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The role of antioxidant compounds in plant heat tolerance

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Abstract

Plants are sessile organisms, therefore cannot move to more favorable environments; consequently, plant growth and developmental processes are affected, often lethally by stress. High temperature or 'Heat' stress is known as major environmental stress that limits plant growth, metabolism, and productivity worldwide. Heat stress is often defined as the rise in temperature beyond a threshold level for a period of time sufficient to cause irreversible damage to plant growth and development. The increase of temperature up to a certain level increases plant growth, photosynthesis, respiration and enzyme activity and after that these parameters tend to decline. One of the ways to deal the with adverse effects of heat stress may involve exploring some molecules that have the potential to protect the plants from the harmful effects of heat stress In recent decades exogenous protectant such as osmoprotectants (proline, glycinebetaine, trehalose, etc.), plant hormone (gibberellic acids, jasmonic acids, brassinosterioids, salicylic acid, etc.), signaling molecules (nitric oxide, hydrogen peroxide, etc.), polyamines (spermidine, spermine, putrescine), trace elements (selenium, silicon, etc.) antioxidants (ascorbic acid, thiamine, glutathione, tocopherol, etc.), have been found effective in mitigating the abiotic stress induced damage in plant. Current report showed that several antioxidants compound such as ascorbic acid and thiamine perform positive effect to combat heat stress in plant is dose dependent manner.

Keywords: Antioxidant; Heat stress; Ascorbic acid; Thiamine; ROS

1. Introduction

Temperature stress is becoming the major concern for plant scientists worldwide due to the changing climate. The difficulty of climate change is further added considering its precisely projecting potential agricultural impacts [1][4]. The global air temperature is predicted to rise by 0.2°C per decade, which will lead to temperatures 1.8 – 4.0°C higher than the current level by 2100 [1][2]. Plants are sessile organisms, therefore cannot move to more favorable environments; consequently, plant growth and developmental processes are affected, often lethally by stress. High temperature or 'Heat' stress is known as a major environmental stress that limit plant growth, metabolism and productivity worldwide [2][3][4]. Heat stress is often defined as the rise in temperature beyond a threshold level for a period of time sufficient to cause irreversible damage to plant growth and development. In general, a transient elevation in temperature, usually 10–15°C above ambient, is considered heat shock or heat stress [5]. The increase of temperature up to a certain level increases plant growth, photosynthesis, respiration and enzyme activity and after that these parameters tend to decline [3]. High temperatures cause yield losses of 15 – 70% dramatically. While the trends of global polulations is increasing every decade, it's estimated global population will become 9 million at 2050. This condition lead the global food security at risk [1].

The cellular changes induced by heat stress include responses those lead to the excess accumulation of toxic compounds, especially reactive oxygen species (ROS). The end result of ROS accumulation is oxidative stress. In response to heat stress, the reaction catalyzed by ribulose-1,5-bisphosphate carboxylase oxygenase (RuBisCO) can lead to the production of H2O2 as a consequence of increases in its oxygenase reactions [[2][3][4]. Plants have evolved a variety of responses to extreme temperatures those minimize damages and ensure the maintenance of cellular

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homeostasis. A considerable amount of works have explored that there is a direct link between ROS scavenging and plant stress tolerance under temperature extremes. Thus, the improvement of temperature stress tolerance is often related to enhanced activities of enzymes involved in antioxidant systems of plants. Plants exposed to extreme temperatures use several non-enzymatic and enzymatic antioxidants to cope with the harmful effects of oxidative stress; higher activities of antioxidant defense enzymes are correlated with higher stress tolerance. Different plant studies have revealed that enhancing antioxidant defense confers stress tolerance to heat stress.

In heat stress condition, modification of physiological and biochemical processes by gene expression changes gradually leads to the development of heat tolerance in the form of acclimation, or in the ideal case, to adaptation. In recent times, exogenous applications of protectants in the form of osmoprotectants (proline, Pro; glycine betaine, GB; trehalose, Tre, *etc.*), phytohormones (abscisic acid, ABA; gibberellic acids, GA; jasmonic acids, JA; brassinosterioids, BR; salicylic acid, SA; *etc.*), signaling molecules (e.g., nitric oxide, NO), polyamines (putrescine, Put; spermidine, Spd and spermine, Spm), trace elements (selenium, Se; silicon, Si; *etc.*) antioxidants compounds (ascorbic acid, thiamine, glutathione, tocopherol, etc.), and nutrients (nitrogen, N; phosphorus, P; potassium, K, calcium, Ca; *etc.*) have been found effective in mitigating heat stress stress-induced damage in plants [3][4]. These protectants showed the capacity to enhance the plant's growth, development, photosynthesis, yield, and antioxidative capacities thus combat several number of stress.

2. Potential role of antioxidant compounds as exogenous protectants to mitigate salt, mannitol, heavy metal and paraquat stress: previous studies

Severeal researcher have reported their finding about the potential role and uses of anitioxidant compound in mitigating the abiotic stress in several important crops. Antioxidant compound could maintain dry matter yield of wheat (*Triticum aestivum L.*) under several condition of heavy metal stress. Exogenous application of 100 ppm ascorbic acid (AsA), thiamine (B1) or salicylic acid (SA) within 3 days resulted in increasing the production of dry matter yields in the shoots and roots of Cu stressed wheat plants as compared with those of untreated plants [6].

Thiamin suppresses protein oxidation and ROS accumulation in paraquat-treated Arabidopsis. Exogenous thiamin greatly decreased the amount of protein carbonylation and accumulated significantly less hydrogen peroxide in paraquat-treated plants, suggesting that thiamine increases plant tolerance to paraquat through the reduction of oxidized protein due to decreasing of ROS accumulation and subsequent oxidative damage [7]. Ascorbic acid induces antioxidant enzyme activities of germinating broad beans under NaCl and mannitol stress. Adding 4 mM ascorbic acid into NaCl or Mannitol stress condition, induced significant increases in SOD and APO activities as compared with those of control in bean seedlings [8].

3. Plant responses to heat stress

Zhao et al. [9], explained that, at very high temperatures, severe cellular injury and even cell death may occur within minutes, which could be attributed to a catastrophic collapse of cellular organization. At moderately high temperatures, injuries or death may occur only after long-term exposure. Direct injuries due to high temperatures include protein denaturation and aggregation,and increased fluidity of membrane lipids. Indirect or slower heat injuries include inactivation of enzymes in chloroplast and mitochondria, inhibition of protein synthesis, protein degradation and loss of membrane integrity.

Heat stress also affects the organization of microtubules by splitting and/or elongation of spindles, formation of microtubule asters in mitotic cells, and elongation of phragmoplast microtubules. These injuries eventually lead to starvation, inhibition of growth, reduced ion flux, production of toxic compounds and reactive oxygen species (ROS). Immediately after exposure to high temperatures and perception of signals, changes occur at the molecular level altering the expression of genes and accumulation of transcripts, thereby leading to the synthesis of stress-related proteins as a stress tolerance strategy [9][10].

Expression of heat shock proteins (HSPs) is known to be an important adaptive strategy in this regard. The HSPs, ranging in molecular mass from about 10 to 200 kDa, have chaperonelike functions and are involved in signal transduction during heat stress [19]. The tolerance conferred by HSPs results in improved physiological phenomena such as photosynthesis, assimilate partitioning, water and nutrient use efficiency, and membrane stability [11][12]. Such improvements make plant growth and development possible under heat stress. However, not all plant species or genotypes within species have similar capabilities in coping with the heat stress. There exists tremendous variation within and between species, providing opportunities to improve crop heat-stress tolerance through genetic means. Some attempts to develop heat-tolerant genotypes via conventional plant breeding protocols have been successful [10]

4. Antioxidative Defense System in Plants

Plants possess complex antioxidative defense system comprising nonenzymatic and enzymatic components to scavenge ROS. In plant cells, specific ROS producing and scavenging systems are found in different organelles such as chloroplasts, mitochondria, and peroxisomes. ROS scavenging pathways from different cellular compartments are coordinated. Under normal conditions, potentially toxic oxygen metabolites are generated at a low level and there is an appropriate balance between production and quenching of ROS [13]. The balance between production and quenching of ROS may be perturbed by a number of adverse environmental factors, giving rise to rapid increases in intracellular ROS levels, which can induce oxidative damage to lipids, proteins, and nucleic acids. In order to avoid the oxidative damage, higher plants raise the level of endogenous antioxidant defense [14]. An antioxidants (AOX) are a molecule that inhibits the oxidation of other molecules. Plants possess complex antioxidative defense system comprising of nonenzymatic and enzymatic antioxidants to scavenge ROS. Various components of antioxidative defense system involved in ROS scavenging have been manipulated, overexpressed or downregulated to add to the present knowledge and understanding the role of the antioxidant systems [15]

4.1 Nonenzymatic Components of Antioxidative Defense System

Nonenzymic components of the antioxidative defense system include the major cellular redox buffers ascorbate (AsA) and glutathione (γ-glutamyl-cysteinyl-glycine, GSH) as well as tocopherol, thiamine, carotenoids, and phenolic compounds [16]. They interact with numerous cellular components and in addition to crucial roles in defense and as enzyme cofactors, these antioxidants influence plant growth and development by modulating processes from mitosis and cell elongation to senescence and cell death. Mutants with decreased nonenzymic antioxidant contents have been shown to be hypersensitive to stress [16][15].

4.2 Enzymatic Components of Antioxidative Defense System

The enzymatic components of the antioxidative defense system comprised of several antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), guaiacol peroxidase (GPX), enzymes of ascorbate-glutathione (AsA-GSH) cycle ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR). These enzymes operate in different subcellular compartments and respond in concert when cells are exposed to oxidative stress. That shows various antioxidant enzymes that play important role in scavenging stress-induced ROS generated in plants [19].

4.3 Antioxidant Activity of Plant-derived Vitamins

The antioxidant vitamins that have been the focus of most attention in plants are carotenoids (pro-vitamin A), ascorbate (vitamin C) and tocochromanols (vitamin E, including both tocopherols and tocotrienols). However, recent evidence indicates that vitamin B compounds could also play a significant role as antioxidants in plants. Thiamine (vitamin B1) has been shown to alleviate the effects of several environmental stresses on Arabidopsis (Arabidopsis thaliana), presumably by protecting the plant from oxidative damage. The antioxidant role of thiamine can be indirect, by providing NADH and NADPH to the antioxidant network, or direct, by acting as an antioxidant [20].

Another important finding is increased sensitivity to photooxidative stress in vitamin B6-deficient Arabidopsis plants. Pyridoxine, pyridoxal, pyridoxamine and their phosphorylated derivates are collectively known as vitamin B6. Singlet oxygen levels increase in the pdx1mutant, which is deficient in de novo vitamin B6 biosynthesis. Other compounds with potential antioxidant activity within the plant cell include folates (vitamin B9) and phylloquinone (vitamin K1). This review focuses on the occurrence, biosynthesis and antioxidant function of vitamins in plants, including classical groups (vitamins A,Cand E) and other compounds (vitamins B and K) [21].

Ascorbic acid is the primary substrate in the cyclic pathway for enzymatic detoxification of hydrogen peroxide (H_2O_2). It can neutralize suoeroxide radicals ($O_2^{\bullet -}$) and singlet oxygen ($^1O_2$). It also can become Secondary antioxidant for recycling of α-tocopherol, another lipophilic antioxidant molecules. While Thiamine is a coenzyme in the catabolism of sugars and amino acids. Thiamine Providing NADH and NADPH to the antioxidant network. It can act as scavenging agent for superoxide radicals ($O_2^{\bullet -}$), hydroxil radicals ($^{\bullet}OH$) [22].

5. Conclusion

Exogenous antioxidant could increase antioxidant activity and decrease accumulation of ROS in plant tissues. Equilibrium between ROS production and reduction plays a crucial role in embarking plant defense response when encountering abiotic stresses. Antioxidants activated gene expression in plant tissues under exposuring of heat stress.

Compliance with ethical standards

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Disclosure of conflict of interest

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Authors' contributions

The authors have participated and work on completing this manuscript and approved the final manuscript.

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