

Metabolic Changes in Plants under Chilling Stress

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Abstract

Stress, causes environmental and biological factors to undergo significant changes in physiological events that occur in plants. Various studies have also shown that the temperature factor is one of the most important factors affecting the metabolism of plants. Chilling stress begins as the temperature falls below the values required for plant growth. Each plant species has its own degree of chilling. In other words, it is the temperature at which the metabolic activity decreases. In plant changes, this change varies according to the degree of chilling. As a result of the formation of oxygen radicals, which cause harm to plant metabolism and break down, due to the stress that occur in plants exposed to cold. The defense system is activated due to the genetic structure of the plant species and variety and the antioxidative enzyme activities in this defense system play an important role.

In this study, the metabolic effects of chilling stress on plants and the defense mechanism that plants developed against cold were investigated.

Keywords; Stress, cold, plant, temperature, antioxidative enzyme activities

Üşüme Stresi Altındaki Bitkilerde Meydana Gelen Metabolik Değişimler

Özet

Stres, çevresel ve biyolojik faktörlerin bitkide gerçekleşen fizyolojik olaylarda belirgin derecede değişimler meydana getirmesidir. Yapılan çeşitli çalışmalar da göstermiştir ki özellikle sıcaklık faktörü bitkilerin metabolizmasını etkileyen en önemli faktörlerden biridir. Sıcaklık değerlerinin bitki gelişimi için gerekli olan değerlerin altına düşmesiyle bitkide üşüme stresi başlar. Her bitki türünün kendine özgü üşüme derecesi, yani metabolik aktivitesinin durduğu bir sıcaklık değeri vardır ve bitki de görülen değişimlerde bu üşüme derecesine göre farklılıklar göstermektedir. Üşümeye maruz kalan bitkilerde oluşan stresten dolayı bitki metabolizmasına zarar veren ve yıkıma uğratan oksijen radikallerinin oluşumu sonucunda bitki tür ve çeşidinin genetik yapısına bağlı olarak savunma sistemini harekete geçirir ve bu savunma sistemi içerisinde bulunan antioksidatif enzim aktiviteleri önemli rol üstlenmektedir.

Bu çalışmada üşüme stresinin bitkiler üzerine metabolik etkileri ve bitkilerin üşümeye karşı geliştirdikleri savunma mekanizması araştırılmıştır.

Anahtar kelimeler; Stres, üşüme, bitki, sıcaklık, antioksidatif enzim aktiviteleri

Introduction

Stress in crop production; one or more of the factors can be defined as affecting the plant environmentally, resulting in slow growth and low productivity. Factors causing plants stress; besides being able to be biotic origin such as disease-causing and harmful ones; salinity, drought, low and high temperatures, lack of nutrients or abundance of the elements may be of abiotic origin. Exposure of plants to these stress factors prevents them from achieving their genetic potential and limits productivity (Yasar 2003). Abiotic stresses, which are the main cause of inferiority in the world, reduce the average yield of important products by 50% or more (Bray et al., 2000, Wang et al., 2004). Cold, which limit the quantity and quality of crops, especially in tropical and semi-tropical regions (Wilson, 1985; Raison and Lyons, 1986; Yang et al., 2005). When the available agricultural areas in the world are classified according to stress factors, drought stress, which is a natural stress factor, contains the largest slice with a share of 26%. This is followed by mineral stress (20%) and cold (15%) stress. While all other stresses account for 29%, only a 10% area is not exposed to any stress factor (Blum, 1986). In this case, chill stress is one of the most common environmental stresses affecting growth and efficiency, inducing many physiological, biochemical, and molecular responses in plants, and consequently decreasing the damage caused by cold by developing tolerance mechanisms that allow plants to adapt to limited environmental conditions (Thomashow, 1999). Accumulated data on how plants respond to biotic and abiotic stress and how stress affects their development in the plant life cycle has led to the development of new approaches to cold stress (Thomashow, 1999; Wasternack, 2007). For this reason, it is very important to clarify the physiological and biochemical mechanisms that provide tolerance and adaptation to the cold in plants, to increase crop yield and to develop cold tolerant plants.

For these reasons, the effects of chilling stress on the plants have been investigated by detailed screening of recent studies on cold stress. In addition, important studies to clarify the mechanisms of response and adaptation of plants to chilling have been taken as a reference, and the literature in this subject is intended to be updated.

Chills Stress and Genetic Factors

Chill stress is an environmental stress factor that plants most commonly encounter during the first period of development, especially germination and shoot-out. The period in which the plants are affected is not only the period of exile that they first started to develop, but they are also influenced by the progressive stages of development at the same time. In the case of low temperatures, damage occurs at different rates depending on the species, age and genetic makeup of the plant (Dodds and Ludford, 1990; Saltveit and Morris, 1990). Chills can cause negative consequences, such as saltiness and drought in other stress factors, that affect the flowering period, the direct planting of the plant in the fruit context and seed formation, and the continuation of the plant growth (Mock and Eberhart, 1972; Mahajan and Tuteja, 2005). Plants in genetic variation also exhibit different responses to plasma membrane function and physiological events such as photosynthesis as well as to seedling, shoot and development activities against cold (Rab and Saltveit, 1996). From here it is necessary to find and develop those tolerant to genetic resources against stress factors, such as chills, even at the sensitive species level. Mock and Eberhart (1972) found corn germplasms, Patterson and Payne (1983) found cold-tolerant types of tomato germplasms. Toğay et al. (2017), they found that the lines tolerated to cold were not changed compared to the control plants and that they were not affected by low temperatures and increased enzyme activities of the same genotypes. Yaşar et al. (2017) In their study of cold stressing different genotypes of beans, some genotypes were more affected than others, while others were less affected and plant development was better.

Perpeption of Low Temperature Signal

Any environmental stress response of the plants occurs through a series of reactions called signal transduction. Low-temperature signaling probably begins with the detection of the cold signal by the receptor located in the cell membrane. This sensor protein tends to find physical phase transitions in the microdomains of the cell membrane as a consequence of temperature change (Murata and Los, 1997). Cold stress induced by cell membrane, can cause solidification of microdomains reorganization of the actin cytoskeleton. It is followed by the activation of Ca + 2 channels, the increase of cytosolic Ca + 2 level and the triggering of the cold-regulated expression of COR genes (Woods et al., 1984; Orvar et al., 2000; Chinnusamy et al., 2006). n addition, receptor protein kinases may play a role as cold receptors (Heino and Palva, 2003). In stress transmission, membrane phospholipids form important stress-transfer molecules such as inositol-1,4,5-triphosphate (IP3), phosphatidic acid (PA) and diacylglycerol (DAG). These molecules are involved in the opening of the Ca + 2 channels in the tonoplast (Kacperska, 2004). Abscisic acid (ABA) is an important plant hormone that plays a critical role in response to various stress

signals and is induced together with stress. ABA and calcium in the cold plant cell (Mahajan and Tuteja, 2005).

Mechanism consisting of chills Stress

Symptoms of cold damage occurring in plants; (Saltveit and Morris, 1990), depending on the temperature, the duration of exposure to cold, the genotype, the developmental stage of the plant, the tissue in contact with the cold, wind, water, nutrients and light. In general, these indications are; reduction of plant growth rate, decrease of leaf width, increase of cellular autolysis and aging, programmed cell death, chlorosis formation due to photooxidation-resultant chlorophyll loss, deterioration of cell membrane structures and consequent deterioration of cellular integrity, protoplasmic flow to minimum level and necrosis Mahajan and Tuteja, 2005; Bertamini et al., 2007; Rymen et al., 2007; Toğay et al., 2017; Yaşar et al. Some researchers have reported that photosynthesis is the first event to be affected in plants, although the mechanisms by which the plants are affected by cold stress are not fully known Wang, (1993); Boese et al. (1997); The negative effect of low temperature on photosynthesis depends on the light intensity. Its importance is also revealed by the degree of damage to the mechanism. When high light intensity chills with simultaneously tested, photosystem II (PS II) saw severe damage and stress in this way, photosynthesis leads to inhibition of non-recycled (Gesch and Heilman, 1996; Terashima et al., 1998; Kingston-Smith et al., 1999; Allen et al., 2002; Van Heerden et al., 2003; Taiz and Zaiger 2006; Garstka et al., 2007).

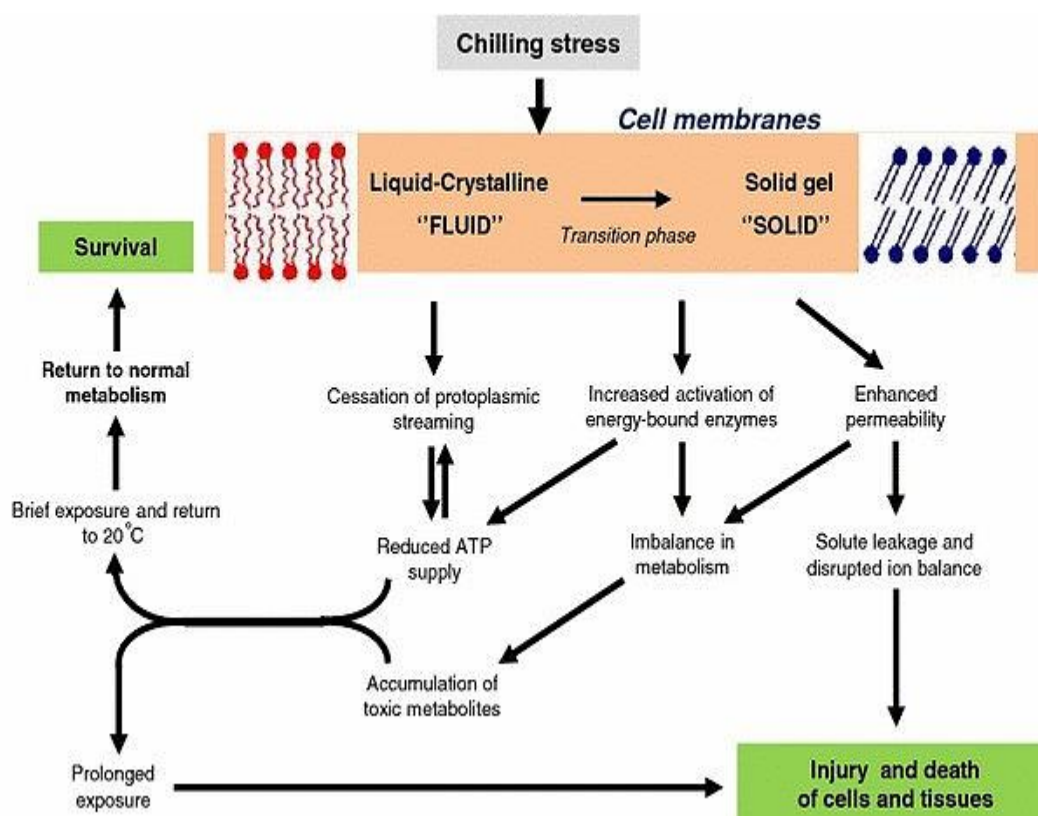


Figure 1. Schematic of the formation mechanism of cold stress (Theocharis ve ark. 2012)

Chilling stress, unlike other stress factors, each molecule in each cell of a plant exhibits a large, instantaneous and synchronous change in the thermodynamic micro-climate (Kratsch and Wise, 2000). In order for each plant to exhibit normal growth and development, a certain optimum temperature grade is required. Changes in the metabolism of plants due to temperature drops in the vegetation during the vegetation period are perceived as cold stress. In addition, while certain temperature conditions are optimal for a plant, it can cause stress for the other plant (Mahajan and Tuteja, 2005). Each plant species has its own degree of temperature, a temperature at which its metabolic activity stops (Mahajan and Tuteja, 2005). The key response to chilling stress, especially in susceptible plants, is the change in saturated and unsaturated fatty acid ratios present in the cell membrane at critical temperature (Graham and Patterson, 1982). Therefore, the ability of cold sensitive plants to develop tolerance to cold stress is

directly related to the ability to change the proportions of saturated and unsaturated fats. As a matter of fact, the lipid in the cell membrane begins to solidify and begin to crystallize at a critical temperature. Because the liquid mosaic-lipid cell is in the form of an extreme liquid-crystal state, the enzymes are optimally active and the permeability is under control (Mahajan and Tuteja, 2005; Bakht et al., 2006; Uemura et al., 2006; Wang et al., 2006; Togay et al., 2017). Below the critical temperature, membrane lipids become crystal-liquid, and this change in permeability increases the porosity and permeability of the membrane (Figure 1.). In this case, the intracellular solution balance is distorted and the permeation of ions and other solutes in the membranes of the damaged cells and organelles, as well as deterioration of the proton transport mechanism, are observed (Yoshida et al., 1979; Taiz and Zaiger, 2006; Toğay et al., 2017). Thus, an increase in the ratio of unsaturated fatty acids may allow the cell membrane to remain functional at lower temperatures. Because it is recyclable changes associated with cold, if the temperature increases after a short period of time, the membrane can return again into the liquid-crystal. However, if cold stress is prolonged and severe, the accumulation of metabolites in the cytoplasm increases because the negative-feedback mechanism of metabolite building is not processed. In addition, material transport through membrane systems is uncontrolled and high, and the plant can be damaged and die (Figure 1.). Although some cultivated plants have the same fatty acid ratios, their susceptibility to cold is also different due to their different sensitivity to metabolites accumulated in the cytoplasm during low temperature stress (Holobrada et al., 1981; Clarkson et al., 1988; Korkmaz and Dođamaz, 2017; Togay et al., 2017).

Cold Acclimation

The atmospheric temperatures affecting the texture of the plants affect the plant in two ways. In the first, reaction rates and activities catalyzed by enzymes that cause changes in plant metabolism. In the second, extreme temperatures cause damage to plants. The problem of maintaining viability in extreme temperature conditions depends on the persistence of the macromolecular content, the structural and functional integrity of the cells (Clarkson et al., 1988). Unlike animals, plants living in the terrestrial environment can not change places to avoid and protect from adverse environmental conditions. For this reason, plants have to develop physiological and biochemical strategies in order to survive the extreme environmental conditions. Hence plants are adaptive to adverse factors in certain processes (Steward et al., 1990; Nilsen and Orcutt, 1996). The droughts due to the high temperature and the frosts due to the low temperature are the main stress factors affecting the viability and development of the plants. Resistance to stress conditions in plants is provided in two ways. These; 1. Avoidance (ability to reduce or inhibit the existing stress factor), 2. Tolerance (ability to survive the stratus with little damage or slight damage). Many plant species in temperate climatic zones are able to resist frost damage by exposure to low temperatures that are not frost-free for a certain period of time. This complicated adaptation process is called cold acclimation or cooling resistance process. During cold acclimation, plants develop different mechanisms to protect against frost stress or tolerance. These are expressed in lipid composition, changes in enzymatic and non-enzymatic antioxidative activities, increases in sugar and amino acid contents, changes in the levels of certain proteins and gene expression (Howarth and Ougham, 1993; Burke, 1995; Thomashow, 1999). Changes in the chemical and enzymatic composition of cell membrane structures may also lead to positive or negative changes in exposure to low temperatures due to the genetic makeup of plants (Wisniewski and Basett, 2003). When plants are exposed to stress, one of their reactions at the molecular level is to increase the levels of enzymatic or non-enzymatic antioxidants. These enzymatic antioxidants, known as stress enzymes, are responsible for eliminating reactive oxygen species from tissues during and after stress. The high activity of these enzymes indicates that there is a positive correlation between the tolerance of plants to stress. These enzymatic antioxidants, known as stress enzymes, are responsible for eliminating reactive oxygen species from tissues during and after stress. The high activity of these enzymes indicates that there is a positive correlation between the tolerance of the plants to their stress factors (Yasar, 2003; Yasar et al., 2006, 2014, 2016, 2017; Korkmaz et al., 2016; Toğay et al., 2017).

Chilling Stress and Photoinhibition

Chlorophyll pigments of plants exposed to low temperatures need more photons to build up and inhibit electron transport throughout the PSII (Sfakianaki et al., 2006). The inhibition of photosynthesis by light is called "photoinhibition". This inhibition leads to the degradation of the D1 reaction center protein of PSII (Szilárd et al., 2005), which is called photodamage. Photoinhibition occurs when the light is excessive for plants. As the temperature falls, the activity of the enzymes in the Calvin cycle also decreases, resulting in a decrease in the photons used and an increase in the photoinhibition. If the high intensity of light is coincident with the cold, the damage in photosynthesis becomes much more severe

(Bertamini et al., 2005, 2007; Ohira et al., 2005). In cold processes such as CO₂ fixation, it reduces the demand for chemical energy, allowing the electrons that jump out of the photosystems to be idle. Idle and unavailable electrons are transferred from the light to oxygen, thus causing photooxidative damage in the D1 protein of the reaction center of the PSI (Bertamini et al., 2005; Ohira et al., 2005). The activity of the enzymes that will remove the activated oxygen is reduced, which is the reduction of these defense systems at low temperatures. For example, catalase has been photoinactivated at cold temperatures in cold susceptible plants (Lukatkin, 2003). This allows hydrogen peroxide to accumulate and escape to other chloroplast or cytosol sites that initiate destructive reactions of active oxygen. In addition to all this, it causes cold stomata to shut down in both light and darkness. Cold-induced stoma closure has two causes. First, direct inhibition of mesophyll photosynthesis leads internally to an increase in CO₂ and eventually to the closure of stomata. The second reason may be water stress, as the hydrolytic conductivity decreases with cold, and water uptake from the soil is significantly inhibited and the stomata can close to prevent water loss (Yang et al., 2005). The shutdown of the stomata leads to a decrease in intrinsic CO₂ and an inhibition of photosynthesis. Many environmental stresses, such as cold, disturb the balance between the absorbing light energy and the used light energy. This leads to the formation of singlet O₂, reactive oxygen species (ROT) instead of reduction of O₂ (Logan et al., 2006). It is called "photooxidative stress" when ROT comes to light. The formation of reactive oxygen species during photosynthesis is reduced most by many components and is eliminated by photooxidative stress regulatory mechanisms. ROTs are rapidly destroyed by rapid and efficient antioxidative systems (Yasar, 2003; Foyer and Noctor, 2005; Yasar et al., 2014, 2016, 2017; Toğay, 2016).

Antioxidative Defense Against Chills

Plants have developed some defense mechanisms against free oxygen radicals in stress conditions. Some of these are responses to enzymatic pathways and responses to the elimination of toxic effects, while others are associated with nonenzymatic substances and pathways. In other words, plants have antioxidants and antioxidative enzymes in various amounts, protecting them against toxic O₂ derivatives (Asada and Takahashi, 1987; Yasar, 2003). The transformation of toxic oxygen radicals into harmless forms by enzymatic means has been actively pursued by the literature, not only in plants, but also in the last few years, preventing cell destruction in all living organisms. Superoxide dismutase (SOD) (EC 1.15.1.1) is the enzyme responsible for detoxification of the superoxide radical. Gossett et al. (1994), SOD, superoxide (O₂⁻) is the most important grinder and this enzymatic activity results in the formation of H₂O₂. Enzymes of ascorbate peroxidase (APX) (EC 1.11.1.11) and glutathione reductase (EC) (EC 1.6.4.2) together play a decisive role in the detoxification of hydrogen peroxide (Cakmak et al., 1993; Cakmak, 1994). Hydrogen peroxide plays a direct role in the oxidation of thyroid-containing enzymes of the Calvin cycle and thus in the inhibition of photosynthesis (Tanaka et al., 1982). Catalase (CAT) (EC 1.11.1.6), ascorbate peroxidase (Chen and Asada, 1989) and several general peroxidases catalyze the breakdown of hydrogen peroxide. However, Asada and Takahashi (1987) report that the actual detoxification is due to a mechanism defined as the 'ascorbate-glutathione cycle' due to the weak catalase effect. Ascorbate peroxidase (APX) has played a decisive role in the detoxification of hydrogen peroxide. To accomplish this function, the ascorbate peroxidase enzyme uses ascorbic acid, and as a result, monodehydro ascorbate and water come out as products. H₂O₂ conversion system linked to ascorbate; In addition to APX, it also needs monodehydroascorbate reductase (EC 1.6.5.4), dehydroascorbate reductase (EC 1.8.5.1) and glutathione reductase (GR) enzymes (Hossain et al., 1984; Bowler et al., 1992). The cooperation of these enzymes is of great importance in removing adverse effects of harmful active oxygen. In the sequence of the reaction in which hydrogen peroxide is made harmless, first the monodehydroascorbate radicals are produced as a result of the enzymatic function of ascorbate peroxidase; they are reduced to dehydroascorbate by NADPH-linked monodehydroascorbate radical reductase. Dehydroascorbate is enzymatically reduced to ascorbate by reduction of glutathione by a non-enzymatic way and by dehydroascorbate reductase enzyme activity. Oxidized glutathione is converted to a reduced structure by the NADPH-linked glutathione reductase enzyme (Gossett et al., 1994a). Certain known substances such as ascorbic acid (ascorbate), vitamin E α -tocopherol, glutathione, β -carotene and zeaxanthin carotenoid are the major antioxidants used by plants against free oxygen radicals that appear toxic in stress conditions (Cakmak and Marschner 1992).

Conclusion

Cold stress, which occurs when the temperature falls below optimum conditions, is one of the most important environmental factors that cause loss of yields by preventing growth and development in plants. When faced with stress factors, plants struggle to survive and survive by developing many ways and responses to their genetic makeup, ecological conditions and nutritional status to protect the strut.

Thus, plants are able to adapt to the factors of the environment they live to survive through the stress responses they develop. However, if the plants are in an effort to adapt to the environment, the increase in world population and the decrease in agricultural areas and agricultural production due to cold stress pose a threat especially to human nutrition. It is thought that this threat will be diminished by researching the tolerance of the plants that are covered by basic nutrients with high nutrient content, by examining the tolerances against the cold, by identifying the cold tolerant types within the existing genetic resources and by cultivating the cold land soils that can not be cultivated.

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