Plant Molecular Biology (2021) 105:11–41
https://doi.org/10.1007/s11103-020-01077-w

REVIEW

Bioregulators: unlocking their potential role in regulation of the plant oxidative defense system

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Received: 14 June 2020 / Accepted: 23 September 2020 / Published online: 29 September 2020

Abstract

Key message **Plant bioregulators play an important role in managing oxidative stress tolerance in plants. Utilizing their ability in stress sensitive crops through genetic engineering will be a meaningful approach to manage food production under the threat of climate change.**

Abstract Exploitation of the plant defense system against oxidative stress to engineer tolerant plants in the climate change scenario is a sustainable and meaningful strategy. Plant bioregulators (PBRs), which are important biotic factors, are known to play a vital role not only in the development of plants, but also in inducing tolerance in plants against various environmental extremes. These bioregulators include auxins, gibberellins, cytokinins, abscisic acid, brassinosteroids, polyamines, strigolactones, and ascorbic acid and provide protection against the oxidative stress-associated reactive oxygen species through modulation or activation of a plant's antioxidant system. Therefore, exploitation of their functioning and accumulation is of considerable significance for the development of plants more tolerant of harsh environmental conditions in order to tackle the issue of food security under the threat of climate change. Therefore, this review summarizes a new line of evidence that how PBRs act as inducers of oxidative stress resistance in plants and how they could be modulated in transgenic crops via introgression of genes. Reactive oxygen species production during oxidative stress events and their neutralization through an efficient antioxidants system is comprehensively detailed. Further, the use of exogenously applied PBRs in the induction of oxidative stress resistance is discussed. Recent advances in engineering transgenic plants with modified PBR gene expression to exploit the plant defense system against oxidative stress are discussed from an agricultural perspective.

Keywords Antioxidant machinery · ROS detoxification · Reactive oxygen species · Oxidative stress · Phytohormones · Transgenic crops

Introduction

Food security is generally referred to as when nutritious food is sufficiently available at all times to people living on the globe (FAO 1996). While food security or agro-productivity are under immense pressure due to a rapid increase in the human population along with an associated conversion of land from food production to residential or industrial use, changing life styles, low soil fertility/water quality, soil erosion and global climate changes (Savvides et al. 2016; Russell et al. 2020). Among these, climate change is seen as a major and exacerbating issue for crop production as its associated environmental impacts of drought, salinity, heat, cold, freezing, flooding, heavy metal toxicity and UV radiation, occurring sequentially and simultaneously, are the main factors limiting enhanced agricultural productivity (Zulfiqar and Hancock 2020). This situation is expected to worsen with the predicted increase in climate change in the coming years and is contemplated as a big challenge to global food security (Balfagón et al. 2019). Ultimately, there will be an unprecedented increase in the intensity of abiotic stresses worldwide. In a relatively recent study by Daryanto et al. (2016), it was concluded from studies published from 1980 to 2015, that drought stress caused a worldwide yield decline of up to 21% and 40% in wheat and maize crops, respectively. Similarly, with each degree Celsius increase

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in global temperature, a wheat production decline of 6% is likely to occur (Asseng et al. 2015).

Abiotic stresses lead to an impairment of water balance, membrane permeability, and uptake and accumulation of mineral nutrients (Singh et al. 2015). Exposure to abiotic stresses such as drought causes disturbance in plant water relations by influencing various factors including leaf and canopy temperature, transpiration, leaf water potential, stomatal regulation, and water use efficiency (Blum 2017). Among these, the most disturbed factor is stomatal conductance, a major determinant of photosynthesis, especially under drought stress (Blum 2017). Abiotic stresses are known to limit respiration and protein synthesis, and to inhibit growth in sensitive plant species (Savvides et al. 2016). Abiotic stress conditions also disturb the nutrient relations of plants especially salinity and drought stress. Abiotic stresses also can significantly limit photosynthesis, whereby the conversion of energy into plant biomass undergoes considerable reduction.

Exposure of plants to harsh environmental conditions results in over-reduction of the electron-transport chain and subsequently causes photooxidation (Gururani et al. 2015). Moreover, these environmental stresses also hamper the photosynthesis process by adversely affecting the ultrastructure of organelles, pigment biosynthesis and concentrations, and the concentrations of key metabolites and enzymes (Ashraf and Harris 2013). In addition, abiotic stresses such as high temperature can reduce the activity of photosystem II (PSII) and impair the regeneration capacity of ribulose 1,5 bisphosphate (Fahad et al. 2017). Reactive oxygen species (ROS) are aerobic metabolic by-products that are abundantly produced in specific organelles such as mitochondria, chloroplasts and peroxisomes in plants due to their high frequency of electron flow and a highly oxidizing metabolic activity (Gill and Tuteja 2010; Hasanuzzaman et al. 2020). ROS play a role of both protective and destructive compounds in plant cells (Savvides et al. 2016). Generally, in plants under abiotic stresses, generation of cellular ROS is a common phenomenon that subsequently results in failure of ROS-metabolizing system and initiation of oxidative stress.

Oxidative stress is the effect of various abiotic stresses and a state of imbalance between the speed of ROS-generation and their metabolism, which damages the cellular organelles and biomolecules, and it perturbs the plant cellular redox homeostasis due to interruption in cellular homeostasis (Noctor et al. 2018). In addition to an obvious regulation by antioxidants, the synthesis of mitochondrial ROS is tightly controlled by a variety of reductant systems (Blokhina and Fagerstedt 2010). Moreover, enhanced production of ROS damages plant cells by triggering oxidation of a variety of key biomolecules including proteins, lipids, and nucleic acids, and stimulation of the programmed cell death pathway, subsequently leading to cell death.

Reducing the productivity loss caused by climatic change is a great challenge for the agriculture and horticulture sectors. There is an urgent need to reform crop improvement programs and to modify agronomic practices to manage future environmental stresses. In this regard, reliance on conventional breeding approaches is a time-consuming and laborious method while transgenic approaches are still not considered a reliable solution because of lack of performance in farmers' fields (Srivastava et al. 2016). This is because stress tolerance is a quantitative trait and linked with polygenes that control the various signaling and metabolic pathways (Srivastava et al. 2016). Moreover, at the field level, plants have to endure multiple stresses and hence, transgenic crop plants transformed with one type of stress resistance genes may not perform well under the multiple stresses at field level. Although, genetic modification at the level of molecular regulators has addressed the issue associated with multiple stresses, resulting transgenic crops have not yet been evaluated for their yield response at field level.

In order to cope with oxidative stress caused by ROS over-accumulation, plants activate their antioxidant defense mechanisms, either enzymatically or non-enzymatically (Noctor et al. 2018; Hasanuzzaman et al. 2020). The antioxidant defense system efficiently detoxifies or scavenges ROS accumulation in response to abiotic stress. In response to this, plants accumulate naturally occurring compounds known as osmoprotectants, which not only aid osmotic regulation in plants, but also stabilize biomolecules including proteins and membranes (Singh et al. 2015).

In addition, transgenic crops are unacceptable in many countries worldwide. Therefore, as an immediate and alternative solution to 'prepare' plants to endure future stresses, there is a widespread agricultural use of plant bioregulators (PBRs) to enhance crop productivity. A substantial part of the biochemical aspect of the Green Revolution in the 1950s was based on bioregulators, such as gibberellins (Silverstone and Sun 2000). Bioregulators or plant growth regulators, both natural and synthetic, play a key role in plant development and metabolism by altering plant key physio-biochemical processes or its structures to achieve enhanced yield or quality (Nickell 1982) under normal (Zulfiqar et al. 2019) and stress condition (Gaion et al. 2018). They also cause the synthesis/accumulation of a variety of plant constituents that impart an ability to plants to resist to abiotic stresses and oxidative stress. Importantly, PBRs are reported to enhance the activities of plant defense systems and ultimately stress tolerance. In this regard, various studies have shown that PBRs exogenously applied at optimum concentrations to plants under stress can upregulate osmoprotectants, enhance expression of stress related genes, and increase the efficiency of plant antioxidant system (Kaya et al. 2018a, b, c, 2019a, b), thereby resulting in increased stress tolerance. Increased activity of the antioxidant system, production of osmoprotectants and ROS scavenging is reported following PBR application under a range of stresses resulting in the mitigation of oxidative damage to plant cellular functioning (Gaion et al. 2018; Samadi et al. 2019; Sadak et al. 2019).

In view of the attention they have attracted in plant science research, understanding the protective functions of PBRs on plants under harsh environmental conditions and the tolerance that plants can acquire following the application of PBRs is of vital significance. A large body of research related to the use of PBRs to maximize agricultural productivity under stress conditions has been published. However, a comprehensive review on the role of PBRs in specifically regulating the plant oxidative defense system is lacking.

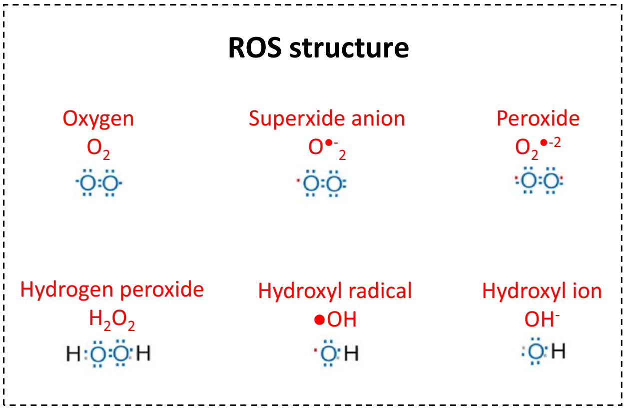

Fig. 1 Reactive oxygen species structure in plants. The red filled circle shows an unpaired electron. [Adopted from https://www.biotek.com/resources/white-papers/an-introduction-to-reactive-oxygen-species-measurement-of-ros-in-cells/]

Generation of different types of ROS

Like all aerobic living organisms, constant production of ROS is an inescapable outcome of aerobic metabolism in plant cells (Ashraf 2009; Hasanuzzaman et al. 2020). The ROS include two major groups; (1) free radicals such as superoxide (O_2^{-}), hydroxyl radicals ($^{\cdot}OH$), and (2) non-radicals such as hydrogen peroxide (H_2O_2) and singlet oxygen ($^1O_2$) (Table 1). All are derived primarily from O_2 (Apel and Hirt 2004). The structures of commonly occurring ROS in plant cell are presented in Fig. 1. In recent years, it has been established that ROS play a vital role in various plant functions including a signaling role in subcellular and intercellular communication, growth, development, and response to both biotic and abiotic stimuli (Sharma et al. 2019). Their major production is confined to chloroplasts (Foyer and Noctor 2016), although they are produced in mitochondria and peroxisomes as well as in some secondary sites such as cell membrane, endoplasmic reticulum, apoplast and cell wall under favorable conditions (Xia et al. 2015). ROS production in different cellular organelles is illustrated in Fig. 2. In plants, three potential mechanisms are present for the production of ROS, (1) from chlorophyll containing molecules, (2) in electron transport chain (ETC) in chloroplasts and mitochondria, and (3) by different oxidases and peroxidases such as lipoxygenase, amine oxidase, NADH oxidase, glycolate oxidase, xanthine oxidase and NADPH oxidase (Blokhina et al. 2003). Photosynthetic products in the chloroplast are major ROS producers (Foyer and Noctor 2016). Further,

Table 1 Functioning of enzymatic and non-enzymatic antioxidants for scavenging toxic ROS in plants

	Functioning in nullifying ROS
Enzymatic antioxidants	
SOD	$O^{\cdot -} + 2\,O_2^{-} + 2H^{+} \rightarrow 2H_2O_2 + O_2$
CAT	$2H_2O_2 \rightarrow O_2 + 2H_2O$
APX	$H_2O_2 + AA \rightarrow 2H_2O + DHA$
MDHAR	$2MDHA + NADH \rightarrow 2AA + NAD$
DHAR	$DHA + 2GSH \rightarrow AA + GSSG$
GR	$GSSG + NADPH \rightarrow 2GSH + NADP+$
GPX	$H_2O_2 + DHA \rightarrow 2H_2O + GSSG$
Non-enzymatic antioxidants	
Ascorbic acid	Scavenges H_2O_2 by the action of APX
Reduced glutathione	Acts as a detoxifying co-substrate for enzymes e.g., glutathione-*S*-transferase, peroxidases, and GR
A-tocopherol	Guards against and detoxifies products of membrane lipid peroxidation
Carotenoids	Quenches excess energy from the photosystems, light harvesting complex
Flavonoids	Directly scavenges H_2O_2, $^1O_2$ and $^{\cdot}OH$
Proline	Scavenges $^{\cdot}OH$ and $^1O_2$ and inhibits damages due to lipid peroxidation

SOD superoxide dismutase, *CAT* catalase, *APX* ascorbate peroxidase, *MDHAR* monodehydroascorbate reductase, *DHAR* dehdroascorbate reductase, *GR* glutathione reductase, *GPX* glutathione peroxidase

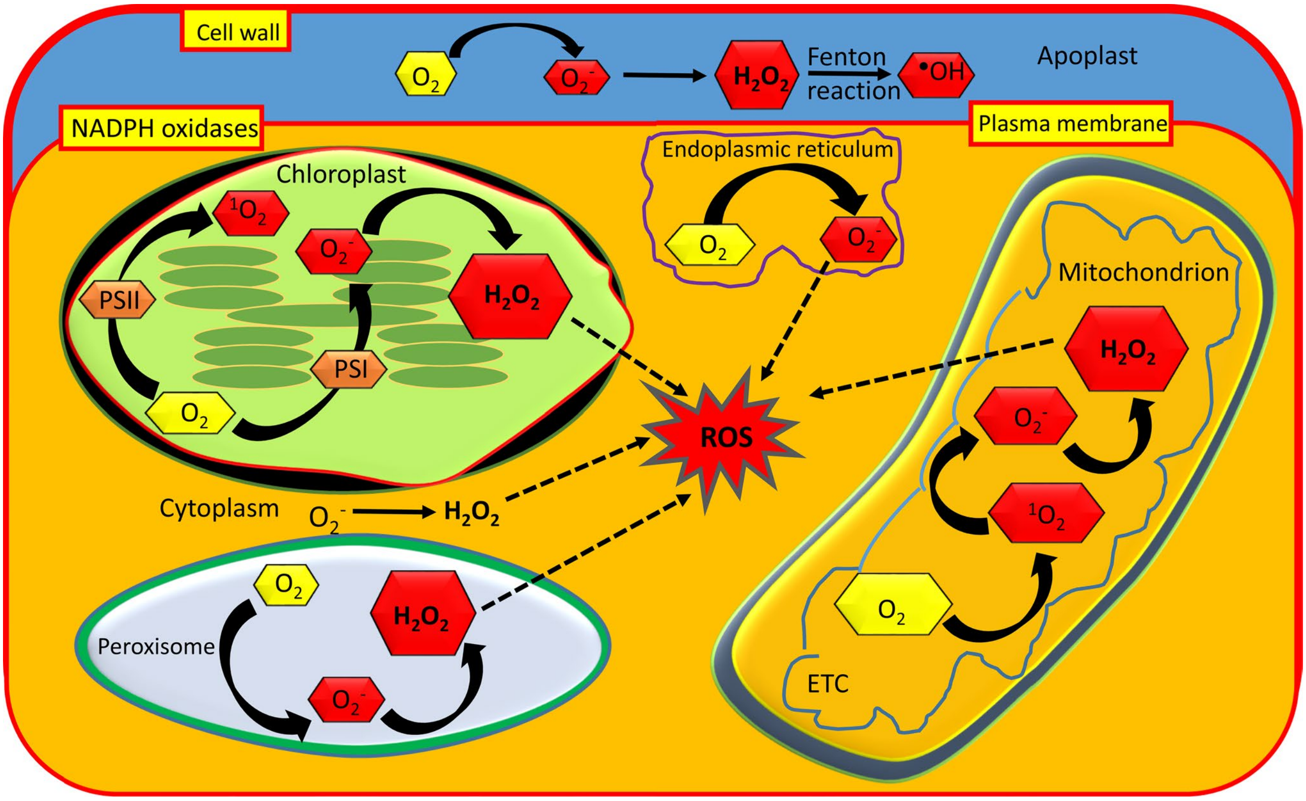

Fig. 2 A schematic representation showing key ROS production in different organelles of plant cells. Excessive ROS production in response to oxidative stress condition leads to cell injury or even death

chlorophyll along with photosensitizers also produce ROS utilizing sunlight (Mittler 2002). In these organelles, ROS signals initiate transcriptional changes and reprogramming of cells leading to either cell protection or cell death (Foyer and Noctor 2005). The protein products of ROS gene network are responsible for the tightly controlled production of ROS (Mittler et al. 2004). At normal level, ROS are unable to cause cellular damage, as they are regularly being scavenged by antioxidant systems (Foyer and Noctor 2005; Mittler et al. 2004). Moreover, ROS family acts as a secondary messenger in various physiological processes of plants and has other important cellular roles in apoptosis, cell proliferation and necrosis under normal growth condition (Choudhury et al. 2013). ROS as a signaling molecule under abiotic stress conditions, regulate various pathways (Choudhury et al. 2016; Hasanuzzaman et al. 2020).

Under pathogens, wounding or environmental stresses, the level of ROS production increases beyond the scavenging capacity of plants, and normal homeostasis results in induction of oxidative stress in plants (Sharma et al. 2019). The oxidative stress results in degradation of important cellular biomolecules such as proteins, carbohydrates, pigments, lipids, and DNA, that ultimately hampers cellular functioning or causes death of plants (Sharma et al. 2019; Foyer and Noctor 2005; Khan and Khan 2017). Of the total oxygen consumption by plants tissues, 1 to 2% is accounted for by ROS generation (Bhattacharjee 2005). So, under harsh environmental stresses, plant survival in response to changes in plant growth conditions, including stress nature, severity and duration depends on the plant capacity to rapidly adjust to the changing energy equation (Miller et al. 2010).

Functioning of oxidative defense system in stressed plants

Plants have evolved with the ROS defense strategy regulated by a well-developed antioxidant system that is capable of efficiently mitigating/modulating the ROS-associated adverse effects occurring during the oxidative stress in plant cells (Table 1). This versatile defense system has two components, enzymatic and non-enzymatic antioxidants. The enzymatic antioxidants include, superoxide dismutase (SOD), catalases (CAT), dehydroascorbate reductase (DHAR), glutathione reductase (GR), glutathione peroxidase (GPX), ascorbate peroxidase (APX), and monodehydroascorbate reductase (MDHAR). The non-enzymatic antioxidants include, ascorbic acid (vitamin C), α-tocopherols, reduced glutathione, carotenoids, and flavonoids. The localization of these antioxidants is illustrated in Fig. 3.

Enzymatic antioxidants

a. *Superoxide dismutase* (*SOD*) The metalloenzyme, SOD, occurs in the sub-cellular compartments including apoplast that are associated with the production of activated oxygen in all aerobic living organisms. SOD acts as a primary protectant in plant cells against the toxic effects of excessive ROS production under stress conditions. It dismutases or disproportionates $O_2^{-\cdot}$ into O_2 and H_2O_2 with a very rapid second order rate constant (Hussain et al. 2019a, b). This ability avoids the risk of $OH^{\cdot}$ formation by the Haber–Weiss reaction (Gupta et al. 2018). Based on their prosthetic ability, essentially SODs are grouped into three isoenzymes including Mn-SODs, Fe-SODs, and Cu/Zn-SODs that are localized in mitochondria, chloroplasts, and cytosol and peroxisomes, respectively. The amino terminal targeting sequence helps target the nuclear encoded types of SOD to specific subcellular sections (Hussain et al. 2019a, b). Numerous studies have demonstrated the enhanced activity of SOD in tolerant/resistant cultivars under various oxidative stress conditions. This increased activity of SOD is often contemplated as one of the potential tolerance mechanisms to prevent oxidative stress situations. Thus, increasing SOD in stress sensitive plants can be a strategy to scavenge the increased ROS that cause oxidative stress under unfavorable conditions. This is further confirmed by the genetic manipulation of plants overexpressing SOD activity and enhancing oxidative stress tolerance in plants.

b. *Catalase (CAT)* CAT is another enzymatic antioxidant found in the peroxisomes of all aerobic organisms including plants (Mhamdi et al. 2010). It is a tetrameric heme-containing enzyme. It scavenges the H_2O_2 produced as a result of several important cellular functions including β-oxidation of fatty acids, mitochondrial electron transport, and photorespiratory oxidation (Mhamdi et al 2010). CAT acts as a catalyst and speeds up the dismutation of H_2O_2 into O_2 and H_2O without reliance on cellular reducing equivalents (Hussain et al. 2019a, b). Similar to SOD, it has widely been reported that an enhancement in CAT activity is usually detected in plants exposed to oxidative stress conditions suggesting that this is an adaptive response of plants. Plant cells under oxidative stress condition are usually starved of

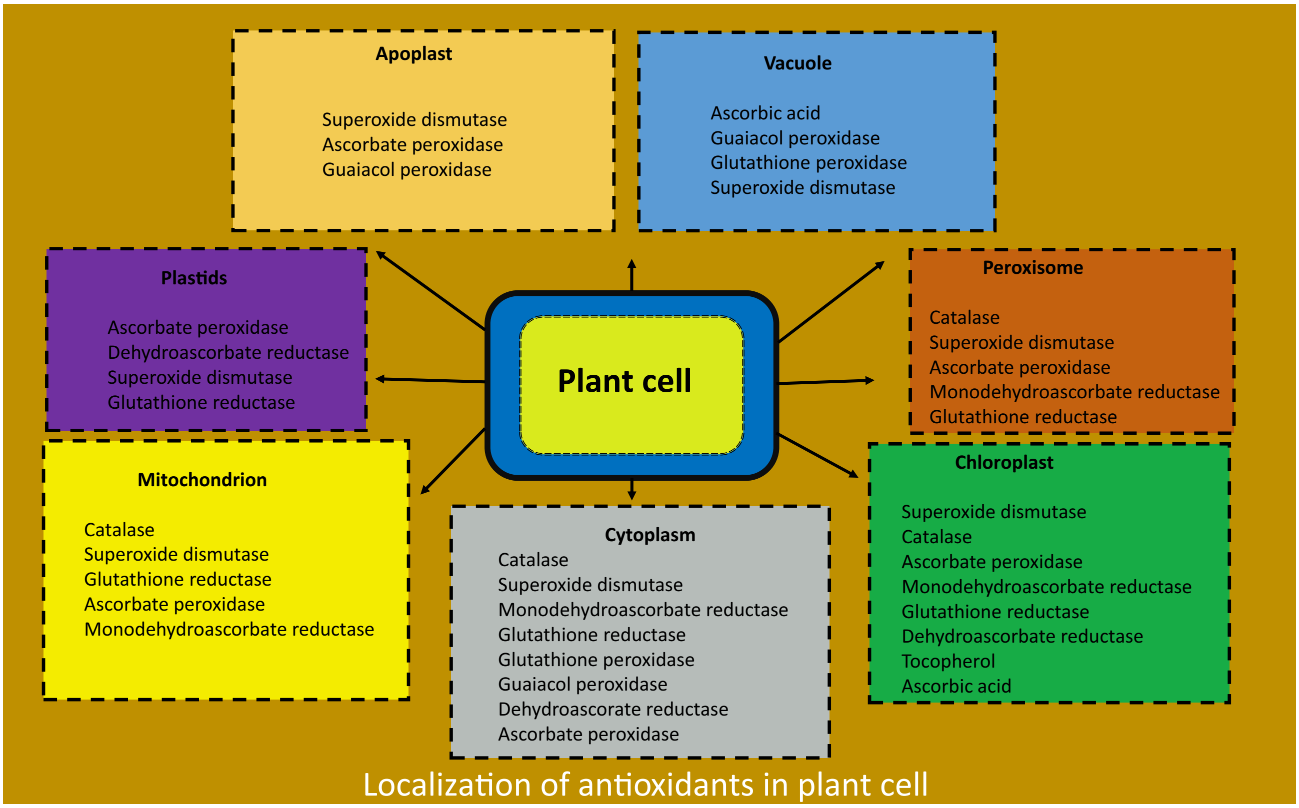

Fig. 3 Cellular localization of antioxidants in plants. Antioxidant machinery regulates ROS homeostasis by their complex and multifaceted protective mechanisms

energy due to their high energy demands, and they generally produce energy via catabolic processes that result in excessive accumulation of H_2O_2. CAT scavenges this H_2O_2 in an energy efficient way. Based on its expression profiles, CAT is grouped into Classes I, II, and III (Hussain et al. 2019a, b). CAT activity either increases or decreases under individual or combined oxidative stress conditions.

c. *Ascorbate peroxidase (APX)* It is another heme-containing enzyme assisting plants to protect themselves from the damaging effects of oxidative stresses. It is critically involved as a vital component in the ascorbate–glutathione cycle. This photosynthetic eukaryote-specific enzyme fine-tune H_2O_2 by catalyzing the conversion of H_2O_2 into water and dehydroascorbate uses ascorbic acid as a reducing agent (Caverzan et al. 2012). APXs isoforms are distributed among the peroxisomes, mitochondria, cytosol, and chloroplast (stroma and thylakoid) (Hussain et al. 2019a, b). Due to its wide occurrence in plant cells, APX is considered a better scavenger of H_2O_2 than CAT under oxidative stress conditions. Monodehydroascorbate reductase is another enzymatic antioxidant that replenishes the cellular ascorbic acid pool from MDHA via NADPH as a reducing agent (Khan and Khan 2017). It is localized in the mitochondria, peroxisomes and chloroplasts where APX scavenging of H_2O_2 occurs along with the oxidation of ascorbic acid. It has different isoenzymes localized in various cellular organelles such as chloroplast, cytosol, peroxisome, mitochondrion, and glyoxysome (Hussain et al. 2019a, b).
d. *Dehydroascorbate reductase* It is another enzymatic antioxidant that maintains the cellular redox state in both apoplast and symplast by regenerating ascorbic acid (Khan and Khan 2017). It converts dehydroascorbate to ascorbic acid, by utilizing an electron donor compound such as reduced glutathione. Monodehydroascorbate reductases are localized in the chloroplasts (Shin et al. 2014).
e. *Glutathione reductase* (*GR*) It is a low molecular weight flavoprotein reductase that reduces glutathione disulfide to glutathione by NADPH. Reduced glutathione (GSH) helps regenerate ascorbic acid from DHA and MDHA, and subsequently is converted to its oxidized form (GSSG). To maintain the cellular GSH/GSSG ratio, GR plays an important role in catalyzing the creation of disulphide bond in glutathione disulfide (Khan and Khan 2017). It also plays its role in preventing the oxidation of the thiol group and reacts with toxic ROS members ($^{\cdot}OH$ and $^1O_2$).
f. *Glutathione peroxidase* It is a heme-containing enzyme, scavenges H_2O_2 under both normal and oxidative stress conditions. It plays a crucial role in both lignin biosynthesis and protection against biotic stress by degrading and utilizing indole-acetic acid and H_2O_2. It favors aromatic compounds, e.g., pyrogallol or guaiacol as electron donors. Thus, this enzyme is considered a key scavenger of H_2O_2 (Hussain et al. 2019a, b).

Non-enzymatic antioxidants

The antioxidant system comprises half enzymatic and half non-enzymatic antioxidants. Non-enzymatic antioxidants also scavenge toxic ROS under oxidative stress.

a. *Ascorbic acid* It is generally known as vitamin C, is a widely studied antioxidant molecule which plays a crucial role as a premier substrate for the ROS detoxification (Foyer and Noctor 2011; Akram et al. 2017). The regenerative behavior and the electron donating ability to different enzymatic and non-enzymatic reactions make ascorbic acid a powerful antioxidant (Noctor and Foyer 1998). In addition, ascorbic acid keeps the ROS levels within an acceptable non-toxic limit (Shao et al. 2008). In plant cells, ascorbic acid is produced principally via the Smirnoff-Wheeler pathway in mitochondria, while a small portion is produced by D-galacturonic acid (Ashraf et al. 2019). Due to its wide occurrence in cytosol and apoplast, ascorbic acid plays a major role in protecting against ROS damage. It functions to protect membranes from oxidative stress either by directly scavenging of the $^{\cdot}OH$, H_2O_2 and O_2 radicals or by regeneration of α-tocopherol from the tocopheroxyl radical (Sadiq et al. 2019). Excessive excitation energy in the chloroplast is dissipated via ascorbic acid as a cofactor of violaxanthin de-epoxidase (Khan and Khan 2017). The ascorbic acid redox system includes ascorbic acid, DHA and MDHA. Ascorbic acid is also involved in the protection of metal binding enzymes in plant cells. In addition, it is reported to eliminate the photooxidation via pH-mediated fine-tuning of the PSII activity as well as its down-regulation by zeaxanthin formation (Akram et al. 2017).
b. *Tocopherols* The lipophilic antioxidant family member, α-tocopherol is not only an integral component of cellular membranes, but also an efficient scavenger of lipid radicals and ROS (Ashraf et al. 2019). Of its four isomers, α-, β-, γ-, and δ-, α-tocopherol possesses the highest antioxidant capacity. Tocopherols are present in the green parts of all photosynthetic organisms including plants (Sadiq et al. 2019).
c. *Glutathione* Another, low molecular weight antioxidant of the thiol tripeptide family is glutathione. It is found in different cellular compartments (Fig. 3) (Gill et al. 2013). It performs diverse functions in plants, because of its strong reductive potential that is due to a central

cysteine residue with nucleophilic character (Gill et al. 2013). It scavenges H_2O_2, $^1O_2$, $^{\cdot}OH$, and O_2^-, thereby protecting cellular biomolecules either by generating adducts (glutathiolated) or by reducing them in the presence of organic free radicals or ROS along with the generation of GSSG as a by-product. It also plays a crucial role in regenerating ascorbic acid to produce GSSG which is converted again into glutathione and creates a balance in the cell. Glutathione plays an important role in the formation of phytochelatins catalyzed by phytochelatin synthase that directly chelates heavy metal ions, thereby detoxifying the potential sources of ROS accumulation in plants (Gill et al. 2013).

d. *Carotenoids* The lipophilic non-enzymatic antioxidants, carotenoids, occur widely in the plastids. They are well known for their photosynthetic apparatus protection potential under oxidative stress conditions. Carotenoids are colored pigments produced by plants. They play important roles in plants biological functions including detoxifying $^1O_{2,}$ thus preventing photoxidative damage. Moreover, carotenoids are also known for their ability to provide stability to light harvesting proteins and thylakoid membranes and are crucial for PSI assembly (Khan and Khan 2017).

e. *Flavonoids* They also act as non-enzymatic antioxidants and are abundantly localized in plant aerial parts, especially leaves, flowers, pollens, and are present in the plant vacuole in the form of glycosides (Ahmad et al. 2019). They play diverse and important roles in plant functioning including flower and fruit pigmentation and plant fertility. Moreover, under oxidative stress conditions, flavonoids act as secondary scavengers of ROS, thereby preventing damage to the photosynthetic apparatus caused by excessive excitation energy under stress conditions. Accessibility of the radicals as well as reduction potential provide flavonoids with a strong antioxidant potential (Khan and Khan 2017). They also detoxify $^1O_2$ and protect the outer covering of the chloroplast membrane. In addition, flavonoids inhibit lipid peroxidation and lipoxygenases. In fact, as a secondary metabolite, flavonoids perform better than other reputed antioxidants such as α-tocopherol and ascorbic acid (Ahmad et al. 2019).

Effect of plant bioregulators on the plant oxidative defense system

In their living environment, plants encounter a vast array of individual or multiple abiotic stresses that enhance the production of ROS resulting in oxidative stress. Plants usually defend themselves by utilizing their natural defense mechanisms that are complex and effective to cope with a diverse array of stresses (Raja et al. 2017). The defense system in plants normally activates on the exposure of plants to extreme environmental conditions and is referred to as the inducible defense system. Hence, susceptibility and resistance of plants to stress depends on their timely ability to recognize the prevailing stress conditions coupled with speedy and efficient induction of oxidative defense responses.

Endogenous production of PBRs is one mechanism by which plants regulate growth and development as well as their defense against biotic and abiotic stresses, as briefly discussed in the previous section. Oxidative stress is the condition/outcome of different extreme environmental conditions such as drought, salinity, heavy metals, and high or low temperatures (Demidchik 2015). During plant natural adaptation and cell reparation against oxidative stress-associated ROS, PBRs play an important role to reduce the risk of damage/oxidation to macromolecules such as proteins or nucleotide denaturation and lipid peroxidation (Raja et al. 2017). Thus, the endogenous levels and functions of natural PBRs are altered with the elevated levels of ROS under oxidative stress conditions (Raja et al. 2017). A broad overview with reference to the specific roles of PBRs under oxidative stress conditions is discussed in the following sections and in Table 2. The possible mechanisms by which exogenously applied PBRs induce oxidative stress tolerance are demonstrated in Fig. 4.

Auxins

Auxins are well known for their growth and developmental roles in plants. Several research reports on plants under oxidative stress have demonstrated that there exists an intricate interplay between auxins and ROS produced during oxidative stress condition and in inducing tolerance of such stresses (Jung et al. 2015; Pellegrini et al. 2016; Li et al. 2018a, b, c, d). ROS alter auxin gradient and hence auxin-mediated signaling under oxidative stress (Xia et al. 2015). Furthermore, auxins possess the ability to generate production and homeostasis of ROS, exhibiting an obvious relationship between auxins and oxidative stress (Tognetti et al. 2012). Plant bioregulators (PBRs) regulate many other plant defense genes by regulating the auxin response genes, thereby causing stress tolerance in plants (Wani et al. 2016). For instance, in a recent study by Li et al. (2018a, b, c, d), mung bean seedlings grown under drought and heavy metal stresses increased adventitious rooting to protect the plants from oxidative stress through regulation of antioxidative defense system. Wang et al. (2019a, b, c) demonstrated that the auxin influx carrier, *OsAUX3* in rice grown under aluminum stress regulated the oxidative stress and root growth due to decreased auxin transport in *osaux3* mutants, causing reduced sensitivity to aluminum-induced oxidative stress. The authors concluded that the auxin acts as a signaling

Table 2 Mitigation of oxidative stress by plant growth regulators (PBRs)

Plant growth regulator	Plant species	Stress type	PBR-induced mitigation of oxidative stress	Reference
IAA	Fenugreek (*Trigonella foenum-graecum*)	Cadmium stress	Reduced $O_2^{\cdot -}$, H_2O_2, and MDA contents and membrane damage	Bashri and Prasad (2016)
	Tomato (*Lycopersicum esculentum*)	Cadmium stress	Reduced $O_2^{\cdot -}$ and H_2O_2, electrolyte leakage and lipid peroxidation	Khan et al. (2019)
	White clover (*Trifolium repens*)	Water stress	Reduced MDA contents and improved the activities of antioxidant enzymes	Li et al. (2018a, b, c, d)
	Maize (*Zea mays*)	Boron toxicity	Reduced H_2O_2, electrolyte leakage, and MDA content	Kaya et al. (2018a, b, c)
IAA and SA	Barley (*Hordeum vulgare*)	Cadmium stress	ROS detoxification	Tamás et al. (2015)
	Okra (*Abelmoschus esculentus*)	Salinity stress	Increased activities of glutathione peroxidase (GPX), SOD, CAT, and DPPH free radical scavenging activity	Esan et al. (2017)
Auxins (IAA, IBA, PAA and cytokinins (tZ, Kin, DPU)	Green alga (*Acutodesmus obliquus*)	Lead stress	Reduced levels of MDA and H_2O_2, and improved antioxidant defense system	Piotrowska-Niczyporuk et al. (2018)
IAA and GA_3	Pea (*Pisum sativum*)	Copper toxicity	Reduced levels of H_2O_2 and MDA, lipid peroxidation and protein oxidation	Ben Massoud et al. (2018)
α-naphthaleneacetic acid (NAA), a synthetic auxin	Soybean (*Glycine max*)	Drought stress	Reduced levels of $O_2^{\cdot -}$ and H_2O_2, and increased activities of antioxidant enzymes (SOD, CAT, APX), and reduced membrane lipid peroxidation	Xing et al. (2016)
GA_3	Okra (*Abelmoschus esculentus*)	Salinity stress	Reduced levels of MDA, and H_2O_2, lipid peroxidation, and electrolyte leakage	Wang et al. (2019a, b, c)
	Sunflower (*Helianthus annuus*)	Drought stress	Reduced levels of MDA and enhanced total phenolics, Pro, and antioxidant enzymes activities	Jan et al. (2019)
	Wheat (*Triticum aestivum*)	Chilling stress	Reduced levels of MDA, H_2O_2 and increased antioxidant enzyme activities	Li et al. (2013)
	Tomato (*Solanum lycopersicum*)	Salinity stress	Reduced lipid peroxidation and enhanced activities of antioxidant defense system	Halo et al. (2015)
Cytokinins	Sunflower (*Helianthus annuus*)	Boron toxicity stress	Improved antioxidant defense system by activating SOD, GR, APX, and CAT	Barbafieri et al. (2018)

Table 2 (continued)

Plant growth regulator	Plant species	Stress type	PBR-induced mitigation of oxidative stress	Reference
	Creeping bentgrass (*Agrostis stolonifera)*	Drought stress	Reduced levels of $O_2^{\cdot -}$ and H_2O_2 and increased activities of APX, CAT and POD	Chang et al. (2016)
Kinetin	Tomato (*Solanum lycopersicum*)	Salinity stress	Reduced levels of H_2O_2 and MDA, and electrolyte leakage and increased activities of SOD, CAT, APX, GR, and GST, and increased levels of Pro and GB	Ahanger et al. (2018)
	Tomato (*Solanum lycopersicum*)	UV-B stress	Reduced levels of $O_2^{\cdot -}$, and H_2O_2 and increased activities of SOD, POD, CAT, GST, PAL and DPPH	Singh et al. (2019)
ABA	*Populus* × *canescens*	Zinc stress	Increased activities of enzymatic and levels of non-enzymatic antioxidants	Shi et al. (2015)
	Bermuda grass (*Cynodon dactylon*)	Cold stress	Reduced levels of $O_2^{\cdot -}$, H_2O_2, and MDA, and increased activities of antioxidant enzymes	Cheng et al. (2016)
	Peach fruit (*Prunus persica*)	Chilling stress	Reduced extent of lipid peroxidation, and levels of $O_2^{\cdot -}$, H_2O_2, $^{\cdot}OH$, MDA, and increased activities of antioxidant defense system	Zhang et al. (2019)
	Rice (*Oryza sativa*)	Alkalinity stress	Reduced levels of $O_2^{\cdot -}$, H_2O_2, and MDA and increased activities of antioxidant defense system	Liu et al. (2019)
	Maize (*Zea mays*)	Drought stress	Reduced levels of MDA, and increased activities of antioxidant enzymes and up-regulation of stress defense genes	Yao et al. (2019)
Polyamines -Spermidine	Bakraii (*Citrus reticulata* × *Citrus limetta*)	Salinity stress	Reduced levels of MDA and H_2O_2, electrolyte leakage and increased activities of antioxidant enzymes	Khoshbakht et al. (2018)
	Boehmeria nivea	Cadmium stress	Reduced levels of MDA and H_2O_2 and increased activities of antioxidants	Gong et al. (2016)
Putrescine	Wheat (*Triticum aestivum*)	Aluminum stress	Reduced cell death, membrane lipid peroxidation, lipoxygenase activity, and H_2O_2, and increased NADPH oxidase activity	Yu et al. (2018)

Table 2 (continued)

Plant growth regulator	Plant species	Stress type	PBR-induced mitigation of oxidative stress	Reference
Spermine (Spm) and Spermidine	*Rosa damascena*	Water stress	Reduced levels of MDA and H_2O_2, and enhanced membrane stability, membrane stability index and improved antioxidant defense system	Hassan et al. (2018)
Polyamines (Spermidine)	Tomato (*Solanum lycopersicum*)	High temperature stress	Reduced levels of MDA, $O_2^{\cdot -}$, and H_2O_2, increased activities of GSH, SOD, POD, CAT, GR, MDHAR, DHAR, dehydroascorbic acid and levels of AsA as well as regulated the expression of *MnSOD, POD, APX2, APX6, GR, MDHAR, DHAR1*, and *DHAR2* genes	Sang et al. (2016)
24-Epibrassinolide	Radish (*Raphanus sativus*)	Zinc toxicity stress	Reduced levels of ·OH, $O_2^{\cdot -}$, and H_2O_2, membrane lipid peroxidation, and protein oxidation, and enhanced activities of lipoxygenase, NADPH oxidase as well as enhanced activities of antioxidant defense system	Ramakrishna and Rao (2012; 2013)
Brassinosteroid	Tomato (*Solanum lycopersicum*)	Zinc-oxide nanoparticles induced stress	Reduced levels of H_2O_2, MDA, oxidized glutathione (GSSG)], and GSH:GSSG ratio and increased glutathione (GSH)	Li et al. (2016a, b)
24-Epibrassinolide (EBL)	Eggplant (*Solanum melongena*)	Zinc stress	Reduced levels of H_2O_2, and MDA, and increased levels of AsA, and activities of GSH, MDHAR, APX, GR and glutathione synthetase (GS)	Wu et al. (2016)
	Maize (*Zea mays*)	Drought stress	Reduced levels of $O_2^{\cdot -}$, H_2O_2, and MDA, electrolyte leakage and increased activities of antioxidant defense system	Talaat et al. (2015)
	Arabidopsis thaliana	Arsenic stress	Reduced levels of MDA and enhanced activities of antioxidant defense system	Surgun-Acar and Zemheri-Navruz (2019)
	Brassica juncea	Lead (Pb) stress	Increased activities of POD, APOX, GR, DHAR, MDHAR, GST, and GPOX	Kohli et al. (2018)

Table 2 (continued)

Plant growth regulator	Plant species	Stress type	PBR-induced mitigation of oxidative stress	Reference
	Rice (*Oryza sativa*)	Salinity stress	Reduced levels of MDA while increased e antioxidant enzyme activities as well as the expression of oxidative defense gene *OsBRI1*	Sharma et al. (2013)
	Brassica juncea	Salinity stress	Reduced electrolyte leakage and the levels of MDA, while increased Pro content	Gupta et al. (2017)
24-epibrassinolide and brassinazole	*Arabidopsis thaliana*	Antimony (Sb) stress	Reduced levels of lipid peroxidation and H_2O_2, and enhanced Pro and activities of antioxidant enzymes	Wu et al. (2019)
24-Epibrassinolide and SA	*Brassica juncea*	Lead (Pb) stress	Reduced levels of $O_2^{\cdot-}$, H_2O_2, and MDA, nuclear damage, membrane damage, while increased Tre, Pro and GB contents	Kohli et al. (2019)
28-Homobrassinolide	Rice (*Oryza sativa*)	Salt and pesticide induced stress	Reduced levels of $O_2^{\cdot-}$, H_2O_2, and MDA and increased activities of SOD, APX, GR and CAT	Sharma et al. (2015)
Melatonin	Poplar (*Populus alba* × *Populus glandulosa*)	Methyl viologen stress	Reduced levels of H_2O_2 and, MDA, electrolyte leakage, and increased activities of SOD, CAT, POD, APX, AsA and GSH and Pro	Ding et al. (2018)
	Tea (*Camellia sinensis*)	Cold, salt and drought stress	Reduced levels of $O_2^{\cdot-}$, MDA, and H_2O_2, and increased levels of GSH, ASA, and activities of antioxidant defense system	Li et al. (2019a, b)
	Creeping bentgrass (*Agrostis stolonifera*)	Heat stress	Reduced electrolyte leakage, lipid peroxidation and altered fatty acid content, while increased activities of antioxidant enzymes	Merewitz and Liu (2019)
	Rice (*Oryza sativa*)	Cold stress	Reduced levels of MDA, $O_2^{\cdot-}$, and H_2O_2 and increased Reduced and Oxidized Glutathione (GSH, GSSG) and activities of antioxidant defense system	Han et al. (2017)
	Naked oat (*Avena nuda*)	Salt stress	Reduced levels of $O_2^{\cdot-}$ and H_2O_2 and increased activity of antioxidant defense system	Gao et al. (2019)
Methyl jasmonate	*Zamioculcas zamiifolia*	Air borne benzene stress	Reduced levels of ROS and increased the activities of antioxidant defense system	Khaksar et al. (2017)

Table 2 (continued)

Plant growth regulator	Plant species	Stress type	PBR-induced mitigation of oxidative stress	Reference
	Cow pea (*Vigna sinensis*)	Chilling stress	Reduced levels of MDA and increased activities of antioxidant defense system	Fan et al. (2016)
	Rape seed (*Brassica napus*)	Salinity stress	Reduced levels of MDA and enhanced Pro as well as the activities of antioxidant defense system	Ahmadi et al. (2018)
Methyl jasmonate and SA	Lemon fruit (*Citrus limon*)	Chilling stress	Reduced levels of ROS and increased activities of antioxidant defense system	Siboza et al. (2017)
Tre	Wheat (*Triticum aestivum*)	Salinity stress	Reduced levels of H_2O_2, lipid peroxidation and increased the phenolics, Pro contents	Alla et al. (2019)
	Pepper (*Capsicum annuum*)	Chilling stress	Reduced levels of membrane permeability and MDA content, and enhanced activities of CAT and POD	Ding et al. (2018)
	Herbaceous peony (*Paeonia lactiflora*)	High temperature stress	Reduced levels of $O_2^{\cdot -}$, H_2O_2, and MDA, and enhanced activities of CAT and SOD	Zhao et al. (2019a, b)
	Rice (*Oryza sativa*)	Salinity stress	Reduced levels of H_2O_2 and MDA and enhanced activities of SOD and POD	Shahbaz et al. (2017)
	Radish (*Raphanus sativus*)	Water-deficit stress	Reduced levels of MDA and increased accumulation of GB and AsA activities of CAT, SOD and POD	Shafiq et al. (2015)
Pro	Sugar beet (*Beta vulgaris*)	Drought stress	Reduced levels of MDA and H_2O_2 and enhanced leaf membrane stability index, Pro, soluble sugars, and activities of antioxidant defense system	Ghaffari et al. (2019)
	Date palm (*Phoenix dactylifera*)	Cadmium stress	Reduced levels of MDA and increased membrane stability index as well as activities of enzymatic and levels of non-enzymatic antioxidants	Zouari et al. (2016)
	Maize (*Zea mays*)	Salinity stress	Reduced levels of H_2O_2 and lipid peroxidation, and increased activities of antioxidant enzymes and Pro metabolism enzymes	De Freitas et al. (2019)

Table 2 (continued)

Plant growth regulator	Plant species	Stress type	PBR-induced mitigation of oxidative stress	Reference
	Olive (*Olea europaea*)	Lead stress	Reduced levels of H_2O_2, lipid peroxidation, electrolyte leakage, and enhanced activities of enzymatic antioxidants	Zouari et al. (2018)
Pro and 24-epibrassinolide	Soybean (*Glycine max*)	Arsenic stress	Reduced levels of electrolyte leakage, MDA, $^{\cdot}OH$, $O_2^{\cdot-}$, H_2O_2, MDA-/HNE-protein adducts, protein hydroperoxide, and protein carbonyl	Zouari et al. (2016)
Pro and GB	Sugar cane (*Saccharum species* hybrid)	Salt stress	Increased activities of SOD and GPX	Patade et al. (2014)
GB	Lettuce (*Lactuca sativa*)	Salt stress	Increased activities of APX, CAT, SOD and POD	Shams et al. (2016)
	Oat (*Avena sativa*)	Water stress	Reduced levels of MDA, H_2O_2 and increased accumulation of Pro along with enhanced activities of antioxidant defense system	Shehzadi et al. (2019)
	Tobacco (*Nicotiana tabacum*)	Cadmium stress	Reduced levels of MDA and increased activities of APX, CAT, SOD and POD	He et al. (2019)
	Alfalfa (*Medicago sativa*)	Salinity	Reduced levels of MDA, and activities of CAT, SOD, and POD and increased concentration of soluble proteins	Lou et al. (2019)
	Soybean (*Glycine max*)	Salinity stress	Reduced levels of MDA and H_2O_2 and increased activities of CAT and SOD	Malekzadeh (2015)
	Lettuce (*Lactuca sativa*)	Salinity stress	Reduced levels of MDA and H_2O_2 and membrane permeability	Yildirim et al. (2015)

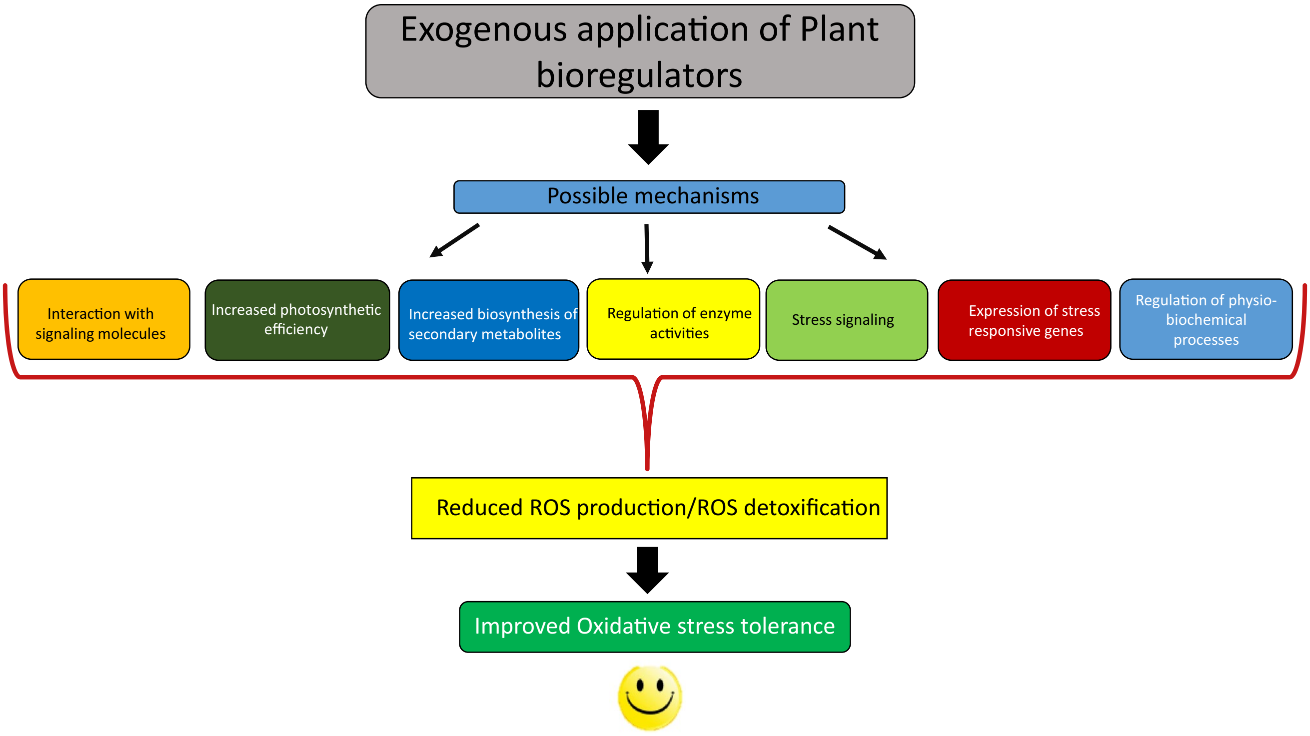

Fig. 4 Possible mechanisms triggered by exogenously applied bioregulator-induced oxidative stress tolerance in plants

molecule against Al stress (Wang et al. 2019a, b, c). Iglesias et al. (2010) demonstrated that an auxin receptor *tir1 afb* mutant possessing impaired auxin perception showed an increased tolerance to oxidative stress condition in *Arabidopsis* by affecting a signaling pathway to adaptive responses.

Exogenous application of auxins has also been shown to mitigate oxidative stress in plants. For example, a low concentration (10 µM) of IAA applied exogenously in *Pisum sativum* alleviated the oxidative stress caused by manganese (Mn) toxicity by decreasing malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) compared with control plants without IAA. The authors concluded that a low concentration of IAA was better able to provide tolerance to pea plants than a high concentration (100 µM) (Gangwar et al. 2011a, b). Similarly, IAA applied exogenously to pea seedlings under copper (Cu) induced stress led to tolerance which was ascribed to low Cu accumulation as well as through the modulation of the thioredoxin/ferredoxin system (Ben Massoud et al. 2018). Furthermore, the balance between regeneration and consumption of cysteine and glutathione reduced forms as well as alterations in thiols and carbonyls profiles contributed to defense against oxidative stress (Ben Massoud et al. 2018). In another study, Piotrowska-Niczyporuk et al. (2018) observed that under lead toxicity (100 µM), exogenously applied auxins (IAA; phenylacetic acid, PAA; indole-3-butyric acid, IBA) and cytokinins (kinetin, Kin; trans-zeatin, tZ; *N*,*N*′-diphenylurea, DPU) to the green alga, *Acutodesmus obliquus,* enhanced its tolerance of oxidative stress compared with that of non-treated alga. While studying the effect of both kinetin and IAA on maize plants grown under boron toxicity, Kaya et al. (2019a, b) reported that increased stress tolerance was associated with reduced uptake of boron and low accumulation of malondialdehyde (MDA) and H_2O_2 as well as low electrolyte leakage (EL), but also with increased activities of some key antioxidant enzymes.

Overall, these results suggest that auxins play a vital role in regulating the oxidative defense mechanism in plants. However, it is not yet clear how far auxin application can effectively circumvent stress-induced oxidative damage in a specific species and how effectively they can trigger the oxidative stress genes. Thus, future research should focus on these unraveled aspects. Furthermore, although auxin signaling pathways have been elucidated considerably, it is not yet known that up to what extent these hormones can counteract the stress-induced oxidative stress and hence improve overall plant stress tolerance. It is also not yet understood that to which other hormones auxins can crosstalk to alleviate the adverse effects of stress-induced oxidative stress on plants exposed to stressful environments.

Gibberellins

Plant response and adaptation to oxidative stress require the coordinated collaboration of hormone signaling pathways to control the expression of stress related genes that allow plants to fine tune stress response (Chen et al. 2020). Gibberellins are crucial PBRs which play a vital role in plant growth and development. Gibberellins in the cell cause synthesis of alpha-amylase, which catalyzes starch into sugar. The sugar so produced enhances the osmotic pressure of the cell due to which water from the external environment enters the cell by the process of osmosis; as a result of which cell enlargement takes place. Like many other hormones, GAs actively participate in signal transduction meant for growth promotion or retardation depending on the plant how it responds to a stress (Colebrook et al. 2014). Gibberellins, either individually, or in combination with other PBRs, are also reported to be involved in triggering oxidative stress resistance in plants (Banerjee and Roychoudhury 2019). For example, Gaion et al. (2018) studied GA-mediated drought tolerance in two tomato cultivars grafted on each other in different combinations. The authors observed that GA sensitivity of root stock and its GA cross talk with ABA produced improved the drought tolerance in the scion by eliminating the oxidative stress, and improving water use efficiency and gene expression related to drought tolerance. Gibberellic acid particularly is known to reduce oxidative stress in plants by modulating thioredoxin/ferredoxin systems thereby protecting proteins from oxidation. In another study with pea plants, copper induced oxidative stress was mitigated by the application of PBRs including GA_3 by decreasing protein oxidation and lipoperoxidation via increased antioxidant enzyme activities. Furthermore, exogenously applied GA increased antioxidant activities in *Solanum lycopersicum* which in turn improved its tolerance to high temperature (Haroun et al. 2018). In another study, ascorbic acid and GA_3 applications to *Phaseolus vulgaris* plants subjected to salinity-induced oxidative stress, synergistically enhanced the plant oxidative defense by decreasing the levels of MDA and H_2O_2 and enhancing protein content, and activities of guaiacol peroxidase and other antioxidant enzymes (Saeidi-Sar et al. 2013). Ding et al. (2015) reported decreased MDA and electrolyte leakage as well as increased proline content and antioxidant activities in stored tomato following GA treatment under chilling stress.

In view of the earlier mentioned reports, it is evident that GA application can mitigate stress-induced oxidative stress. Indeed, these existing evidences suggest that exogenous application of GR has led to induce oxidative stress tolerance. However, the molecular mechanisms underlying pathway crosstalk remains partly understood. Moreover, future research related to genetic transformation for enhanced gibberellic acid biosynthesis to offset stress-induced oxidative stress in plants is vital.

Cytokinins

Cytokinins (CK) regulate a number of developmental processes in plants. The main role of CK is to promote cell division from seed germination to adult stages of the plant. They play an effective role in the S-phase and G2/M phase of the cell cycle. They regulate the activities of key enzymes involved in metabolism and the biosynthesis of growth factors. They also play a critical role in the transport of nutrients and assimilates within the plant body. However, they are known to effectively safeguard the plants against environmental adversaries (Cortleven et al. 2019). Furthermore, there is an ample evidence that they can modulate oxidative stress condition in plants (Cortleven et al. 2019; Jiang et al. 2019a, b). Recent reports have demonstrated that CK applications to crop plants under stress conditions can enhance the plant ability to cope with such stress by enhancing the antioxidant potential as protective response (Jiang et al. 2019a, b; Hönig et al. 2018). Chang et al. (2016) reported enhanced drought tolerance in *Agrostis stolonifera* following the exogenous application of CK which was found to be associated with decreased electrolyte production by 21% using 100 μM CK, O_2^- production 11% and H_2O_2 accumulation 9% as well as increased activities of superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and guaiacol peroxidase (POD) (Chang et al. 2016). In a more recent study, the ability of CK to mitigate selenium induced oxidative stress was demonstrated by enhanced antioxidant activity and detoxification as well as by reduced selenium uptake in *Arabidopsis* (Jiang et al. 2019a, b).

Ma et al. (2016) conducted a study on perennial rye grass to investigate the effect of exogenous CK application in mitigating the salinity induced oxidative stress. They observed regulation of various physiological characteristics as well as ROS scavenging following the application of CK via increased activities of SOD, ascorbate peroxidase, catalase, monodehydroascorbate reductase, and GR. Furthermore, exogenous application of CK was found to up-regulate the gene expression levels for GR and ascorbate peroxidase, resulting in oxidative stress tolerance Ma et al. (2016). Samea-Andabjadid et al. (2018) reported enhancement in the antioxidant activities and reduction in the lipid peroxidation in *Vicia faba* under salinity stress. In a recent study by Kaya et al. (2019a, b), maize grown under boron toxicity demonstrated considerable oxidative stress. While the application of IAA and synthetic CK enhanced the activities of antioxidant enzymes and proline content, it lowered EL, and H_2O_2 and MDA contents, indication a reduction of oxidative stress. Similarly, Singh et al. (2019) conducted an experiment on the *S. lycopersicum* under UV-B oxidative stress. The authors demonstrated that seedlings treated with kinetin and then exposed to UV-B stress had enhanced the antioxidant potential (activities of SOD, POD, CAT and DPPH and GST) and thereby experienced a marked reduction in oxidative stress.

The promising role of cytokinins in mitigating stress-induced oxidative stress impairment is evident form the afore-mentioned reports. However, further research needs to be performed to engineer plants with enhanced biosynthesis of cytokinins as well as to unravel how far they interact with other potential PGRs to circumvent the oxidative stress.

Abscisic acid

Abscisic acid (ABA) is referred to as a potential plant growth inhibitor. ABA-induced growth inhibition is ascribed to the inhibition in GA-induced promotion of the activities of α-amylase and other key hydrolases such as ribonuclease and protease observed during seed germination in different plants. ABA is known to cause inhibition in stomatal regulation and induce dormancy in plants. Despite regulating a variety of physiological processes, ABA is believed to provide an effective adaptation in plants against several abiotic stresses. It also plays an effective role as a signaling mediator for controlling the adaptive responses of plants to various stress environments (Sah et al. 2016). Due to its biosynthesis in response to stress conditions, it is now known as a stress hormone (Tuteja 2007). Specifically, it acts as an endogenous messenger in the plant's water regulation system by targeting or controlling guard cells to adjust water shortage (Zhu 2002).

ABA acts as an oxidative protectant by modulating the expression level of appropriate genes and analysis of *cis*- and *trans*-acting regulatory elements of responsive promoters. Moreover, it interacts with the stress response signaling molecules and other phytohormones as well as osmoprotectants. Furthermore, the endogenous levels of ABA under oxidative stress also change (Vishwakarma et al. 2017). For example, while examining the effect of exogenously applied ABA on drought tolerance of maize cultivars, Yao et al. (2019) reported increased ABA content, antioxidant enzyme activities, osmotic substances, and expressive quantity of the *Asr1* gene, but reduced oxidative stress damage. The cross-talk of both ABA and nitric oxide is believed to increase the oxidative stress tolerance in plants. For instance, in a recent study by Zhang et al. (2019), it was shown that exogenous application of ABA reduced the cold-induced oxidative stress in peach fruit by enhancing the activities of both enzymatic and non-enzymatic antioxidants, partially mediated by nitric oxide. Nitric oxide may act as a downstream signal of ABA as reported in wheat grown under molybdenum-induced oxidative stress (Wu et al. 2018).

Hence, the crosstalk between ABA and nitric oxide may be a topic of great interest for future studies. In this regard, Deng et al. (2019) have studied the effect of ABA, sodium tungstate and sodium nitroprusside (donor of NO) on the post-harvest physiology of cut roses. They reported that ABA along with NO decreased senescence in cut-flowers by enhancing the activities of SOD, POD and ascorbate peroxidase. In another study, while studying the effect of ABA and NO and their interaction in vitro in walnut (*Juglans regia*) shoots under chilling stress, Dong et al. (2017) reported enhanced chilling tolerance which was associated with enhanced activities of antioxidants and reduced electrolyte leakage and MDA content, and other oxidative stress parameters partially mediated via NO. Furthermore, it was also demonstrated that ABA-triggered NO production enhanced the chilling tolerance by counteracting oxidative stress. However, how ABA-regulates NO production under chilling induced oxidative stress conditions still needs to be clarified. ABA levels may differ in crop varieties/genotypes differing in stress tolerance. For example, Silva et al. (2018) examined the difference in ABA levels in coffee grafting clones differing in drought tolerance potential. It was demonstrated that drought tolerant clones showed the ability to accumulate high amounts of ABA in both roots and shoots under drought stress and in these tolerant clones reduced oxidative stress was found which was associated with up-regulation of the antioxidant defense system.

In a recent study, Shi et al. (2019) reported that lead toxicity induced oxidative stress in *Populus* × *canescens* was reduced by the exogenous application of ABA. They observed reduced ABA levels as well as enhanced amelioration of ROS in both leaves and roots, which was mediated through increased activities of CAT, POD, and APX. In another study, in cold stressed sugarcane seedlings, Huang et al. (2015) reported that ABA application effectively mitigated oxidative stress and cell membrane injury by decreasing the MDA and GA_3 contents while increasing the endogenous ABA, proline, and the ratio of ABA/GA_3. On the basis of the aforementioned studies, it is evident that ABA enhances plant tolerance to different abiotic stresses by counteracting oxidative stress. However, more detailed studies related to their crosstalk with other hormones and gene expression are required to better cognize their regulatory action under oxidative stress.

Ethylene

Ethylene, a gaseous hormone, is known for causing the "triple response" in plants. For example, it effectively shortens the length of shoots and makes them thick; it also promotes lateral root growth. It is referred to as a stress hormone produced in plants subjected to environmental cues. It plays an effective role in plant adaptation to a variety of stresses (Mattoo and White 2018) by interacting with some key biological signals throughout plant life cycle (Kolbert et al. 2019). Its action as promoter or inhibitor of growth and senescence depends on its level, application timing, and the nature of plant species (Khan and Khan 2017). It also plays a vital role in flower development and fruit ripening. The endogenous levels of ethylene generally increase under stress conditions (Abiri et al. 2017; Pei et al. 2017). However, ethylene along with some other potential growth regulators such as JA and SA play roles as second messengers thereby regulating oxidative stress (Jang et al. 2020).

For example, in a recent investigation, exogenously supplemented 1-methylcyclopropene (1-MCP), an ethylene inhibitor, to rice plants under salinity stress regulated several processes and provided tolerance of salinity induced oxidative stress (Hussain et al. 2019a, b). The authors observed that 1-MCP improved chlorophyll contents, rate of photosynthesis, SOD activity, and protein synthesis and, diminished the levels of H_2O_2, MDA and proline in salt stressed rice plants thereby improving growth and grain yield.

To examine the role of ethylene in tomato plants under chilling stress, Yu et al. (2019) used two types of fruits, one expressing antisense *SlACS2 (ethylene inhibition) and the other a* wild-type, Lichun (normal ethylene biosynthesis) to confirm the role of ethylene biosynthesis in the relative expression of *SlCBF1* and the degree of chilling tolerance. The authors observed *more chilling stress* in ethylene inhibited tomatoes accompanied by enhanced ion leakage and MDA content, reduced antioxidant activities, lower soluble protein and proline content, and lower expression of *SlCBF1*, a cold stress tolerance gene in tomato (Yu et al. 2019). From these studies, it can be concluded that ethylene plays diverse roles in plant tolerance to stress-induced oxidative stress. Abiotic stresses are believed to influence the expression of genes involved in ethylene synthesis and perception, but the role of ethylene in oxidative defense system still remains to be comprehended. However, future research should focus on their role in triggering molecular mechanisms under oxidative stress.

Brassinosteroids

Brassinosteroids (BRs), plant steroidal hormones, play an effective role in regulating plant growth and development. Although they were initially considered as promoters of cell elongation analogous to what GAs do, their functions in plants have been identified to be highly diverse including development of roots, formation and development of anther and pollen, differentiation of vascular tissue and biosynthesis of cellulose, etc. (Yang et al. 2011). Brassinosteroids play vital roles in plant development, regulating multiple processes such as cell elongation, cell division, photomorphogenesis, vascular differentiation, and reproduction as well as responses to both biotic and abiotic stresses (Fariduddin et al. 2014). The maintenance and regulation of endogenous levels of BRs are crucial for various biological functions in plants. Brassinosteroids are known to play an important role in amelioration of oxidative stress conditions in plants exposed to different stresses. For example, Li et al. (2016a, b) studied the zinc-oxide nanoparticles induced oxidative stress in tomato plants that was caused by increased accumulation of H_2O_2 and lipid peroxidation (MDA content) and increased activities of antioxidant enzymes (SOD, CAT, APX and GR), which thereby altered the redox state (GSH, GSSG, and their ratio) especially at 50 mg/L (highest dose) of ZnO nanoparticles. The addition of 24-brassinolide (EBR) to the growing media along with ZnO nanoparticles reduced the levels of MDA and H_2O_2, glutathione and further increased the activities of antioxidant enzymes which alleviated the oxidative stress conditions.

Not only environmental stresses but also some organic pollutants can cause oxidative stress. For example, while examining the role of 24-epibrassinolide (EBR) in controlling oxidative stress induced in *Cucumis sativus* plants by the organic pollutants chlorpyrifos, 2,4,6-trichlorophenol, and oxytetracycline, Ahammed et al. (2017) reported that exogenously supplied EBR mitigated the oxidative stress in plants by decreasing H_2O_2, MDA and NO content, and increasing the activities of antioxidant enzymes and altering the expression of detoxification genes. Furthermore, flavonoid content, free radical scavenging capacity, and the activity and transcription of secondary metabolism related enzymes also increased in response to applied EBR. While studying the effect of nickel stress on *S. lycopersicum*, Nazir et al. (2019) observed that the exogenously applied epibrassionolide and H_2O_2 regulated plant growth and ameliorated oxidative stress by restricting Ni uptake and reducing oxidative burst by lowering endogenous H_2O_2 contents, electrolyte leakage, and superoxide, and by increasing the activities of CAT by 65.23%, GPOX 75.02% and SOD by 84.61% as well as proline accumulation (Nazir et al. 2019). Moreover, similar studies have also confirmed the BR-induced enhancement of antioxidant activities in plants in response to other stresses (Shahzad et al. 2018; Tanveer et al. 2018).

It is now evident that BR signal transduction pathway interacts with redox signaling in plants subjected to environmental cues (Tian et al. 2018). A strong evidence also shows that BR triggers oxidative defense system in plants grown under stressful regimes (Planas-Riverola et al. 2019). BR has been reported to improve stress tolerance by employing the processes regulated by hydrogen peroxide and nitric oxide (Planas-Riverola et al. 2019). An indirect relationship of synthesis of BR and accumulation of superoxide radical has been reported which suggests a crosstalk between BR and ROS (Lv et al. 2018).

Undoubtedly, extensive research has been conducted during the last few decades to unravel BR multiple functions including key metabolic processes, signal transduction and cross-talks with other PGRs as well as ROS involved in growth and development in plants subjected to stressful environments. However, the crosstalk of BR with each individual ROS needs to be yet explored. Since BRs have pleiotropic effects on plants so it would be plausible to understand their specific roles in offsetting stress-induced oxidative stress. In view of some latest reports, tissue-specific and temporally operating different BR signaling pathways exist in plants (Nolan et al. 2019; Planas-Riverola et al. 2019), but how far these spatio-temporal different signaling mechanisms interact with each other and also with those of the other hormones during oxidative stress, is not known yet. Thus, this area of research needs to be dealt with strenuously.

Jasmonates

Jasmonates (JAs) belong to a group of diverse chemical compounds known as plant oxylipins. Jasmonates (JAs) include prominently jasmonic acid (JA) and its derivative methyl jasmonate (MeJA), although some other derivatives [*cis*-jasmone, jasmonoyl isoleucine (JA-Ile), jasmonoyl ACC] of JA are also known to play a critical role in plant growth regulation (Ahmad et al. 2016). Jasmonates, in general, are considered as a defense and fertility hormone, so they play a critical role in physiological processes involved in plant stress adaptation (Pauwels and Goossens 2011). Jasmonates are known to trigger a myriad of responses in plants subjected to biotic or abiotic stresses. For example, exogenous application of methyl jasmonate improved oxidative stress tolerance by decreasing the MDA and increasing the antioxidant defense system in rapeseed (*Brassica napus*) grown under salt stress (Ahmadi et al. 2018). In a recent study, Sarabandi et al. (2019) showed that under boron toxicity, foliar application of methyl jasmonate eliminated the boron induced oxidative stress by enhancing the activities of SOD, CAT, and phenylalanine ammonia lyase while by decreasing the proline and MDA content in the leaves of Iranian grape cultivars. In a recent study, Moharramnejad et al. (2019) showed that growing *Stevia rebaudiana* in vitro on a medium amended with salicylic acid or methyl jasmonate enhanced oxidative stress tolerance by increasing the activities of SOD and POX, as well as the levels of total phenolics, potential non-enzymatic antioxidants. As with abiotic stresses, jasmonates can also effectively alleviate biotic stress-induced oxidative stress. For example, Chakraborty and Basak (2019) reported mitigation of oxidative stress in *Vigna mungo* caused by mung bean yellow mosaic India virus. The authors observed decreased MDA and increased membrane stability index value. Furthermore, the methyl jasmonate application up-regulated the expression of antioxidant related genes that caused an effective ROS homeostasis in plants. Therefore, it is necessary to identify and transfer the genes related to jasmonates as well as to optimize the doses and number of exogenous applications to achieve maximum mitigation of stress-induced oxidative stress.

Although the roles of different classical hormones in offsetting the adverse effects of stress-induced oxidative stress on plants are well reported in the literature, the role of jasmonates in plants subjected to abiotic stresses is currently being aggressively researched. Moreover, a strong evidence reveals that crosstalk between jasmonates and several other hormone signaling pathways takes place under different stress environments (Riemann et al. 2015). For example, the key components of the JA signaling pathway in some plants such as Arabidopsis, tobacco, and rice are identified as CORONATINE INSENSITIVE 1 (COI1) protein, JASMONATE ZIM DOMAIN PROTEIN (JAZ), and MYC (Yang et al. 2019). In this complex, COI1, plays a critical role in identifying JA signalling (Xie et al. 1998; Yang et al. 2019). The inhibition of jasmonate response is reported to be carried out by JAZ protein (Yang et al. 2019). The interaction between JAZ and COI1 may take place by the action of JAZ protein (Gimenez-Ibanez et al. 2015). Moreover, a widely reported transcription factor for negatively regulating plant growth, MYC2, is contemplated as a universal switch of the JA signaling pathway (Yang et al. 2019). It actively participates in the crosstalks between JA and several other hormone signaling pathways (Gangappa et al. 2013). It has been also observed that different stressful cues cause the accumulation of JA/JA-Ile (JA-isoleucine) in plants (Heitz et al. 2016; Hazman et al. 2019). It is believed that under stressful environments JA–Ile is significantly activated, which is recognized by COI1 (JA receptor). Then the binding of SKP1/CULLIN/F-box $(SCF)^{COI1}$ to JAZs results in ubiquitination followed by degradation through the 26S proteasome, thereby causing the discharge of the MYCs and the upregulation of JA responses (Dubois et al. 2018; Hazman et al. 2019; Yang et al. 2019). Such information will now be useful to comprehensively elucidate the metabolic role JA-Ile in plant stress response to adverse environments and fine-tune JA signaling under stressful conditions.

Tocopherols

Tocopherols belong to vitamin E family and are potential antioxidants, lipophilic in nature. There are four different forms of tocopherols, i.e., α-, β-, γ- and δ-, which differ in the position and number of methyl groups in their molecular structures (Munné-Bosch 2005). The main site of the biosynthesis of tocopherols is plastids. Tocopherol biosynthesis alters during different phases of plant development, and in response to different stresses (Ma et al. 2020). Tocopherols mainly scavenge lipid peroxy radicals and quench singlet oxygen. Acting as antioxidants, tocopherols form tocopherol quinone, which in turn undergoes degradation or recycling (Munné-Bosch 2005). Their potential antioxidative characteristic is attributable to their capability to scavenge lipid peroxyl radicals and other readily produced ROS in plant tissues under stress conditions, so fatty acids are protected from lipid peroxidation (Fritsche et al. 2017). For example, Sadiq et al. (2018) reported that α-tocopherol applied exogenously to mung bean (*Vigna radiata*) grown under limited irrigation eliminated the oxidative stress by improving endogenous levels of glycine betaine (GB) and proline (Pro) as well as the activities of SOD, POD, and CAT, whereas it reduced non-reducing sugars, endogenous tocopherol, total soluble proteins, free amino acids. MDA and H_2O_2. Similarly, in another study, α-tocopherol quenched the ROS production induced by salinity stress by decreasing the levels of H_2O_2 and the rate of superoxide radical generation, and increasing the carotenoids, chlorophyll b, endogenous Pro, and soluble proteins in *Carex leucochlora* (Ye et al. 2017). Alpha-tocopherol or ascorbic acid application (400 mg/L) to salt stressed flax (*Linum usitatissimum*) plants reduced lipid peroxidation and increased the activities of polyphenol oxidase, SOD and CAT, thereby mitigating the oxidative stress (El-Bassiouny and Sadak 2015).

Since there are very few studies on the role of alpha-tocopherol in offsetting stress-induced oxidative stress, so it is not easy to draw a conclusive inference its effectiveness. However, there is a general perception that high levels of alpha-tocopherol can effectively improve plant stress tolerance, whereas low levels lead to oxidative impairment. Moreover, it is also reported that in the absence of alpha-tocopherol, a variety of other potential antioxidants can manage to protect plants from oxidative damage (Munné-Bosch 2005).

Thus, further research is desired to be performed to ascertain that up to what extent alpha-tocopherol can individually protect the plants from oxidative injury. The recent literature demonstrates that the genes for the synthesis of all vitamin E components including tocopherols are now considerably elucidated. However, since there are different forms of tocopherols occurring in plants, so it is naïve to expect that the different isoforms may play a differential role in plant stress adaptation and signaling pathways operative under oxidative stress condition. Thus, future research on these aspects may enable us to understand the comprehensive role of tocopherols along with all other components of vitamin E in circumventing oxidative stress.

Polyamines

Although in living organisms polyamines (PAs) occur in three different forms, i.e., free, covalently conjugated and non-covalently conjugated (Chen et al. 2019), in higher plants the commonly occurring PAs are the free form. The main PAs occurring in plants are putrescine (Put), spermidine (Spd), and spermine (Spm); they are believed to play an active role in regulating a myriad of physiological processes (Mustafavi et al. 2018) including mainly senescence, flower development, fruit maturation, embryogenesis, organogenesis, etc. (Chen et al. 2019) as well as plant responses to different stressful environments (Mustafavi et al. 2018; Chen et al. 2019). It is believed that polyamines are involved in complex hormonal cross-talks. For example, the cross-talk of polyamines with the signaling pathways of abscisic acid as well as with reactive oxygen species are evident (Diao et al. 2017). They are also known to generate nitric oxide, and regulate the activities of ion channels, ATP synthesis, cell membrane stability, transcription, translation, etc.. They are reported to play a critical role in plant growth and development, most importantly under stressful environments (Li et al. 2018a, b). For example, while examining the role of polyamines in conferring drought tolerance in white clover using exogenous spermidine (Spd) and a Spd inhibitor, dimethylthiourea (DCHA), (Li et al. 2016a, b) reported that exogenously applied Spd increased the endogenous polyamine levels, while DCHA decreased them. Furthermore, Spd application increased cytokinins and GA, but decreased IAA contents under drought stress. Spd application particularly enhanced the antioxidant activities. On the contrary, the Spd inhibitor, DCHA, impaired the antioxidant system, inhibited MT gene expression and decreased proline metabolism thereby exacerbating the drought-induced oxidative damages. The authors concluded that changes in polyamines and other plant hormones leads to oxidative stress mitigation, inhibition of leaf senescence and regulation of growth under drought stress.

In another study with maize plants, Li et al. (2018a) reported enhanced oxidative tolerance in drought stressed maize plants by exogenously applied Spd. The authors observed increased endogenous levels of polyamines, IAA, zeatin riboside (ZR), and $GA_{3,}$ but decreased jasmonate and SA contents following Spd applications under drought stress. Exogenously supplied Spd application reduced the levels of MDA, H_2O_2 and oxidized glutathione. Activities of APX, SOD, and GR increased, while the activities of dehydroascorbate and monodehydroascorbate reductase decreased as well as the ratios of ascorbate, dehydroascorbate and glutathione, oxidized glutathione. The authors concluded that exogenous Spd reduced oxidative damage by improving the antioxidant components, enhancing the redox state of ascorbate and glutathione, and changing the polyamine pool, thereby improving drought tolerance in maize. The positive influence of polyamines on plant growth was correlated with enhanced antioxidant activity but still there is a need to search for the genes (molecular mechanisms) which regulate this phenomenon.

There is a plethora of literature which clearly depicts that polyamines supplied through external means or intrinsically over-produced through advanced biotechnological tools, can markedly promote plant adaptation against stressful cues including oxidative stress. However, it remains to be elucidated how and up to what extent polyamines regulate plant growth and development under oxidative stress condition.

Glycine betaine

Glycine betaine is a soluble quaternary ammonium compound which acts as a potential osmoprotectant in plants particularly when they are exposed to stress conditions (Zulfiqar et al. 2020). Glycine betaine is believed to stabilize protein structures, so the enzyme activities are reasonably maintained (Cleland et al. 2004). Glycine betaine not only can protect proteins from denaturation, but it can stabilize membranes, protect photosystem II, and alleviate oxidative injury (Chen and Murata 2011). Moreover, GB can promote the expression of many intrinsic genes in transgenic plants (Giri 2011). Thus, the role of GB in plants is diverse (Ahmad et al. 2013). Despite playing a critical role as a compatible osmolyte for osmoregulation, GB has the ability to interact with both hydrophilic and hydrophobic domains of membrane proteins. Due to this characteristic, GB can effectively maintain and stabilize the ultra-structures of these key biomolecules and safeguard them from the injurious effects of ROS (Ashraf and Foolad 2007; Annunziata et al. 2019). Although it has been widely reported that GB can effectively mitigate stress-induced oxidative stress, the mechanism by which it counteracts various reactive oxygen species is still not quite clear. However, while using GB as an exogenous supply to plants, several studies have reported its beneficial effects on different plants exposed to a variety of stressful cues. For example, Shehzadi et al. (2019) have determined the role of exogenous GB application in confronting the negative effects of drought stress on oat plants. They reported an effective counteraction of oxidative stress due to GB application, which was found to be associated with a reduction in H_2O_2 levels and increases in SOD activity and endogenous GB content in drought stressed oat plants. GB applied exogenously to cadmium stressed tobacco cultivars mitigated, to a great extent, the damage caused by oxidative stress by reducing Cd and MDA contents and enhancing the activities of key antioxidative enzymes (He et al. 2019). Similarly, Ahmed et al. (2019) observed that winter wheat under limited irrigation but treated with GB were better able to counteract key reactive oxygen species (H_2O_2 and MDA) than untreated plants. In alfalfa grown under salinity stress, an exogenous spray of GB significantly reduced soluble proteins, MDA content and Na^+ /K^+ ratio and increased the activities of SOD, POD, and CAT. The authors concluded that 5 mM GB application was an appropriate concentration to ameliorate the salinity induced oxidative stress damages in alfalfa (Lou et al. 2019).

These studies clearly indicate the positive influence of GB in controlling stress-induced oxidative stress. However, the potential of GB must be explored with a wide range of crop plants in order to better understand how far it can effectively offset oxidative stress. Furthermore, introgression of genes responsible for high accumulation of GB particularly in GB-non-accumulator plant species has a great promise.

Proline

Proline, an imino acid, accumulates to varying levels in higher plants grown under adverse environmental cues (Saradhi et al. 1995; Kuznetsov and Shevyakova 1997; Ashraf and Foolad 2007). It acts as a prospective osmoprotectant as well as a quencher of ROS (Hayat et al. 2012). As an important compatible solute, it plays a vital role in osmoregulation in plants exposed to stressful environments (Ashraf and Foolad 2007). It has been considered as a metabolic energy sink as well as stress signal (Werner and Finkelstein 1995; Zhang and Becker 2015). Although a plethora of reports show that proline plays an effective role in plants exposed to stressful environments (Van Rensburg et al. 1993; Kavi Kishor et al. 1995; Ashraf and Foolad 2007), some other reports have shown that proline accumulation in stressed plants is an indication of a stress (Madan et al. 1995; Hare and Cress 1997). Thus, the role of Pro in stress tolerance is yet controversial (Hayat et al. 2012). Either through exogenous supply or endogenous manipulation it can regulate a myriad of physio-biochemical processes in stressed plants because it is regarded as a vital organic osmolyte as well as a potential antioxidant. It can also stabilize cellular macromolecules and cell wall structural components. Recently, de Freitas et al. (2019) studied salt stressed sorghum plants supplied exogenously with proline (30 mM) as a plant bioregulator/osmoprotectant. It was demonstrated that exogenous Pro application increased the endogenous Pro level, the activity of proline metabolism enzymes, and glutamine level, as well as the expression of *p5cs1* and *prodh* proline related genes. This shows that proline application is helpful in mitigating salinity induced oxidative damage in plants. In another study, de Freitas et al. (2018) reported that exogenously applied proline alleviated salt-induced oxidative damage by altering the antioxidant system and inorganic solute content as well as by decreasing H_2O_2 content and lipid peroxidation. Ghaffari et al. (2019) also demonstrated that under drought induced oxidative stress, Pro application down-regulated the levels of MDA and H_2O_2 and up-regulated the antioxidant defense system. When comparing the effectiveness of Pro and GB in counteracting Pb-induced oxidative stress, Pro was comparatively better in controlling stress than GB. Similarly, Zouari et al. (2018) also reported that proline application provided a better PBR/osmoprotectant than the glycine betaine. Further studies need to be carried out to understand the Pro biosynthetic pathway especially at the genetic level.

Trehalose

Trehalose (Tre), a non-reducing disaccharide, is widely reported as a plant stress mitigator. Trehalose is contemplated as a vital signal biomolecule having an ability to maintain the levels of sucrose up to optimum levels within plants. Its role in starch metabolism and synthesis of key organic acids has been widely reported. Trehalose is believed to act as a critical osmoprotectant which can effectively stabilize key proteins and enzymes (Zulfiqar et al. 2020). Although in plants it usually occurs in small amounts, its concentration rises in plants when they are subjected to abiotic stresses (Kosar et al. 2019). Externally supplemented trehalose in low quantity has been reported to assuage stress-induced physio-biochemical disorders (Kosar et al. 2019). There are several reports in the literature that depict its effectiveness in counteracting stress-induced oxidative stress. For example, Zhao et al. (2019a, b) examined the role of exogenously applied Tre on peony (*Paeonia lactiflora* Pall.) plants grown under high temperature stress. The Tre application significantly reduced the levels of ROS including $O_2^{\cdot -}$, MDA, H_2O_2, but enhanced the activities of key antioxidant enzymes such as SOD and CAT.

In salt stressed wheat plants raised from Tre pre-treated seeds, Alla et al. (2019) demonstrated that pre-sowing treatment with 10 mM Tre lowered the levels of H_2O_2 and lipid peroxides by elevating endogenous Pro and phenolics, sugars, K contents, and K/Na ratio as well enhancing the expression of *AOX*, *SOS1*, and *NHX1*, thereby ameliorating overall the oxidative stress effect. In quinoa (*Chenopodium quinoa*), Tre application under water deficit conditions mitigated oxidative stress by decreasing lipid peroxidation, H_2O_2, and lipoxygenase activity, and by increasing antioxidant enzyme activities, including those of APX, SOD, CAT, and POX (Sadiq et al. 2019). In radish, (*Raphanus sativus*) Shafiq et al. (2015) reported that Tre applied via pre-sowing seed treatment or as a foliar spray reduced MDA content, increased the levels of ascorbic acid, total tocopherols, phenolics, GB and total soluble proteins, as well as the activities of antioxidant system (SOD, CAT, POD) under 60% field capacity.

Trehalose accumulation in plants is generally not so high to effectively mitigate the negative effects of different stresses. Thus, efforts have been made to engineer plants by incorporating microbial trehalose biosynthesis genes. However, although these transgenic plants had low accumulation of trehalose, they were still resistant to abiotic stresses including most specifically water deficit stress (Iordachescu and Imai 2011). Under such circumstances, a balance between the levels of exogenous and those of intrinsic trehalose needs to be determined which should be effective in mitigating the stress-induced oxidative stress or other related attributes in plants. Furthermore, crosstalk of trehalose with other PBRs should be the focus of future research.

Melatonin

The occurrence of melatonin has been reported in several plant species. It has been contemplated as a vital growth regulator as well as a morphogenetic factor for plants (Hardeland 2016). In plants, melatonin is demonstrated to be a regulatory molecule for diverse metabolic processes involved in plant growth, such as seed protection and germination, root development, fruit ripening, and senescence (Zhao et al. 2019a, b). Melatonin has been reported to regulate H_2O_2/NO signaling pathways, and enhance plant stress tolerance by stimulating key antioxidant enzymes, regulating transcription factors, and mitigating photosynthesis inhibition (Zhao et al. 2019a, b). Melatonin is thought to cross-talk with other stress hormones such as ethylene, jasmonic acid, and salicylic acid (Zhao et al. 2019a, b). The major role of melatonin is believed to reinforce stress-induced oxidative defense system. Thus, melatonin functions as the most important defense against any stressful cue (Martinez et al. 2018). Its functions are believed to be analogous to those of auxins, and acting as a signaling molecule it is effectively involved in regulation of pathways of ABA, jasmonates, ethylene, and salicylic acid (Hardeland 2016). Thus, it can play a critical role in plant tolerance of stress-induced oxidative stress. For example, Martinez et al. (2018) demonstrated that the combination of heat and salinity (35 °C + 75 mM NaCl) caused considerable oxidative stress in tomato plants. However, exogenously applied melatonin (100 µM) under the combined stress condition helped the plants to tolerate the oxidative stress and prevented damage to biological membranes and proteins by modulating antioxidant related genes (*APX, GR, GPX* and *Ph-GPX*). Ultimately, the ROS accumulation decreased, while the antioxidant activities increased (Martinez et al. 2018). In another study, Huang et al. (2019) reported that under drought-induced oxidative stress, melatonin applied either via leaf spraying or through the root growing medium decreased the oxidative stress induced ROS, degradation of proteins, and severe cell death, particularly via root application.

While working with Kiwifruit (*Actinidia deliciosa*) plants, Liang et al. (2018) found that seedlings grown under heat stress (45 °C) showed cellular membrane damage, inhibition of photosynthesis and, ultimately, reduced biomass production. However, exogenously applied melatonin

(200 μM) reduced lipid peroxidation, protein degradation, and cell membrane injuries, but, in contrast, increased the levels of endogenous osmoprotectants (2.1 times), and also improved photosynthesis by regulating electron transport in PSII and the genes related to CO_2 fixation. Furthermore, pretreatment with melatonin increased POD two times, CAT one time and reduced the decline in SOD activity to half under heat stress compared to that in untreated stressed plants. Although the above-mentioned studies indicate the positive effect of melatonin in offsetting stress-induced oxidative stress, further research is needed to confirm the extent to which melatonin can modulate the oxidative defense mechanisms in different plants under stressful environments.

Strigolactones

Strigolactones (SLs) are carotenoid derived PBRs that play a vital role in effectively regulating plant tolerance to a variety of stressful environments (Mostofa et al. 2018). Strigol and orobanchol are natural, while $GR24^{5DS}$ and $GR24^{ent-5DS}$ are synthetic analogues of SLs (Rameau et al. 2019). They play a crucial role in the regulation of vital developmental processes such as development of shoot, leaf and root. SLs perform a crucial role in key bioprocesses through an interaction with a protein receptor (Carlsson et al. 2018). Several reports have shown that SLs interact with abiotic stresses by up-regulating the plant oxidative defense system. For example, in a recent study, while studying the effect of rac-GR24 (synthesized strigolactone) at three different levels (1, 3 and 5 μM) on grape (*Vitis vinifera* L.) seedlings under drought stress, Min et al. (2019) reported reduced stomatal opening, electrolyte leakage, and ROS, but enhanced chlorophyll contents, photosynthesis, and relative water content in GR24 treated plants. Moreover, under drought stress conditions, GR24 applications decreased IAA and zeatin riboside contents but increased ABA in leaves and roots. The authors concluded that strigolactone applications can mitigate the negative effects of drought-induced oxidative stress in plants by regulating physiological processes and antioxidant defense system as well as cross-talking with other hormones such as IAA and ABA. In another study using the exogenous application of GR24, Lu et al. (2019a, b) reported that under low light stress, foliar-applied GR24 (15 μM) increased the antioxidant activity as well as gene expression, the electron transport rate of PSII and PSI, non-photochemical quenching, the oxidized plastoquinone pool size, and ratio of the quantum yield of cyclic electron flow to Y(II), while reduced the contents of H_2O_2 by 26% and MDA 33%. The authors concluded that strigolactone application can efficiently mitigate the negative effects of low light induced oxidative damages to photosystem in tomato plant thereby improving plant growth. Strigolactones are also reported to enhance plant tolerance to saline stress. For example, SL supply (0.18 μM GR24) to rape seed (*B. napus*) increased the activities of SOD and POD, and the efficiency of photosystem II quantum yield, but decreased non-photochemical quenching and MDA content (Ma et al. 2017). Furthermore, transcriptome analysis revealed that tolerance against salinity was associated with plant hormone signal transduction, gene expression of tryptophan metabolism, and photosynthesis. The role of SLs in mitigating metal-induced oxidative stress has also been reported (Tai et al. 2017). For example, the authors demonstrated that GR24, alleviated the cadmium induced stress in switch grass (*Panicum virgatum*) by regulating photosynthesis, relative water content, activities of antioxidant enzymes, chlorophyll contents and nutrient uptake (Fe, Mn, Zn, Cu) as well as by reducing the uptake and accumulation of cadmium in plants. Furthermore, it was observed that the endogenous SL level increased in plants following the application of exogenous SL application.

SLs are believed to function in conjunction with other PGRs. For example, while assessing the effect of SL and SA on winter wheat under drought stress, Sedaghat et al. (2017) reported that, individually, these PBRs increased the drought stress tolerance by decreasing the electrolyte leakage and increasing the antioxidant activities, relative water content, membrane stability index, and leaf stomatal limitations, but the effect on these parameters was more pronounced when both PBRs were applied in combination. The foregoing reports on different stresses clearly indicate that SLs have a potential role in mitigating the adverse effects of oxidative stress induced by different stresses. However, the detailed mechanism how SLs regulate oxidative stress is not amply clear. Furthermore, like in most of the relatively new PGRs, the SL dose–response relationship in different plant species is also not clear. Thus, future research in this direction would offer more insight into the roles of SLs in counteracting stress-induced oxidative stress.

Salicylic acid (SA)

SA is regarded as an important PBR, which is believed to play a vital role as a key effector of growth and development of plants (Jahan et al. 2019). SA has been reported as a vital signalling molecule in plants, regulating growth and development and protection against stresses (Guo et al. 2019). It is also known as a key signalling molecule which plays a crucial role in systemic acquired resistance (SAR) in plants (Guo et al. 2019). SA is reported to bind to and change the activities of several key proteins (Pokotylo et al. 2019). SA has been demonstrated to interact in a complex manner with the antioxidative metabolism in plants, adjusting cellular redox homeostasis and ultimately causing changes in transcription factor activities and defense-related gene activation particularly under stress conditions (Sharma et al. 2019). For instance, under salinity stress (50 mM), Samadi et al. (2019) reported enhanced stress tolerance in strawberry following SA supplementation. The authors tested two levels of SA (100 and 500 µM) and observed that 100 µM SA application enhanced the levels of some key osmoprotectants, CAT by 67% and endogenous trehalose as well as increased the efficiency of PSII photosystem and phenol metabolism, along with a decrease in MDA content compared to those in untreated salt stressed plants. The authors concluded that SA application (100 µM) could mitigate the salinity-induced oxidative stress in strawberry plants. While studying the effect of SA on heat stress in tomato, Jahan et al. (2019) reported enhanced tolerance in plants through the stress relieving role of SA (1 mM) due to improved gas exchange characteristics, photosystem II functioning, antioxidant defense system (SOD, POD, CAT, and APX by 36.6%, 136.3%, 250%, and 65.8%, respectively), endogenous proline content by 165%, scavenging of ROS, and reduced levels of H_2O_2 and MDA. The authors concluded that SA (1 mM) application played a protective role in mitigating the heat stress induced oxidative damages to plants via improving the photosynthesis and antioxidative defense system.

Similarly, in case of drought stress, exogenous application of SA (250 µM) along with sodium nitroprusside (a donor of NO 25 µM) was reported to mitigate the adverse effects of drought stress in safflower (*Carthamus tinctorius*) by enhancing CAT activity by 43%, SOD by 43%, enhanced production of osmoprotectants (particularly proline), and improving membrane stability as well as by reducing lipid peroxidation and the synthesis of free radicals (Chavoushi et al. 2019). The authors concluded that individual, and particularly the combined, application of both these PBRs brought the safflower plants to approximately normal growth. In another study, SA application (500 µM) in combination with thiamine (150 µM) alleviated boron-induced oxidative stress in wheat by regulating the synthesis/accumulation of carbohydrates, soluble proteins, amino acids and H_2O_2 (El-Shazoly et al. 2019). Although in the afore-mentioned reports it is evident that SA can efficiently mitigate stress-induced oxidative stress, the mechanism by which it triggers the oxidative stress defense system is not yet very clear. Moreover, its crosstalk with other known plant hormones as well as signaling pathways are also not well studied. Thus, further research is necessary to uncover the mechanism of action of SA in mitigating oxidative stress in plants.

Genetic transformation for enhanced synthesis/accumulation of bioregulators in plants and their mitigation effects on oxidative stress

Because conventional breeding has the drawbacks of being laborious, time-consuming, and cost-intensive, PBR genetic engineering can prove a good platform for biotechnologists efficiently to develop transgenic crops with inbuilt enhanced tolerance to abiotic stress. Thus, it is contemplated as a promising approach that includes the introgression of genes/genetic manipulation for enhanced accumulation of PBRs to alleviate oxidative stress associated crop yield losses in future. Specific genes responsible for regulating complex mechanisms of tolerance need to be identified and classified so as to better comprehend the fundamental metabolism. For instance, in a recent study, Agarwal et al. (2016) developed transgenic tobacco overexpressing SA-inducible *JcWRKY* that showed increased membrane stability, soluble sugar accumulation, reduced electrolyte leakage, and generation of H_2O_2 and $O_2^{\bullet-}$ compared with the wild type under salinity stress. Additionally, the transcript expression of *ICS1* (SA biosynthetic gene), *CAT* and *SOD* showed upregulation during stress conditions (Sedaghat et al. 2017). In another study, Quan et al. (2018) developed *Arabidopsis* overexpressing *pGC1, AtPYL5*, an ABA receptor, which showed enhanced drought tolerance via reduced electrolyte leakage, H_2O_2 content, and increased antioxidant activities. In another study, Luo et al. (2016) developed tobacco over-expressing *RrANR* which showed increased accumulation of ABA via up-regulation of ABA biosynthesis and ROS scavenging genes under methylviologen induced stress.

Li et al. (2019a, b) have developed transgenic tobacco overexpressing *Lycium chinense LcSABP*, a gene for SA binding protein 2, which showed enhanced drought tolerance via increased levels of endogenous SA and ABA contents, *LcSABP* transcripts, increased scavenging of ROS and stress responsive genes, increased activities of antioxidant enzymes (CAT, SOD, POD) and lower accumulation of MDA, H_2O_2, and O_2^-. In transgenic tomato, overexpression of *SlGRAS40*, a gibberellin biosynthesis and auxin signaling gene, enhanced drought and salinity tolerance by decreasing MDA, H_2O_2, and O_2^- and increasing CAT, SOD and POD activities (Liu et al. 2017). Jiang et al. (2019a, b) reported enhanced tolerance against salinity and sclerotinia stem rot stress in broccoli overexpressing *BoERF1*, related to ethylene response factors, via decreased H_2O_2, relative electric conductivity, and MDA and increased activities of CAT, SOD and POD compared with those in the wild type. Wang et al. (2019a, b, c) developed transgenic tobacco by inserting *KvP5CS1* (proline producing genes) from *Kosteletzkya virginica* using an *Agrobacterium*-mediated method and observed increased salinity tolerance in transgenic tobacco via reduced MDA contents, and greater antioxidant activities and proline content than those in the wild type. Overexpression of *GhABF2*, an ABA associated gene, in *Arabidopsis* and cotton (*Gossypium hirsutum*) under drought and salinity stress showed enhanced gene expression related to ABA and stress (Liang et al. 2016). Moreover, proline content and the activities of SOD and CAT increased in the transgenic *Arabidopsis* plants compared with the wild type leading to enhanced salinity and drought tolerance (Liang et al. 2016).

Lu et al. (2019a, b) transferred a cotton gene, *DTX/MATE* associated with translocation of ABA, to develop transgenic *Arabidopsis*. The authors observed greater tolerance to drought, salt and cold in transgenic plants than in wild type plants, which was found to be associated with enhanced antioxidant (SOD and CAT) activities, and reduced MDA content as well as increased expression of the stress related genes. While developing transgenic tobacco introduced with a brassinosteroids biosynthetic gene (*SoCYP85A1* taken from *Spinacia oleracea*), Duan et al. (2017) observed enhanced drought tolerance in transgenic plants which possessed increased endogenous BRs level, Pro contents and antioxidant activities, and reduced ROS and MDA contents as well as enhanced expression of stress related genes compared with those in wild plants under drought stress conditions. In another study, Wang et al. (2017) developed transgenic cotton using *Agrobacterium*-mediated genetic transformation of *ABP9* gene associated with ABA, and observed enhanced osmotic and salt tolerance via enhanced Pro, soluble sugars, antioxidant activities (CAT, SOD, POD and GST) and reduced MDA content in transgenic cotton compared with those in the wild type. From these studies, it is obvious that there is a potential for developing transgenic plants with greater ability to over-accumulate PBRs so as better to tolerate extreme environment-related oxidative stresses.

Conclusion and future prospects

Environmental stresses are the main barriers to achieving enhanced crop production globally. In the agriculture sector, such issues are believed to be intensified by climate change. On the other hand, the demand for food is continuously increasing due to a consistent increase in human population. Thus, pragmatic strategies to cope with deleterious oxidative stresses are essential. PBRs are known to play a vital role in conferring oxidative stress tolerance in plants. It is pertinent to note that undoubtedly the levels/activities of antioxidants are potential markers of stress tolerance, but it is not always true that enhanced levels/activities of antioxidants positively relate to stress tolerance. However, there is still a need to explore the scope of different PBRs via both exogenous application or through genetic engineering. Different PBRs have different potential to mitigate oxidative stress in plants, and thus there is a need to assess the costs incurred in the use of specific PBRs. In the case of a very expensive PBR, efforts should be made to explore cheap plant sources which could yield optimal amount of the desired PBR. Alternatively, cost-effective analogues of PBRs with considerable effectiveness need to be also explored.

Furthermore, greater focus must be on understanding the role of PBRs under oxidative stress condition induced by multiple field stresses. This would allow a better understanding of the role of PBRs in plants grown under field conditions. The findings, summarized here clearly depict how environmental stress induced oxidative stress can be mitigated through the use of PBRs. Development of stress-resistant crops needs detailed studies of plant responses under stress conditions. Achievement in generating stress tolerant crop lines/cultivars depends upon the integration of several research areas including molecular biology, genetics, and cell physiology. In many studies, efforts have been made to develop transgenic plants utilizing PBRs oriented genes, which have shown greater survivability under severe stressful environments. Further studies related to the exogenous PBRs application or introduction of PBRs biosynthesis genes may further enhance the knowledge related to oxidative stress tolerance in plants.

Acknowledgements The authors gratefully acknowledge Prof. Phil Harris, Coventry University, UK for his critical reading of the whole manuscript.

Author contributions MA conceived the idea and helped in revising manuscript. FZ contributed in literature collection, writing of manuscript, tables and figures. Both Authors reviewed and updated the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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