

# Chapter 20

## Physiological Interventions of Antioxidants in Crop Plants Under Multiple Abiotic Stresses



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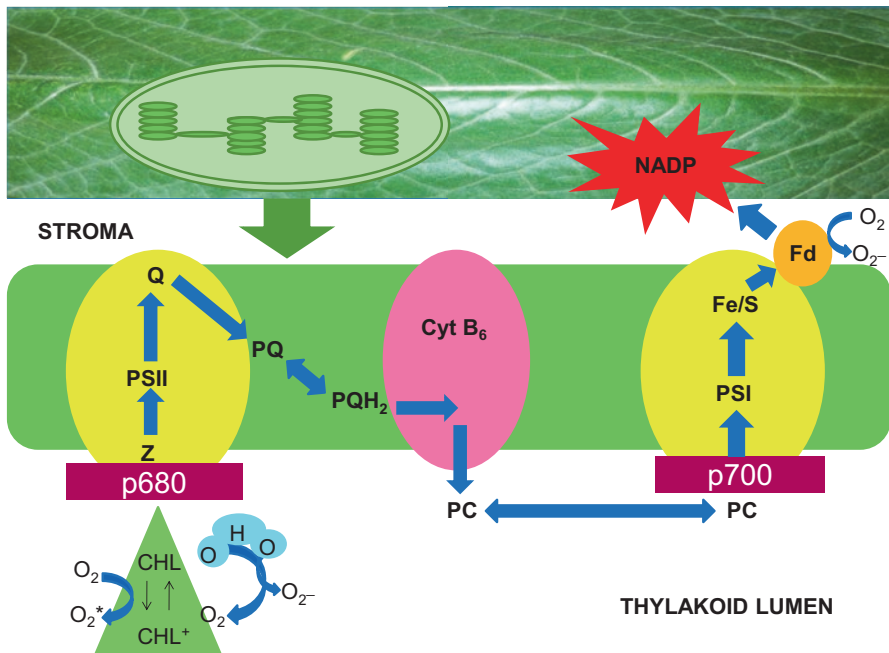
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### Introduction

The current environmental changes across the globe are serious threats to agriculture and all living organisms (Devendra, 2012). As a result of these environmental changes, global temperature may rise up to 3–4°C (WMO, 2014), which may lead to serious problems such as food shortage and starvation. Owing to these climate changes, plants are persistently facing different stresses such as salinity, heavy metals, drought, chilling, heat, increased sunlight, etc. Due to aforesaid stresses, yield of crops is being dwindled (Lamaoui, 2018; Dhangaye & Gadre, 2015; Gao et al., 2014) that will certainly affect increasing human population (Poljsak et al., 2013).

From chemistry point of view, oxidative stress on plants due to the abovementioned external stimuli imbalances the ROS-antioxidant interrelations (Fig. 20.1). Excess ROS production in response to various stresses has also been known to speed up peroxidation of lipids, DNA impairment, and carbonylation of proteins (Munns, 2008). Plants produced enzymatic and nonenzymatic antioxidants as a



**Fig. 20.1** Production of superoxide radical and singlet oxygen in chloroplast at PSII and PSI, respectively

defensive strategy to avoid cytotoxic effects (Shalata et al., 2001) but ultimately hindered plant growth obtained under saline conditions (Taarit et al., 2012a, b). Therefore, there is a need to grow plants under simulated saline conditions using exogenous enzymatic and nonenzymatic antioxidants. In this way, the toxic effects of salinity on the plant growth can be diminished, which is witnessed by various studies (Khan et al., 2013a, b, 2017; Husen et al., 2018).

### ***Strategies of Plants to Cope with Stress***

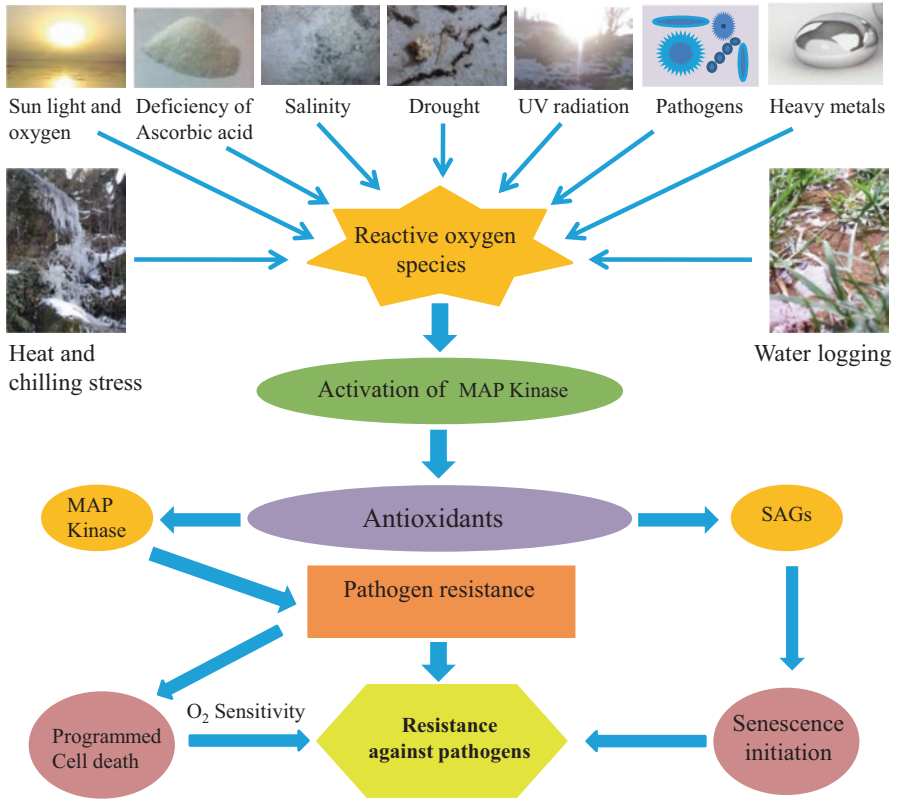
Plants adapted different strategies at cellular, physiological, biochemical, and molecular levels to cope with salinity stress (Gupta & Huang, 2014; Tamang & Fukao, 2015; Wang et al., 2018). For instance, plants respond to salinity by Na<sup>+</sup> selectivity and compartmentalization of Na<sup>+</sup> ions at cellular as well as tissue levels. Mechanisms of salt tolerance thus could be categorized into two major groups, that is, physiological and molecular.

Physiological mechanisms can further be explained by osmotic adjustment and/or water homeostasis, ion exclusion/inclusion and/or ion homeostasis, ROS scavenging, and hormonal biosynthesis (Batool et al., 2015). Among these mechanisms, water and ion homeostasis are mainly thought to counter antagonistic impacts of salinity on plant growth.

Moreover, many transcription factors such as heat shock factors (HSF) or ABA-responsive elements (ABF/ABRE) may induce salinity tolerance in plants (Vinocur & Altman, 2005). Stress-induced activation of molecular networks, signal transduction (starting from the roots toward cellular and whole plant levels), metabolites and specific gene expression are among decisive factors of plants to adapt against environmental stresses (Nguyen et al., 2018; Ismail et al., 2014; Ashraf, 2009; Vinocur & Altman, 2005). In plants, resistance to biotic stresses is usually controlled in a simple way, but salinity tolerance as an abiotic factor is controlled by the interaction of several genes (i.e., a few major genes along with several minor genes) (Ashraf & Harris, 2004; Batool et al., 2015). At the transcriptomic level, genes related to stress signaling, transcription regulation, ion transport mechanism, and biosynthesis of specific metabolites of complex signaling pathways are responsible for salt stress tolerance in plants (Cotsaftis et al., 2011; Kawasaki et al., 2001; Kumar et al., 2013; Walia et al., 2007).

### ***Abiotic Stresses and Plants***

Plants growth is significantly affected by various abiotic stresses, which resulted in low crop yields. Abiotic stresses included salinity, heavy metals, drought, chilling, temperature, water logging, and increased exposure to UV radiations (Dhamgaye & Gadre, 2015). Figure 20.2 explained the response of plants to various stresses.



**Fig. 20.2** Diagram showing response of plants to various stresses

Among multiple abiotic stresses, salinity is considered the most alarming, which constrained the agricultural production and adversely affected growth and yield of chief crops. Salt stress has affected 25% of the agricultural lands all over the globe due to application of saline irrigation water. Salinity reduced the water availability to crop plants (Taffouo et al., 2010; Ashraf, 2009). High concentrations of salts inhibited the growth of plants due to stumpy osmotic potential of lands, imbalanced nutrition, and selected ion effects (Parvaiz & Satyawati, 2008).

Drought, another abiotic factor, is threatening and has disturbed the economy of the world by reducing crop production (Cenacchi, 2014). Transgenic plants have been prepared to use genes that encoded proteins involved in drought tolerance. Accumulation of osmolytes is also one of the important mechanisms that helped the plants to tolerate drought stress in plants (Bechtold & Field, 2018).

Chilling stress also affects plant metabolism thus hindering plant growth and reproduction. The plants changed their pattern of gene expression to cope with chilling stress, thereby producing a suite of metabolites to protect plants against chilling (Sanghera et al., 2011).

UV radiations also cause a serious threat on the environment and oxidative damage in plants (Du et al., 2011). Due to stress environment, plants switched on their antioxidant system to reduce the toxic effects of stress (Carletti et al., 2013). Although UV-absorbing compounds mainly protected the DNA (Stapleton & Walbot, 1994), these compounds also played a key role in the plant antioxidative defense system and pathogens (Tuteja et al., 2001).

Moreover, heavy metals in the environment is a serious threat to agro-ecosystem and crop plants (Ashraf et al., 2015, 2017a, b; Mani & Kumar, 2014). Toxic levels of heavy metal in plants often result in the oxidative damage and disruption of structural and functionality of plant cells (Ashraf et al., 2018, 2020; Ashraf & Tang, 2017). The oxidative stress disturbs the equilibrium between prooxidant and antioxidant homeostasis (Flora et al., 2008). Waterlogging and salinity go parallel with each other and create severe problems for plant growth. One of the first responses to plant against waterlogging is reduction in stomatal conductance (Folzer et al., 2006). The deficiency of oxygen due to waterlogging generally leads to the substantial decline in photosynthetic efficiency (Kaur et al., 2018a, b; Ashraf et al., 2011; Ashraf & Arfan, 2005) and causes oxidative stress. Due to oxidative stress, reactive oxygen species produced and disturbed the metabolic process of plants (Ashraf et al., 2011; Ashraf, 2009). Excess of water also inhibit electron transport chain, respiration, and ATP formation due to hypoxia (low oxygen concentrations (Ashraf et al., 2011). The nutrient uptake and growth of the plants reduced due to the contrary effects of waterlogging (Ashraf et al., 2011).

Furthermore, the magnitude of temperature stress increased as the ambient temperature increases from a threshold level, which results in alteration in physio-biochemical mechanisms in plants (Kong et al., 2017). The extent of possible damage owing to increased temperature in plants depends on plant developmental stage experiencing the high temperature stress (Slafer & Rawson, 1995; Wollenweber et al., 2003).

### ***Antioxidants Combat Plant Abiotic Stresses***

Antioxidant defense system is the best strategy adapted by the plants to ameliorate the abiotic stresses. Plants produce a variety of enzymatic, nonenzymatic antioxidants, and hormones endogenously in response to aforesaid stresses (Albaladejo et al., 2017; Almeselmani et al., 2006; Kandil et al., 2017; Massoud et al., 2018). Enzymatic antioxidants included enzymes such as superoxide dismutase (SOD), peroxidase (POX), ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR), and polyphenol oxidase (PPO), whereas  $\alpha$ -tocopherol, carotenes, and ascorbic acid (vitamin C) are nonenzymatic antioxidants produced by the plants to alleviate the impacts of abiotic stresses on plants. It is noticed that the abovementioned endogenous production of antioxidant secondary metabolites is the best way but not enough in amount to cope with elevated salinity conditions (Srinieeng et al., 2015). It has been reported that antioxidants being supplied exogenously to plants

are also fruitful to mitigate plant stresses, particularly salinity (Agada, 2016). Al Kharusi et al. (2019) performed an experiment on date palm to induce salinity tolerance by application of antioxidants.

Ascorbic acid has been found to be involved in cell wall expansion, enhancement of cell division, leaf area, biosynthesis of photosynthetic pigments, and improvement in plant tolerance against multifarious stresses by scavenging ROS (Dey et al., 2016; Kasote et al., 2015). Moreover, salicylic acid also modulates the important physiological processes such as photosynthesis, osmoregulation, and nitrogen metabolism (Khan et al., 2013a, b). Salicylic acid also plays its role in the tolerance of plants against chilling, drought, salinity, UV radiations, pathogen, heavy metals, waterlogging, and heat stresses (Farheen et al., 2018; Khan et al., 2015; Palma et al., 2013). Exogenous application of trehalose alleviates the adverse effects of salinity stress in wheat by changing the physiological process (Alla et al., 2019; Mervat & Sadak, 2019; NematAlla et al., 2019). Ellagic acid, a natural polyphenolic antioxidant in various vegetables and fruits (Lima et al., 2014), is distributed in the vacuoles as water-soluble ellagitannin and played a vital role in plant defense against a number of stresses by capturing ROS effectively (Nagarani et al., 2014; Priyadarsini et al., 2002; Saul et al., 2011).

In addition, brassinolide captured ROS effectively and protects the plants from oxidative stress. Various literature reports confirmed its oxidative potential when applied exogenously against different stresses (Zhou et al., 2015; Behnamnia 2015; Javid et al., 2011; Li & Chory, 1999). Moreover, tocochromanols are effective and useful group of lipophilic phenolic antioxidants (Housam et al., 2014), which could protect key cell components by scavenging free radicals before prior to lipid peroxidation and/or DNA damage. The tocochromanols break the chain reactions involved in lipid peroxidation and shield the cellular membranes by repair and replacement of lipid in bilayer membranes (Falk and Munnè-Bosch, 2010; Mène-Saffrané & DellaPenna, 2010). On the other hand, exogenous GABA application improved stress tolerance by regulating the physio-biochemical processes and redox balance (Jin et al., 2019; Li et al., 2016). Similarly, carotenoids are important antioxidants used as photosynthetic apparatus in plants, algae, and cyanobacteria, which protected against photooxidative damage and contributed to light harvesting for photosynthesis (Ksas et al., 2015).

## **Mode of Exogenous Applications of Antioxidants**

### ***Foliar Applications of Antioxidants***

Foliar spray of an antioxidants is considered a shotgun approach to ameliorate the toxic effects of salinity. Foliar application is very economic mode of application to save the nutrients. Previously, Khan et al. (2006) and Athar et al. (2009) have performed experiments on wheat by applying different concentrations (0 and 100 mg

L<sup>-1</sup>) of ascorbic acid and found substantial improvements in the growth and development of wheat plants. Malik and Ashraf (2012) also performed experiment on wheat by applying different concentration of ascorbic acid and hydrogen peroxide to mitigate the effects of drought. Ahmad et al. (2014) studied the effect of salicylic acid and hydrogen peroxide (each 0, 20, and 40 mgL<sup>-1</sup>) on maize at low temperature stress. Noreen et al. (2009) reported that exogenous salicylic acid application improved salt stress tolerance in sunflower. Baber et al. (2014) also reported that salicylic acid application improved the performance of fenugreek under saline conditions. Noreen and Ashraf (2008) reported that exogenous salicylic acid application improved the physiology and growth of sunflower under saline conditions. Li et al. (2014a, b) stated that foliar spray of salicylic acid improved the photosynthesis and antioxidant system in *Torreya grandis*. Exogenous salicylic acid application improved the germination and early growth of wheat under salt stress (Sahli et al., 2019). Moreover, Desoky and Merwad (2015) performed an experiment on foliar applications of ascorbic acid and salicylic acid and found that co-application of both resulted in improved the growth and development of wheat under saline conditions (Hamideldin et al., 2017; Morsi et al., 2018; Rihan et al., 2017).

### ***Applications of Antioxidants Through Rooting Media***

In a number of studies, much attention has been given on stress tolerance by the application of antioxidants through rooting medium. It was observed that antioxidants increased photosynthetic rate via stomatal regulation, which was positively associated with stress tolerance. For example, Athar et al. (2009) found improved growth of wheat when ascorbic acid was applied through rooting medium at vegetative stage under salt stress. Malik and Ashraf (2012) also conducted experiment on wheat and applied ascorbic acid through rooting medium under drought stress and found substantial improvements in growth. In another study, Xu et al. (2015) evaluated the positive effects of ascorbic acid on *Festuca arundinacea* through rooting medium under water stress. Arfan et al. (2007) found improved growth of wheat when applied with the salicylic acid through rooting under saline conditions.

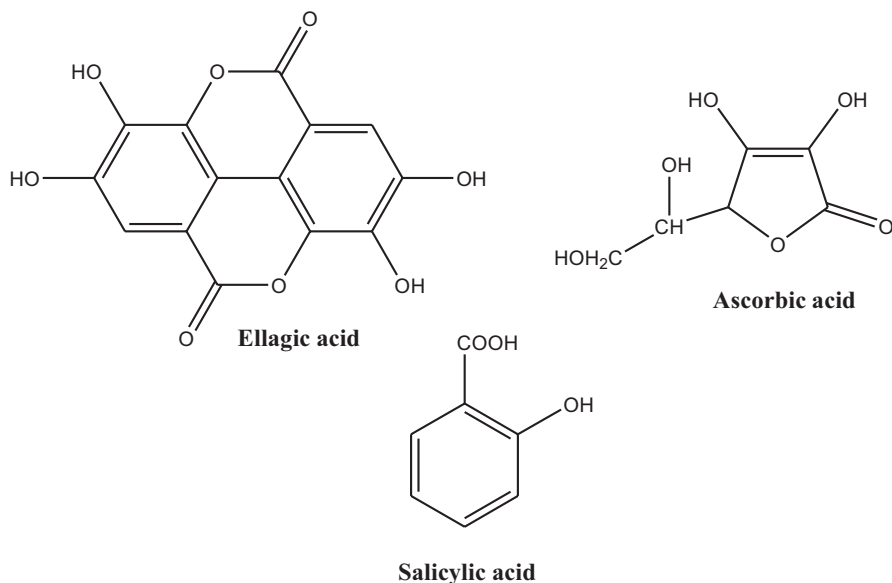
### ***Applications of Antioxidants by Seed Soaking***

Exogenous application of antioxidant compounds as a pre-sowing treatment has gained a considerable attention in ameliorating the adverse effect of salt stress. In this regard, El-Soud et al. (2013) observed that seed treatment of chickpea seeds with ellagic acid improved seed germination under PEG-induced stress. Seed soaking of soybean and other crops in distilled water or ASC solution for 4 h improved germination under associated physio-biochemical mechanisms under saline

conditions (Çavuşoğlu and Bilir 2015; Malik & Ashraf, 2012; Dehghan et al., 2011). Kasim et al. (2016) soaked radish seeds in *Pterocladia capillacea* and *Codium taylorii* extracts and found improved growth under saline conditions. Khan et al. (2006) observed positive effects of pretreatment of wheat seeds with ascorbic acid under saline conditions. Overall, pre-treatment of seeds with antioxidants increased endogenous level of ascorbic acid that had a protective effect on photosynthetic pigments against salt-induced oxidative stress; thus, antioxidants are involved in the regulation of many physiological functions to improve the performance of plants under stress conditions.

## Nonenzymatic Antioxidants

To fight against stresses, plants produced antioxidants (Fig. 20.3) that maintained the growth and provided strength under stress and non-stress conditions. Most commonly studied nonenzymatic antioxidants to mitigate the stresses on plant growth included ellagic acid, ascorbic acid, salicylic acid,  $\alpha$ -tocopherol, anthocyanins, brassinolides, and carotenes.



**Fig. 20.3** Structures of some important carboxylic acids used as antioxidants against salinity stress



## Ellagic Acid

Ellagic acid is a naturally occurring polyphenolic antioxidant that is present in several fruits including grapes, nuts, pomegranate, and a wide variety of berries as well as in vegetables (Malini et al., 2011). However, ellagic acid played several essential roles in plants under stress conditions such as DNA binding, scavenging of ROS, and inhibition of ROS production (Fig. 20.4) and protection of DNA from alkylating injury (Barch et al., 1996). Ellagic acid is also responsible for the restoration of normal functioning of various biomolecules. ROS depolarized cell membranes and hence disturbed the cell metabolism through seepage of essential ingredients from the cell (Hasanuzzaman, 2013). Ellagic acid has displayed antioxidant (Han et al., 2006; Sepúlveda et al., 2011), antibacterial (Han et al., 2006; Sepúlveda et al.,

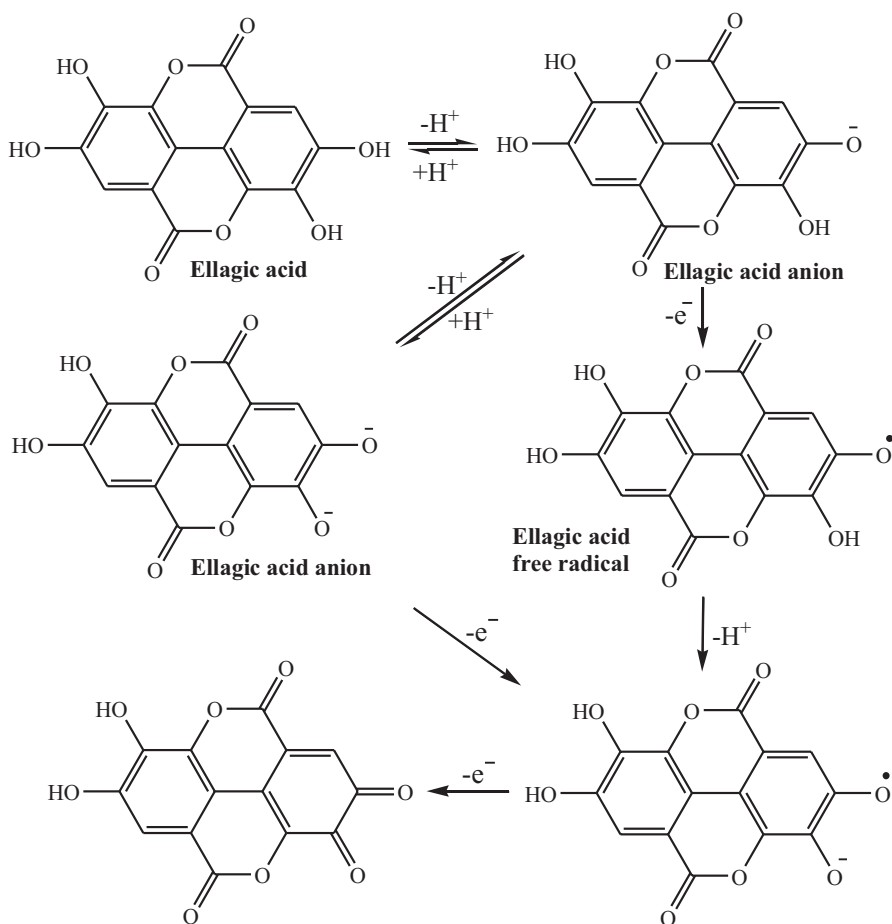


Fig. 20.4 Plausible free radical capturing mechanism of ellagic acid

2011), antiviral (Han et al., 2006; Sepúlveda et al., 2011), anti-inflammatory (Mehan et al., 2015), and anticancerous activities (Han et al., 2006; Mehan et al., 2015; Sepúlveda et al., 2011) in humans and inhibited UV-induced oxidative stress in plants with protection against lipid peroxidation (Bhandari, 2012).

More importantly, it effectively captured ROS at physiological pH to protect cells against toxic effects. Under such conditions, the ellagic acid anion is well known for its protective role, which continuously regenerated after capturing two free radicals, and thus proves more beneficial even at low concentrations (Galano et al., 2014). Moreover, the ellagic acid metabolites have also the ability to scavenge free radicals efficiently showing that its working performance is not reduced after being metabolized. This is an uncommon and constructive characteristic of ellagic acid, which made it particularly valuable against oxidative damage (Galano et al., 2014). Moreover, it has also been reported that ellagic acid provided better protection against oxidative stress and lipid peroxidation than vitamin E.

In another study, it has been investigated that the antioxidant activity of ellagic acid is mainly due to the presence of two pairs of neighboring hydroxyl groups in its structure, and it is very effective in inhibiting lipid peroxidation even at micromolar (low) concentrations. The scavenging activity of ellagic acid resembled those of other antioxidants such as vitamins E and C (Parthasarathi & Park, 2015; Galano, 2014; Indira et al., 2002).

A recent study showed that ellagic acid is bound to DNA by intercalating with the minor groove because of its planar structure. In this function, it activated various signaling pathways such as apoptosis, protected from oxidative DNA damage, and altered growth factor expression (Parthasarathi & Park, 2015). However, detailed investigations are still needed on bioavailability and absorption capacity of ellagic acid.

In a study, ellagic acid (50 ppm) was applied as a pre-seed treatment on chickpea seedlings, and it was found that ellagic acid accelerated the germination and growth with enhanced total antioxidant capacity and contents of compatible components (proline and glycine betaine) and antioxidant enzymes. Furthermore, ellagic acid decreased the lipid peroxidation levels, glutathione content, and seepage of solutes. Thus, the study discovered an improved salt tolerance of gram seedlings under osmotic stress by decreasing contents of  $H_2O_2$  and increasing total antioxidant capacity after ellagic acid treatment (Aguilera-Carbo et al., 2008; El-Soud et al., 2013).

### *Ascorbic Acid*

Ascorbic acid (Fig. 20.3) is a potential antioxidant to scavenge ROS produced under stresses (Kumar et al., 2014). Ascorbic acid possesses antioxidant and cellular reductant abilities, promotes plant growth and development, and regulates plant cellular mechanisms against environmental stresses (Hameed et al., 2015). Generally, ascorbic acid is present in all plant parts, subcellular compartments including the

cell wall and vacuole (Ferne & Szilvia, 2015) except dry seeds (Davey et al., 2000), and its concentration varies in different parts of plants (Klaue et al., 2016). Ascorbic acid is synthesized by almost all higher plants, while animals capable to oxidize L-gulono-1,4-lactone can synthesize ascorbic acid. It has been discovered that synthesis of ascorbic acid is regulated by the presence of jasmonate, which induced the transcription level and enhanced its production inside the cell (El Hariri et al., 2010; Smirnoff, 2005).

Plants release ascorbic acid in response to stresses. It not only captured free radicals but also activated complex biological defense mechanisms at cellular levels (Conklin & Barth, 2004) (Fig. 20.5). Exogenous ascorbic acid application reduced lipid peroxidation in seedlings of *S. fruticose* (Hameed et al., 2012) and *Brassica napus* (Dolatabadian et al., 2008) and *Phaseolus vulgaris* (Saeidi-Sar et al., 2013) and in perennial halophytes (Hameed et al., 2015) under salinity stress. Shalata and Neumann (2001) described the protective role of exogenous ascorbic acid that appeared to be associated to its antioxidant activity. Ascorbic acid via rooting medium, pre-sowing seed treatment, and foliar spray has been found reliable to reduce the effect of salinity in wheat (Azzedine et al., 2011; Raafat et al., 2011; Athar et al., 2008, 2009; Khan et al., 2006; Shalata & Neumann, 2001; Janda et al., 1999). It can also mitigate the toxic effects of oxidants, inhibit the uptake of sodium, and enhance the uptake of potassium (Conklin & Barth, 2004).

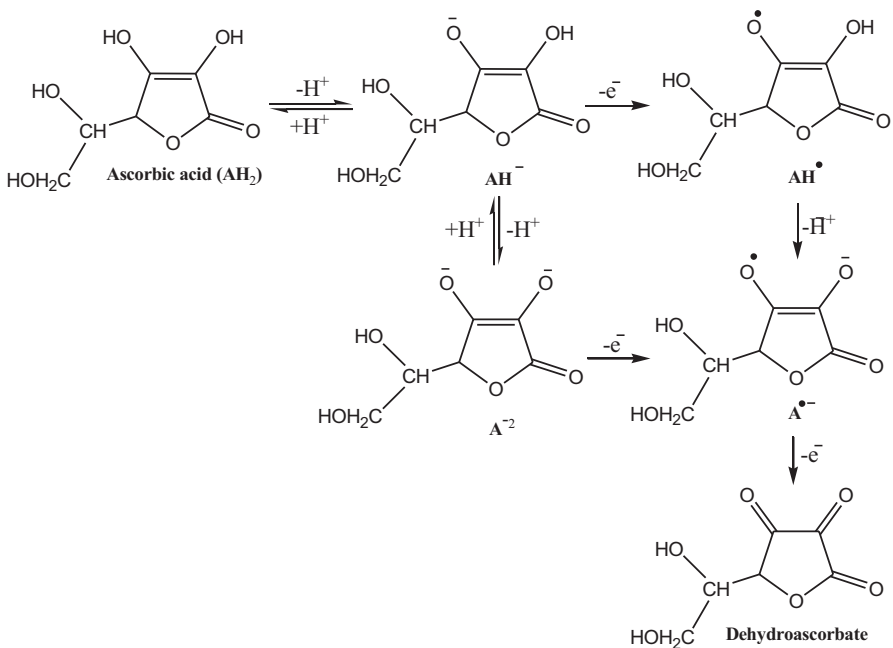


Fig. 20.5 Plausible free radical capturing mechanism of ascorbic acid

It has been indicated that ascorbic acid is centrally correlated with different physiological processes that involved plant growth and production (Hameed et al., 2012; Younis et al., 2010) and rapidly reached the target area owing to its greater solubility in water (Herschbach et al., 2010). Therefore, foliar application of ascorbic acid improved salt tolerance of crop plants in a number of ways (Athar et al., 2008; Dolatabadian et al., 2008; El Hariri et al., 2010; Farahat et al., 2013).

Chemically, ascorbic acid acts as a strong reducing agent and oxidized reversibly to dehydroascorbic acid. The investigation on the interactions of various chemicals with ascorbic acid and metal ions has shown that ascorbic acid, its oxidation product (dehydroascorbic acid), and intermediate, monodehydroascorbic acid free radical might function as cycling redox couples in electron transport and membrane electrochemical potentiation. It quenches oxidizing free radicals and other highly reactive oxygen-derived species such as the hydrogen peroxide, hydroxyl radical, and singlet oxygen by inactivating them in water-soluble compartments such as the plasma, cytosol, and extracellular fluid (Nimse & Pal, 2015).

Exogenous ascorbic acid application induces salt tolerance in wheat and improved  $\text{Na}^+$  ions accumulation, leaf chlorophyll contents, and photosynthetic machinery (Akram et al., 2017; Khan et al., 2006). Foliar application of ascorbic acid enhanced the plant biomass accumulation, photosynthetic pigments, and absorption of potassium and calcium ions (Khan et al., 2013a, b).

Application of ascorbic acid on roots not only enhanced the root growth, antioxidant activities, and photosynthetic rate but also improved the antioxidant activities (Athar et al., 2009). Ascorbic acid helped in the accumulation of potassium and calcium ions in the leaves; however, application of ascorbic acid on roots did not improve the growth of salt-stressed wheat plants (Athar et al., 2008). The exogenous application of ascorbic acid on leaves or via irrigation accelerated the antioxidant activities with enhanced contents of proline in wheat (Batool et al., 2012). The pre-treatment of barley with ascorbic acid improved seed germination traits, early growth, biomass accumulation, and anatomical features of barley under saline conditions (Çavuşoğlu & Bilir, 2015).

Foliar spray of ascorbic acid on *Cyamopsis tetragonoloba* grown under sea salt irrigation improved plant growth, photosynthetic pigments, protein contents, and potassium contents (Gul et al., 2015). Similarly, ascorbic acid improved seed germination, growth, yield, and ionic composition of eggplant under salt stress (Jan et al., 2016).

## ***Salicylic Acid***

Salicylic acid is one of the important antioxidants owing to its involvement in endogenous signal mediating local and systemic plant defense response against stresses. Salicylic acid is a growth regulator that promoted the growth of plants under stress and non-stress conditions (Rivas-San & Plasencia, 2011) (Fig. 20.3). Salicylic acid acts as a potential nonenzymatic antioxidant, which plays a key role

in regulations of various physiological processes in crop plants (Jayakannan et al., 2015; Arfanet al., 2007). It has also been found that plants release salicylic acid in response to multiple abiotic stresses such as heavy metal toxicity, water stress or drought, chilling stress, temperature, and osmotic stress (Jayakannan et al., 2015). Some earlier reports showed that exogenous application of salicylic acid could minimize the damaging effect of drought on wheat (Waseem et al., 2006) and heavy metals in rice (Khan et al., 2015).

Salicylic acid is a phenolic compound involved in many physiological and biochemical processes such as nitrogen metabolism, photosynthesis, proline metabolism and production of antioxidant system, glycine betaine, and plant water relations under stress conditions and thereby provided protection in plants against abiotic stresses (Viehweger, 2014; Miura & Tada, 2014; Khan et al., 2013a, b). In another study, salicylic acid was reported to induce salinity tolerance and increased biomass of *Torreya grandis* owing to improved chlorophyll content and antioxidant activity that eventually alleviated the oxidative stress (Li et al., 2014a, b).

The deficiency of salicylic acid in plants could make the effects of salt stress more worse and lead to substantial decline in plant growth (Mirdehghan & Ghotbi, 2014). Salicylic acid-induced pre-adaptation status in plants remained helpful in the acclimation to subsequent salt stress via reducing lipid peroxidation in terms of reduced malondialdehyde (MDA) content (Li et al., 2014a, b; Deng et al., 2012). In wheat, exogenous salicylic acid negated the salt stress-induced growth inhibition (Arfan et al., 2007).

Salicylic acid has variable effects on plants regarding plant adaptation to salt stress; however, the magnitude of protective effects depends on plant species, application dose, application method, and time of application (Metwally et al., 2003). Salicylic acid has obtained special attention owing to its protective effects on plants under NaCl salinity. Several studies have shown that the effects of cytotoxicity induced by salt stress can be overcome by exogenous application of salicylic acid (Dong et al., 2015). Salicylic acid can also act as an endogenous phytohormone, which may regulate various physiological and biochemical processes in plants (Abedini & Hassani, 2015). Foliar application of salicylic acid promoted growth, enzymatic, and photosynthetic activities in salt-stressed sunflower plants (Noreen et al., 2009). Foliarly applied salicylic acid on maize grown in saline soil showed positive effect at the vegetative stage of maize plants. Exogenous salicylic acid application prominently improved sugar, protein, and proline contents and antioxidant enzyme activities. On the other hand, chlorophyll, carotenoids, osmotic potential, and membrane stability index were reduced (Fahad & Bano, 2012).

In addition, exogenous application and salicylic acid concentrations significantly improved plant growth and development (Akhtar et al., 2013). The foliar spray of salicylic acid also protected citrus seedlings subjected to salt stress. Growth, chlorophyll (Chl) contents, relative water contents (RWC), maximal quantum yield of PS-II photochemistry, and gas-exchange attributes were negatively affected by salinity. In addition, cell membrane damage and proline contents were enhanced by salinity. It appeared that the best ameliorative remedies of salicylic acid were obtained when citrus seedlings were sprayed by 0.50 and 1.0 mM salicylic acid

solutions (Khoshbakht & Asgharei, 2015). Cucumber seedlings were treated with foliar salicylic acid applications at low concentrations, and it was noted that salt stress negatively affected the growth, chlorophyll content, and mineral uptake of cucumber plants. However, foliar applications of salicylic improved plant biomass accumulation. Moreover, salicylic acid application improved water contents of salt-stressed cucumber plants and reduced electrolyte leakage (Yildirim et al., 2008).

## Tocopherols

Tocopherols (Fig. 20.6) are lipophilic antioxidants, which are synthesized in plants and some photosynthetic microorganisms. Four isoforms ( $\alpha$ ,  $\beta$ ,  $\gamma$ ,  $\delta$ ) of tocopherols and tocotrienols, which vary in the positions and number of methyl groups in the chromanol ring, are found in nature (Eitenmiller et al., 2007). Plants mainly

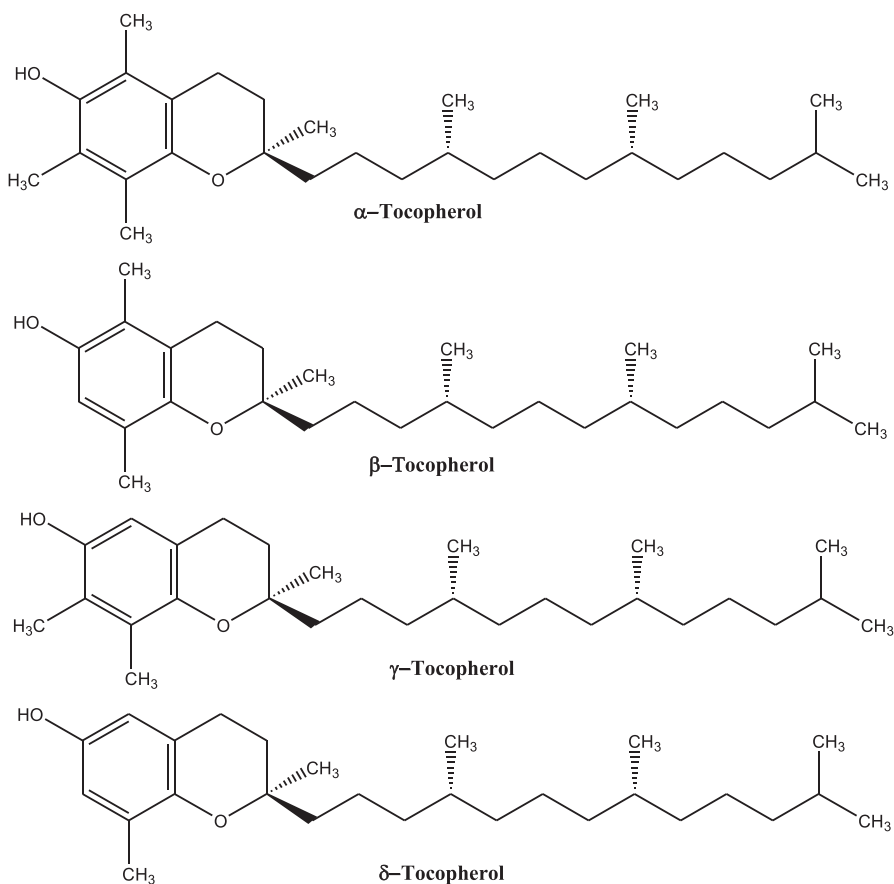


Fig. 20.6 Structures of important tocopherols

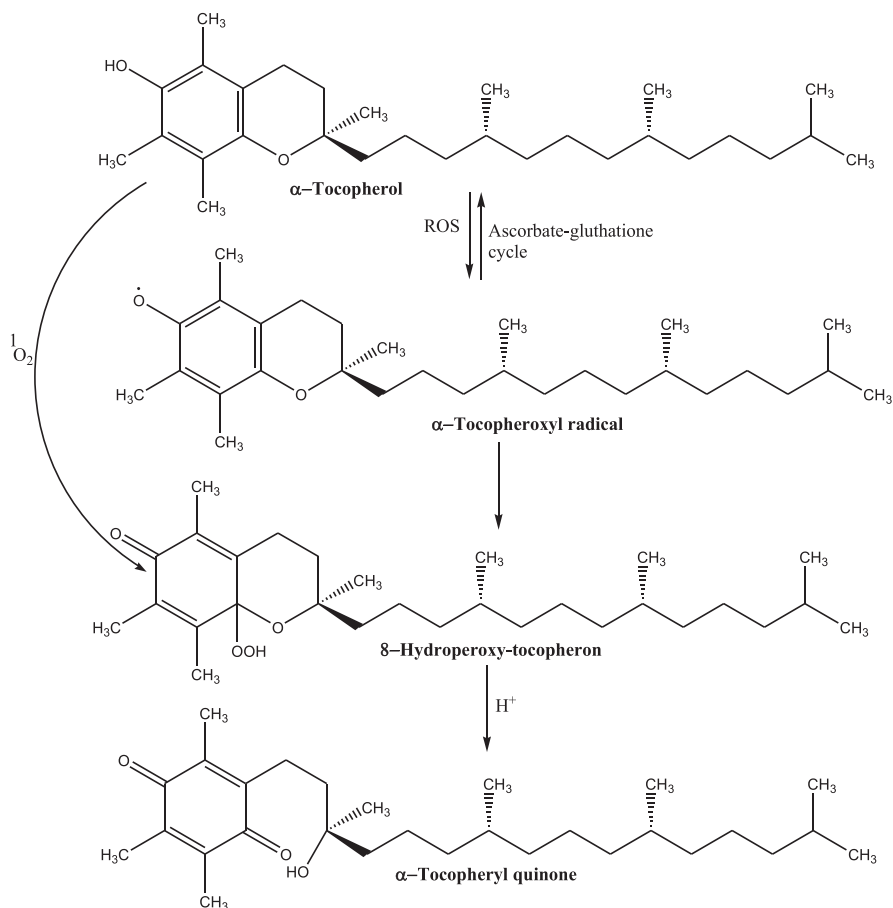
accumulated tocopherols to reduce the lipid oxidation (Falk & Munné-Bosch, 2010). Some evidences suggested that the effectiveness of antioxidant may vary between natural and synthetic source of tocopherols (Ahsan et al., 2015). To date, little is known about the specific roles of  $\alpha$ - and  $\gamma$ -tocopherols in different plant tissues. Tocopherol biosynthesis happens at inner envelope membrane of chloroplasts of photosynthetic organisms (Fritsche et al., 2014), which provides protection to photosynthetic machinery from oxidative damage and lipid peroxidation owing to enhanced ROS production under stress conditions. The important aspect of the biosynthetic pathway of tocopherols in plants has already been identified, whereas the enzyme tocopherol cyclase has been identified as a key enzyme of tocopherol biosynthesis (Ali et al., 2015).

Up to the 1990s, the function of  $\alpha$ -tocopherol in plants is believed to be associated only with antioxidant activity and maintenance of membrane integrity. Later on, it was found that  $\alpha$ -tocopherol has the ability to transmit cellular signals in plants as well as in animal cells. Experiments performed on mutant plants, which are unable to synthesize tocopherols, have proved this assumption. Tocopherols are the most effective group of lipophilic phenolic antioxidants, which protect key cell components by neutralizing free radicals before they can cause damage to cellular structures and functions (Espinosa-Diez et al., 2015).

Among tocopherols,  $\alpha$ -tocopherols (vitamin E), which contain three methyl groups, have an excellent antioxidant activity (Kamal-Eldin & Appelqvist, 1996). Protective mechanism of vitamin E is the quenching of ROS and removal of the polyunsaturated fatty acid radical species (Fig. 20.7), which are generated during lipid peroxidation (Shin et al., 2016; Raederstorff et al., 2015; Munne-Bosch, 2013; Bramley et al., 2000).

Vitamin E reduced the effect of seawater stress on growth, yield, and physiological and antioxidant responses of faba bean plant. Similarly, foliar application with  $\alpha$ -tocopherol on faba bean plants alleviated injuries and caused diluted seawater irrigation. The positive effects are related to the enhancement of protective parameters such as antioxidant enzymes, proline, carotenoids, and inorganic ions ( $K^+$  and  $Ca^{2+}$ ). Tocopherols also improved faba bean plant growth, yield, and quality of seeds (Orabi & Abdelhamid, 2016). Foliar application of tocopherols increased relative growth rate, plant nitrogen contents, and net assimilation rate and showed positive changes in all other parameters and productivity of soybean plants when grown under irrigation with moderately saline water (Rady et al., 2015). The antioxidants appraised to alleviate salinity-induced stresses in plants, which has been mentioned in Table 20.1.

Exogenous application of  $\alpha$ -tocopherols substantially improved salt stress tolerance in onion plants by inhibiting endogenous  $H_2O_2$  and lipid peroxidation and enhancing enzymatic (i.e., SOD, CAT, APX, and GR) and nonenzymatic (i.e., ascorbic acid and glutathione) antioxidant activities. Moreover,  $\alpha$ -tocopherol application improved photosynthetic efficiency and plant water status. Therefore, foliar application of  $\alpha$ -tocopherols could be used to induce salt tolerance in plants (Semida et al., 2014).



**Fig. 20.7** Conversion of  $\alpha$ -tocopherol into  $\alpha$ -tocopherylquinone by its reaction with ROS

## Anthocyanins

Anthocyanins are water-soluble, polar, and pigmented flavonoids (Bendary et al., 2013; Prior, 2006; Harborne, 1998; Holton & Cornish, 1995), which also contributed to the antioxidant properties (Longo & Vasapollo, 2006) in plants grown under saline conditions. Major sources of anthocyanins are cherries, strawberries, blueberries, raspberries, purple grapes, and black currants (Mazza, 2007) and found in the vacuoles of the epidermal and mesophyll cells (Chalker-Scott, 1999). Anthocyanins accumulated in expanding juvenile tissues and autumnal senescing leaves of deciduous species under stress (Amal et al., 2015; Close & Beadle, 2003). Anthocyanin supplementation through foods and beverages plays an important role in the prevention of diverse cardiovascular diseases, cancer, and a plethora of other diseases due to their strong antioxidant, detoxification, anti-proliferation, anti-angiogenic, and anti-inflammatory activities (Ames et al., 1993; Nikkhah et al., 2008).



**Table 20.1** Antioxidants used in various crops to alleviate salinity-induced effects

Sr. No.	Antioxidant	Crop	Mode	References
1	Ellagic acid	<i>Cicer arietinum</i> (chickpea)	Seed soaking	El-Soud et al. (2013)
2	Ascorbic acid	<i>Triticum aestivum</i> (wheat)	Foliar	Khan et al. (2006)
			Rooting	Athar et al. (2008)
			Seed soaking	Athar et al. (2009)
		<i>Helianthus annuus</i> (sunflower)	Foliar	Khan et al. (2013a, b)
		<i>Saccharum spontaneum</i> (wild sugarcane)	Foliar/rooting	Batool et al. (2015)
		<i>Solanum melongena</i> (eggplant)	Foliar	Elwan et al. (2007) and Jan et al. (2016)
		<i>Hordeum vulgare</i> (barley)	Seed soaking	Çavuşoğlu and Bilir (2015)
3	Salicylic acid	<i>Cyamopsis tetragonoloba</i> (guar)	Foliar	Gul et al. (2015)
		<i>Sesamum indicum</i> (sesame)	Seed soaking	Tabatabaei and Naghibalghora (2013)
		<i>Helianthus annuus</i> (sunflower)	Foliar	Noreen et al. (2009)
		<i>Zea mays</i> (maize)	Foliar	Fahad and Bano (2012)
		<i>Vigna radiata</i> (mung bean)	Foliar	Akhtar et al. (2013)
		<i>Citrus sinensis</i> (citrus)	Foliar	Khoshbakht and Asgharei (2015)
4	Tocopherols	<i>Cynara scolymus</i> (artichoke)	Foliar	Bagherifard et al. (2015)
		<i>Cucumis sativus</i> (cucumber)	Foliar	Yildirim et al. (2008)
		<i>Vicia faba</i> (horsebean)	Foliar	Orabi and Abdelhamid (2016)
		<i>Glycin max</i> (soybean)	Foliar	Rady et al. (2015)
		Mung bean seedling ( <i>Vigna radiata</i> )	Soaking	Farheen et al. (2018)
5	Anthocyanin	<i>Allium cepa</i> (onion)	Foliar	Semida et al. (2014)
		<i>Linum usitatissimum</i> (Linseed)	Foliar	Sadak and Dawood (2014)
		Role of anthocyanin in plant defense	Endogenous	Lev-Yadun and Gould (2009)
		Higher plants	Endogenous	Eryılmaz (2006)
		<i>Hibiscus esculentus</i> (okra)	Endogenous	Dkhil and Denden (2012)
6	Flavonoids	<i>Triticum aestivum</i> (wheat)	Endogenous	Tereshchenko et al. (2012)
		The photoprotective role of anthocyanin pigments in leaf tissues	Endogenous	Hughes (2007)
		Flavonoids production in plants under stress condition Giovanni	Endogenous	Agati et al. (2013)

(continued)

**Table 20.1** (continued)

Sr. No.	Antioxidant	Crop	Mode	References
7	Brassinosteroids	<i>Triticum aestivum</i> (wheat)	Foliar spray	Shahbaz and Ashraf (2007) and Eleiwa et al. (2011)
			Seed soaking	El-Feky et al. (2014)
		<i>Lycopersicon esculentum</i> (tomato)	Foliar	Behnamnia et al. (2015)
		<i>Leymus chinensis</i> Trin.	Foliar	Niu et al. (2016)
		<i>Oryza sativa</i> (rice)	Seed soaking	Sharma et al. (2015)
		<i>Citrullus lanatus</i> (water melon)	Spray	Cheng et al. (2015)
		<i>Lycopersicon esculentum</i> (tomato)	Spray	Slathia et al. (2012)
		<i>Leymus chinensis</i> (Chinese lyme grass)	Spray	Jin et al. (2015)
		<i>Zea mays</i> (maize)	Foliar	Anjum et al. (2011)
		<i>Solanum lycopersicum</i> (garden tomato)	Foliar	Hayat et al. (2012)
		<i>Gossypium hirsutum</i> (cotton)	Seed soaking	Fathima et al. (2011)
<i>Raphanus sativus</i> (radish)	Seed soaking	Mahesh et al. (2013)		
8	28-HBL	<i>Cicer arietinum</i> (chickpea)	Seed soaking	Ali et al. (2007)
		<i>Zea mays</i> (maize)	Seed soaking	Arora et al. (2008)
		<i>Triticum aestivum</i> (wheat)	Foliar	Eleiwa et al. (2011)
		<i>Brassica juncea</i>	Foliar	Hayat et al. (2012)
		<i>Triticum aestivum</i> (wheat)	Foliar	Yusuf et al. (2011)
			Seed soaking	El-Feky (2014)
		<i>Brassica juncea</i> (Chinese mustard)	Foliar	Alyemini et al. (2013)
9	24-EBL	<i>Pisum sativum</i> (garden pea)	Rooting	Fedina (2013)
		<i>Pisum sativum</i> L. (pea)	Seed soaking	Shahid et al. (2011)
		<i>Cucumis sativus</i> (cucumber)	Foliar spray	Fariduddin et al. (2013)
		<i>Solanum melongena</i> (eggplant)	Rooting	Wu et al. (2017)
			Rooting	Ding et al. (2012)
		<i>Cajanus cajan</i> (pigeon pea)	Rooting	Dalio et al. (2013)
		<i>Capsicum annuum</i> (pepper)	Foliar	Abbas et al. (2013)
		<i>Lactuca sativa</i>	Foliar and Seed soaking	Ekinci et al. (2012)
		<i>Brassica juncea</i>	Seed soaking	Kaur et al. (2018a, b)
		<i>Triticum aestivum</i> (wheat)	Foliar	Qayyum et al. (2007) and Shahbaz et al. (2008)
			Foliar	Talaat and Shawky (2013)
		<i>Acacia gerrardii</i>	Foliar	Abd Allaha et al. (2018)
		<i>Cucumis sativus</i> (cucumber)	Foliar	Anwar et al. (2018)
		<i>Phaseolus vulgaris</i>	Foliar	Rady (2011)
		<i>Hordeum vulgare</i> (barley)	Seed soaking	Kartal et al. (2009)
		<i>Cajanus cajan</i>	Rooting	Dalio et al. (2011)
<i>Fragaria x ananassa</i>	Foliar	Karlidag et al. (2011)		
<i>Grass seedlings</i>	Rooting	Wu et al. (2017)		

The promising antioxidant properties of anthocyanins in humans caused also an interest to study their role on plant growth under saline conditions. However, the ecophysiological roles of anthocyanins are manifold as compatible solutes in osmotic regulation, antioxidants, and photoprotectants by masking photosynthetic pigments and capturing ROS (Carletti et al., 2013; Hatier & Gould, 2008; Nakabayashi et al., 2014; Steyn et al., 2002). Anthocyanins are well recognized as an important component of *Quinoa* grains owing to their high nutritional value and health benefits (Alvarez-Suarez et al., 2014). The induced synthesis and accumulation of anthocyanins under stress at grain filling could be an important functional trait for grain nutritional quality of *Quinoa*. Anthocyanin captures free radicals generated from the cyanidin oxidation (Castañeda-Ovando et al. (2009) as well as defends plants against environmental stresses such as ultraviolet radiation, drought, temperature variations, and attraction of pollinators (Chalker-Scott, 1999; Close & Beadle, 2003; Leão et al., 2014; Stone et al., 2001).

Anthocyanins improve drought resistance in plants due to its ability to stabilize the water potential and thus hypothesized to be involved in osmotic regulation (Chalker-Scott, 2002; Oosten et al., 2013). Ploenlap and Pattanagul (2015) suggested that the increase in anthocyanin levels under water stress is mainly due to the photoprotection of chlorophylls by anthocyanins. The anthocyanin level was increased in the juvenile leaves under drought stress, however the accumulation of anthocyanins inhibited under severe stress conditions. Similarly, flavonoids with radical scavenging activity mitigated oxidative and drought stress in *Arabidopsis thaliana* (Nakabayashi et al., 2014). Moreover, it has been demonstrated that anthocyanins are potent antioxidants, displaying up to four times the ROS scavenging potential of trolox (Wang et al., 1997), an industry standard in gauging antioxidant potential. Moreover, in vivo monitoring of an oxidative burst (following mechanical wounding) showed that  $H_2O_2$  decreased more rapidly in red (anthocyanic) *Pseudowintera colorata* leaves than green ones. While the vacuolar storage of anthocyanins was found against their action as direct scavengers of ROS produced in the chloroplast, possibly due to cytoplasmic anthocyanins, which act as antioxidants. For example, Zhang et al. (2012) showed that leaves of an acyanic *Arabidopsis thaliana* mutant subjected to a high irradiance displayed a reduced DPPH (2,2-diphenyl-1-picryl-hydrazylhydrate) scavenging potential and increased oxidative damage (estimated by cell membrane permeability) as compared to wild-type anthocyanic leaves. It was further observed that anthocyanins in *Sambucus* spp. peduncles are responsible for ameliorating light stress during senescence, and anthocyanins may additionally prolonged the senescence period. This dichotomy in anthocyanin research is unwarranted, and its significance is still poorly acknowledged. Identification and exploration of those functions that anthocyanins perform in either reproductive or vegetative organs are necessary to understand the adaptive significance of anthocyanin production in plants.

## ***Brassinosteroids***

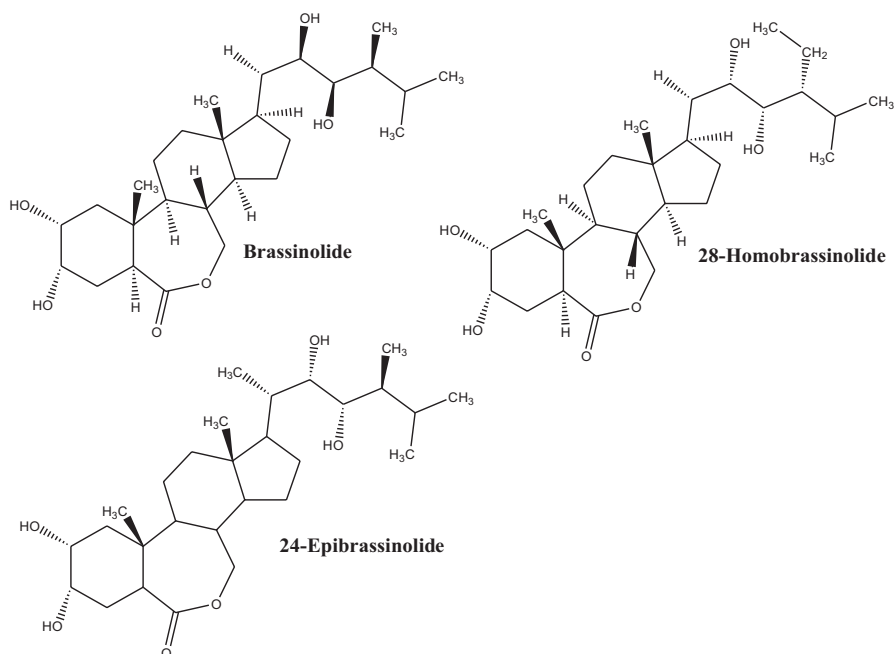
Brassinosteroids belong to a group of steroid plant hormones with significant growth promoting potential (Bishop & Yokota, 2001; Clouse & Sasse, 1998; Chory et al., 1989). Brassinosteroids have multiple effects on seed germination, growth, leaf abscission, and senescence (Sasse, 1997) although its mechanism is still obscure (Mathur et al., 1998). Moreover, brassinosteroids exert anti-stress effects on plants such as those caused by cold, heat, drought, and salt (Anuradha & Rao, 2003; Dhaubhadel et al., 2002; El-Feky, 2014; Kagale et al., 2007; Ogweno et al., 2008; Sharma et al., 2018). The brassinosteroids' stress response is an intricate sequence of biochemical reactions such as induction of protein biosynthesis, activation or suppression of key enzymatic reactions, and the production of multiple chemical defense compounds (Bajguz & Hayat, 2009; Jin et al., 2015).

Exogenous applications of brassinosteroids under salinity have long been known to improve growth and yield in many economically useful plant species (Cheng et al., 2015). In cereals, brassinosteroids promoted growth and yield attributes, whereas in leguminous crops, the number of pods per plant and total seed yield remained higher after the exogenous application of brassinosteroids (Rao et al., 2002). Growth and seed yield of rapeseed plants were also promoted by brassinosteroid application (Hayat et al., 2012; Sharma et al., 2018), and the same was reported for seed yield in cotton (Ramraj et al., 1997). Brassinosteroids removed the salinity-induced inhibition of seed germination and seedling growth in rice (*Oryza sativa*) and improved the chlorophyll biosynthesis and enhanced nitrate reductase activity under salt stress (Anuradha & Rao, 2003; Bajguz & Hayat, 2009).

Furthermore, brassinosteroids had no prominent effect on the leaf cell ultrastructure under normal conditions; however, damages imposed by salt stress on nuclei and chloroplasts were significantly reduced by brassinosteroid treatment in barley (Krishna, 2003). When salt solution was supplemented with brassinosteroids, the inhibitory effect of salt on rice seed germination was considerably reduced that is possibly associated with enhanced levels of nucleic acids and soluble proteins (Anuradha & Rao, 2009). The exogenous application of 28-homobrassinolide on *Pusa Basmati*<sup>1</sup>, a commercially important rice variety, resulted in reduced growth and protein and chlorophyll contents and increased proline and MDA contents of at early growth stages (Sharma et al., 2015).

The plants resulting from the seeds soaked in 28-homobrassinolide exhibited higher activities of nitrate reductase (23%) and carbonic anhydrase (31%), improved dry mass (34%) and nodule number (30%), content of leghemoglobin (28%), and nitrogenase activity (30%), while contents of nodule nitrogen and carbohydrate were decreased by 5% and 6%, respectively, with ultimate increase in yield (26%) in chickpea (Ali et al., 2007). The structures of some important brassinolides are given in Fig. 20.8.

In addition, the activities of antioxidative enzymes and protein contents were promoted in 28-HBL-treated maize plants. Moreover, application of 28-HBL reduced lipid peroxidation in salt-treated maize plants (Arora et al., 2008). Similarly,



**Fig. 20.8** The structures of some selected brassinolides

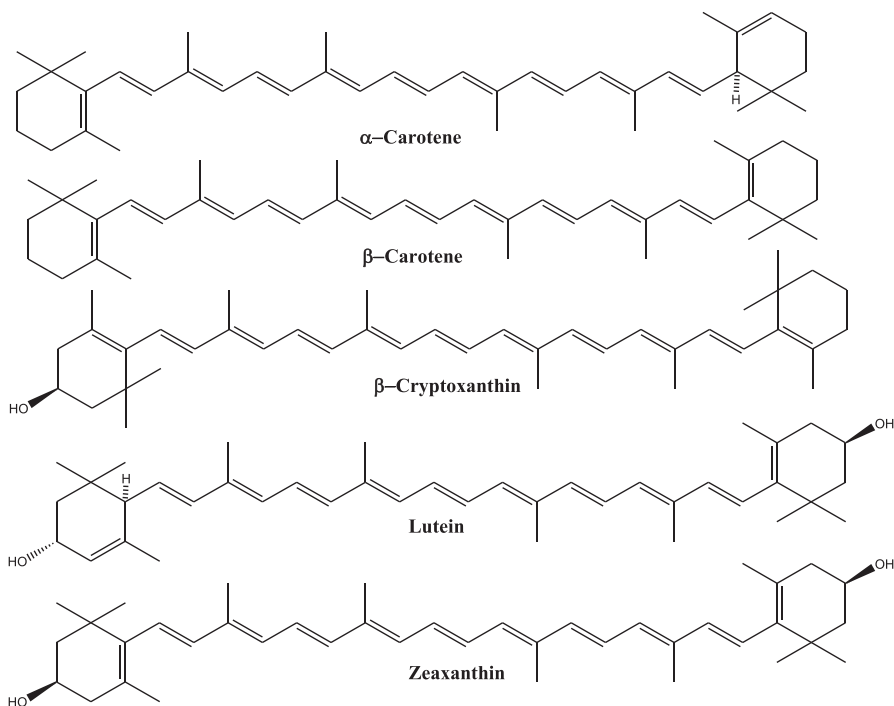
foliar spray of 28-HBL increased growth and yield attributes and photosynthetic pigments in wheat (Eleiwa et al., 2011). Activities of nitrate reductase and carbonic anhydrase, photosynthetic rate, and seed yield were decreased along with content of chlorophyll under salt stress; however, application of 28-HBL solutions stimulated morpho-physiological attributes in *Brassica juncea* (Alyemeni et al., 2013). Application of 24-epibrassinolide (24-EBL) attenuated the hostile effects of salinity on *Eriobotrya japonica* plants; however, the effect of 24-EBL was significant at 0.5 mgL<sup>-1</sup> under saline conditions (Sadeghi & Shekafandeh, 2014; Xue, 2012). Similarly, the grass seedlings were treated with 24-EBL and induce salinity tolerance (Wu et al., 2017). In similar studies, foliar spray of 24-EBL improved growth parameters of wheat and *Acacia gerrardii* plants significantly under saline and non-saline conditions; however, there was no prominent increase in the mineral contents of wheat plants (Abd Allaha et al., 2018; Ali et al., 2006; Shahbaz et al., 2008; Shahbaz & Ashraf, 2007). Exogenous application of brassinolide (1.0 mgL<sup>-1</sup>) enhanced growth, carbohydrate, and total soluble proteins in roots and shoots of wheat and improved the activities of hydrolytic enzymes, amylase, and protease as well under salt stress (El-Fekyl, 2014; Durigan et al., 2011). No doubt, brassinosteroids alleviated the inhibitory effects of salinity on germination, seedling growth, and crop yields; however, further studies are needed to uncover the tolerance mechanism imparted by brassinosteroids under stress conditions.

## Carotenoids

Carotenoids are among the most important nutrients in food and found in all plants as natural pigments. They are derived from acyclic C<sub>40</sub> isoprenoid lycopene that can be classified as a tetraterpene (Heider et al., 2014). Carotenoids are lipophilic microconstituents that have beneficial effects on human health and provide protection against cancer, cardiovascular diseases, and muscular regeneration (Rao & Rao, 2007; Sommer & Vyas, 2012). Till date, there are approximately 700 known carotenoids that can be categorized as  $\alpha$ -carotene,  $\beta$ -carotene, and lycopene and xanthophylls (zeaxanthin, lutein, and  $\beta$ -cryptoxanthin), which denote the oxygenated carotenoids fraction. The  $\alpha$ -carotene,  $\beta$ -carotene, and  $\beta$ -cryptoxanthin are promoters of vitamin A and are represented in Fig. 20.9.

In plants, carotenoids function a crucial role in protecting chlorophyll owing to their antioxidant properties, and the endogenous carotenoid contents are affected by several factors such as environmental, genetic, or man-made strategies (Fanciullino et al., 2006). The carotenoid-rich extract is usually used in food supplements, food additives, medicines, and cosmetics (Mezzomo & Ferreira, 2016).

The extent of expression of carotenogenic genes varied with stress conditions. For instance, carotenoid molecules present in the tissues are capable of neutralizing



**Fig. 20.9** The structures of some selected carotenoids

ROS; however, the mechanism of action of these molecules is based on the modifications of the cell metabolic functions, aimed at interacting with the polyunsaturated acyl groups of lipids to stabilize membranes and playing a protective role against ROS and synergic function with other antioxidants (Raposo et al., 2015). Table 20.2. shows uses and sources of some selected antioxidants.

**Table 20.2** Sources and uses of some important antioxidants

Serial No.	Compound	Class	Sources	Uses	References
1	Ellagic acid	Polyphenolic	Vegetables, nuts, grapes, pomegranate, berries	Antioxidant, antiviral, antibacterial, anti-inflammatory, anticancerous	Galano et al. (2014), Bhandari (2012) and Malini et al. (2011)
2	Ascorbic acid	Vitamin	All plant parts except dry seeds, citrus fruit	Antioxidant, growth regulator, anti-saline	Kumar et al. (2014), Hameed et al. (2015) and Klause et al. (2016)
3	Salicylic acid	Phenolic carboxylic acid	Berries, dates, grapes, guavas, apricots, green pepper, olives, tomatoes	Antioxidant, growth regulator, anti-saline	Viehweger (2014), Li et al. (2014a, b) and Abedini and Daie Hassani (2015)
4	Tocopherols	Phenolics	Vegetables and vegetable oils, nuts, grains	Antioxidants	Ahsan et al. (2015), Fritsche et al. (2014) and Raederstorff et al. (2015)
5	Anthocyanins	Flavonoids	Blueberries, cherries, raspberries, strawberries, black currants, purple grapes, red wine	Antioxidant, detoxification activity, anti-proliferation activity, anti-angiogenic activity, anti-inflammatory activity	Chukwu et al. (2012), Leão et al. (2014) and Nakabayashi et al. (2014)
6	Brassinosteroids	Steroid	Plants	Antioxidant, anti-stress, enhanced growth and yield	El-Feky (2014), Cheng et al. (2015) and Jin et al. (2015)
7	Carotenoids	Tetraterpenes	Tomatoes, carrots, and apricots, all fruit or vegetable	Anticancer, cardioprotective, antioxidant	Fanciullino et al. (2006)

## Enzymatic Antioxidants

The ROS are the by-products of aerobic metabolism, and their production is generally enhanced under stress conditions (Ashraf & Harris, 2013; Gómez-Bellot et al., 2013; Mugnai et al., 2009) through enhanced oxidizing metabolic activities occurring in chloroplasts, mitochondria, and microbodies and disruption of electron transport system (Pinheiro & Chaves, 2011). In this context, enzymatic antioxidants, that is, CAT, POX, and SOD, served as efficient ROS scavenging systems to evade the oxidative damage (Mittler et al., 2011; Saisanthosh et al., 2018) in plants under stress conditions.

### *Catalases (CAT)*

The CAT is a tetrameric protein of 244 kDa comprising four identical subunits of 59.7 kDa, and each subunit contains 527 amino acid residues, one haem group, namely, iron (III) protoporphyrin IX, and a tightly bound molecule of NADPH (Sofa et al., 2015). Stress conditions predispose the photosynthetic system of leaves to photoinhibition resulting in a light-dependent inactivation of the primary photochemistry associated with photosystem II (Ashraf & Harris, 2013). At low concentrations, H<sub>2</sub>O<sub>2</sub> acts as a signal molecule involved in the regulation of growth and development, specific biological/physiological processes, cell cycle, photosynthetic functions, and plant responses to biotic and abiotic stresses (Kovalchuk, 2010; Seki et al., 2007; Vadez et al., 2012). Oxidative stress and eventual cell death in plants can be caused by excess H<sub>2</sub>O<sub>2</sub> accumulation. Since stress factors provoked production of H<sub>2</sub>O<sub>2</sub> in plants, severe damage to biomolecules can be possible due to enhanced and non-metabolized cellular H<sub>2</sub>O<sub>2</sub> (Sofa et al., 2015; Foyer & Shigeoka, 2011; Apel & Hirt, 2004). Considering the key role of CAT in photorespiration, many authors focused on the role of CAT-catalyzed pathway under both drought and salt stress. Indeed, the maintenance of CAT activity in leaves of drought-stressed plants likely allowed the removal of photorespiratory H<sub>2</sub>O<sub>2</sub> produced (De Pinto et al., 2013). Under stress conditions, the photorespiration works as energy sink preventing the over-reduction of the photosynthetic electron transport chain and photo-inhibition (De Pinto et al., 2013). On this basis, photorespiration and CAT pathway cannot be considered wasteful processes but appreciated as a key subsidiary component of photosynthesis and important parts of stress responses in green tissues for preventing ROS accumulation (Bauwe et al., 2012; Voss et al., 2013).

Enzymes, that is, APX, GPX, and CAT, are able to scavenge H<sub>2</sub>O<sub>2</sub> with different mechanisms. Regulation of the CAT gene expression played an important role in the levels of CAT activity. The catalase gene expression is regulated by various mechanisms involving peroxisome proliferator-activated receptors (Ford et al., 2011; Sofa et al., 2015).



## ***Peroxidases***

Peroxidases (POXs) having molecular weight ranging from 30 to 150 kDa are widely distributed in nature. The POXs are involved in the detoxification of toxic pollutants, and its detoxification ability is dependent upon the reduction of peroxides such as  $H_2O_2$  (Saxena et al., 2011). These enzymes are produced by a variety of sources including plants, animals, and microbes, whereas POXs have the potential for bioremediation of wastewater contaminated with phenols, cresols, and chlorinated phenols used for biopulping and biobleaching in paper industry (Malar et al., 2014). Moreover, the POXs are also used as biosensors. The term POX represents a group of specific enzymes such as NADH-POX, glutathione-POX, and iodine-POX as well as a variety of nonspecific enzymes that are simply known as POXs. These oxidases and POXs have been reported as excellent antioxidants to degrade dyes (Caverzan et al., 2012). Specifically, the POX activity involved donating electrons that are bound to other substrates such as ferricyanide and ascorbate to break them into harmless components. Moreover, the POX donates two electrons to reduce peroxides by forming selenols and eliminates peroxides as potential substrate for the Fenton reaction (Liochev & Fridovich, 2003, 2010).

In addition, the use of POX for the degradation of pollutants has thrown more light on sustainable bioremediation strategies for polluting compounds and environmental protection using different enzymes. Environmental protection is influenced by interwoven factors such as environmental legislation, ethics, and education. Each of these factors played an important role in influencing national-level environmental decisions and personal-level environmental values and behaviors. For environmental protection to become a reality, it is important for societies and the nations to develop each of these areas that together will inform and drive environmental decisions.

## ***Superoxide Dismutase (SOD)***

Plant-antioxidant defense machinery comprising antioxidant enzymes and nonenzymatic antioxidant components metabolized ROS and their reaction products to avert oxidative stress conditions (Gill & Tuteja, 2010; Hasanuzzaman et al., 2012). The SOD is a metalloenzyme and one of the most effective components of the antioxidant defense system in plant cells against ROS toxicity. The SODs catalyzed the dismutation of  $O_2^{\cdot-}$  to  $H_2O_2$  and  $O_2$  in all subcellular compartments such as chloroplasts, peroxisomes, mitochondria, cytoplasm, nuclei, and the apoplast (Alscher et al., 2002; Gill & Tuteja, 2010). Moreover, the SODs are available at an intracellular concentration of  $10^{-5}$  M and occur in all oxygen-metabolizing cells and all subcellular compartments (Alscher et al., 2002; Fink & Scandalios, 2002). The SODs constituted the first-line defense against abiotic stress-induced enhanced ROS production and its reaction products. Nevertheless, all the SOD isoforms are

nuclear coded and, where necessary, transported to their subcellular targets by means of NH<sub>2</sub>-terminal targeting sequences (Pan et al., 2006).

Four different isoforms of SODs have been distinguished depending on the metal at the active center, which is manganese, iron, copper, and zinc (Miller & Sorkin, 1997). Previous studies denoted that most of the SODs are intracellular enzymes; these are Cu/Zn SOD (which is also extracellular), Mn-SOD, and Fe-SOD. Cu/Zn-SODs are generally found in the cytosol of eukaryotic cells and chloroplasts. The Mn-SODs are found in mitochondria and reported in chloroplasts and peroxisomes in some plants. The dimeric Fe-SODs, which are not found in animals, have been reported in chloroplasts of some plants (Gomez et al., 2003; Droillard & Paulin, 1990; Camp et al., 1994; Fridovich, 1995; Salin & Bridges, 1980).

In summary, to detoxify ROS, enzymatic and nonenzymatic antioxidant systems become upregulated, whereas H<sub>2</sub>O<sub>2</sub> is scavenged by CAT and POX. The SOD plays a determinant role in the protection against the toxic effects of oxidative stress by scavenging superoxide radicals and providing their conversion into O<sub>2</sub> and H<sub>2</sub>O<sub>2</sub> (Verma et al., 2003; Bowler et al., 1992). Overall, the enzymatic antioxidants are first-line defense of plants against oxidative stress owing to multiple biotic and abiotic factors.

## Conclusion

Throughout the world, environmental stresses are proved to be a fatal threat for agricultural productivity. Plants being sessile in nature have to face multiple abiotic stresses. Crops in arid and semiarid regions have to face uncertain periods of drought and extreme weather conditions. Thus, improving crop yields under such climatic conditions yield is vital to satisfy the increasing food demand. Phytohormones and plant growth regulators could play important role in this regard owing to their stress alleviatory role. Exogenous application of some phytohormones and plant growth regulators could substantially improve the enzymatic and nonenzymatic antioxidants to scavenge ROS and brought promising results regarding growth and productivity of crops under stress conditions. Moreover, the antioxidants play a diverse role in inducing abiotic stress tolerance in plants. Till now, a number of exogenous antioxidants have been reported, but still there is a need to discover more economical antioxidants so that they can be used for beneficial purposes.

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