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Regulation of plant growth and metabolism by alpha-tocopherol under stress and non-stress conditions

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Abstract

Alpha-tocopherol is a member of the vitamin E family and is lipid soluble. Its biosynthesis is by the reaction of isopentyl diphosphate and homogentisic acid in plastid membranes. The biochemical activities of tocopherols are linked with the formation of tocopherol in quinone species, which subsequently undergo degradation and recycling within cells/ tissues. Alpha-tocopherol plays a key role in a variety of plant metabolic processes throughout the ontogeny of plants. It can maintain the integrity and fluidity of photosynthesizing membranes. Alpha-tocopherol can also neutralize lipid peroxidation radicals, consequently blocking lipid peroxidation by quenching oxidative cations. It preserves membrane integrity by retaining membranous structural components under environmental constraints such as water deficiency, high salt content, toxic metals, high/low temperatures and radiations. Alpha-tocopherol also induces cellular signaling pathways within biological membranes. Its biosynthesis varies during growth and developmental stages as well as under different environmental conditions. The current review primarily focuses on how alpha-tocopherol can regulate various metabolic processes involved in promoting plant growth and development under stress and non-stress conditions and how it can effectively counteract the stress-induced high accumulation of reactive oxygen species (ROS). Currently, exogenous application of alpha-tocopherol has been widely reported as a potential means of promoting resistance in plants to a variety of stressful environmental conditions.

Keywords: α -Tocopherol, Antioxidants, Abiotic stress, Exogenous application.

Introduction

Tocopherols are lipophilic antioxidant compounds that belong to vitamin E family. They are naturally synthesized in green photosynthetic organisms (Munné-Bosch & Alegre, 2002) [74]. Tocopherols play an important role in protecting plant cells from oxidative damage. Ronald M. Evans *et al.*, (1974) first described α - and β -tocopherols and isolated them from the seed oil of wheat. (*Triticum aestivum* L.). Subsequently, γ - and δ -tocopherols were extracted from other oil-producing plants (Stern *et al.*, 1947) [102].

All tocopherols contain a hydrophilic chromanol head that is oriented toward the outer membrane surface and a hydrophobic phytol tail that extends into the inner membrane. Structural differences among tocopherols arise due to variations in the methyl groups on the chromanol ring (Munné-Bosch, 2007) [73]. Among these forms, α - and γ -tocopherols are commonly present in plant membranes. α -Tocopherol is mainly found in the photosynthetic membranes of plant leaves, whereas γ -tocopherol is predominantly present in fruits, seeds and nuts (Grilo *et al.*, 2014) [37]. Tocopherol biosynthesis mainly occurs in the chloroplast, particularly in the envelope, thylakoid membranes, and plastoglobuli, although it may also occur in the protoplast and vacuole of plant cells (Rautenkranz *et al.*, 1994) [84]. In plants, singlet oxygen is produced under photo-oxidative stress due to the formation of reactive oxygen species (ROS) (Asada, 2006) [7]. Tocopherols, which are abundant in cellular membranes, help scavenge these free radicals and prevent lipid peroxidation in membranes (Munné-Bosch, 2007) [73]. The tocopheroxyl radical can be reduced back to tocopherol by antioxidants such as vitamin C, ubiquinol, glutathione, or lipoic acid, thereby maintaining the antioxidant defence system

in plant cells. The tocopheroxyl radical can be reduced back to tocopherol by antioxidants such as vitamin C, ubiquinol, glutathione, or lipoic acid, which are further regenerated by NADH or NADPH (Yang *et al.*, 2011) ^[110]. Therefore, tocopherols play an important role in both plants and animals. Photosynthetic organisms are the primary source of tocopherol production for other living organisms. Deficiency of tocopherols may lead to severe physiological disorders and may even be lethal in both plants and animals (Azzi & Stocker, 2000; Maeda & DellaPenna, 2007) ^[13, 14]. In addition to protecting cellular membranes from oxidative damage, tocopherols also regulate the expression of certain genes (Munné-Bosch, 2007; Li *et al.*, 2008; Suo *et al.*, 2017) ^[73]. In recent decades, considerable attention has been given to improving the oxidative defence system of plants exposed to various environmental stresses. This can be achieved either through genetic engineering to enhance antioxidant production or through the exogenous application of antioxidant compounds such as tocopherols. The exogenous application approach has gained more attention because it is relatively simple, efficient, and economical. However, it is still unclear whether tocopherol alone or in combination with other antioxidants can significantly improve plant growth under normal or stress conditions. Therefore, recent studies have focused on understanding the role of tocopherols, particularly α -tocopherol, in enhancing plant growth and stress tolerance under both stress and non-stress conditions. Studies on *Arabidopsis thaliana* revealed that mutation in the *vte1* gene results in the deficiency of all four tocopherol isoforms due to the lack of tocopherol cyclase. This enzyme is located in the plastoglobuli of chloroplasts and is essential for the synthesis of the chromanol ring of tocopherol. Similarly, limited expression of the *vte1* gene in *Oryza sativa* (rice) plants made them more sensitive to stress, whereas its overexpression increased stress tolerance in rice and *Nicotiana tabacum* (tobacco). Furthermore, overexpression of the γ -tocopherol methyltransferase gene in genetically engineered *Brassica juncea* plants converted γ -tocopherol into α -tocopherol and enhanced stress tolerance (Yusuf *et al.*, 2010) ^[112]. These findings suggest that, transgenic approaches involving genes responsible for the synthesis and accumulation of α -tocopherol can improve stress tolerance, particularly in oilseed crops. Successful manipulation of such

genes may also help in improving the oil quality of oilseed plants like soybean.

Tocopherol and Its Types

The vitamin E family consists of two major groups: tocopherols and tocotrienols. Both groups contain a 6-chromanol ring as the head and an isoprenoid side chain. Each group includes four forms—alpha (α), beta (β), gamma (γ) and delta (δ)—which differ in the position of methyl groups on the chromanol ring (Shahidi & de Camargo, 2016) ^[97, 98]. Thus, the vitamin E family includes eight compounds in total: four tocopherols and four tocotrienols. Among these, only the RRR-form occurs naturally in biological systems. Among the vitamin E compounds, α -tocopherol is the most abundant form found in plant and animal tissues and more than 95% of research studies have focused on this form (Sen *et al.*, 2007) ^[94]. The main structural difference between tocopherols and tocotrienols is that tocotrienols have unsaturated side chains, whereas tocopherols possess saturated side chains (Fu *et al.*, 2017) ^[33]. Tocopherols are synthesized mainly in photosynthetic organisms such as algae and higher plants (Hussain *et al.*, 2013) ^[48]. They act as antioxidants by donating phenolic hydrogen to neutralize reactive free radicals. Among the different types of tocopherols, α -tocopherol has the highest antioxidant activity. In comparison, β - and γ -tocopherols show moderate antioxidant activity, while δ -tocopherol exhibits relatively lower antioxidant potential (Kapoor *et al.*, 2015) ^[53].

Physio-Biochemical Role of Alpha-Tocopherol in Plants

All plants contain lipophilic antioxidants such as fatty acids, carotenoids and α -tocopherol as important components of photosynthetic membranes (Semida *et al.*, 2016) ^[93]. Plastid membranes are rich in polyunsaturated fatty acids and α -tocopherol plays a key role in the antioxidant defence system of mesophyll cells in plant. α -Tocopherol helps to prevent lipid peroxidation by scavenging reactive oxygen species and their by-products, thereby maintaining the stability and integrity of biological membranes (Wang & Quinn, 2000; Sharma *et al.*, 2012; Spicher *et al.*, 2016) ^[99, 109]. For instance, a single molecule of α -tocopherol can neutralize nearly 120 molecules of singlet oxygen under stress conditions before being degraded (Semida *et al.*, 2014) ^[92].

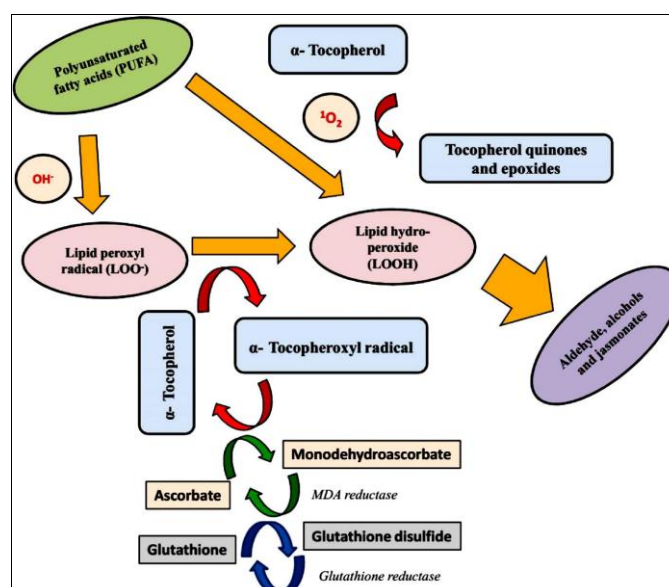


Fig 1: Schematic diagram of α -tocopherol mediated scavenging of ROS.

The α -tocopherol molecule is involved in the direct scavenging of singlet oxygen ($^1O_2$) as well as in the conversion of lipid peroxy radical ($LOO\cdot$) to lipid hydro-peroxide ($LOOH$). Regeneration of α -tocopherol from α -tocopheroxyl radical is mediated through ascorbate- glutathione redox couple.

Tocopherol acts as an antioxidant by donating an electron from its chromanol ring to reactive lipid radicals, such as lipid peroxy radicals ($LOO\cdot$), converting them into more stable products ($LOOH$). Through this mechanism, α -tocopherol protects cellular membranes from oxidative damage and helps maintain normal physiological and biochemical processes in plants. During the antioxidant reaction, α -tocopherol is converted into a tocopheroxyl radical after donating an electron to neutralize free radicals. This radical can be regenerated back to α -tocopherol through interactions with other antioxidants such as ascorbate and glutathione. The protective role of α -tocopherol in preventing the oxidation of polyunsaturated fatty acids in membranes involves several mechanisms (Sandorf & Hollander-Czytko, 2002) ^[90]. Reactive oxygen species (ROS) are produced as by-products of photosynthesis and other metabolic processes in plants (Bhattacharya, 2015). Excess accumulation of ROS can cause lipid degradation and membrane damage (Munné-Bosch & Alegre, 2003) ^[75]. However, α -tocopherol acts as an effective antioxidant that scavenges these free radicals and protects cellular membranes from lipid peroxidation. For example, Clement *et al.*, (2002) ^[23] reported that α -tocopherol effectively reduced free radical activity and prevented membrane lipid peroxidation in soybean.

Molecular Aspects of Tocopherol-Induced Stress Tolerance

Tocopherols are lipid-soluble compounds belonging to the

vitamin E family. It includes four isoforms: α , β , γ , and δ . These compounds play an important role in protecting plants from oxidative stress by scavenging and neutralizing reactive oxygen species (ROS) (Ouchi *et al.*, 2014) ^[80]. Among these isoforms, α -tocopherol showed the highest antioxidant activity due to the presence of methyl groups in its phenolic ring structure (Hussain *et al.*, 2013) ^[48]. The structure of tocopherol, which includes a benzoquinone ring and a phytol side chain, enables it to participate in redox reactions and neutralize singlet oxygen. It has been reported that, one molecule of α -tocopherol can neutralize nearly 120 singlet oxygen molecules in the photosynthetic system before it is degraded (Gill & Tuteja, 2010) ^[36]. The oxidized form of tocopherol can be regenerated by other antioxidants such as coenzyme Q, glutathione (GSH) and ascorbic acid (AsA) (Karuppanapandian *et al.*, 2011) ^[54]. Under the stress conditions, the synthesis of tocopherol may increase to compensate for its degradation in plant cells (Szarka *et al.*, 2012) ^[104]. In plants, the hydroxyl group of α -tocopherol can form α -tocopheryl acetate, which retains vitamin E activity (Gregory, 2007) ^[38]. α -Tocopherol also plays a role in the photosynthetic process. It participates in electron transport around Photosystem II by interacting with cytochrome b559 (Kruk & Strzalka, 2001) ^[58]. In addition, α -tocopherol influences the formation of the light-driven trans-membrane proton gradient (ΔpH) across the thylakoid membrane, which is important for ion transport and ATP synthesis. The proton gradient also regulates the xanthophyll cycle, where violaxanthin is converted into zeaxanthin. This process helps dissipate excess light energy as heat in chloroplasts and protects the photosynthetic apparatus from damage under stress conditions (Demmig-Adams *et al.*, 2008) ^[26].

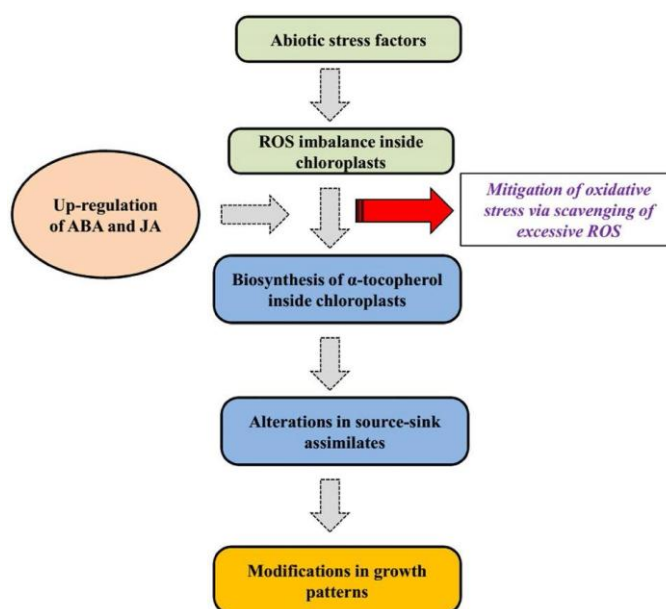


Fig 2: Anti-oxidative regulation by α -tocopherol in plant chloroplasts during abiotic stress.

Physiological Basis of Tocopherol-Induced Stress Tolerance

Alpha-tocopherol is an important component of the seeds of oilseed crops such as safflower, sunflower and wheat germ (Reboul *et al.*, 2006) ^[85]. It plays a significant role in the germination of oil seeds by protecting the tissues from oxidative stress during the germination process (Sattler *et al.*, 2004) ^[91]. Generally, oilseeds contain higher levels of tocopherol compared to photosynthetic tissues. A considerable amount of α -tocopherol is present in plastoglobuli vesicles of chloroplasts. It helps to protect photosynthetic tissues from the harmful effects

of abiotic stresses. The distribution of α -tocopherol between thylakoid membranes and plastoglobuli is an important physiological feature and varies with the growth stages of plants such as *Nicotiana tabacum* and *Arabidopsis thaliana* (Matringe *et al.*, 2008) ^[68].

Under low temperature conditions, α -tocopherol helps to prevent the destabilization of cellular membranes. In phospholipid bilayer membranes, α -tocopherol maintains membrane stability by influencing the movement of fatty acid chains in the liquid crystal phase (Hinch, 2008) ^[45]. Through these mechanisms, α -

tocopherol contributes to improved physiological tolerance of plants under different environmental stresses.

Photo-Protective Function of α -Tocopherol in Plants

Photosynthesis converts solar energy into chemical energy in the form of carbohydrates. During photosynthesis process, excess light energy is safely dissipated as heat to maintain a balance between light absorption and energy utilization. Under normal conditions, most of the captured energy is used for plant growth, development, and only a small photoprotective mechanism is required.

However, under unfavourable environmental conditions, photosynthesis may be inhibited, leading to the accumulation of excess light energy. In such situations, plants activate protective mechanisms to dissipate this extra energy and prevent damage to the photosynthetic system. Plants may modify their leaf structure and physiological processes to cope with excess energy, including mesophyll adaptation, changes in pigment composition, accumulation of anthocyanins to reduce light intensity and adjustments in light absorption efficiency (Terashima *et al.*, 2001) ^[107].

Excess energy can lead to the formation of reactive oxygen species (ROS) in chloroplasts, which may cause oxidative damage to cellular components (Asada, 2006) ^[7]. α -Tocopherol plays an important role in protecting the photosynthetic apparatus by scavenging ROS and preventing lipid peroxidation. It also contributes to the dissipation of excess energy as heat within chloroplasts, thereby protecting plants from photo-oxidative damage.

Role of Alpha-Tocopherol in Plant Resistance against Abiotic Stresses

Tocopherols play an important role in plant adaptation to various abiotic stresses such as drought, salinity, extreme temperatures, radiation and toxic metals. Different plant species show variation in tocopherol-mediated stress tolerance depending on their sensitivity and metabolic responses to stress conditions (Kapoor *et al.*, 2015) ^[53]. Studies have shown that, stress-tolerant plant species generally contain higher levels of α -tocopherol compared to stress-sensitive species (Munné-Bosch & Alegre, 2002) ^[74]. The level of α -tocopherol in plants exposed to stress is usually regulated in two phases. In the first phase, the synthesis of α -tocopherol increases to scavenge reactive oxygen species (ROS) produced during stress. In the second phase, under severe stress conditions, degradation of tocopherol may occur. The first phase is more prominent in stress-tolerant species, while the degradation phase is mainly observed in stress-sensitive plants (Munné-Bosch, 2005). Environmental stresses such as drought, salinity, extreme temperatures, heavy metals and radiation negatively affect plant growth and lead to the accumulation of reactive oxygen species in plant cells and tissues. A gradual increase in ROS can disrupt important metabolic processes and cause oxidative damage to cellular components. Under severe stress conditions, the accumulation of reactive oxygen species (ROS) can damage cellular components and may ultimately lead to cell death. To protect themselves from such oxidative damage, plants activate defence mechanisms by producing both low and high molecular weight antioxidants (Lushchak, 2011) ^[65].

The accumulation of tocopherols in plants depends on the intensity and severity of the stress conditions, as well as the species-specific responses of plants. Higher levels of tocopherols help plants reduce oxidative damage and improve their tolerance to adverse environmental conditions.

Drought Stress

Under drought stress, plants often close their stomata to reduce water loss. This leads to increased photo-oxidation and the production of reactive oxygen species (ROS), which can disrupt photosynthesis through lipid peroxidation (Cela *et al.*, 2009b) ^[20, 21]. To counteract this effect, many plant species increase the production of α -tocopherol under water-deficit conditions. Increased α -tocopherol levels have been reported in plants such as *Arabidopsis thaliana* and *Nicotiana tabacum* (Liu *et al.*, 2008) ^[64], *Rosmarinus officinalis* (Munné-Bosch *et al.*, 1999) ^[76], *Salvia officinalis* and *Melissa officinalis* (Munné-Bosch & Alegre, 2003) ^[75] ^[74] and *Quercus ilex* (Munné-Bosch *et al.*, 2004) ^[77].

Studies have also shown that, transgenic drought-tolerant plants often produce higher levels of tocopherols. For example, transgenic brassica juncea plants showed that, greater drought tolerance due to increased α -tocopherol content compared to wild types (Kumar *et al.*, 2013) ^[59]. Similarly, Cela *et al.*, (2009a) reported higher α -tocopherol levels in a drought-tolerant transgenic line of *Arabidopsis thaliana*.

The VTE2 gene as an important gene involved in α -tocopherol synthesis under water-stress conditions, helping to protect the photosynthetic system from photo-oxidative damage (Espinoza *et al.*, 2013) ^[29]. In *Cistus clusii*, early drought stress activated the expression of the homogentisate phytyl transferase gene, which increased α -tocopherol levels by about 62% (Munné-Bosch *et al.*, 2009) ^[78]. Additionally, Liu *et al.*, (2008) ^[64] observed that, higher total tocopherol content in transgenic *Nicotiana tabacum* plants under drought stress due to overexpression of the VTE1 gene from *Arabidopsis thaliana*. Abdallah *et al.*, (2013) ^[2] studied the combined effect of mycorrhiza and α -tocopherol on *Helianthus annuus* plants grown under 60% field capacity conditions. Their results showed that, significant improvement in growth parameters, mineral ion uptake and yield components compared to untreated plants.

Similarly, Sadiq *et al.*, (2016) ^[86] reported that, foliar application of α -tocopherol enhanced plant growth and increased antioxidant enzyme activity in *Vigna radiata* under moisture-deficit conditions. These findings suggest that, α -tocopherol can improve plant tolerance to drought stress by enhancing antioxidant defence mechanisms.

Salinity Stress

Salinity is more harmful than drought because it causes both ionic stress and osmotic stress in plants. It negatively affects important physiological processes such as water and nutrient uptake, respiration and photosynthesis. Salinity also increases the production of reactive oxygen species (ROS) and leads to membrane lipid peroxidation, which ultimately reduces plant growth and yield (Mahajan & Tuteja, 2005) ^[66].

Skłodowska *et al.*, (2009) ^[100] studied salt-stressed tomato plants (*Solanum lycopersicum*) treated with 50 and 150 mM NaCl. They observed increased lipid peroxidation, reduced chlorophyll content and changes in antioxidant enzyme activities along with an increase in α -tocopherol levels. The antioxidative role of α -Tocopherol was associated with higher activities of glutathione S-transferase (GST) and glutathione peroxidase (GPX) during the early growth stage. However, at later stages, α -Tocopherol was involved in signalling pathways related to plant senescence. Similarly, treatment with 100-200 mM NaCl increased total tocopherol content in *Brassica juncea* plants. However, at 400 mM NaCl, total tocopherol levels decreased due to a reduction in α -tocopherol and an increase in γ -tocopherol. Overexpression

of the γ -tocopherol gene did not change the total tocopherol content but increased the conversion of γ -tocopherol to α -tocopherol (Yusuf *et al.*, 2010) ^[112].

Hussein *et al.*, (2007) ^[49] reported that, exogenous application of 200 mg L⁻¹ α -tocopherol improved the growth of cowpea plants. Similarly, Mohamed and Aly (2008) ^[70] found that, α -tocopherol application reduced the harmful effects of salt stress in onion plants and increased the levels of total phenolics and flavonoids. Farouk (2011) ^[32] reported that, foliar application of α -tocopherol significantly increased antioxidant enzyme activity and the accumulation of ascorbic acid (AsA), phenolics, accessory pigments, calcium, potassium and magnesium in wheat plants compared with untreated plants. In addition, soaking sunflower seeds in different concentrations of α -tocopherol helped reduce the negative effects of salinity stress (Rady *et al.*, 2011) ^[82]. These studies indicate that, foliar application of α -tocopherol under salinity stress enhances plant tolerance by stabilizing important biochemical processes. As a result, it helps maintain plant growth and improves biomass and seed yield production.

Extreme Temperatures

Increasing global warming creates stress conditions for crops, particularly in tropical regions (Kumar *et al.*, 2013) ^[59]. High temperature stress adversely affects plant growth and development at different growth stages (Hatfield and Prueger, 2015) ^[43]. Elevated temperatures can denature cellular and sub-cellular proteins, leading to disruption of membrane integrity (Hatfield and Prueger, 2015). In addition, high temperature causes enzyme inactivation in chloroplasts and mitochondria, which blocks many metabolic reactions (Howarth, 2005) ^[47]. Generally, high temperature stress reduces photosynthesis, causes nutrient deficiency and impairs transpiration (Oukarroum *et al.*, 2012) ^[81]. It also leads to pigment degradation and slower plant growth. However, several studies have reported a positive relationship between high temperature stress and the increased synthesis or accumulation of tocopherols (Falk and Munné-Bosch, 2010) ^[31].

For example, exposure of *Helianthus annuus* plants to 35 °C increased tocopherol levels during the reproductive stage and also enhanced seed oil content (Dong *et al.*, 2007) ^[27]. In lettuce, high temperature activated tocopherol cyclase, which increased the biosynthesis of vitamin E (Tang *et al.*, 2011) ^[106]. Generally, tocopherol accumulation in plants is considered a light-dependent process (Lichtenthaler, 2007) ^[63], as reported in *Arabidopsis* (Szymańska and Kruk, 2010) ^[105]. However, Chennupati *et al.*, (2011) ^[22] reported that, high temperature conditions of 33/25 °C (day/night) significantly increased α -tocopherol levels while decreasing γ -tocopherol and δ -tocopherol concentrations at different developmental stages of soybean plants. Similarly, Carrera and Seguin (2016) ^[19] observed that, increased temperature combined with soil moisture deficiency enhanced the accumulation of α -tocopherol but reduced δ -tocopherol levels in soybean.

Low Temperature

Low temperature also adversely affects the plant growth and development. This problem is more common in countries that experience continuously low temperatures, although chilling stress can also occur during the winter season in tropical regions. Both high and low temperature extremes have been reported to promote tocopherol accumulation in several plant species (Kanayama *et al.*, 2013) ^[52]. However, the concentration of α -tocopherol varies among different plant species under chilling

stress (Streb *et al.*, 1999) ^[103]. Under low temperature conditions, tocopherols help to protect the plastid membranes from oxidative damage (Matringe *et al.*, 2008) ^[68].

For example, exposure of *Medicago sativa* plants to low temperature (10 °C) increased lipid peroxidation (MDA) and hydrogen peroxide (H₂O₂) levels. During the recovery period, α -tocopherol helped to scavenge the free radicals produced due to oxidative stress. The increased levels of α -tocopherol were associated with higher activities of antioxidant enzymes such as catalase (CAT), superoxide dismutase (SOD) and ascorbate peroxidase (APX), which helped to reduce the accumulation of reactive oxygen species (ROS) (Bafeel and Ibrahim, 2008) ^[16]. In response to cold stress, plants maintain their metabolic activities by accumulating various cryoprotective compounds, which enhance their tolerance to chilling conditions.

Metal Toxicity

Metal toxicity can negatively affect various physiological and biochemical processes in plants (Hasanuzzaman and Fujita, 2013) ^[39, 40]. Similar to other environmental stresses, metal stress can also influence the levels of tocopherols in plants processes. For example, Artetxe *et al.*, (2002) ^[6] reported that duckweed plants exposed to zinc (Zn) and cadmium (Cd) stress showed the increased levels of tocopherols in plant. A similar response was observed in lupine plants subjected to lead (Pb) stress, where tocopherol synthesis was enhanced.

In wheat, treatment with 50 and 100 mM nickel (Ni) for nine days resulted in 38% and 60% higher tocopherol levels, respectively, compared with the control plants (Gajewska and Skłodowska, 2007) ^[34]. Similarly, in *Arabidopsis*, copper (Cu) and cadmium (Cd) stress induced approximately six-fold and five-fold increases in tocopherol content compared with control plants (Collin *et al.*, 2008) ^[24]. In *Brassica juncea*, Yusuf *et al.*, (2010) ^[112] reported that, 1.5-fold and 9.3-fold increases in α -tocopherol and γ -tocopherol contents, respectively, in plants treated with CdCl₂ (20 mM).

Ultraviolet (UV) Radiation

Global warming and climate change are causing depletion of the stratospheric ozone layer, which increases the exposure of the earth to ultraviolet (UV) radiation. The reduction in ozone concentration leads to higher levels of UV-B radiation reaching the Earth's surface (Mpoloka, 2008) ^[72]. UV-B radiation can cause various harmful effects in plants, including reduced growth, biochemical changes and decreased yield. α -Tocopherol is considered an important protective compound against UV-B stress. Endogenous α -Toc present in plastids helps reduce reactive oxygen species (ROS), lipid peroxidation and hydrogen peroxide (H₂O₂) levels, thereby maintaining membrane integrity under UV-B stress in different plant species (Sharma *et al.*, 2012) ^[99].

For example, exposure of *Spinacia oleracea* leaves to UV-B radiation increased malondialdehyde (MDA) formation, indicating enhanced lipid peroxidation (DeLong and Steffen, 1998) ^[25]. However, increased endogenous α -Toc levels helped reduce lipid peroxidation and neutralize oxidative stress. In addition, α -Tocopherol also protects the membranous antioxidant system (DeLong and Steffen, 1998). In contrast, some studies have reported that, no positive effect of UV-B on α -Tocopherol levels. For instance, UV-B stress significantly reduced α -Tocopherol content in maize (Carletti *et al.*, 2003) ^[18] and cucumber seedlings (Jain *et al.*, 2003) ^[50], while no significant effect was observed in soybean leaves (Galatro *et al.*, 2001) ^[35].

Therefore, α -tocopherol may help reduce the harmful effects of UV radiation in some plant species under certain conditions.

Tocopherols and Cellular Signalling

Antioxidants play an important role in redox reactions and help regulate the expression of genes involved in plant acclimatization to abiotic stress. Stress conditions and environmental factors trigger various signals that activate the plant's internal defence mechanisms. In cellular systems, α -tocopherol plays an important role in initiating signalling processes in cell. (Azzi, 2007) [13]. The level of bioactive α -Tocopherol involved in signalling varies depending on the severity of stress conditions. This highlights the important role of α -Tocopherol in maintaining redox homeostasis in plant cells (Traber and Atkinson, 2007) [108]. In addition, α -Tocopherol can influence gene expression and modify source-sink relationships in plants, indicating its involvement in cellular signalling processes (Hofius *et al.*, 2004) [46].

Studies on transgenic potato plants have shown that, tocopherol can regulate gene expression and increase the transcription of several defence-related proteins, such as proline biosynthesis enzyme (P5CS), jasmonic acid synthesis enzyme (AOC) and proteinase inhibitor II (PIN2) (Lichtenthaler, 2007) [63]. Furthermore, plants deficient in α -tocopherol were found to be more sensitive to stress, whereas mutant plants containing γ -tocopherol instead of α -tocopherol showed greater tolerance to osmotic stress (Abbasi, 2007) [1].

Exogenous Application of Tocopherols

Exogenous application is considered a simple, effective method to help plants cope with various abiotic stresses (Ashraf *et al.*, 2010) [9]. Under stress conditions, the internal levels of phytohormones and antioxidants in plants often decrease. These reduced levels can be improved through external application of such compounds. The exogenous application of non-enzymatic antioxidants has become a common practice to reduce the harmful effects of abiotic stresses in plants (Kaya *et al.*, 2010) [55]. Vitamins act as antioxidants and also function as co-enzymes in many metabolic processes. Although they are required in small amounts, they may act as limiting factors for plant growth (Hassanein *et al.*, 2009) [42].

Several studies have reported that, beneficial effects of applying vitamins, phytohormones, and antioxidants to protect plants against abiotic stresses. These protective substances enhance plant stress tolerance by regulating metabolic processes, which ultimately improves plant growth and crop productivity (Hasanuzzaman *et al.*, 2013) [39, 40]. To maintain cellular homeostasis in response to intra and extracellular stimuli, chloroplasts regulate many intercellular signalling pathways. Plastids are often located close to plasmodesmata, which allows external molecules to easily reach these organelles (Bobik and Burch-Smith, 2015) [17]. The movement of molecules between cells is mediated by proteins located in plasmodesmata and by the activity of callose synthase (Lee *et al.*, 2011) [62]. These findings indicate that, existence of cross-talk between low molecular weight compounds, including tocopherols and plasmodesmata-mediated signalling. Tocopherols, including α -tocopherol, are lipophilic compounds, which enables them to easily enter cells through biological membranes (Sattler *et al.*,

2004) [91]. The chloroplast is the primary site of α -tocopherol biosynthesis and most of the enzymes involved in this process are located on the inner membrane of the chloroplast envelope. In addition, plastoglobules associated with the thylakoid membrane are also believed to participate in tocopherol biosynthesis (Atkinson *et al.*, 2008) [11]. Therefore, tocopherols or related chemicals can be applied externally to plants through different methods such as seed treatment, foliar spray, or application through the growing medium via roots (Tables 1 and 2).

Pre-sowing Seed Treatment

Seed soaking is an effective technique to improve seed germination and seedling growth under both stress (Agholaghi and Sedghi, 2014) [4] and non-stress conditions (Saleem *et al.*, 2014) [89]. It is a controlled hydration process in which metabolic activities within the seed are initiated, but radicle emergence is prevented (Ashraf and Foolad, 2005) [8]. Jie *et al.*, (2008) [51] reported that, pre-treatment of *Leymus chinensis* seeds with 0.05-10.0 mmol L⁻¹ vitamin E increased antioxidant enzyme activity and proline content, while reducing malondialdehyde (MDA) levels in plants grown from treated seeds. Similarly, soaking sunflower seeds in an α -tocopherol (α -Tocopherol) solution reduced the harmful effects of salinity stress (Rady *et al.*, 2011) [82]. vSakr and El-Metwally (2009) [88] also reported that, wheat seeds pre-treated with α -Tocopherol produced plants with higher levels of ascorbic acid (AsA) and phenolic compounds. These plants showed that, improved antioxidant activity, which helped protect them from the damaging effects of salinity stress. Although only a limited number of studies are available, seed soaking with α -tocopherol appears to be a practical and economical method for improving seed germination under stress conditions. This treatment can lead to better crop establishment and increased yield.

Foliar Spray

Foliar application is an effective method for improving plant growth and crop yield (Shahi and Srivastava, 2016) [97]. It is commonly used to supply micronutrients directly to plant leaves in order to overcome nutrient deficiencies. The response of plants to foliar application depends on the crop species and the prevailing agro-climatic conditions (Aslam *et al.*, 2016) [10]. Foliar application becomes particularly useful when the root system cannot absorb sufficient nutrients due to factors such as soil compaction, low soil moisture or nutrient loss through leaching. It can also compensate for the plant's inability to synthesize adequate amounts of certain nutrients (Fageria *et al.*, 2009; Herrera *et al.*, 2016) [30, 44].

After foliar application, many water-soluble compounds can easily enter the plant through stomata, the cuticle or the entire leaf surface (Latha and Nadanassababady, 2003) [61]. Several studies have reported that, foliar nutrient application during the vegetative stage increases internal mineral levels in plants and ultimately improves crop yield (Kolota and Osinska, 2001) [56]. Vitamin E (α -tocopherol) is a non-enzymatic antioxidant which, when applied as a foliar spray, can enhance plant growth and yield, particularly under stress conditions (Soltani *et al.*, 2012) [101].

Table 1: Improvement in growth and different metabolic functions by external application of α -tocopherol in various plants during control conditions.

Mode of application	Concentration	Plant species	Major effects observed	Reference
Foliar spray	0.1, 0.5, 1.0, 2.0 and 4.0 mM	<i>Phaseolus vulgaris</i> , <i>Pisum sativum</i>	Increased pods per plant, 100-seed weight and seed dry weight	El-Hakim (2014)
Foliar spray	400, 800 and 1200 mg L ⁻¹	<i>Antirrhinum majus</i>	Improved plant height, leaf number, shoot and root biomass and floral characters	Badawy <i>et al.</i> , (2015)
Foliar spray	0, 500 and 1000 mg L ⁻¹ (Vitamin E)	<i>Vicia faba</i>	Increased plant height, biomass, branches and pod number	Marzauk <i>et al.</i> , (2014)
Foliar spray	75 and 150 mg L ⁻¹	<i>Phaseolus vulgaris</i>	Improved plant height, leaf number, leaf dry weight and seed quality	Shafeek <i>et al.</i> , (2014)
Foliar spray	50 mL L ⁻¹	<i>Capsicum annuum</i>	Increased plant height, leaf area, dry weight and fruit yield	Abeer <i>et al.</i> , (2015)
Foliar spray	50 and 100 mg L ⁻¹	<i>Allium cepa</i>	Increased bulb length and diameter, protein and soluble sugars	Hassan <i>et al.</i> , (2013)
Foliar spray	50 and 100 mg L ⁻¹	<i>Calendula officinalis</i>	Enhanced shoot growth and seed yield	Soltani <i>et al.</i> , (2012)
Foliar spray	50 mg L ⁻¹	<i>Helianthus annuus</i>	Increased plant height, leaf number, head diameter and yield traits	Al-Qubaie (2012)
Foliar spray	50, 100 and 150 mg L ⁻¹	<i>Pelargonium graveolens</i>	Increased biomass, plant length and crude protein; reduced lipid peroxidation	Ayad <i>et al.</i> , (2009)

Sereflioglu *et al.*, (2017) ^[95] reported that, α -tocopherol acts as a signalling molecule from soybean leaves to roots under salinity stress. The external application of α -Tocopherol improved root length and root weight, increased endogenous auxin (IAA) concentration and peroxidase enzyme activity and reduced the levels of malondialdehyde (MDA), proline and hydrogen peroxide (H₂O₂) in soybean roots.

Ye *et al.*, (2017) ^[111] treated *Carex leucochlora* plants with 0.8 mM α -Tocopherol under salinity stress and observed that it alleviated the harmful effects of salinity. The treatment increased carotenoid content, free proline and chlorophyll b, while significantly reducing the production of superoxide

radicals and hydrogen peroxide.

Rahmawati and Damanik (2018) ^[83] reported that, foliar application of 500 mg L⁻¹ α -Tocopherol significantly increased root and shoot dry weight, number of branches, chlorophyll content and total soluble proteins in soybean under salt stress. Similarly, Sadiq *et al.*, (2018) ^[87] studied the effect of exogenous α -Tocopherol on mungbean plants under field water deficit conditions. They found that, α -Tocopherol application increased plant biomass, photosynthetic pigments, proline, glycine betaine, sugars and antioxidant enzyme activities. It also reduced the accumulation of hydrogen peroxide (H₂O₂) and malondialdehyde (MDA).

Table. 2: Improvement in growth and different metabolic functions by external application of α -tocopherol in different plants under stress conditions

Nature of stress	Mode of application	Concentration	Plant species	Major effects observed	Reference
Seawater salt stress	Foliar spray	200 mg L ⁻¹	<i>Allium cepa</i>	Increased total phenolics and flavonoids	Mohammad and Aly (2008)
Drought stress	Foliar spray	1 mM	<i>Gossypium barbadense</i>	Increased chlorophyll a, chlorophyll b, total soluble sugars and free amino acids	Mekki <i>et al.</i> , (2015)
Salinity stress	Foliar spray	100 mg L ⁻¹	<i>Triticum aestivum</i>	Increased ascorbic acid, phenolics and mineral ions (Mg, K, Ca)	Farouk (2011)
Drought stress	Seed pre-treatment	0.05, 1.0 and 10 mmol L ⁻¹	<i>Leymus chinensis</i>	Increased antioxidant enzymes (SOD, POD) and proline; decreased MDA	Jie <i>et al.</i> , (2008)
Salt stress	Foliar spray	0.5 mM	<i>Citrus aurantium</i>	Improved membrane stability and chlorophyll; reduced lipid peroxidation and H ₂ O ₂	Kostopoulou <i>et al.</i> , (2014)
Salt stress	Foliar spray	100 mg L ⁻¹	<i>Glycine max</i>	Improved photosynthetic pigments, relative water content and K ⁺ concentration	Mostafa <i>et al.</i> , (2015)
Salt stress	Foliar spray	50 and 100 mg L ⁻¹	<i>Vicia faba</i>	Increased antioxidant enzymes, proline and carotenoids; reduced MDA	Orabi and Abdelhamid (2016)
Salt stress	Seed soaking	25 and 50 mg L ⁻¹	<i>Helianthus annuus</i>	Increased total soluble sugars and antioxidant enzyme activity	Rady <i>et al.</i> , (2011)

Conclusions and Future Prospects

Vitamin E *i.e.* α -Tocopherol is an important antioxidant that helps to improve the plant growth and enhances tolerance to various abiotic stresses. It plays a significant role in protecting plants from oxidative damage under both normal and stress environmental conditions. However, the exact mechanisms by which α -tocopherol regulates stress tolerance at physiological, biochemical and molecular levels are still not fully understood and require further investigation.

Tocopherols may also be involved in complex signalling

pathways associated with reactive oxygen species (ROS), phytohormones, antioxidants and secondary metabolites. Therefore, it is important to identify the factors that regulate tocopherol expression under both stress and non-stress conditions.

Several studies have shown that, exogenous application of α -tocopherol increases its internal concentration in plants and improves growth and stress tolerance. However, more research is needed to understand how tocopherol-related enzymes regulate the redox signalling and how α -tocopherol interacts

with other metabolic pathways to help the plants adapt to unfavourable environmental conditions. Further studies are also required to clarify the role of tocopherols in regulating metabolic processes in plant at both cellular and whole-plant levels. In addition, it is important to evaluate the practical use of tocopherols under field conditions, considering their cost-benefit ratio and environmental impact. So far, very few studies have confirmed the positive effects of exogenous tocopherol application on crops grown under natural field conditions. Therefore, more field-based experiments are required to determine whether the results obtained under laboratory or greenhouse conditions can be successfully applied under variable field environments.

References

- Abbasi AR. Functional analysis of tocopherol biosynthesis in plants [PhD thesis]. Tehran, Iran: University of Tehran; 2007.
- Abdallah MM, Abdel-Monem AA, Hassanein RA, El-Bassiouny HMS. Response of sunflower plant to the application of certain vitamins and arbuscular mycorrhiza under different water regimes. *Australian Journal of Basic and Applied Sciences*. 2013;7(1):915-932.
- Abeer SI, Shafeek MR, Ahmed HI, Abdel-Al FS. Improving growth, fruit setting, total yield and fruit quality of sweet pepper plants (*Capsicum annuum* L.) by using antioxidant and seaweed extracts. *Middle East Journal of Agricultural Research*. 2015;4(2):154-161.
- Agholaghi MA, Sedghi M. The effect of halo- and hydro-priming on germination characteristics of millet seeds under salinity stress. *Cercetări Agronomice în Moldova*. 2014;47(2):41-48.
- Al-Qubaie AI. Response of sunflower cultivar Giza-102 (*Helianthus annuus* L.) plants to spraying some antioxidants. *Natural Science*. 2012;10(11):1-6.
- Artetxe U, García-Plazaola JI, Hernández A, Becerril JM. Low light grown duckweed plants are more protected against the toxicity induced by Zn and Cd. *Plant Physiology and Biochemistry*. 2002;40(9):859-863.
- Asada K. Production and scavenging of reactive oxygen species in chloroplasts and their function. *Plant Physiology*. 2006;141(2):391-396.
- Ashraf M, Foolad MR. Pre-sowing seed treatment: A shotgun approach to improve germination, plant growth, and crop yield under saline and non-saline conditions. *Advances in Agronomy*. 2005;88:223-271.
- Ashraf M, Ahmad R, Bhatti AS, Afzal M, Sarwar A, Maqsood MA, *et al.* Amelioration of salt stress in sugarcane (*Saccharum officinarum* L.) by supplying potassium and silicon in hydroponics. *Pedosphere*. 2010;20(2):153-162.
- Aslam M, Sultana B, Anwar F, Munir H. Foliar spray of selected plant growth regulators affected the biochemical and antioxidant attributes of spinach in a field experiment. *Turkish Journal of Agriculture and Forestry*. 2016;40(2):136-145.
- Atkinson J, Epand RF, Epand RM. Tocopherols and tocotrienols in membranes: A critical review. *Free Radical Biology and Medicine*. 2008;44(5):739-764.
- Ayad HS, El-Din KG, Reda F. Efficiency of stigmasterol and α -tocopherol application on vegetative growth, essential oil pattern, protein and lipid peroxidation of geranium (*Pelargonium graveolens* L.). *Journal of Applied Sciences Research*. 2009;5(7):887-892.
- Azzi A. Molecular mechanism of α -tocopherol action. *Free Radical Biology and Medicine*. 2007;43(1):16-21.
- Azzi A, Stocker A. Vitamin E: Non-antioxidant role. *Progress in Lipid Research*. 2000;39(3):231-255.
- Badawy M, Magda M, Kandil M, Iman M. Influence of diatomite, putrescine and α -tocopherol on some vegetative growth and flowering of *Antirrhinum majus* L. plants. *Journal of Horticultural Science and Ornamental Plants*. 2015;7(1):7-18.
- Bafeel SO, Ibrahim MM. Antioxidants and accumulation of α -tocopherol induce chilling tolerance in *Medicago sativa*. *International Journal of Agriculture and Biology*. 2008;10(5):593-598.
- Bobik K, Burch-Smith TM. Chloroplast signaling within, between and beyond cells. *Frontiers in Plant Science*. 2015;6:1-26.
- Carletti P, Masi A, Wonisch A, Grill D, Tausz M, Ferretti M. Changes in antioxidant and pigment pool dimensions in UV-B irradiated maize seedlings. *Environmental and Experimental Botany*. 2003;50(2):149-157.
- Carrera CS, Seguin P. Factors affecting tocopherol concentrations in soybean seeds. *Journal of Agricultural and Food Chemistry*. 2016;64(50):9465-9474.
- Cela J, Falk J, Munné-Bosch S. Ethylene signaling may be involved in the regulation of tocopherol biosynthesis in *Arabidopsis thaliana*. *FEBS Letters*. 2009;583(6):992-996.
- Cela J, Arrom L, Munné-Bosch S. Diurnal changes in photosystem II photochemistry, photoprotective compounds and stress-related phytohormones in the CAM plant, *Aptenia cordifolia*. *Plant Science*. 2009;177(3):404-410.
- Chennupati P, Seguin P, Liu W. Effects of high temperature stress at different development stages on soybean isoflavone and tocopherol concentrations. *Journal of Agricultural and Food Chemistry*. 2011;59(24):13081-13088.
- Clement SA, Tan CC, Guo JL, Kita K, Suzuki YJ. Roles of protein kinase and α -tocopherol in regulation of signal transduction for GATA-4 phosphorylation in HL-1 cardiac muscle cells. *Free Radical Biology and Medicine*. 2002;32(4):341-349.
- Collin VC, Eymery F, Genty B, Rey P, Havaux M. Vitamin E is essential for the tolerance of *Arabidopsis thaliana* to metal-induced oxidative stress. *Plant, Cell & Environment*. 2008;31(2):244-257.
- DeLong JM, Steffen KL. Lipid peroxidation and α -tocopherol content in α -tocopherol supplemented thylakoid membranes during UV-B exposure. *Environmental and Experimental Botany*. 1998;39(2):177-185.
- Demmig-Adams B, Adams WW, Barker DH, Logan BA. Using chlorophyll fluorescence to assess the fraction of absorbed light allocated to thermal dissipation of excess excitation. *Physiologia Plantarum*. 2008;98(2):253-264.
- Dong G, Liu X, Chen Z, Pan W, Li H, Liu G. The dynamics of tocopherol and the effect of high temperature in developing sunflower (*Helianthus annuus* L.) embryo. *Food Chemistry*. 2007;102(1):138-145.
- El-Hakim WMA. Response of some vegetable legume plants to foliar application of some antioxidants. *Journal of American Science*. 2014;10(12):1-12.
- Espinoza A, Martín AS, López-Climent M, Ruiz-Lara S, Gómez-Cadenas A, Casaretto JA. Engineered drought-induced biosynthesis of α -tocopherol alleviates stress-induced leaf damage in tobacco. *Journal of Plant Physiology*. 2013;170(14):1285-1294.
- Fageria NK, Filho MB, Moreira A, Guimaraes CM. Foliar fertilization of crop plants. *Journal of Plant Nutrition*.

- 2009;32(6):1044-1064.
31. Falk J, Munné-Bosch S. Tocochromanol functions in plants: Antioxidation and beyond. *Journal of Experimental Botany*. 2010;61(6):1549-1566.
 32. Farouk S. Ascorbic acid and α -tocopherol minimize salt-induced wheat leaf senescence. *Journal of Stress Physiology & Biochemistry*. 2011;7(3):58-79.
 33. Fu JY, Htar TT, De Silva L, Tan DMY, Chuah LH. Chromatographic separation of vitamin E enantiomers. *Molecules*. 2017;22(2):1-17.
 34. Gajewska E, Skłodowska M. Relations between tocopherol, chlorophyll and lipid peroxides contents in shoots of Ni-treated wheat. *Journal of Plant Physiology*. 2007;164(3):364-366.
 35. Galatro A, Simontacchi M, Puntarulo S. Free radical generation and antioxidant content in chloroplasts from soybean leaves exposed to ultraviolet-B. *Physiologia Plantarum*. 2001;113(4):564-570.
 36. Gill SS, Tuteja N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiology and Biochemistry*. 2010;48(12):909-930.
 37. Grilo EC, Costa PN, Gurgel CSS, Beserra AFDL, Almeida FND, Dimenstein R. Alpha-tocopherol and gamma-tocopherol concentration in vegetable oils. *Food Science and Technology*. 2014;34(2):379-385.
 38. Gregory JF. Vitamins. In: Damodaran S, Parkin KL, Fennema OR, editors. *Fennema's Food Chemistry*. 4th ed. Boca Raton, FL: CRC Press; 2007. p. 439-523.
 39. Hasanuzzaman M, Fujita M. Exogenous sodium nitroprusside alleviates arsenic-induced oxidative stress in wheat (*Triticum aestivum* L.) seedlings by enhancing antioxidant defence and glyoxalase system. *Ecotoxicology*. 2013;22(3):584-596.
 40. Hasanuzzaman M, Nahar K, Fujita M. Plant response to salt stress and role of exogenous protectants to mitigate salt-induced damages. In: Ahmad P, Azooz MM, Prasad MNV, editors. *Ecophysiology and Responses of Plants under Salt Stress*. New York: Springer; 2013. p. 25-87.
 41. Hassan NMK, Shafeek MR, Saleh SA, El-Greadly HMN. Growth, yield and nutritional values of onion (*Allium cepa* L.) plants as affected by bioregulators and vitamin E under newly reclaimed lands. *Research Journal of Applied Sciences*. 2013;9(11):795-803.
 42. Hassanein RA, Bassuony FM, Baraka DM, Khalil RR. Physiological effects of nicotinamide and ascorbic acid on *Zea mays* plant grown under salinity stress: Changes in growth and oxidative defence systems. *Research Journal of Agricultural and Biological Sciences*. 2009;5(1):72-81.
 43. Hatfield JL, Prueger JH. Temperature extremes: Effect on plant growth and development. *Weather and Climate Extremes*. 2015;10:4-10.
 44. Herrera JM, Rubio G, Häner LL, Delgado JA, Lucho-Constantino CA, Islas-Valdez S, *et al.* Emerging and established technologies to increase nitrogen use efficiency of cereals. *Agronomy*. 2016;6(2):1-19.
 45. Hinch DK. Effects of α -tocopherol (vitamin E) on the stability and lipid dynamics of model membranes mimicking chloroplast membranes. *FEBS Letters*. 2008;582(25-26):3687-3692.
 46. Hofius D, Hajirezaei M, Geiger M, Tschiersch H, Melzer M, Sonnewald U. RNAi-mediated tocopherol deficiency impairs photoassimilate export in transgenic potato plants. *Plant Physiology*. 2004;135(3):1256-1268.
 47. Howarth CJ. Genetic improvements of tolerance to high temperature. In: Ashraf M, Harris PJ, editors. *Abiotic Stresses: Plant Resistance Through Breeding and Molecular Approaches*. New York: Howarth Press Inc.; 2005. p. 277-300.
 48. Hussain N, Irshad F, Jabeen Z, Shamsi IH, Li Z, Jiang L. Biosynthesis, structural, and functional attributes of tocopherols in plants: Past, present, and future perspectives. *Journal of Agricultural and Food Chemistry*. 2013;61(26):6137-6149.
 49. Hussein MM, Balbaa LK, Gaballah MS. Developing a salt tolerant cowpea using alpha tocopherol. *Journal of Applied Sciences Research*. 2007;3(10):1234-1239.
 50. Jain K, Kataria S, Guruprasad KN. Changes in antioxidant defences of cucumber cotyledons in response to UV-B and AAPH. *Plant Science*. 2003;165(3):551-557.
 51. Jie G, Liu GS, Guo J, Zhang J. Effects of vitamin E on protective enzymes and membrane lipid peroxidation in *Leymus chinensis* under drought stress. *Chemical Research in Chinese Universities*. 2008;24(1):80-83.
 52. Kanayama Y, Sato K, Ikeda H, Tamura T, Nishiyama M, Kanahama K. Seasonal changes in abiotic stress tolerance and concentrations of tocopherol, sugar, and ascorbic acid in sea buckthorn leaves and stems. *Scientia Horticulturae*. 2013;164:232-237.
 53. Kapoor D, Sharma R, Handa N, Kaur H, Rattan A, Yadav P, *et al.* Redox homeostasis in plants under abiotic stress: Role of electron carriers, metabolism mediators and proteinaceous thiols. *Frontiers in Environmental Science*. 2015;3:1-12.
 54. Karuppanapandian T, Moon JC, Kim C, Manoharan K, Kim W. Reactive oxygen species in plants: Their generation, signal transduction, and scavenging mechanisms. *Australian Journal of Crop Science*. 2011;5(6):709-725.
 55. Kaya C, Tuna AL, Dikilitas M, Cullu MA. Responses of some enzymes and key growth parameters of salt-stressed maize plants to foliar and seed applications of kinetin and indole acetic acid. *Journal of Plant Nutrition*. 2010;33(3):405-422.
 56. Kolota E, Osinska M. Efficiency of foliar nutrition of field vegetables grown at different nitrogen rates. In: *International Conference on Environmental Problems Associated with Nitrogen Fertilization of Field Grown Vegetable Crops*. 2001. p. 87-91.
 57. Kostopoulou Z, Therios I, Molassiotis A. Resveratrol and its combination with α -tocopherol mediate salt adaptation in citrus seedlings. *Plant Physiology and Biochemistry*. 2014;78:1-9.
 58. Kruk J, Strzalka K. Redox changes of cytochrome b559 in the presence of plastoquinones. *Journal of Biological Chemistry*. 2001;276(2):86-91.
 59. Kumar S, Singh R, Nayyar H. α -Tocopherol application modulates the response of wheat (*Triticum aestivum* L.) seedlings to elevated temperatures by mitigation of stress injury and enhancement of antioxidants. *Journal of Plant Growth Regulation*. 2013;32(2):307-314.
 60. Lalarukh I, Shahbaz M. Alpha-tocopherol induced modulations in morpho-physiological attributes of sunflower (*Helianthus annuus*) grown under saline environment. *International Journal of Agriculture and Biology*. 2018;20(3):661-668.
 61. Latha MR, Nadanassababady T. Foliar nutrition in crops. *Research Reviews*. 2003;24(3):229-234.
 62. Lee JY, Wang X, Cui W, Sager R, Modla S, Czymbek K, *et al.* A plasmodesmata-localized protein mediates crosstalk

- between cell-to-cell communication and innate immunity in Arabidopsis. *Plant Cell*. 2011;23(9):3353-3373.
63. Lichtenthaler HK. Biosynthesis, accumulation and emission of carotenoids, α -tocopherol, plastoquinone, and isoprene in leaves under high photosynthetic irradiance. *Photosynthesis Research*. 2007;92(2):163-179.
 64. Liu X, Hua X, Guo J, Qi D, Wang L, Liu Z, *et al*. Enhanced tolerance to drought stress in transgenic tobacco plants overexpressing VTE1 for increased tocopherol production from *Arabidopsis thaliana*. *Biotechnology Letters*. 2008;30(7):1275-1280.
 65. Lushchak VI. Environmentally induced oxidative stress in aquatic animals. *Aquatic Toxicology*. 2011;101(1):13-30.
 66. Mahajan S, Tuteja N. Cold, salinity and drought stresses: An overview. *Archives of Biochemistry and Biophysics*. 2005;444(2):139-158.
 67. Marzauk N, Safeek M, Helmy Y, Ahmed A, Shalaby M. Effect of vitamin E and yeast extract foliar application on growth and yield of broad bean (*Vicia faba* L.). *Middle East Journal of Applied Sciences*. 2014;4(1):61-67.
 68. Matringe M, Ksas B, Rey P, Havaux M. Tocotrienols can function as antioxidants and lipid protectors in tobacco leaves. *Plant Physiology*. 2008;147(2):764-778.
 69. Mekki BED, Hussien HA, Salem H. Role of glutathione, ascorbic acid and α -tocopherol in alleviation of drought stress in cotton plants. *International Journal of Chemical and Technological Research*. 2015;8(4):1573-1581.
 70. Mohamed AA, Aly AA. Alterations of secondary metabolites and enzyme activity using exogenous antioxidants in onion under salt stress. *American-Eurasian Journal of Scientific Research*. 2008;3(2):139-146.
 71. Mostafa MR, Mervat SS, Safaa REL, Ebtihal MAE, Magdi TA. Exogenous α -tocopherol improves growth of soybean (*Glycine max* L.) under saline conditions. *Journal of Horticultural Science and Biotechnology*. 2015;90(2):195-202.
 72. Mpoloka SW. Effects of prolonged UV-B exposure in plants. *African Journal of Biotechnology*. 2008;7(25):4874-4883.
 73. Munné-Bosch S. α -Tocopherol: A multifaceted molecule in plants. *Vitamins and Hormones*. 2007;76:375-392.
 74. Munné-Bosch S, Alegre L. The function of tocopherols and tocotrienols in plants. *Critical Reviews in Plant Sciences*. 2002;21(1):31-57.
 75. Munné-Bosch S, Alegre L. Drought-induced changes in antioxidants in chloroplasts. *Plant Physiology*. 2003;131(4):1816-1825.
 76. Munné-Bosch S, Schwarz K, Alegre L. Enhanced formation of α -tocopherol in water-stressed rosemary plants. *Plant Physiology*. 1999;121(3):1047-1052.
 77. Munné-Bosch S, Peñuelas J, Asensio D, Llusà J. Airborne ethylene alters antioxidant protection in holm oak. *Plant Physiology*. 2004;136(2):2937-2947.
 78. Munné-Bosch S, Falara V, Pateraki I, Lopez-Carbonell M, Cela J, Kanellis AK. Responses of isoprenoid pathway under drought. *Journal of Plant Physiology*. 2009;166(2):136-145.
 79. Orabi SA, Abdelhamid MT. Protective role of α -tocopherol on two *Vicia faba* cultivars against seawater-induced lipid peroxidation by enhancing capacity of antioxidative system. *Journal of the Saudi Society of Agricultural Sciences*. 2016;15(2):145-154.
 80. Ouchi A, Nagaoka SI, Suzuki T, Izumisawa K, Koike T, Mukai K. Synergistic and cancel effects on aroxyl radical-scavenging rate and suppression of prooxidant effect for coexistence of α -, β -, γ -, and δ -tocopherols. *Journal of Agricultural and Food Chemistry*. 2014;62(32):8101-8113.
 81. Oukarroum A, Strasser RJ, Schansker G. Heat stress and photosynthetic electron transport chain of the lichen *Parmelina tiliacea* in dry and wet states. *Photosynthesis Research*. 2012;111(1-2):303-314.
 82. Rady MM, Sadak MSH, El-Bassiouny HMS, Abdel-Monem AA. Alleviation of adverse effects of salinity stress in sunflower cultivars using nicotinamide and α -tocopherol. *Australian Journal of Basic and Applied Sciences*. 2011;5(10):342-355.
 83. Rahmawati N, Damanik RIM. Effect of foliar application of α -tocopherol on vegetative growth and biochemical constituents of soybean genotypes under salt stress. *IOP Conference Series: Earth and Environmental Science*. 2018;122(1):012049.
 84. Rautenkranz AAF, Li L, Machler F, Matinoia E, Oertli JJ. Transport of ascorbic acid and dehydroascorbic acids across membranes in barley (*Hordeum vulgare* L.). *Plant Physiology*. 1994;106(1):187-193.
 85. Reboul E, Richelle M, Perot E, Desmoulins-Malezet C, Pirisi V, Borel P. Bioaccessibility of carotenoids and vitamin E from dietary sources. *Journal of Agricultural and Food Chemistry*. 2006;54(23):8749-8755.
 86. Sadiq M, Akram NA, Javed MT. Alpha-tocopherol alters endogenous oxidative defence system in mungbean under water-deficit conditions. *Pakistan Journal of Botany*. 2016;48(6):2177-2182.
 87. Sadiq M, Akram NA, Ashraf M. Impact of exogenous tocopherol on physio-biochemical and yield attributes in mungbean (*Vigna radiata* L.). *Acta Physiologiae Plantarum*. 2018;40(1):1-14.
 88. Sakr MT, El-Metwally MA. Alleviation of harmful effects of soil salinity on wheat using antioxidants. *Pakistan Journal of Biological Sciences*. 2009;12(8):624-630.
 89. Saleem MS, Sajid M, Ahmed Z, Ahmed S, Ahmed N, Islam SU. Effect of seed soaking on germination and growth of bitter melon cultivars. *International Journal of Agriculture and Veterinary Science*. 2014;6(6):7-11.
 90. Sandorf I, Hollander-Czytko H. Jasmonate involvement in tocopherol biosynthesis in *Arabidopsis thaliana*. *Planta*. 2002;216(1):173-179.
 91. Sattler SE, Gilliland LU, Magallanes-Lundback M, Pollard M, DellaPenna D. Vitamin E is essential for seed longevity and preventing lipid peroxidation. *Plant Cell*. 2004;16(6):1419-1432.
 92. Semida WM, Taha RS, Abdelhamid MT, Rady MM. Foliar-applied α -tocopherol enhances salt tolerance in *Vicia faba*. *South African Journal of Botany*. 2014;95:24-31.
 93. Semida WM, Abd El-Mageed TA, Howladar SM, Rady MM. Foliar-applied alpha-tocopherol enhances salt tolerance in onion plants. *Australian Journal of Crop Science*. 2016;10(7):1030-1039.
 94. Sen CK, Khanna S, Rink C, Roy S. Tocotrienols: The emerging face of natural vitamin E. *Vitamins and Hormones*. 2007;76:203-261.
 95. Sereflioglu S, Dinler BS, Tasci E. Alpha-tocopherol-dependent salt tolerance related to auxin synthesis in soybean roots. *Acta Biologica Hungarica*. 2017;68(1):115-125.
 96. Shafeek MR, Helmy YI, Ahmed AA, Shalaby MAF. Productivity of snap bean plants by antioxidant spraying under sandy soil conditions. *Middle East Journal of*

- Agricultural Research. 2014;3(1):100-105.
97. Shahi S, Srivastava M. Foliar application of manganese for salinity tolerance in mungbean. *International Journal of Applied Biology and Pharmaceutical Technology*. 2016;7(1):148-153.
 98. Shahidi F, de Camargo AC. Tocopherols and tocotrienols in dietary sources: Occurrence and health benefits. *International Journal of Molecular Sciences*. 2016;17(10):1-29.
 99. Sharma P, Jha AB, Dubey RS, Pessarakli M. Reactive oxygen species and antioxidative defence mechanisms in plants. *Journal of Botany*. 2012;2012:1-26.
 100. Skłodowska M, Gapin M, Gajewska E, Gabara B. Tocopherol content and antioxidant activities in NaCl-stressed tomato plants. *Acta Physiologiae Plantarum*. 2009;31(2):393-400.
 101. Soltani Y, Saffari VR, Moud AAM, Mehrabani M. Effect of α -tocopherol and pyridoxine on growth and flowering of *Calendula officinalis*. *African Journal of Biotechnology*. 2012;11(56):11931-11935.
 102. Stern MH, Robeson CD, Weisler L, Baxter JG. α -Tocopherol: Isolation from soybean oil and properties. *Journal of the American Chemical Society*. 1947;69(4):869-874.
 103. Streb P, Shang W, Feierabend J. Resistance of winter rye leaves to photo-oxidative stress. *Plant, Cell & Environment*. 1999;22(10):1211-1223.
 104. Szarka A, Tomasskovics B, Bánhegyi G. The ascorbate-glutathione- α -tocopherol triad in abiotic stress response. *International Journal of Molecular Sciences*. 2012;13(4):4458-4483.
 105. Szymańska R, Kruk J. Plastoquinol synthesis and conversion to plastochromanol in *Arabidopsis*. *Plant and Cell Physiology*. 2010;51(4):537-545.
 106. Tang YL, Ren WW, Zhang L, Tang KX. Molecular cloning and characterization of a tocopherol cyclase gene from *Lactuca sativa* (Asteraceae). *Genetics and Molecular Research*. 2011;10(2):693-702.
 107. Terashima I, Miyazawa SI, Hanba YT. Why are sun leaves thicker than shade leaves? Consideration based on analyses of CO₂ diffusion in the leaf. *Journal of Plant Research*. 2001;114(1):93-105.
 108. Traber MG, Atkinson J. Vitamin E: Antioxidant and nothing more. *Free Radical Biology and Medicine*. 2007;43(1):4-15.
 109. Wang X, Quinn PJ. The location and function of vitamin E in membranes. *Molecular Membrane Biology*. 2000;17(3):143-156.
 110. Yang W, Cahoon RE, Hunter SC, Zhang C, Han J, Borgschulte T, *et al.* Vitamin E biosynthesis: Functional characterization of the monocot homogentisate geranylgeranyl transferase. *Plant Journal*. 2011;65(2):206-217.
 111. Ye YR, Wang WL, Zheng CS, Fu DJ, Liu HW, Shen X. Foliar application of α -tocopherol enhanced salt tolerance of *Carex leucochlora*. *Biologia Plantarum*. 2017;61(3):565-570.
 112. Yusuf MA, Kumar D, Rajwanshi R, Strasser RJ, Tsimilli-Michael M, Sarin NB. Overexpression of γ -tocopherol methyl transferase gene in transgenic *Brassica juncea* plants alleviates abiotic stress: Physiological and chlorophyll a fluorescence measurement. *BBA - Bioenergetics*. 2010;1797(8):1428-1438.
 113. Velíšek J, Cejpek K. Biosynthesis of food constituents: Amino acids: 2. The alanine-valine-leucine, serine-cysteine-glycine, and aromatic and heterocyclic amino acids groups. *Czech Journal of Food Sciences*. 2006;24(2):45-58.
 114. Yamamoto Y, Hori H, Kai S, Ishikawa T, Ohnishi A, Tsumura N, *et al.* Quality control of photosystem II: Reversible and irreversible protein aggregation decides the fate of photosystem II under excessive illumination. *Frontiers in Plant Science*. 2013;4:1-9.
 115. Zhou R, Yu X, Ottosen CO, Rosenqvist E, Zhao L, Wang Y, *et al.* Drought stress had a predominant effect over heat stress on three tomato cultivars subjected to combined stress. *BMC Plant Biology*. 2017;17(1):1-13.