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Genetic Engineering Applications in Inducing Stress Tolerance in Plants Through Antioxidants

Deepu Pandita

Abstract

Reactive oxygen species (ROS) is a necessary evil for the adaptation of plants in an oxygen-containing environment. ROS is mainly produced by electron transport system of chloroplasts (photosynthesis), mitochondria (during respiration), peroxisomes, and plant cell membrane. ROS in low concentrations is critical in some important plant metabolic pathways. It is estimated that beyond all the O_2 absorbed, approximately 1% of it is diverted to generate ROS. Higher levels of ROS concentration can damage plant cells, chlorophyll, lipids, proteins, carbohydrates, and nucleic acids by oxidative damage and can cause disruption of transport of ions, loss of enzyme activity, protein cross-linking, DNA damage, and programmed cell death (PCD) pathway activation and death of cells. In order to evade the oxidative damage, chloroplasts, mitochondria, and peroxisomes in plants provide complex antioxidative defense against ROS by numerous enzymatic and nonenzymatic antioxidant components. Abiotic stress tolerance and stress-induced oxidative protection/tolerance has been accomplished in several crop plants by generation of transgenics through detoxification strategies of overexpression of a battery of enzymatic and nonenzymatic antioxidants that scavenge oxygen radicals.

Keywords

Antioxidants · Genetic engineering · Stress tolerance · Reactive oxygen species (ROS) · Oxidative stress

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D. Pandita (✉)
Government Department of School Education, Jammu, Jammu and Kashmir, India

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5.1 Introduction

An inevitable consequence of adaptation of life to an oxygen-comprising environment was the nonstop production of reactive oxygen species (ROS) as the metabolism derivative in a biological system. ROS is mainly produced by electron transport chain system of chloroplasts (photosynthesis), mitochondria (during respiration), peroxisomes, and plant cell membrane or as a derivative of numerous cellular metabolic pathways. ROS originates from molecular oxygen and accumulate in plant tissues. In normal plant growth scenarios, production rate of ROS is low in different cell compartments. Exogenous abiotic environmental stresses for instance, chilling, drought, extreme heat, salinity, toxicity of heavy metals, pollutants, deficiency of nutrients, and UV can interrupt the cellular homeostasis, cell defense, and intra- and extracellular cell signaling and can induce the production and concentration of biochemically active reactive oxygen species (ROS) molecule through oxygen metabolism in that plant (Zurbriggen et al. 2009; Pandita 2021). But higher levels of ROS concentration can damage plant cells, chlorophyll, lipids, proteins, carbohydrates, and nucleic acids by oxidative damage and can cause disruption of transport of ions, loss of enzyme activity, protein cross-linking, DNA damage, and programmed cell death (PCD) pathway activation and death of cells. Hence, plants have evolved several complex mechanisms to maintain the ROS concentrations under balance by stringent reconnaissance (Ali and Alqurainy 2006; Ahmad et al. 2011a, b; Ozgur et al. 2013; Sharma et al. 2012). The ROS consists of both free radical (alkoxy radical (RO), superoxide radical ($O2^{\cdot -}$), hydroperoxyl radical ($HO_2^{\cdot}$), hydroxyl radical ($^{\cdot}OH$), and peroxy radical (ROdrogen peroxide (H_2O_2)). The free radical and nonradical forms are plant cytotoxic (Dismukes et al. 2001; Pandita 2021).

Toxic and destructive ROS production in plant cell alters metabolic functions of cell organelles like chloroplast and mitochondria. Their increased production is destructive and causes oxidative damage to organellar membranes and other vital biomolecules. Reactive oxygen species or reactive oxygen intermediate (ROI) are partially a reduced form of atmospheric oxygen (O_2). Their production is due to the excitation of oxygen (O_2) to form singlet oxygen ($^1O_2$) or transfer of one or two or three electrons to O_2 to form superoxide radical (O_2^-) or hydroxyl radical (HO^-). ROS acts as signal molecule for the activation of stress-response and defense mechanism in plant body. Oxygen is vital for the cell; however, under stress conditions, it undergoes a series of reactions to form reactive oxygen species and jeopardize survival of cells (Ahmad et al. 2010a, b, 2011a, b; Ahmad and Umar, 2011; Choudhury and Panda 2013). ROS and antioxidant balance completely scavanges ROS. This leads to the loss of ROS, which is a significant second messenger in intracellular signaling cascade. Disturbance of this balance leads to oxidative stress (Dalton et al. 1999; Tuteja, 2007; Khan and Singh, 2008; Tuteja, 2010; Ahmad et al. 2010a, b, 2011a, b; Ahmad and Umar, 2011). To avoid the oxidative damage, chloroplasts, mitochondria, and peroxisomes in plants provide complex antioxidative defense against ROS by producing numerous enzymatic and nonenzymatic antioxidant components (Sharma and Dubey, 2007; Zurbriggen et al.

2009; Gill and Tuteja, 2010; Saed-Moucheshi et al. 2014). Plants accumulate compatible solutes as well under abiotic stresses (Ashraf and Fooland 2007).

5.2 Reactive Oxygen Species (ROS) and Oxidative Stress

Molecular reduction of O_2 results in the production of ROS containing O_2-, H_2O_2, OH, and $^1O_2$ (Asada, 1999; Ahmad et al. 2008, 2010a, b, 2011a, b; Ahmad and Prasad 2012a, b; Ahmad et al. 2013). ROS free radicals comprise of oxygen with at least one unpaired electron. Unpaired electrons pair with other electrons for a stable conformation. These free radical forms swiftly react with other molecules and generate supplementary free radicals (Foyer and Halliwell, 1976).

Abiotic stresses increase generation and assemblage of very reactive reactive oxygen species. This sequentially leads to oxidative stress. Compounds responsible for tolerance, e.g., heat shock proteins (HSP) in temperature stress, also activate oxidative bursts (Panchuk et al. 2002; Lee et al. 2000). Advancement of ROS detoxification is emblematic of the reaction to abiotic and biotic stresses (Munné-Bosch et al. 2004). Disruption in cellular homeostasis reduces molecular oxygen and changes it into ROS by high energy electrons (Rizhsky et al. 2002a, b; Mittler, 2002). In living conditions, $^1O_2$, H_2O_2, $O_2^{\cdot}-$, and $^{\cdot}OH$ reactive oxygen species damage all organic components (Snider et al. 2008). ROS generates at low levels in chloroplasts, mitochondria apoplasm, and peroxisomes and endoplasmatic reticulum (Polle 2001; Ashraf 2009; Ahmad and Umar 2011; Ahmad and Prasad 2012a, b; Ahmad et al. 2013). Under normal conditions of growth, ROS production increases during environmental stress conditions (Laloi et al. 2004; Ahmad and Umar 2011; Ahmad and Prasad 2012a, b; Zare and Pakniyat 2012; Ahmad et al. 2013; Rasool et al. 2013) and reacts directly with numerous metabolites for instance, lipids (peroxidation), proteins (degradation, inactivation) and nucleic acids (DNA/RNA disruption) pigments, and other vital cellular molecules causing cell membrane injury and cell death (Apel and Hirt 2004; Bencze and Veisz 2005; Gao et al. 2008; Ashraf 2009; Mittler et al. 2011).

Abiotic or biotic stresses produce ROS by NADPH oxidases (Pei et al. 2000). Plants have three main pathways for ROS generation:

1. Electron transport chain (ETC) in photosynthetic chloroplasts and powerhouses of mitochondria.
2. A number of peroxidases and oxidase processes (glycolate oxidase, NADH oxidase, NADPH oxidase, amine oxidase, xanthine oxidase, and lipoxygenase).
3. Photosensitizer molecules holding chlorophyll (Blokhina et al. 2003).

Inadequate CO_2 fixation along with reduced ETC is the principal goal of ROS generation in chloroplasts. During photorespiration, glycolate oxidation into glyoxylic acid produces H_2O_2 in plant peroxisomes (Mittler et al. 2004). Stress disturbs functions of mitochondria, resulting in accumulation of ROS and in turn oxidative damage to lipids of membranes (Vacca et al. 2004; Suzuki and Mittler

2006). Electrons from NADH produced by enzymes of Krebs cycle reduce O_2 to reactive oxygen intermediates (ROI) by ETC (Davidson and Schiestl 2001). This process suppresses ROI production during stress conditions and induces several defense genes, e.g., scavenging enzymes of ROI (Mittler 2002). The ROS signaling molecule has roles in growth, development, biotic and abiotic stress, and the programmed cell death of plants. ROS overproduction causes oxidative stress. In oxidative stress, capability of cellular defense system to eliminate ROS molecules is lesser than ROS generation. The balance between the production of ROS and the consumption of ROS shifts toward higher generation of ROS (Ahmad et al. 2008, 2010a, b, 2011a, b; Ahmad and Umar 2011). The swift ROS production known as oxidative burst is an indispensable process. Respiratory burst oxidase homolog (Rboh) genes, which encode NADPH oxidases, are key producers of signal transduction-associated ROS (Miller et al. 2009). Certain signaling pathways exponentially enhance the ROS amount to battle against infection and stress in plants. This exponentially increased ROS is labeled as the oxidative burst. The positive power of ROS in low concentrations is decisive in certain vital plant pathways. The estimations state that beyond all the O_2 absorbed, approximately 1% of O_2 is sidetracked to ROS production (Tuteja 2010; Sharma et al. 2012). The localized and temporal ROS production and ROS scavenging are probably very critical in cellular and intracellular transduction of ROS signals (Panchuk et al. 2002). Therefore, two slightly opposite functions of ROS highlight the necessity to regulate steady state level of ROS in plant cells. This provides an extra potent approach for improving crop tolerance to various stresses (Suzuki and Mittler 2006). ROS-scavenging mechanisms protect plants (Yabuta et al. 2002; Yoshimura et al. 2004).

5.3 Scavenging of Reactive Oxygen Species (ROS)

Stress factors induce oxidative stress and antioxidative enzyme expression in bacteria, yeast, and plants (Morgan et al. 1986; Davidson et al. 1996; Jaleel et al. 2007; Esfandiari et al. 2007). ROS is a by-product of stress in plants, which damages cellular organelles (Xiaozhong and Huang 2000; Polle 2001). For protection of cellular and subcellular systems from oxidative damage, plant's responses have developed various ROS scavengers consisting of functionally interlocked protective detoxification systems of enzymatic and nonenzymatic antioxidants for neutralizing cytotoxic effects of ROS (Sairam and Tyagi 2004). The detoxification systems include protective molecules like isoprene, glycine betaine, α-tocopherol (vitamin E), and carotenoids and antioxidant metabolites, for instance, ascorbic acid and glutathione (Sakamoto and Murata 2001; Young et al. 2004; Markovska et al. 2009). Several plants under stressed condition synthesize and accumulate antioxidant enzymes as defensive mechanism. Antioxidant system consists of a battery of enzymes that scavenge oxygen radicals, for instance, dehydroascorbate reductase, ascorbate peroxidase (APX), superoxide dismutase (SOD), catalase (CAT), glutathione reductase, glutathione peroxidase (GPX), and peroxiredoxin (PrxR) (Kubo et al. 1999; Sairam et al. 2000; Shah et al. 2001; Iba 2002; Mittler et al. 2004).

Antioxidants in excess bind to ROI molecule and detoxify or scavenge it. Antioxidative activities of antioxidants upregulate under stress, but their activities are diverse in different species (Smirnoff 2005).

5.3.1 Nonenzymatic Antioxidants

The nonenzymatic antioxidants include glutathione (GSH), tocopherols, carotenoids, ascorbate (AsA), flavonoids, flavones, and anthocyanins (Fig. 5.1) (Schafer et al. 2002; Gupta et al. 2005; Ahmad et al. 2008, 2010a, b, 2011a, b; Ahmad and Umar 2011; Ahmad and Prasad 2012a, b; Ahmad et al. 2013; Rasool et al. 2013). These antioxidants function as redox buffers, which show ROS interaction and acts as metabolic interface that modulates proper induction of acclimation responses (Foyer and Noctor 2005). Ascorbate and glutathione are vital nonenzymatic antioxidants of ascorbate-glutathione cycle (Rasool et al. 2013; Ahmad et al. 2013).

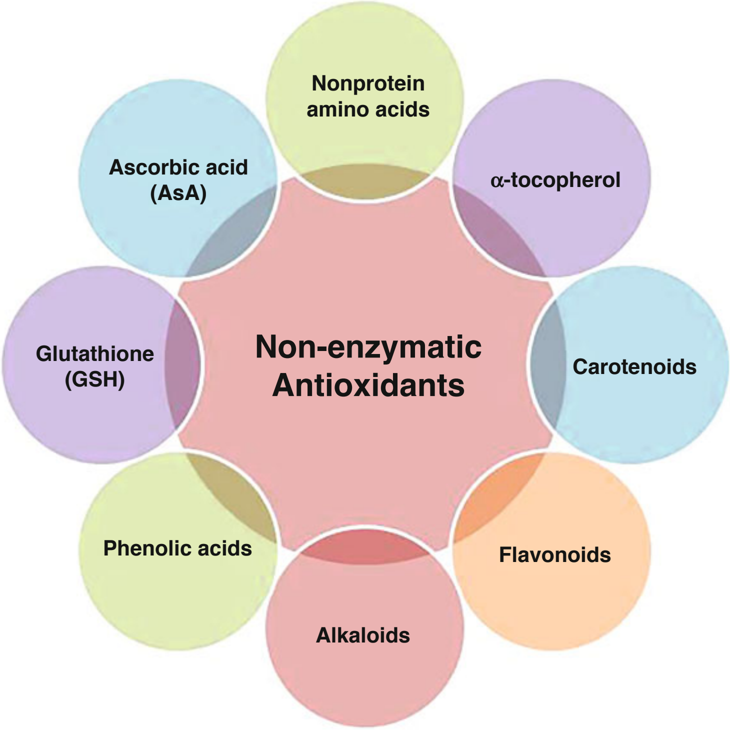

Fig. 5.1 Nonenzymatic antioxidants

5.3.1.1 Glutathione (GSH)

Glutathione (GSH) is tripeptide γ-glutamylcysteinylglycine (γ-glu-cys-gly) metabolite with significant role in plants. GSH appears in reduced form in tissues of plant. GSH is localized in cytosol, apoplast, chloroplasts, peroxisomes, mitochondria, vacuoles, endoplasmic reticulum, and scavenges peroxides (Noctor and Foyer 1998; Jimenez et al. 1998; Asada 1999; Gill and Tuteja 2010; Szarka et al. 2012; Ramírez et al. 2013). Inside plant cells, GSH exists in reduced form (GSH) and oxidized disulfide form (GSSG) (Shu et al. 2011).

GSH is the most important antioxidant and plays a vital function in antioxidative defense system and pathogen tolerance and detoxifies ROS by the regeneration of ascorbic acid through ascorbate-glutathione cycle and protects plants from oxidative damage (Foyer and Halliwell 1976; Noctor and Foyer 1998; Ogawa 2005; Shiu and Lee 2005; Shan et al. 2011). GSH is a substrate of glutathione S-transferase (GST) and detoxifies dehydroascorbate reductase (DHAR) and xenobiotics (Mendoza-Cozatl and Moreno-Sanchez 2006). GSH conserves cellular redox equilibrium by combining with its GSSG under stressful or normal conditions (Wang et al. 2008).

5.3.1.2 Ascorbate (Ascorbic Acid)

Ascorbate is a water soluble metabolite, ubiquitous antioxidant, and enzyme cofactor molecule, with localization in different organelles of cell, such as apoplast, chloroplast, cytosol, mitochondria, and peroxisome, has roles in photosynthesis, photo protection, growth of cell wall, and development, and fights against stress, biosynthesizes ethylene, gibberellins, hydroxyproline and anthocyanins (Wolucka and Van Montagu 2003; Mellidou et al. 2012). It plays central role in the removal of H_2O_2 and singlet oxygen (Noctor and Foyer 1998; Asada 1999). Ascorbic acid frequently occurs in reduced state (ascorbic acid/vitamin C) in plant leaves and chloroplasts under normal conditions and two oxidized ascorbate forms of mono-ascorbic acid and dehydroascorbic acid. The ratio of reduced and oxidized ascorbate forms is a principal factor that influences plant tolerance to oxidative stress (Conklin et al. 2000; Zechmann 2011; Cruz-Rus et al. 2012). Concentration of ascorbic acid in cells increases to millimolar range (Smirnoff 2005).

Ascorbate is the most powerful compound for detoxification of reactive oxygen species due to its capability to provide electrons in various nonenzymatic or enzymatic reactions. Ascorbic acid directly quenches O_2^-, $^1O_2$, and hydroxyl radicals, reduces H_2O_2 via glutathione-ascorbate cycle, and takes part in redox signaling, gene expression modulation, and enzymatic activity regulation (Foyer et al. 1997; Zechmann 2011). Ascorbate on reaction with reactive oxygen species produces monodehydroascorbate (MDHA), which disproportionates into dehydroascorbate (DHA) and ascorbate (Smirnoff et al. 2001). Ascorbic acid recovers tocopherols from tocopheroxyl radical and offers protection of membrane. Consequently, increased ascorbic acid levels in plants balance detrimental influences of oxidative stress (Smirnoff 2005).

5.3.1.3 Proline

Proline accumulates safeguard cellular redox potential and protects plants as ROS detoxification molecule. It maintains integrity of cell membranes and stabilizes antioxidant enzymes. Proline over accumulation has toxic effect on plant cells (Rizhsky et al. 2004a, b).

5.3.1.4 Tocopherols

Tocopherols (α-tocopherol) are lipid soluble metabolites with antioxidant and nonantioxidant potential, present in all plant parts produced by photosynthetic organisms with localization in biological membranes (Munné-Bosch 2005; Holländer-Czytko et al. 2005; Maeda and DellaPenna 2007; Ashraf 2009; Quadrana et al. 2013). Tocopherols detoxify lipid radicals and ROS (Holländer-Czytko et al. 2005). Plant tocopherols have four isomers (α-, β-, γ-, and δ-) (Ashraf 2009). It removes. OH radicals, superoxide radical, and singlet oxygen (Asada and Takahashi 1987). Leaves store most abundant form of α-tocopherol, and seeds store γ-tocopherol. The β-tocopherols and δ-tocopherols are less copious in plants. The α-tocopherol is biosynthesized from γ-tocopherol in green chloroplasts by γ-tocopherol methyl transferase (γ-TMT, VTE4) (DellaPenna 2005; Lichtenthaler 2007; Szymanska and Kruk 2008; Gill and Tuteja 2010; Szarka et al. 2012; Velasco et al. 2013). The α-tocopherol changes during stress into two phases. In initial phase, α-tocopherol content enhances under stress and reduces ROS levels. In second phase, under severe stress, α-tocopherol degradation is more than biosynthesis. Stress-tolerant plants face first phase, and stress sensitive plants have second phase. In photosynthetic biological organisms, fluctuations in tocopherol content were confirmed under drought, salinity, heavy metal, or high radiation stresses (Collakova and DellaPenna 2003; Ledford et al. 2004; Munné-Bosch 2005; Tounekti et al. 2011a, b).

5.3.1.5 Carotenoids

Carotenoids are lipophilic isoprenoids derived from organic pigment antenna molecules, localized in plant chloroplasts with multiple functions in plant metabolism and tolerance to oxidative stresses (Taiz and Zeiger 2006; Fraser et al. 2007). It scavenges singlet oxygen and protects chlorophyll from photoxidation (Demmig-Adams and Adams III 1992; Neubauer and Yamamoto 1992). The chlorophyll to carotenoid ratio is the indicator of seed tolerance to stress (Smolikova et al. 2011).

5.3.1.6 Flavonoid

Flavonoid phenolic pigments found floral parts; pollens and leaves of plants have antioxidant properties against various oxidizing compounds. Innumerable flavonoids act as potential inhibitors of lipoxygenase enzyme. Lipoxygenase enzyme transforms polyunsaturated fatty acids to oxygen comprising derivatives (Nijveldt et al. 2001).

5.3.2 Enzymatic Antioxidants

Enzymatic antioxidants take part in ROS detoxification in abiotic stress (Jiang and Huang 2001; Vacca et al. 2004). Peroxidase (POD), catalase (CAT), superoxide dismutase (SOD) and GR, monodehydroascorbate reductase (MDHAR or MDAR), ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR or DAR), and glutathione reductase (GR) scavenge superoxide and H_2O_2 and MDAR and GR regenerate ascorbate (Fig. 5.2) (Mittler 2002; Nagesh-Babu and Devaraj 2008; Ahmad et al. 2008, 2010a, b, 2011a, b; Ceylan et al. 2013). Accumulation of ROS, for instance, H_2O_2 under various environmental stresses, increased CAT and POX activities.

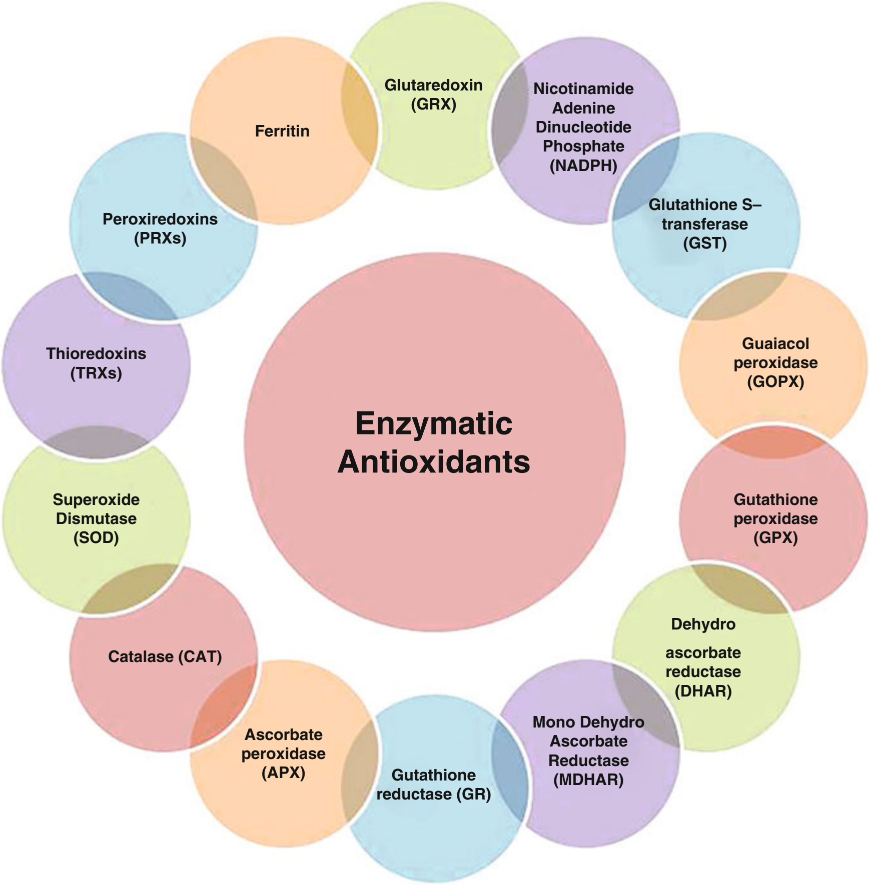

Fig. 5.2 Enzymatic antioxidants

5.3.2.1 Superoxide Dismutase (SOD)

The main and universal multimeric metalloprotein enzymatic antioxidant defense system in plants is SOD localized in chloroplast, cytsol, mitochondria, peroxisome, apoplast (Gür et al. 2010). SOD catalyzes dismutation/scavenging of two superoxide radicals O_2- into molecular oxygen and hydrogen peroxide (H_2O_2) (Abedi and Pakniyat 2010; Zare and Pakniyat 2012) and thus reduces hydroxyl radical (OH) formation, which is very toxic (Bowler 1992; Scandalios 1993). SOD isoforms, localized within cell apoplast, are differentially expressed in plants (Wingsle et al. 1999). According to SOD metal cofactor existing at their active sites, plants contain different types like manganese (Mn) (MnSOD), copper/zinc (Cu-Zn) (CuZnSOD), iron (Fe) (FeSOD), and nickel (Ni-SOD) in chloroplasts and mitochondria (Alscher et al. 2002; Halliwell 2006; Abedi and Pakniyat 2010; Zare and Pakniyat 2012).

Bacteria also contain these four SODs (Halliwell and Gutteridge 2006). After SOD changes superoxide radical to H_2O_2, then either CAT, APX, or POD reduce H_2O_2 to H_2O and O_2 in cytoplasm and cell organelles (Howarth 2005). Stress increases SOD enzyme activity for the detoxification of superoxide radicals (Abedi and Pakniyat 2010; Zare and Pakniyat 2012).

5.3.2.2 Catalase

Catalases (CATs) are tetrameric iron porphyrins. In plants, CATs generate inside peroxisomes and glyoxisomes. CAT catalyzes redox reaction in which H_2O_2 changes into oxygen and water. CAT specifically detoxifies H_2O_2. It also reacts with various organic hydroperoxides, for instance, methyl hydrogen peroxide (MeOOH) (Mittler 2002; Ali and Alqurainy 2006).

5.3.2.3 Ascorbate Peroxidase

Peroxidases remove the scavenging of H_2O_2 through oxidization of various cosubstrates. Various peroxidases are not specific and use various cosubstrates (Mano et al. 2001). Ascorbate peroxidase (APX) is a vital antioxidant enzyme having different isoforms in chloroplasts, mitochondria, cytosol, peroxisome, apoplast, and microsomes. These ascorbate isoforms detoxify H_2O_2 (Asada and Takahashi 1987; Asada 1999; Rasool et al. 2013; Ahmad et al. 2013). APX converts toxic H_2O_2 on reaction with ascorbate substrate to monodehydroascorbate (MDHA) (Payton et al. 2001; Blokhina et al. 2003). In plant cells, four classes of APX are chloroplast thylakoid bound (tAPX), glyoxisome membrane (gmAPX), chloroplast stromal soluble (sAPX), and cytosolic (cAPX). The ascorbic acid antioxidant plays a positive role for plant defense against oxidative stress. Ascorbic acid recovers by MDAR, DHAR, and GR, oxidized by APX. The stress increased APX gene expression in chloroplasts of tobacco plants and in turn increases resistance to salt stress and drought (Rizhsky et al. 2002b; Abedi and Pakniyat 2010; Zare and Pakniyat 2012). APX increases during stress and recovery from stress in tolerant genotypes approves that glutathione-ascorbate cycle is extra proficient in tolerants and provides tolerance to seedlings (Pang and Wang 2010). Plant glutathione peroxidases (GPXs) have Cys instead of seleno-Cys at their active sites. This decreases their catalytic action. Actually, some enzymes favor thioredoxin to GSH (Rodriguez-Milla et al. 2003).

5.3.2.4 Monodehydroascorbate Reductase (MDHAR)

Chloroplast, mitochondria, and cytosol cause the reduction of MDHA to ascorbate (Jimenez et al. 1997).

5.3.2.5 Dehydroascorbate Reductase (DHAR)

DHAR localized in chloroplast, mitochondria, and peroxisomes plays an important function in defense system and regenerates ascorbate from dehydroascorbate (Asada 1994).

5.3.2.6 Glutathione Reductase (GR)

GR is another enzyme localized primarily in chloroplasts or in low amounts in cell cytosol and mitochondria, which inhibits oxidation of enzymes and cell membranes from HTS and protects plants (Creissen et al. 1994; Almeselmani et al. 2006). It helps in reducing the glutathione (Edwards et al. 1990; Creissen et al. 1994).

Peroxiredoxins are homodimers with significant H_2O_2-scavenging systems (Rhee et al. 2005) and are 2-Cys peroxiredoxins, atypical 2-Cys peroxiredoxins, and 1-Cys peroxiredoxins (Georgiou and Masip 2003).

5.4 Genetic Engineering-Based Stress Tolerance in Plants Through Antioxidants

Most types of abiotic stress factors, for instance, high light, water deficiency, salinity, flooding, and temperature extremes, interrupt the metabolic balance of plant cells, resulting in highly stress-induced overproduction of ROS, which causes cellular damages and damage to lipids, nucleic acids, proteins, and carbohydrates (Kanofsky and Sima 1991; Mittler 2002; Mano 2002; Mittler et al. 2004; Foyer and Noctor 2005; Rodriguez and Redman 2005; Ahmad et al. 2009, 2010; Sharma et al. 2012; Suzuki et al. 2012a). Abiotic stress tolerance and stress-induced oxidative protection/tolerance have been accomplished in several crop plants by the generation of transgenics through detoxification strategies of overexpression of glutathione peroxidase, ascorbate peroxidase, superoxide dismutase, and glutathione reductase and other enzymatic and nonenzymatic antioxidants (Roxas et al. 1997; Zhu et al. 1999; Lee et al. 2007a, b; Zaefyzadeh et al. 2009; Kosová et al. 2011). The low molecular nonenzymatic antioxidants, for instance, carotenoids, ascorbate, tocopherols, and glutathione, play key role to survive with oxidative stress (Xie et al. 2008; Liu et al. 2009; Ahmad et al. 2010; Gill and Tuteja 2010; Miller et al. 2010; Shu et al. 2011; Mostafa and Ibrahim 2012).

A number of forms of nuclear-encoded SOD have been cloned in plants. FeSOD genes (FSD1, FSD2, and FSD3), Cu/ZnSOD genes (CSD1, CSD2, and CSD3), and MnSOD gene (MSD1) with an amino terminal targeting sequence occur in *Arabidopsis thaliana* (Scandalias 1990; Kliebenstein et al. 1999). CAT isozymes such as CAT1 and CAT2 are restricted to peroxisomes and cytosol and CAT3 to mitochondria in *Helianthus annuus* and *Brassica* (Polidoros and Scandalios 1999; Azpilicueta et al. 2007). CAT isozymes show temporal and spatial regulation and respond differentially to light (Scandalias 1990; Willekens et al. 1994). CAT1 is associated with genes of β-oxidation of fatty acids and superoxide dismutase. CAT3 is a senescence-associated gene (SEN2), whereas CAT1 displays mainly higher expression in male flower parts. H_2O_2 accumulation dramatically reduces in the transgenic cassava plants with upregulated CAT expression (Xu et al. 2013). The plants with knocked down catalase show correlation between the availability of intracellular H_2O_2 and GSH-GSSG ratios. The improved availability of H_2O_2 declines the status of GSH pools (Queval et al. 2009; Mhamdi et al. 2010). Catalase-deficient barley, tobacco, and *Arabidopsis* plants show distressed glutathione status because of the higher load on catalase-independent pathways for metabolizing H_2O_2 at intracellular levels (Smith et al. 1984; Rizhsky et al. 2002a; Queval et al. 2007). In tobacco and barley, Cat1 deficiency of Cat1-deficient plants produced white necrotic lesions on plant leaves after exposure to higher light intensities due to reduced ability to eliminate exogenous H_2O_2 and disturbs other defense system components (Kendall et al. 1983; Willekens et al. 1997). APX, CAT, and GPX central players remove H_2O_2 in plants. CAT deficiency induces APX mitAOX, MDA reductase, and GPX to compensate for CAT suppression (Mittler 2002). Decline in peroxisomal catalase activity increases sensitivity to ozone, and H_2O_2 induced cell death in *Arabidopsis thaliana*. Deleterious effects of salinity reduce by pretreatment with H_2O_2 and raised catalase activity in maize (Gondim et al. 2012). Modifications in grade of thiol–disulfide balance catalase deficiency and create an oxidized cellular redox in mutants (Queval et al. 2009). High light induces photorespiration and APX and GPX accumulation in catalase-deficient *Nicotiana tabacum* (Willekens et al. 1997). GPX induction in Cat2 deficient mutants acts as a well-defined alternate pathway to manage decomposition of H_2O_2 in catalase deficiency *Arabidopsis* (Queval et al. 2007; Mhamdi et al. 2010). Overexpression of BjCAT3 gene in *Brassica juncea* increased CAT activity by twofolds, which boosted Cd tolerance (Guan et al. 2009). Transgenic rice overexpressing CAT gene (katE) from *Escherichia coli* was salinity tolerant (Nagamiya et al. 2007; Moriwaki et al. 2008). ABA-induced expression of CAT1 is mediated by MAPK cascade-mediated ABA signaling in *Arabidopsis*. Therefore, close-fitting connection of H_2O_2 and ABA signaling due to CAT1 may be part of H_2O_2 signaling (Xing et al. 2008; Michelet et al. 2013). GST and CAT1 gene co-expression increased CAT and SOD activity in transgenic rice seedlings on exposure to both salinity and paraquat, whereas increased GST activity in transgenics took place only in plants stressed with paraquat (Zhao and Zhang 2006). Site-specific modifications in the activity of antioxidant enzymes have been reported. CAT stimulates in root and shoot; APX in endosperm and GR and POD are upregulated in shoots of drought-tolerant wheat genotypes (Devi et al. 2012).

The modification of DHAR expression is imperative for genetic engineering plants with property of stress tolerance (Amako and Ushimaru 2009). MDHAR overexpression reduces damaging consequences of ecological stresses (Eltayeb et al.

2007). In transgenics, overexpression of DHAR tolerates Al stress, tolerates salinity in *Arabidopsis*, and results in water deficiency and tolerance to ozone toxicity in tobacco plants by maintaining high ASC pool (Yin et al. 2010; Chen and Gallie 2005; Ushimaru et al. 2006; Eltayeb et al. 2006). DHAR overexpressing plants show enhanced growth of roots and lesser content of H_2O_2, less peroxidation of lipids, and levels of oxidative damage to DNA in Al stress (Yin et al. 2010). Transgenic tobacco overexpresses AtMDAR1 and showed 2.1-fold higher MDHAR activity and 2.2-fold higher level of reduced AsA and enhanced tolerance to O3, salinity, and drought stress (Eltayeb et al. 2007). Tobacco transformants express DHAR, GR, and GST genes and display changed antioxidant metabolism and better resistance to salt and chilling stress (Martret et al. 2011). Tomato fruits having enhanced MDAR activity showed improved chilling tolerance (Stevens et al. 2008). Salt and osmotic stress-tolerant transgenic tobacco plants show MDAR overexpression (Eltayeb et al. 2007).

APX family has four different isoforms, i.e., chloroplast stromal soluble form (sAPX), thylakoid (tAPX), glyoxisome membrane form (gmAPX), and cytosolic form (cAPX) (Noctor and Foyer 1998). In response to water deficit, salt, or ozone, APX expression increases in plants (Noctor and Foyer 1998; Yoshimura et al. 2000). In chloroplasts of tobacco, overexpression of APX enhances tolerance of plants to salinity and water deficiency (Badawi et al. 2004a, b). The ascorbate-glutathione cycle enzymes, for instance, APX and GR, were upregulated under high temperature in lily plants. These enzymes play an indispensable role in the alleviation of H_2O_2 accumulation. At transcriptional level, APX upregulation and generation of novel thermostable APX isoforms in *Arabidopsis thaliana* alleviate H_2O_2 accumulation (Panchuk et al. 2002).

Heat-tolerant genotype of cabbage exhibited higher GSH content. Due to increase in expression of APX, DHAR, and GR enzymes in apple leaves on exposure to heat stress, content of AsA, total glutathione, GSH, and GR also increase (Ma et al. 2008). APX and GR stop the oxidation of enzymes and cell membranes and henceforth play an imperative part in the protection of plants from heat (Almeselmani et al. 2006). The pAPX (peroxisomal type ascorbate peroxidase) scavenges H_2O_2 in peroxisomes (Shi et al. 2001). A gene pAPX (HvAPX1) from *Hordeum vulgare* was transferred to transgenic *Arabidopsis thaliana* plant against oxidative stress (Shi et al. 2001). Both CAT and APX enzymes detoxify H_2O_2 into H_2O and O_2. In oxidative stress conditions, CAT activity is declined in peroxisomes (Shi et al. 2001). In normal conditions, total APX enzyme activity does not fluctuate. Overexpression of HvAPX1 transgenic against salt tolerance only affects single APX isoenzyme instead of improving total APX enzyme activity (Tsugane et al. 1999). The cytosolic APX mRNA increases under ozone stress and causes detoxification of ROS (Kubo et al. 1995; Örvar et al. 1997). Antisense version of cytosolic APX reduced tolerance to ozone in tobacco plants (Örvar et al. 1997). OsAPXa overexpressing rice plants exhibited improved APX activity and lower levels of H_2O_2 and MDA in cold stress (Sato et al. 2011). Two different signals were likely generated in thylakoid ascorbate peroxidase (tylapx) and cytosolic ascorbate peroxidase 1 (apx1) gene knockout double mutants. The absence of chloroplastic H_2O_2 removing enzymes enhances heat tolerance in plants (Miller et al. 2007). The thylakoid-bound APX genes (LetAPX) from tomato on overexpression in tobacco lead to enhanced salinity tolerance (Sun et al. 2009).

Heavy metals cause oxidative stress because of better ROS production (Dietzk et al. 1999). SbMYB15 transgenic tobacco displayed heavy metal tolerance. SbMYB15 overexpression improved CAT and SOD activities, MnSOD (twofold), and $CdCl_2$ (three- or ninefold), and CAT1 (62-fold) (Sapara et al. 2019). Overexpression of CaGrx from chickpea increased heavy metal tolerance into *A. thaliana*. Transgenics exhibited enhanced activities of GRX, GST, GR, GPX, CAT, APX, SOD, and MDHAR in AsIII and Cr stress (Kumar et al. 2020). The gene expression for GSH biosynthetic enzymes was enhanced in Cd-tolerant transgenic *Brassica juncea* (Zhu et al. 1999). Yeast cadmium factor (YCF1) is a glutathione-S-conjugate transporter. In yeast, it transports Cd21 GSH in a vacuolar membrane protein (YCF1) and confers tolerance to Cd21 (Decottignies and Goffeau 1997; Morgan et al. 2013). GS or g-ECS overexpression in *B. juncea* showed improved stress resistance to various HMs (Cd, Zn, As, and Pb) because of higher capacity of GSH and PC biosynthesis (Reisinger et al. 2008). Aluminum (Al^{+3}) toxicity inhibits root growth (Tabaldi et al. 2009). Tolerant lines showed Al^{+3} tolerances because of improved GST activity (Darkó et al. 2004). Ascorbate-glutathione enzymes increased in Al^{+3}-stressed rice seedlings to cope with oxidative stress (Sharma and Dubey 2007). MDHAR or DHAR transgenic tobacco plants tolerate Al^{+3} stresses by regeneration of reduced AsA (Yin et al. 2010). Higher proline synthesizing transgenic plants showed better resistance to several abiotic stresses and oxidative damage. Transgenic green microalga *Chlamydomonas reinhardtii* overexpressing P5CS show tolerance to toxic cadmium heavy metal stress by accumulation of above twofold free proline content and GSH redox state (Siripornadulsil et al. 2002).

GR overexpression increased tolerance to plant oxidative stress because of increased antioxidant capacity. Transgenic plants produced by manipulation of various antioxidant enzymes of ascorbate-glutathione cycle show tolerance to salinity (Ashraf 2009; Kocsy et al. 2001). The cold tolerant coffea sp. shows higher level of Cu/Zn-SOD, APX, ascorbate, and tocopherol molecules for controlling oxidative stress produced during chilling (Fortunato et al. 2010). Acerola PMM transgenic tobacco has threefold more ascorbate content (Badejo et al. 2009b). In *Arabidopsis thaliana*, mutations in genes of D-Man/L-Gal pathway decreased AsA content (Dowdle et al. 2007; Linster et al. 2007). Overexpression of these genes improved AsA levels (Dowdle et al. 2007; Linster et al. 2008). *Arabidopsis* ERF (AtERF98) gene regulates AsA synthesis through the activation of synthesis associated genes (Zhang et al. 2012). The ascorbate content enhanced twofolds in transgenic tobacco transformed with GME and GGP than individual gene. The expression of acerola was 5- to 700-fold higher than in *Arabidopsis* (Badejo et al. 2009a). In *Solanum lycopersicon*, overexpression of GDP-Man-3, 5-epimerase gene (SlGME) increases AsA content and tolerance to salinity and cold (Zhang et al. 2011). Overexpressed GDP-D-mannose pyrophosphorylase (GMPase) gene of acerola shows a two- to threefold rise in ascorbate content in *Solanum lycopersicon* (Badejo et al. 2008). The GMPase levels change due to the change in AsA content on the basis of the presence or absence of light (Wang et al. 2011, 2013). GMPase gene shows overexpression in transgenics in normal conditions and heat stress. The activities of GMPase, DHAR, MDHAR, and APX and contents of DHA and AsA increase. Thus, potato and *Solanum lycopersicon* tolerate temperature stress because of overexpression of GMPase, which in turn increase AsA levels (Li et al. 2011a, b). During stress, expression of AsA induces and increases AsA biosynthesis in *Solanum lycopersicon* (Ioannidi et al. 2009). There is an association between the rise in content of AsA and expression of GDP-L-galactose phosphorylase (GGP) and GDP-D-mannose, 3′, 5′-epimerase (GME) in kiwifruit (Bulley et al. 2009).

Overexpression of either Gly I or Gly II glyoxalase system enzymes increases tolerance to abiotic stress in plants (Singla-Pareek et al. 2003, 2006, 2008; Lin et al. 2010; Wu et al. 2012; Viveros et al. 2013). GalUR overexpression in transgenic potato plants shows better tolerance to salinity and salinity-induced oxidative stress, accumulation of AsA, restricted increase in MG levels, higher GSH/GSSG ratio, and increased activities of APX, DHAR, GR, GST, GPX, and Gly I and Gly II. Increased ROS, MG detoxification, changes in GSH, and AsA redox state enhanced salinity tolerance in transgenics (Upadhyaya et al. 2011). The induction of plant-specific Tau class GSTU genes by various abiotic stresses provides improved protection of plants to oxidative damage (Jha et al. 2011). The effect of heat on glutathione and ascorbic acid levels was reported (Kocsy et al. 2002, 2004; Kumar et al. 2012; Dai et al. 2012). The transgenic tomato showed higher GPX activity and more resilience to abiotic stress but more susceptibility to biotic stress (Herbette et al. 2011). Tobacco GST with GPX overexpression in Nicotiana *tabacum* L. improved seedling growth in heat and salinity stress (Roxas et al. 2000). The proline biosynthesis suppression in transgenic plants with inducible gene coding for P5CR in the antisense direction improved drought sensitivity (de Ronde et al. 2000, 2001). Salt hypersensitive *Arabidopsis* mutant (p5cs1) had reduced root growth, proline content, and NADP1 to NADPH ratio and enhanced ROS production, severe chlorophyll destruction, elevated H_2O_2, and level of lipid peroxidation under severe oxidative stress (Szekely et al. 2008; Sharma et al. 2011). *Nicotiana tabacum* transformed with P5CS gene exhibited an increase in activities of APX, CAT, and proline accumulation and salinity tolerance (Razavizadeh and Ehsanpour 2009). “Swingle” citrumelo rootstocks were transformed with P5CSF129A gene encoding for proline biosynthesis (De campos et al. 2011). APX, CAT, SOD, and GR exhibited differential regulation in leaves of Swingle citrumelo transgenics with high endogenous accumulation of proline under drought stress and normal conditions (De Carvalho et al. 2013). P5CS gene overexpression in both sense and antisense directions was done in transgenic soybean plants. Antisense transgenics showed severe H_2O_2 and lipid hydrogen peroxide levels, higher GSH pool, and ROS injury. The sense transgenics showed slightest injury due to lower accumulation of H_2O_2 and higher proline and AsA pool in drought or combined heat and water deficiency stress (Kocsy et al. 2005). Transgenic sugarcane plants overexpress P5CS gene with 2.5-fold higher proline content but no osmotic adjustment under drought (Molinari et al. 2007). A rice transgenic overexpressing P5CSF129A gene showed higher salinity tolerance and reduced lipid peroxidation (Kumar et al. 2010). Salinity leads to excessive ROS generation and oxidative stress in plants produced as a derivative of aerobic metabolism (Chaparzadeh et al. 2004; Parida and Das 2005; Noreen et al. 2009; Ashraf 2009; Wang et al. 2012a, b).

OsOAT gene transgenic rice showed higher GSH pool, enhanced activities of GPX and POD, ROS scavenging activity, proline accumulation, and better water deficiency and osmotic stress tolerance (You et al. 2012). Transgenic *Solanum tuberosum* overexpressing l-gulono-c-lactone oxidase (GLOase) gene boosted basal levels of AsA content and showed improved persistence under various abiotic stresses (Hemavathi et al. 2010). The a-tocopherol overexpression increases plant tolerance to oxidative stress. Tocopherol cyclase (VTE1) catalyzes second last step of tocopherol biosynthesis. VTE1 overexpressing transgenic tobacco exhibited declined lipid peroxidation, electrolyte leakage, and H_2O_2 content in water deficiency conditions (Liu et al. 2008).

Synchronized overexpression of Cu/Znsod and apx or only apx in transgenic tobacco plants lessened the damage of drought stress (Faize et al. 2011). SOD (SOD-OX) overexpression in leaves enhanced tolerance to both acute and longer-term high temperatures (Artlip et al. 2009). In *Ipomoea batatas*, expression of Cu/ZnSOD and APX improved water deficiency resistance and the recovery rate from water deficiency stress (Lu et al. 2010). Expression of CuZnSOD, APX, and DHAR in transgenic tobacco plants was extra effective than single or double expression with improved tolerance to various stresses (Lee et al. 2007a, b).

Overexpression of MuWRKY3 gene from horse gram into groundnut plants leads to lower contents of MDA, H_2O_2, and $O_2{\cdot}-$ and improved SOD (three- to fivefolds) and APX (three- to sevenfolds) activities and increased water deficiency tolerance (Kiranmai et al. 2018). MdATG18a overexpression in apple increased the activities of CAT and POD and improved tolerance to drought stress by high frequency of autophagy and restriction of oxidative damage (Sun et al. 2018). Overexpression of chrysanthemum DgNAC1 gene lowered the accumulation of MDA, H_2O_2, and O2• − and significantly improved SOD, CAT, and POD activities and salinity tolerance in transgenics (Wang et al. 2017). PaSOD (*Potentilla atrosanguinea*) and RaAPX (*Rheum australe*) were overexpressed in potato dual transgenic. Transgenic potato increased activities of SOD and APX positive regulators to enhance tolerance to salinity by ROS regulation and lignin biosynthesis signaling (Shafi et al. 2017). DaAPX overexpression and supplementation of transgenic plants with H_2O_2 improved APX activity and improved flooding and cold tolerance (Chen et al. 2019). AtDREB1A overexpression in tomato plants increased activities of SOD and CAT and superior chilling stress tolerance (Karkute et al. 2019). Overexpression of StSOD1 gene improved SOD, POD, and CAT activities and improved cold tolerance in transgenic plants (Che et al. 2020). Chrysanthemum CmSOS1 overexpression enhanced SOD and CAT in transgenic plants (Wang et al. 2019). A summary of transgenic plants with increased antioxidant defense system activities under various stresses is documented in Table 5.1.

Table 5.1 Transgenic plants tolerant to oxidative stress

Mutant/ transgenic plant	Gene	Stress response	Reference/s
Arabidopsis thaliana	CaMT	Enzyme activities of APX, POD, GPX, and GRX enhance in transgenic plants	Dubey et al. (2019)
Arabidopsis thaliana	MpDGK2	Enzyme activities of CAT, APX, and POD enhance in transgenic plant.	Tan and Wang (2020)
Arabidopsis thaliana	OsSultr1;1	Enzyme activity is enhanced, i.e., GSH with As (III) toxicity	Kumar et al. (2019)
Arabidopsis thaliana	BnERF2.4	Enzyme activities of SOD, POD, and CAT enhanced in under waterlogging	Lv et al. (2016)
Arabidopsis thaliana	MaRAP2-4	Enzyme activities of CAT, GPX, and SOD enhance in transgenic plants under waterlogging	Phukan et al. (2018)
Arabidopsis thaliana	DaAPX	Enzyme activity of APX enhanced in transgenic plants	Chen et al. (2019)
Arabidopsis thaliana	HvERF2.11	Enzyme activities of SOD, POD, CAT, alcohol dehydrogenases by 2.1-, 2.3-, and 1.9-fold enhanced in three transgenic lines under waterlogging	Luan et al. (2020)
Arabidopsis thaliana	apx1/apx2	APX2 knockout lines produced more seeds under prolonged heat stress	Suzuki et al. (2012b)
Arabidopsis thaliana	HSF3/APX2	Enhanced ROS accumulation in plants	Panchuk et al. (2002)
Arabidopsis thaliana	CAM3	Thermotolerance reduced in CAM3 mutants and rescued/ enhanced in CAM3 overexpression	Zhang et al. (2009)
Arabidopsis thaliana	CAM3	AtCaM3 is involved in NO signal transduction as a downstream factor and is dependent on increased HS transcription factor DNA-binding activity and HSP accumulation	Xuan et al. (2010)

(continued)

Table 5.1 (continued)

Mutant/ transgenic plant	Gene	Stress response	Reference/s
Arabidopsis thaliana	Apx1/Apx2	H_2O_2 takes part in heat stress signaling pathway and in HSF activation during the early phase of heat stress	Volkov et al. (2006)
Arabidopsis thaliana	Mammalian L-gulono-lactone oxidase	Four- to sevenfold increase in ascorbate	Jain and Nessler (2000)
Arabidopsis thaliana	DHAR	Increased Salinity tolerance	Ushimaru et al. (2006); Chen and Gallie (2005)
Arabidopsis thaliana	GPX-2	Salinity, heavy metal, drought, cold, oxidative, and MV	Gaber et al. (2006)
Arabidopsis thaliana	APX2 and APX 3	Heat tolerance	Chiang et al. (2015)
Arabidopsis thaliana	MDHAR+ DHAR	Freezing oxidative tolerance	Shin et al. (2013)
Arabidopsis thaliana	AtERF98	Activation of ascorbic acid biosynthesis	Zhang et al. (2012)
Arabidopsis thaliana	VvWRKY30	POD, CAT, and SOD activities enhance in transgenic plants	Zhu et al. (2019)
Arachis hypogaea	MuWRKY3	Enzyme activities of SOD enhanced by 3–5 and APX by three- to sevenfolds in transgenic plants	Kiranmai et al. (2018)
Brassica campestris	Cu-Zn SOD + CAT	Salinity and SO2	Tseng et al. (2007)
Brassica juncea	GS	Heavy metal tolerance	Reisinger et al. (2008)
Chrysanthemum	DgNAC1	Enzyme activities of SOD by twofolds, CAT by twofolds, and POD by threefolds enhanced in transgenic plants	Wang et al. (2017)
Chrysanthemum morifolium	CmSOS1	SOD and CAT activities enhanced in transgenic plants	Wang et al. (2019)
E. coli	GR	Heat and MV	Achary et al. (2015)
Festuca arundinacea	Mn SOD +APX	Multiple abiotic stresses	Lee et al. (2007a, b)
Glycine max	GmMYB84	Enzyme activities of SOD, POD, and CAT enhanced significantly in transgenic plants	Zhang et al. (2020)

(continued)

Table 5.1 (continued)

Mutant/ transgenic plant	Gene	Stress response	Reference/s
Gossypium hirsutum	GR	Cold and photooxidative tolerance	Kornyeyev et al. (2003)
Lycopersicon esculentum	cAPX	Drought, heat, cold, and UV light	Wang et al. (2005a)
Malus domestica	MdATG18a	Enzyme activities of CAT and POD enhanced by 1.57–2.05-fold in transgenic plants	Sun et al. (2018)
Malus domestica	MdATG18a	Enzyme activities of SOD, POD, CAT, AsA, and GSH enhanced in transgenic plants, and decrease in ratio of GSH/GSSG under extreme temperature	Huo et al. (2020)
Manihot esculenta	APX and Cu-Zn SOD	MV and cold	Xu et al. (2014)
Nicotiana tabacum	ZmSO	Increased activity of GSH in transgenic plants	Xia et al. (2018)
Nicotiana tabacum	SbMYB15	Enzyme activities of CAT and SOD enhanced in transgenic plants and increase the expression of MnSOD, CdCl2 and CAT1	Sapara et al. (2019)
Nicotiana tabacum	TaFBA1	Enzyme activities of SOD, POD, and APX enhanced and CAT activity decreased in transgenic plants under heat stress	Li et al. (2018)
Nicotiana tabacum	Cu-Zn SOD	Salinity and drought	Badawi et al. (2004c)
Nicotiana tabacum	katE	Salinity	Al-Taweel et al. (2007)
Nicotiana tabacum	AtMDHAR1	Salinity, ozone and drought	Eltayeb et al. (2007)
Nicotiana tabacum	swpa4	Salinity, osmotic and oxidative	Kim et al. (2008)
Nicotiana tabacum	DHAR	Salinity and drought; ascorbic acid biosynthesis; aluminum	Eltayeb et al. (2007), Zhou et al. (2015b), Yin et al. (2010)

(continued)

Table 5.1 (continued)

Mutant/ transgenic plant	Gene	Stress response	Reference/s
Nicotiana tabacum	GPX	Salinity, cold and oxidative stress tolerance	Yoshimura et al. (2004)
Nicotiana tabacum	VTE1	Drought tolerance	Liu et al. (2008)
Nicotiana tabacum		Drought and ozone tolerance	Ushimaru et al. (2006)
Nicotiana tabacum	APX and Cu-Zn SOD	Methyl viologen and oxidative damage; salinity tolerance	Kwon et al. (2002), Negi et al. (2015)
Nicotiana tabacum	Cu-Zn SOD	MV and cold tolerance; oxidative and salinity tolerance; drought tolerance	Gupta et al. (1993), Jing et al. (2015), Negi et al. (2015)
Nicotiana tabacum	APX, Cu-Zn SOD and DHAR	Salinity and paraquat tolerance	Xu et al. (2014)
Nicotiana tabacum	EsSPDS1	Drought tolerance	Zhou et al. (2015a)
Nicotiana tabacum	CAT3	Heavy metal tolerance	Gichner (2004)
Nicotiana tabacum	SoCYP85A1	Enhanced activity of POD by 1.3- to 1.5-folds and SOD by 1.36- to 1.39-fold	Duan et al. (2017)
Nicotiana tabacum	GDP-L-galactose guanylyl transferase and GDP-mannose3’,5′-epimerase	Sevenfold	Bulley et al. (2009)
Nicotiana tabacum	Arabidopsis cytosolic DHAR	Tolerance to water deficiency and ozone stresses	Eltayeb et al. (2006)
Nicotiana tabacum	sHSPs	H_2O_2 is required for activation of sHSP synthesis	Konigshofer et al. (2008)
Nicotiana tabacum	BADH	Overexpression increased thermotolerance induced by accumulation of glycine betaine and repair of PSII from heat-enhanced photo inhibition in transgenic plants	Yang et al. (2007)
Nicotiana tabacum	MDHAR	MDHAR overexpression increased tolerance to salt and osmotic stresses	Eltayeb et al. (2007)

(continued)

Table 5.1 (continued)

Mutant/ transgenic plant	Gene	Stress response	Reference/s
Nicotiana tabacum	Human DHAR gene	Tolerance to cold and salinity stress	Kwon et al. (2003)
Nicotiana tabacum	Wheat DHAR gene	Tolerance to ozone	Chen and Gallie (2005)
Oryza sativa	Cu-Zn SOD	Salinity, drought, and oxidative tolerance	Prashanth et al. (2008)
Oryza sativa	P5CS	Drought and salinity tolerance in transgenic plants	Su and Wu (2004)
Oryza sativa	MDHAR	Salinity tolerance in transgenic plants	Sultana et al. (2012)
Oryza sativa	Cytosolic GR	Photooxidative stress tolerance	Kouril et al. (2003)
Oryza sativa	MnSOD	Salinity tolerance	Tanaka et al. (1999)
Oryza sativa	CAM1-1 CaM1-1	Isoform interpret a Ca21 signature regulating transcription of nucleoplasmic small HSP gene during heat stress	Wu and Jinn (2012)
Petunia hybrida	P5CS	Drought tolerance	Yamada (2005)
Populus davidiana X *Populus bolleana*	MnSOD	Salinity tolerance	Wang et al. (2005b)
Prunus domestica cv. Claudia Verde	SOD +APX	Salinity tolerance	Diaz-Vivancos et al. (2013)
Solanum lycopersicum	DREB1A/CBF3	Drought stress tolerance	Rai et al. (2013)
Solanum lycopersicum	AtDREB1A	Enzyme activities of SOD and CAT enhanced in transgenic plants	Karkute et al. (2019)
Solanum lycopersicum	CodA	Overexpression of choline oxidase shows higher levels MT-sHSP, HSP70, and HSC70 during heat stress in transgenic plants	Li et al. (2011c)
Solanum lycopersicum	GDP-L- galactose	Several fold	Bulley et al. (2012)

(continued)

Table 5.1 (continued)

Mutant/ transgenic plant	Gene	Stress response	Reference/s
Solanum lycopersicum	cAPX	cAPX overexpression enhanced resistance to heat in transgenic plants	Wang et al. (2006)
Solanum lycopersicum	Increased MDHAR	Chilling tolerance	Stevens et al. (2008)
Solanum tuberosum	GDP-L- galactose	Several fold	Bulley et al. (2012)
Solanum tuberosum	StSOD1	Enzyme activities of SOD enhanced by 1.38-folds, POD by 1.24-folds, and CAT by 1.37-folds in transgenic plants	Che et al. (2020)
Solanum tuberosum	GLOase	Accumulation of vitamin C with enhanced abiotic stress	Hemavathi et al. (2010)
Solanum tuberosum	APX and Cu-Zn SOD	Heat, oxidative stress and MV	Tang et al. (2006)
Solanum tuberosum	GLOase	L-ascorbic acid accumulation and tolerance to salinity and MV	Hemavathi et al. (2010)
Solanum tuberosum	P5CS	Accumulation of proline in response to salinity	Hmida-Sayari et al. (2005)
Solanum tuberosum	PaSOD, RaAPX	SOD enhanced by two- to sixfolds in PaSOD and one- to threefolds in double transgenic plants (DTP); APX enhanced by 5- to 11-fold in APX and four- to eightfold in DTP	Shafi et al. (2017)
Strawberry fruits	D-galacturonic acid	Two- to threefolds	Agius et al. (2003)
Triticum aestivum	MnSOD	Oxidative and photooxidative tolerance	Melchiorre et al. (2009)
Triticum aestivum	P5CS	Drought tolerance	Vendruscolo et al. (2007)

5.5 Conclusions

Stress from their neighboring environment affects plants in a complex modus. The schedule and localization of ROS production and scavenging during stress play strategic roles. Identification and characterization of synchronization of signaling events between ROS and oxidative stress will enable the generation of stress resilient crop plants. The findings stated above evidently validate pivotal functions of enzymatic and nonenzymatic antioxidants in inducing oxidative stress tolerance.

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