rice cells // *Plant and Cell Physiology*. – 2000, vol. 41, No. 7, p. 840–849
- Kato-Noguchi H. Low temperature acclimation to chilling tolerance in rice roots // *Plant Growth Regulation*. – 2007, vol. 51, No. 2, p. 171–175
- Kingston-Smith A. H., 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*. – 2000, vol. 51, No. 342, p. 123–130
- Kingston-Smith A. H., Harbinson J., Foyer C. H. Acclimation of photosynthesis, H<sub>2</sub>O<sub>2</sub> content and antioxidants in maize (*Zea mays*) grown at suboptimal temperatures // *Plant, Cell and Environment*. – 1999, vol. 22, No. 9, p. 1071–1083
- Knight H., Trewavas A. J., Knight M. R. Cold calcium signaling in *Arabidopsis* involves two cellular pools and a change in calcium signature after acclimation // *The Plant Cell*. – 1996, vol. 8, p. 489–503
- Kocsy G., Toth B., Berzy T., Szalai G., Jednakovits A., Galiba G. Glutathione-reductase activity and chilling tolerance are induced by a hydroxylamine derivative Brx-156 in maize and soybean // *Plant Science*. – 2001, vol. 160, No. 5, p. 943–950
- Kodama H., Hamada T., Horiguchi G., Nishimura M., Iba K. Genetic enhancement of cold tolerance by expression of a gene for chloroplast  $\omega$ -3-fatty-acid desaturase in transgenic tobacco // *Plant Physiology*. – 1994, vol. 105, No. 2, p. 601–605
- Kojima M., Suzuki H., Ohnishi M., Ito S. Effects of growth temperature on lipids of adzuki bean cells // *Phytochemistry*. – 1998, vol. 47, No. 8, p. 1483–1487
- Koscielniak J., 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*. – 2000, vol. 184, No. 1, p. 1–12
- Koscielniak J., Markowski A., Skrudlik G., 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*. – 1996, vol. 32, No. 1, p. 53–61
- Koster K. L., Tengbe M. A., Furtula V., 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*. – 1994, vol. 17, No. 12, p. 1285–1294
- Kratsch H. A., Wise R. R. The ultrastructure of chilling stress // *Plant, Cell and Environment*. – 2000, vol. 23, No. 4, p. 337–350
- Lawrence C., Holaday A. S. Effects of mild night chilling on respiration of expanding cotton leaves // *Plant Science*. – 2000, vol. 157, No. 2, p. 233–244
- Leipner J., Basilides A., Stamp P., Fracheboud Y. Hardly increased oxidative stress after exposure to low temperature in chilling-acclimated and non-acclimated maize leaves // *Plant Biology*. – 2000, vol. 2, No. 2, p. 243–251
- Leipner J., Fracheboud Y., Stamp P. Acclimation by suboptimal growth temperature diminishes photooxidative damage in

- maize leaves // *Plant, Cell and Environment*. – 1997, vol. 20, No. 3, p. 366–372
- Lejeune P., Bernier G. Effect of environment on the early steps of ear initiation in maize (*Zea mays* L.) // *Plant, Cell and Environment*. – 1996, vol. 19, No. 2, p. 217–224
- Levitt J. Responses of plants to environmental stresses. Vol. 1. Chilling, freezing and high temperatures stresses. – New York, 1980, 426 p.
- Lewis D. A. Protoplasmic streaming in plants sensitive and insensitive to chilling temperatures // *Science*. – 1961, vol. 124, No. 1, p. 75–76
- Li Q. B., Haskell D. W., 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*. – 1999, vol. 39, No. 1, p. 21–34
- Li X.-G., Wang X.-M., Meng Q.-W., Zou Q. Factors limiting photosynthetic recovery in sweet pepper leaves after short-term chilling stress under low irradiance // *Photosynthetica*. – 2004, vol. 42, No. 2, p. 257–262
- Lock J., Price A. H. Evidence that disruption of cytosolic calcium is critically important in oxidative plant stress // *Proceedings of the Royal Society of Edinburgh. Section B: Biology*. – 1994, vol. 102, p. 261–264
- Lukatkin A. S. Contribution of oxidative stress to the development of cold-induced damage to leaves of chilling-sensitive plants: 1. Reactive oxygen species formation during plant chilling // *Russian Journal of Plant Physiology*. – 2002 (a), vol. 49, No. 5, p. 622–627
- 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*. – 2002 (b), vol. 49, No. 6, p. 782–788
- Lukatkin A. S. Contribution of oxidative stress to the development of cold-induced damage to leaves of chilling-sensitive plants. 3. Injury of cell membranes by chilling temperatures // *Russian Journal of Plant Physiology*. – 2003, vol. 50, No. 2, p. 243–246
- Lukatkin A. S. The use of cucumber callus cultures to study cold damage // *Biology Bulletin / Izvestiya Rossiiskoi Akademii Nauk, Seriya Biologicheskaya*. – 1999, vol. 26, No. 3, p. 242–246
- Lukatkin A. S. Use of maize callus cultures for assessing chilling stress resistance // *Russian Agricultural Sciences*. – 2010, vol. 36, No. 5, p. 331–333
- Lukatkin A. S., Bashmakov D. I., Kipaikina N. V. Protective role of thidiazuron treatment on cucumber seedlings exposed to heavy metals and chilling // *Russian Journal of Plant Physiology*. – 2003, vol. 50, No. 3, p. 305–307
- Lukatkin A. S., Geras'kina A. V. Screening for the improved cold resistance of the cucumber cell cultures // *Biotechnology in Russia*. – 2003, No. 3, p. 64–72
- Lukatkin A. S., Isaikina E. E. Calcium status and chilling injury in maize seedlings // *Russian Journal of Plant Physiology*. – 1997, vol. 44, No. 3, p. 339–342
- Lukatkin A. S., Levina T. E. Effect of exogenous modifiers of lipid peroxidation on chilling injury in cucumber leaves // *Russian Journal of Plant Physiology*. – 1997, vol. 44, No. 3, p. 343–348
- Lukatkin A. S., Sharkaeva E. Sh., Zauralov O. A. Exosmosis of electrolytes from maize leaves under chilling stresses // *Russian Journal of Plant Physiology*. – 1993, vol. 40, No. 5, p. 770–775
- Lukatkin A. S., Sharkaeva E. Sh., Zauralov O. A. Lipid peroxidation in the leaves of heat-loving plants as dependent on the duration of cold stress // *Russian Journal of Plant Physiology*. – 1995, vol. 42, No. 4, p. 538–542
- Lukatkin A. S., Zauralov O. A. Exogenous growth regulators as a means of increasing the cold resistance of chilling-sensitive plants // *Russian Agricultural Sciences*. – 2009, vol. 35, No. 6, p. 384–386
- Lurie S., Ronen R., Lipsker Z., 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*. – 1994, vol. 91, No. 4, p. 593–598
- Lyons J. M. Chilling injury in plants // *Annual Review of Plant Biology*. – 1973, vol. 24, p. 445–466
- Lyons J. M., Raison J. K., Steponkus P. L. The plant membrane in response to low temperature: an overview // *Low temperature stress in crop plants: the role of the membrane*. – New York, USA, 1979, p. 1–24
- Mahajan S., Tuteja N. Cold, salinity and drought stresses: an overview // *Archives of Biochemistry and Biophysics*. – 2005, vol. 444, p. 139–158
- Mandrich M. E., Saltveit M. E. Effect of chilling, heat shock, and vigor on the growth of cucumber (*Cucumis sativus*) radicles // *Physiologia Plantarum*. – 2000, vol. 109, No. 2, p. 137–142
- Marangoni A. G., Butuner Z., Smith J. L., Stanley D. W. Physical and biochemical changes in the microsomal membranes of tomato fruit associated with acclimation to chilling // *Journal of Plant Physiology*. – 1990, vol. 135, No. 6, p. 653–661
- Markowski A. Sensitivity of different species of field crops to chilling temperature. II. Germination, growth and injuries of seedlings // *Acta Physiologiae Plantarum*. – 1988, vol. 10, No. 3, p. 275–283
- Markowski A., Augustyniak G., Janowiak F. Sensitivity of different species of field crops to chilling temperature. III. ATP content and electrolyte leakage from seedlings leaves // *Acta Physiologiae Plantarum*. – 1990, vol. 12, No. 2, p. 167–173
- Matsuo T., Graham D., Patterson B. D., Hockley D. B. An electrophoretic method to detect cold-induced dissociation of proteins in crude extracts of higher plants // *Analytical Biochemistry*. – 1994, vol. 223, No. 2, p. 181–184
- McMahon M. J., Permit A. J., Arnold J. E. Effects of chilling on *Episcia* and *Dieffenbachia* // *Journal of the American Society for Horticultural Science*. – 1994, vol. 119, No. 1, p. 80–83
- Mercado J. A., Reid M. S., Valpuesta V., Quesada M. A. Metabolic changes and susceptibility to chilling stress in *Capsicum annuum* plants grown at suboptimal temperature // *Australian Journal of Plant Physiology*. – 1997, vol. 24, No. 6, p. 759–767
- Michaeli R., Riov J., Philosophhadass S., Meir S. Chilling-induced leaf abscission of *Ixora coccinea* plants. II. Alteration of auxin economy by oxidative stress // *Physiologia Plantarum*. – 1999, vol. 107, No. 2, p. 174–180
- Minorsky P. V. A heuristic hypothesis of chilling injury in plants: a role for calcium as the primary physiological transducer of injury // *Plant, Cell and Environment*. – 1985, vol. 8, p. 75–94
- Mitchell D. E., Madore M. A. Patterns of assimilate production and translocation in muskmelon (*Cucumis melo* L.). 2. Low-temperature effects // *Plant Physiology*. – 1992, vol. 99, No. 3, p. 966–971
- Munro K. D., Hodges D. M., DeLong J. M., Forney C. F., 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*. – 2004, vol. 121, No. 3, p. 488–497
- Murata N., Tasaka Y. Glycerol-3-phosphate acyltransferase in plants // *Biochimica et Biophysica Acta*. – 1997, vol. 1348, No. 1–2, p. 10–16
- Nie G. Y., Long S. P., Baker N. R. The effects of development at sub-optimal growth temperatures on photosynthetic capacity and susceptibility to chilling-dependent photoinhibition in *Zea mays* // *Physiologia Plantarum*. – 1992, vol. 85, No. 3, p. 554–560
- Nishida I., Murata N. Chilling sensitivity in plants and cyanobacteria. The crucial contribution of membrane lipids // *Annual Review of Plant Physiology and Plant Molecular Biology*. – 1996, vol. 47, p. 541–568
- Noh S. A., Park S. H., Huh G. H., Paek K. H., Shin J. S., Bae J. M. Growth retardation and differential regulation of expansin genes in chilling-stressed sweetpotato // *Plant Biotechnology Report*. – 2009, vol. 3, p. 75–85
- Oktem H. A., Eyidogan F., Selcuk F., Oz M. T., da Silva J. A. T., Yucel M. Revealing response of plants to biotic and abiotic stresses with microarray technology // *Genes, Genomes and Genomics*. – 2008, p. 15–48

- Ordentlich A., Linzer R. A., Raskin I. Alternative respiration and heat evolution in plants // *Plant Physiology*. – 1991, vol. 97, No. 4, p. 1545–1550
- Pardossi A., Vernieri P., Tognoni F. Involvement of abscisic acid in regulating water status in *Phaseolus vulgaris* L. during chilling // *Plant Physiology*. – 1992, vol. 100, No. 3, p. 1243–1250
- Pareek A., Singla S. L., Grover A. Proteins alterations associated with salinity, desiccation, high and low-temperature stresses and abscisic acid application in seedlings of Pusa 169, a high-yielding rice (*Oryza sativa* L.) cultivar // *Current Science*. – 1997, vol. 75, No. 10, p. 1023–1035
- Patterson B. D., Paull R., Graham D. Adaptation to chilling: survival, germination, respiration and protoplasmic dynamics // *Low temperature stress in crop plants: the role of the membrane*. – New York, USA, 1979, p. 25–35
- Platt-Aloia K. A., Thomson W. W. Freeze-fracture evidence for lateral phase separation in the plasmalemma of chilling-injured avocado fruit // *Protoplasma*. – 1987, vol. 136, No. 2–3, p. 71–80
- Prasad T. K., Anderson M. D., Martin B. A., Stewart C. R. Evidence for chilling-induced oxidative stress in maize seedlings and a regulatory role for hydrogen peroxide // *Plant Cell*. – 1994 (a), vol. 6, p. 65–74
- Prasad T. K., Anderson M. D., Stewart C. R. Acclimation, hydrogen-peroxide, and abscisic acid protect mitochondria against irreversible chilling injury in maize seedlings // *Plant Physiology*. – 1994 (b), vol. 105, No. 2, p. 619–627
- Price A. H., Taylor A., Ripley S. J., Griffiths A., Trewavas A. J., Knight M. R. Oxidative signals in tobacco increase cytosolic calcium // *Plant Cell*. – 1994, vol. 6, p. 1301–1310
- Provart N. J., Gil P., Chen W., Han B., Chang H. S., Wang X., Zhu T. Gene expression phenotypes of *Arabidopsis* associated with sensitivity to low temperatures // *Plant Physiology*. – 2003, vol. 132, p. 893–906
- Purvis A. C., Shewfelt R. L. Does the alternative pathway ameliorate chilling injury in sensitive plant tissues? // *Physiologia Plantarum*. – 1993, vol. 88, No. 4, p. 712–718
- Quinn P. J. Effect of temperature on cell membranes // *Plants and Temperature: Symposium of Society for Experimental Biology*. – Cambridge, UK, 1988, p. 237–258
- Rab A., Saltveit M. E. Differential chilling sensitivity in cucumber (*Cucumis sativus*) seedlings // *Physiologia Plantarum*. – 1996 (a), vol. 96, No. 3, p. 375–382
- Rab A., Saltveit M. E. Sensitivity of seedling radicles to chilling and heat shock-induced chilling tolerance // *Journal of the American Society for Horticultural Science*. – 1996 (b), vol. 121, No. 4, p. 711–715
- Raison J. K., Lyons J. M. Chilling injury: a plea for uniform terminology // *Plant, Cell and Environment*. – 1986, vol. 9, p. 685–686
- Raison J. K., Lyons J. M., Thompson W. W. The influence of membranes on the temperature-induced changes in the kinetics of some respiratory enzymes of mitochondria // *Archives of Biochemistry and Biophysics*. – 1971, vol. 142, p. 83–90
- Reyes L., 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*. – 1997, vol. 122, No. 2, p. 190–194
- Ribascarbo M., Aroca R., Gonzalez-Meler M. A., Irigoyen J. J., Sanchezdiaz M. The electron partitioning between the cytochrome and alternative respiratory pathways during chilling recovery in 2 cultivars of maize differing in chilling sensitivity // *Plant Physiology*. – 2000, vol. 122, No. 1, p. 199–204
- Routaboult J. M., Fisher S. F., Browse J. Trienoic fatty acids are required to maintain chloroplast function at low temperatures // *Plant Physiology*. – 2000, vol. 124, No. 4, p. 1697–1705
- 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*. – 2007, vol. 143, No. 3, p. 1429–1438
- Sabehat A., Lurie S., We N. D. Expression of small heat-shock proteins at low-temperatures. A possible role in protecting against chilling injuries // *Plant Physiology*. – 1998, vol. 117, No. 2, p. 651–658
- Sharom M., Willemot C., Thompson J. E. Chilling injury induces lipid phase changes in membranes of tomato fruit // *Plant Physiology*. – 1994, vol. 105, No. 1, p. 305–308
- Shen W., Nada K., Tachibana S. Involvement of polyamines in the chilling tolerance of cucumber cultivars // *Plant Physiology*. – 2000, vol. 124, No. 1, p. 431–439
- Skog L. J. Chilling injury of horticultural crops. Ontario Ministry of Agriculture, Food and Rural Affairs Factsheet. – 1998. <<http://www.omafra.gov.on.ca/english/crops/facts/98-021.htm>>[accessed 11 05 2011]
- Skrudlik G., Koscielniak J. Effects of low-temperature treatment at seedling stage on soybean growth, development and final yield // *Journal of Agronomy and Crop Science*. – 1996, vol. 176, No. 2, p. 111–117
- Skrudlik G., Baczek-Kwinta R., 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*. – 2000, vol. 184, No. 4, p. 233–240
- Sonoike K. Photoinhibition of photosystem I – its physiological significance in the chilling sensitivity of plants // *Plant and Cell Physiology*. – 1996, vol. 37, No. 3, p. 239–247
- Sonoike K. The different roles of chilling temperatures in the photoinhibition of photosystem I and photosystem II // *Journal of Photochemistry and Photobiology B: Biology*. – 1999, vol. 48, No. 2–3, p. 136–141
- 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*. – 1998, vol. 111, No. 1101, p. 121–129
- Steward C. R., Martin B. A., Reding L., Cerwick S. Respiration and alternative oxidase in corn seedling tissues during germination at different temperatures // *Plant Physiology*. – 1990, p. 92, No. 3, p. 755–760
- Strauss A. J., Kruger G. H. J., Strasser R. J., 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*. – 2007, vol. 131, No. 1, p. 89–105
- Su Ch.-F., Wang Y.-Ch., Hsieh T.-H., Lu Ch.-A., Tseng T.-H., Yu S.-M. A novel MYBS3-dependent pathway confers cold tolerance in rice // *Plant Physiology*. – 2010, vol. 153, No. 4, p. 145–158
- Suzuki N., Mittler R. Reactive oxygen species and temperature stresses: a delicate balance between signaling and destruction // *Physiologia Plantarum*. – 2006, vol. 126, No. 1, p. 45–51
- Szalai G., Janda T., Bartok T., Paldi E. Role of light in changes in free amino-acid and polyamine contents at chilling temperature in maize (*Zea mays*) // *Physiologia Plantarum*. – 1997, vol. 101, No. 2, p. 434–438
- Takeda Y., Ogawa T., Nakamura Y., Kasamo K., Sakata M., Ohta E. <sup>31</sup>P-NMR study of the physiological conditions in intact root cells of mung bean seedlings under low temperature stress // *Plant and Cell Physiology*. – 1995, vol. 36, No. 5, p. 865–871
- Tao Z., Zou Q., Cheng B. Effect of low temperature during imbibition on ultrastructure in hypocotyls // *Acta Botanica Sinica*. – 1991, vol. 33, No. 7, p. 511–515
- Terashima I., Noguchi K., Itohnemoto T., Park Y. M., Kubo A., Tanaka K. The cause of PSI photoinhibition at low temperatures in leaves of *Cucumis sativus*, a chilling-sensitive plant // *Physiologia Plantarum*. – 1998, vol. 103, No. 3, p. 295–303
- Terzaghi W. B., Fork D. C., Berry J. A., Field C. B. Low and high temperature limits to PS II. A survey using transpirinamic acid, delayed light emission and F<sub>0</sub> chlorophyll fluorescence // *Plant Physiology*. – 1989, vol. 91, No. 4, p. 1494–1500
- Thompson G. A. Molecular changes in membrane lipids during cold stress // *Environmental Stress in Plants: Biochemical and Physiological Mechanisms / NATO ASI series. Series G, Ecological Sciences*. – Berlin, Germany, 1989, vol. 19, p. 249–257
- Ting C. S., Owles T. G., Wolfe D. W. Seedling growth and chilling stress effect on photosynthesis in chilling-sensitive and chilling-

- tolerant cultivars of *Zea mays* // Journal of Plant Physiology. – 1991, vol. 137, No. 5, p. 559–564
- Tsuda H., Niimura Y., Katoh T. Chill injury in Saintpaulia leaf with special reference to leaf spot formation // Journal of Agricultural Science. – Tokyo Nogyo Daigaku. – 2003, vol. 47, No. 4, p. 283–289
- 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. – 2003, vol. 26, No. 2, p. 323–337
- 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. – 2000, vol. 85, No. 6, p. 799–807
- Venema J. H., Posthumus F., de Vries M., 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. – 1999, vol. 105, No. 1, p. 81–88
- Ventura Y., 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. – 1999, vol. 74, No. 5, p. 602–607
- Vernieri P., Pardossi A., Tognoni F. Influence of chilling and drought on water relations and abscisic acid accumulation in bean // Australian Journal of Plant Physiology. – 1991, vol. 18, No. 1, p. 25–35
- Wang C. Y. Approaches to reduce chilling injury of fruit and vegetables // Horticulture Review. – 1993, vol. 15, p. 63–95
- Wang C. Y. Physiological and biochemical responses of plants to chilling stress // HortScience. – 1982, vol. 17, No. 2, p. 173–186
- Wang C. Y. Temperature preconditioning affects glutathione content and glutathione reductase activity in chilled zucchini squash // Journal of Plant Physiology. – 1995, vol. 145, No. 1–2, p. 148–152
- Wang C. Y., Kramer G. F., Whitaker B. D., Lusby W. R. Temperature preconditioning increases tolerance to chilling injury and alters lipid composition in zucchini squash // Journal of Plant Physiology. – 1992, vol. 140, No. 2, p. 229–235
- Wang C., Ma X. L., Hui Z., Wang W. Glycine betaine improves thylakoid membrane function of tobacco leaves under low-temperature stress // Photosynthetica. – 2008 (b), vol. 46, No. 3, p. 400–409
- Wang N., Fang W., Han H., Sui N., Li B., Meng Q. W. Overexpression of zeaxanthin epoxidase gene enhances the sensitivity of tomato PSII photoinhibition to high light and chilling stress // Physiologia Plantarum. – 2008 (a), vol. 132, No. 3, p. 384–396
- Whitaker B. D. Lipid changes in microsomes and crude plastid fractions during storage of tomato fruits at chilling and non-chilling temperatures // Phytochemistry. – 1993, vol. 32, No. 2, p. 265–271
- Wilkinson S., Clephan A. L., 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. – 2001, vol. 126, No. 4, p. 1566–1578
- Wilson J. M. Leaf respiration and ATP levels at chilling temperatures // New Phytologist. – 1978, vol. 80, No. 2, p. 325–334
- Wilson J. M. The economic importance of chilling injury // Outlook on Agriculture. – 1985, vol. 14, p. 197–204
- 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. – 1991, vol. 67, No. 3, p. 205–212
- Wolk W. D., Herner R. C. Chilling injury of germinating seeds and seedlings // HortScience. – 1982, vol. 17, No. 2, p. 169–173
- Woods C. M., Polito V. S., Reid M. S. Response to chilling stress in plant cells. II. Redistribution of intracellular calcium // Protoplasma. – 1984 (a), vol. 121, No. 1, p. 17–24
- Woods C. M., Reid M. S., Patterson B. D. Response to chilling stress in plant cells. I. Changes in cyclosis and cytoplasmic structure // Protoplasma. – 1984 (b), vol. 121, No. 1, p. 8–16
- Xu C. C., Lin R. C., Li L. B., Kuang T. Y. Increase in resistance to low temperature photoinhibition following ascorbate feeding is attributable to an enhanced xanthophyll cycle activity in rice (*Oryza sativa* L.) leaves // Photosynthetica. – 2000, vol. 38, No. 2, p. 221–226
- Yadegari L. Z., Heidari R., Carapetian J. Chilling pretreatment causes some changes in respiration, membrane permeability and some other factors in soybean seedlings // Research Journal of Biological Sciences. – 2008, vol. 3, No. 9, p. 1054–1059
- Yamagitchi-Shinozaki K., Shinozaki K. Transcriptional regulatory networks in cellular response and tolerance to dehydration and cold stresses // Annual Review of Plant Biology. – 2006, vol. 57, p. 781–803
- Yamori W., Noguchi K., Hikosaka K., Terashima I. Cold-tolerant crop species have greater temperature homeostasis of leaf respiration and photosynthesis than cold-sensitive species // Plant and Cell Physiology. – 2009, vol. 50, No. 2, p. 203–215
- Yin G., Sun H., Xin X., Qin G., Liang Z., Jing X. Mitochondrial damage in the soybean seed axis during imbibition at chilling temperatures // Plant and Cell Physiology. – 2009, vol. 50, iss. 7, p. 1305–1318
- Yordanov I. Response of photosynthetic apparatus to temperature stress and molecular mechanisms of its adaptations // Photosynthetica. – 1992, vol. 26, No. 4, p. 517–531
- Yoshida R., Kanno A., Sato T., Kareya T. Cool temperature-induced chlorosis in rice plants. I. Relationship between the induction and a disturbance of etioplast development // Plant Physiology. – 1996, vol. 110, No. 3, p. 997–1005
- Yoshida S. Low temperature-induced cytoplasmic acidosis in cultured mung bean (*Vigna radiata* L. Wilczek) cells // Plant Physiology. – 1994, vol. 104, No. 4, p. 1131–1138
- Yoshida S., Matsuura C., Etani S. Impairment of tonoplast H<sup>+</sup>-ATPase as an initial physiological response of cells to chilling in mung bean (*Vigna radiata* L. Wilczek) // Plant Physiology. – 1989, vol. 89, No. 2, p. 634–642
- Zauralov O. A., Lukatkin A. S. Aftereffect of low temperatures on the respiration of heat-loving plants // Russian Journal of Plant Physiology. – 1997, vol. 44, No. 5, p. 640–644
- Zauralov O. A., Lukatkin A. S., Sharkaeva E. Sh. Intracellular pH of maize leaf tissues upon different degrees of chilling // Biology Bulletin. – 1997, vol. 24, No. 1, p. 82–84
- Zavala E. M., Lin C. L. Anatomical and polypeptide alterations in corn root tips in response to cold stress // American Journal of Botany. – 1989, vol. 76, No. 1 (suppl.), p. 71–72
- Zemetra R. S., Cuany R. L. Variation among inbreds for seed response to low temperatures in maize (*Zea mays* L.) // Maydica. – 1991, vol. 36, No. 1, p. 17–23
- Zhang J. X., Cui S. P., Li J. M., Wei J. K., Kirkham M. B. Protoplasmic factors, antioxidant responses, and chilling resistance in maize // Plant Physiology and Biochemistry. – 1995, vol. 33, No. 5, p. 567–575
- Zhu S.-Q., Zhao H., Liang J.-S., Ji B.-H., 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. – 2008, vol. 50, No. 2, p. 194–202
- Zia M. S., Salim M., Aslam M., Gill M. A., Rahmatullah. Effect of low temperature of irrigation water on rice growth and nutrient uptake // The Journal of Agricultural Science. – 1994, vol. 173, No. 1, p. 22–31
- Zocchi G., Hanson J. B. Calcium influx into corn roots as a result of cold shock // Plant Physiology. – 1982, vol. 70, p. 318–319
- Волкова П. И., Титов А. Ф., Таланова В. В., Дроздов С. Н. Изменения в системе ауксинов в начальный период теплового и холодного закаливания вегетирующих растений // Физиология растений. – 1991, т. 38, № 3, с. 538–544 (in Russian)
- Володько Н. К. Микроэлементы и устойчивость растений к неблагоприятным факторам среды. – Минск, 1983, 192 с. (in Russian)
- Генкель П. А., Кушниренко С. В. Холодостойкость растений и термические способы ее повышения. – Москва, 1966, 223 с. (in Russian)

- Дроздов С. Н., Сычева В. Ф., Будыкина Н. П., Курец В. К. Эколого-физиологические аспекты устойчивости растений к заморозкам. – Ленинград, 1977, 228 с. (in Russian)
- Жолкевич В. Н. К вопросу о причинах гибели растений при низких положительных температурах // Тр. ин-та физиологии растений им. К. А. Тимирязева АН СССР. – 1955, т. 9, с. 3–28 (in Russian)
- Зауралов О. А. Влияние охлаждения проростков огурца на последующий рост и интенсивность фотосинтеза // Физиология и биохимия культурных растений. – 1993, т. 25, № 4, с. 380–387 (in Russian)
- Зауралов О. А., Курова Е. А., Лукаткин А. С. Влияние цитокининовых препаратов и охлаждения на ростовые реакции растений кукурузы // Агробиология. – 2000, № 3, с. 55–59 (in Russian)
- Зауралов О. А., Лукаткин А. С. Влияние экзогенных аналогов фитогормонов на холодоустойчивость теплолюбивых растений // Агробиология. – 1996, № 1, с. 109–119 (in Russian)
- Коровин А. И. Об отношении растений к низким положительным температурам и заморозкам и пути повышения ее холодо- и заморозкоустойчивости // Устойчивость растений к низким положительным температурам и заморозкам и пути ее повышения. – Москва, 1969, с. 5–15 (in Russian)
- Лукаткин А. С. Окислительный стресс и холодное повреждение растений. – Саранск, 2002, 208 с. (in Russian)
- Лукаткин А. С., Грищенко Н. Н., Мартынова Л. П. К вопросу об акклимации проростков кукурузы к пониженной положительной температуре выращивания // Сельскохозяйственная биология. – 2006, № 1, с. 86–91 (in Russian)
- Лукаткин А. С., Дерябин А. Н. Повышение стрессоустойчивости растений с использованием клеточных технологий *in vitro* // Аграрная наука. – 2009, № 2, с. 15–17 (in Russian)
- Лукаткин А. С., Еремкина Т. Н. Активность  $Ca^{2+}$ -АТФазы в листьях растений кукурузы под влиянием охлаждения и в последствии // Сельскохозяйственная биология. – 2002, № 3, с. 73–76 (in Russian)
- Лукаткин А. С., Кобылина И. В., Духовскис П., Сакалаускайте Ю., Баранаускас К. Влияние пониженных температур на выход протонов из клеток листьев кукурузы // Физиология и биохимия культурных растений. – 2007, т. 39, № 6, с. 476–487 (in Russian)
- Лукаткин А. С., Овчинникова О. В. Влияние препарата цитодефа на рост и холодоустойчивость теплолюбивых растений // Агробиология. – 2009, № 12, с. 32–38 (in Russian)
- Лукаткин А. С., Шаркаева Э. Ш., Апарин С. В. Ростовые реакции клеток конуса нарастания теплолюбивых растений при действии и последствии пониженных температур // Физиология и биохимия культурных растений. – 2010, т. 42, № 3, с. 256–269 (in Russian)
- Попов В. Н., Антипина О. В., Трунова Т. И. Перекисное окисление липидов при низкотемпературной адаптации листьев и корней теплолюбивых растений табака // Физиология растений. – 2010, т. 57, № 1, с. 153–156 (in Russian)
- Таланова В. В., Титов А. Ф., Боева Н. П. Изменение уровня эндогенной абсцизовой кислоты в листьях растений под влиянием холодовой и тепловой закалки // Физиология растений. – 1991, т. 38, № 5, с. 991–997 (in Russian)
- Титов А. Ф., Шерудило Е. Г. Степень подавления процессов тепловой и холодовой адаптации растений ингибиторами синтеза РНК и белка при разных закалывающих температурах // Физиология и биохимия культурных растений. – 1990, т. 22, № 4, с. 384–388 (in Russian)

ISSN 1392-3196

Žemdirbystė=Agriculture, vol. 99, No. 2 (2012), p. 111–124

UDK 634.1:581.17:576.3

## Žemų temperatūrų poveikis jautriems augalams: apžvalga

A. S. Lukatkin<sup>1</sup>, A. Brazaitytė<sup>2</sup>, Č. Bobinas<sup>2</sup>, P. Duchovskis<sup>2</sup>

<sup>1</sup>Mordovijos valstybinis universitetas, Rusija

<sup>2</sup>Lietuvos agrarinių ir miškų mokslų centro Sodininkystės ir daržininkystės institutas

### Santrauka

Žemos teigiamos (1–10° C) temperatūros sąlygoja daugybę fiziologinių sutrikimų tokioms temperatūroms jautrių augalų ląstelėse, o tai lemia tropinių ir subtropinių augalų, pavyzdžiui, daugelio daržovių, žūtį. Literatūros apžvalga parodė, kad šilumamėgių augalų laikymas žemų teigiamų temperatūrų sąlygomis nulemia visų fiziologinių procesų (vandens režimo, mineralinės mitybos, fotosintezės, kvėpavimo, medžiagų apykaitos) pažeidimus. Šilumamėgių augalų medžiagų apykaitos inaktyvacija, nustatyta žemų temperatūrų sąlygomis, priklauso ir nuo temperatūros, ir nuo jos trukmės. Augalų atsakas į žemų teigiamų temperatūrų poveikį yra susijęs su keletu mažos molekulinės masės baltymų genų transkripcijos greičiu.

Apžvalgoje analizuojami žemų temperatūrų pažeidimų sampratos kaitos istoriniai aspektai ir šiuolaikinių tyrimų kryptys. Remiantis autorių tyrimais ir literatūros duomenimis, pasiūlyta žemų teigiamų temperatūrų pažeidimų koncepcija, pagal kurią didžiausia reikšmė tenka oksidaciniam stresui kaip stresinės reakcijos sukėlėjui. Pagal šią koncepciją pasiūlyti keli būdai, kaip padidinti žemų temperatūrų toleranciją. Jie suskirstyti į kelias grupes: terminis poveikis (grūdinimas žemomis temperatūromis, temperatūrinis kondicionavimas, tarpinis atšildymas, šilumos streso poveikis), cheminis apdorojimas (mikroelementais, sintetiniai augimo reguliatoriais, antioksidantais) ir genų bei ląstelių inžinerijos panaudojimas.

Reikšminiai žodžiai: antioksidantai, fiziologiniai procesai, ląstelės, oksidacinis stresas, žemoms teigiamoms temperatūroms jautrūs augalai.