frontiers in
ENVIRONMENTAL SCIENCE

REVIEW ARTICLE
published: 12 January 2015
doi: 10.3389/fenvs.2014.00067

Brassinosteroids make plant life easier under abiotic stresses mainly by modulating major components of antioxidant defense system

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Various abiotic stress factors significantly contribute to major worldwide-losses in crop productivity by mainly impacting plant's stress tolerance/adaptive capacity. The latter is largely governed by the efficiency of antioxidant defense system for the metabolism of elevated reactive oxygen species (ROS), caused by different abiotic stresses. Plant antioxidant defense system includes both enzymatic (such as superoxide dismutase, SOD, E.C. 1.15.1.1; catalase, CAT, E.C. 1.11.1.6; glutathione reductase, GR, E.C. 1.6.4.2; peroxidase, POD, E.C. 1.11.1.7; ascorbate peroxidase, APX, E.C. 1.11.1.11; guaiacol peroxidase, GPX, E.C. 1.11.1.7) and non-enzymatic (such as ascorbic acid, AsA; glutathione, GSH; tocopherols; phenolics, proline etc.) components. Research reports on the status of various abiotic stresses and their impact on plant growth, development and productivity are extensive. However, least information is available on sustainable strategies for the mitigation of abiotic stress-mediated major consequences in plants. Brassinosteroids (BRs) are a novel group of phytohormones with significant growth promoting nature. BRs are considered as growth regulators with pleiotropic effects, as they influence diverse physiological processes like growth, germination of seeds, rhizogenesis, senescence etc. and also confer abiotic stress resistance in plants. In the light of recent reports this paper: (a) overviews major abiotic stresses and plant antioxidant defense system, (b) introduces BRs and highlights their significance in general plant growth and development, and (c) appraises recent literature available on BRs mediated modulation of various components of antioxidant defense system in plants under major abiotic stresses including metals/metalloids, drought, salinity, and temperature regimes. The outcome can be significant in devising future research in the current direction.

Keywords: abiotic stress, reactive oxygen species, antioxidant defense system, tolerance, brassinosteroids

INTRODUCTION

ABIOTIC STRESSES AND PLANT ANTIOXIDANT DEFENSE SYSTEM

Plants are inevitably exposed to various environmental stress factors of like abiotic and biotic types. In particular, abiotic stresses such as temperature (heat, chilling, and freezing), water (drought, water logging), salt, heavy metals, light (intense and weak), radiation (UV-A/B) etc. are serious threats to agriculture worldwide (Bray et al., 2000). Elevation in the generation of various reactive oxygen species (ROS; such as superoxide radicals, O^{2-}; hydroxyl radicals, OH^-; perhydroxyl radicals, HO^{2-}; alkoxy radicals, RO^-; hydrogen peroxide, H_2O_2; singlet oxygen, $_{1}O^{2}$.) is a common consequence in plants growing under abiotic stresses (Anjum et al., 2010, 2012, 2014; Gill and Tuteja, 2010). Important signal transduction functions and triggering and/or orchestration of plant responses to varied (abiotic) stresses can be possible with minimal levels of ROS. However, major ROS and their reaction products that escape antioxidant-mediated scavenging can disturb the ROS/antioxidant homeostasis in plant cells, cause oxidative stress, bring critical damages to the primary metabolites of plants viz., proteins, lipids, carbohydrates and DNA and halt cellular metabolism (Anjum et al., 2010, 2012, 2014; Gill and Tuteja, 2010). To survive such stresses, plants have evolved many intricate defense mechanisms to increase their tolerance and survive under such extreme environmental conditions. Plant stress tolerance requires the activation of complex metabolic activities including antioxidative pathways, especially ROS-scavenging systems within the cells that in turn can contribute to continued plant growth under stress conditions (El-Mashad and Mohamed, 2012). Plant antioxidant defense system consists of the enzymes such as superoxide dismutase (SOD: EC 1.15.1.1), catalase (CAT: EC 1.11.1.6), peroxidase (POD: EC 1.11.1.11), ascorbate peroxidase (APX: E.C. 1.11.1.11), glutathione reductase (GR: EC 1.6.4.2), glutathione sulfo-transferase (GST: EC), polyphenol oxidase (PPO: E.C. 1.14.18.1), guaiacol peroxidase (GPX: EC 1.11.1.7), monodehydroascorbate reductase (MDHAR: EC 1.1.5.4), dehydroascorbate reductase (DHAR: EC 1.8.5.1) etc. Whereas, non-enzymatic components may include osmolytes like proline, glycine betaine, sorbital, mannitol etc., and reduced glutathione (GSH), ascorbic acid (AsA) that are needed for osmotic adjustment, stabilization of membranes, and ROS-scavenging (Anjum et al., 2010, 2012, 2014; Gill and Tuteja, 2010) (**Figure 1**).

BRASSINOSTEROIDS

OVERVIEW

Brassinosteroids (BRs) are a new type of polyhydroxy steroidal phytohormones with significant growth-promoting influence (Vardhini, 2012a,b; Bajguz and Piotrowska-Niczyporuk, 2014). Mitchell et al. (1970) discovered BRs which were later extracted from the pollen of *Brassica napus* by Grove et al. (1979). BRs can be classified as C_{27}, C_{28} or C_{29} BRs according to the number of carbons in their structure (Vardhini, 2013a,b). Sixty BRs related compounds have also been identified (Haubrick and Assmann, 2006). However, brassinolide (BL), 28-homobrassinolide (28-HomoBL) and 24-epibrassinolide (24-EpiBL) are the three bioactive BRs those are widely used in most physiological and experimental studies (Vardhini et al., 2006) (**Figure 2**). BRs are considered ubiquitous in plant kingdom as they are found in almost all the phyla of the plant kingdom like alga, pteridophyte, gymnosperms, dicots and monocots (Bajguz, 2009). BRs are considered also as a new group of plant growth hormones that perform a variety of physiological roles like growth, seed germination, rhizogenesis, senescence, and resistance to plants against various abiotic stresses (Rao et al., 2002).

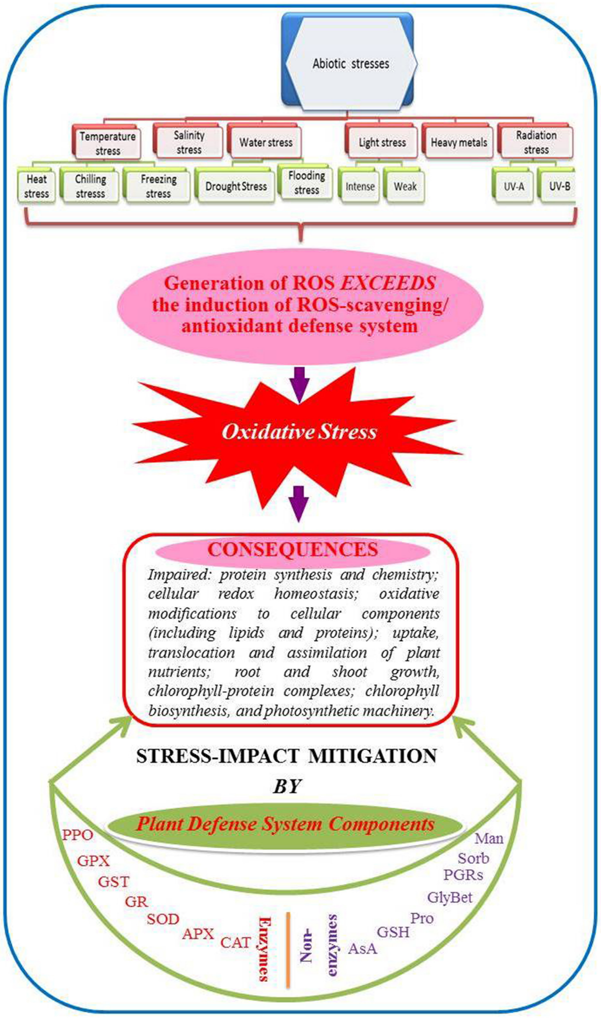

FIGURE 1 | Schematic representation of major abiotic stresses, their consequences and the components of plant antioxidant defense system. (CAT, catalase; APX, ascorbate peroxidase; GR, glutathione reductase; GPX, glutathione peroxidase; GST, glutathione sulfo-transferase; SOD, superoxide dismutase; PPO, polyphenol oxidase; AsA, reduced ascorbic acid; GSH, reduced glutathione; Pro, proline; Man, mannitol; Sorb, sorbitol; GlyBet, glycine betaine; PGRs, plant growth regulators; ROS, reactive oxygen species) (Modified after Anjum et al., 2014).

SIGNIFICANCE IN GENERAL PLANT GROWTH AND DEVELOPMENT

BRs have to their credit a host of roles in general plant growth and development. BRs can activate the cell cycle during seed germination (Zadvornova et al., 2005), control progression of cell cycle (González-Garcia et al., 2011), induce exaggerated growth in hydroponically grown plants (Arteca and Arteca, 2001), and also control proliferation of leaf cells (Nakaya et al., 2002). In addition, reports are also available on the role of BRs in growth promotion of apical meristems in potato tubers (Meudt et al., 1983), acceleration of rate of cell division in isolated protoplasts of *Petunia hybrida* (Ho, 2003) and cell division and leaf expansion (Zhiponova et al., 2013). Initially BRs were identified based on their growth promoting activities; however, subsequent physiological and genetic studies revealed additional functions of BRs in regulating a wide range of processes, including source/sink

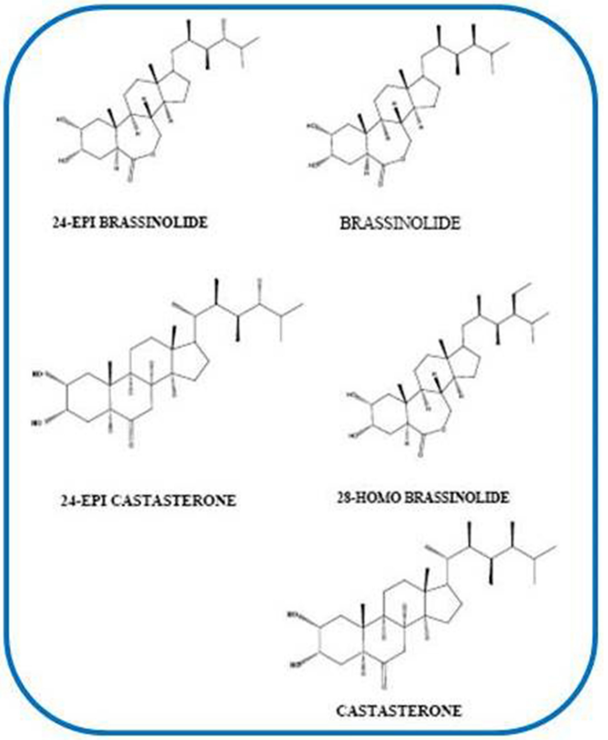

FIGURE 2 | Examples of commonly used bioactive brassinosteroids.

relationships, seed germination, photosynthesis, senescence, photomorphogenesis, flowering and responses to different abiotic and biotic stresses (Deng et al., 2007). The work with BR biosynthetic mutants in *Arabidopsis thaliana* (Tao et al., 2004) and *Pisum sativum* (Nomura et al., 1997) have provided strong evidences that BRs are essential for plant growth and development and BR- signaling plays a positive in plant growth and development (Fábregas and Caño-Delgado, 2014). A simple BR- analog 2α, 3α-dihydroxy-17β-(3-methyl butynyloxyl) 7-oxa-B-homo-5α androstan-6-one induces bean second node splitting which is considered as the prominent physiological feature of BRs (Strnad and Kohout, 2003). Dwarf and de-etiolated phenotypes and BR—deficient species of some *Arabidopsis* mutants were rescued by application of BRs (Bishop and Yakota, 2001). Even *Pharbitis nil*, *Uzukobito* was a defective BR- biosynthetic dwarf mutant strain (Suzuki et al., 2003) which emphasized that BR-deficient and defective BR-biosynthetic species exhibited abnormal growth. Friedrichsen et al. (2002) also reported that three redundant BR genes encode transcription factors which are required for normal growth, indicating the necessity of BRs for normal growth. Similarly, the inhibition of growth (Asami et al., 2000) and secondary xylem development (Nagata et al., 2001) of cress (*Lepidius sativus*) by brassinozole, a specific inhibitor of BL synthesis was reversed by the exogenous application of BL, further emphasizing the necessity of BRs for normal plant growth.

BRs also exhibit synergistic effect with other phyohormones in regulating the plant growth and metabolism. BRs interact with auxins, cytokinins, gibberellins (Domagalska et al., 2010), abscisic acid (ABA) (Domagalska et al., 2010), ethylene (ET) (Manzano et al., 2011) salicylic acid (SA) (Divi et al., 2010) and jasmonic acid (JA) (Creelman and Mullet, 1997; Peng et al., 2011) to promote plant growth and metabolism. Ability of 24-EpiBL to control the basic thermotolerance and salt tolerance of the mutants has been evidenced (Divi et al., 2010). In addition, these authors also reported synergistic role of 24-EpiBL, where treatment with 24-EpiBL increased expression of various hormone marker genes in both wild type and mutant *Arabidopsis* seedlings those were either deficient in or insensitive to ABA, ET, JA, and SA. Notably, BRs may be applied/supplied to plants at different stages of their life cycle viz., vegetative stage (Vardhini and Rao, 1998), flowering stage (Vardhini, 2012a, 2013a), meiosis stage (Saka et al., 2003), grain filling stage (Vardhini, 2012a), anthesis stage (Liu et al., 2006) etc. as foliar spray (Vardhini et al., 2008), seed treatment (Zhang et al., 2007; Kartal et al., 2009), root application (Shang et al., 2006; Song et al., 2006) and even as shot gun approach (Hayat et al., 2010a). Examples of a range of other major functions of BRs and related compounds reported in different plants can be found in **Figure 3**.

BRASSINOSTEROIDS-MEDIATED MODULATION OF PLANT ANTIOXIDANT DEFENSE SYSTEM UNDER MAJOR ABIOTIC STRESS

Extensive research over the years' has established stress-impact-mitigating role of BRs and associated compounds in different plants exposed to various abiotic stresses such as high temperature (Zhou et al., 2004; Kurepin et al., 2008; Janeczko et al., 2011), low temperature in terms of chilling (Divi and Krishna, 2010; Liu et al., 2011; Wang et al., 2014) as well as freezing (Janeczko et al., 2009). Reports are available on the significance of BRs and associated compounds in different plants exposed to salinity (Avalbaev et al., 2010; Abbas et al., 2013), light (Wang et al., 2010, 2012; Kurepin et al., 2012; Li et al., 2012a), drought (Anjum et al., 2011; Li et al., 2012b; Mahesh et al., 2013), flooding (Lu et al., 2006; Liang and Liang, 2009), metals/metalloids (Arora et al., 2010a,b; Ashraf et al., 2010; Bajguz, 2010), herbicides (Sharma et al., 2013a), pesticides (Xia et al., 2006), insecticides (Xia et al., 2009b, 2011), organic pollutants (Ahammed et al., 2012a, 2013a), newly reclaimed sandy soil (Ahmed and Shalaby, 2013) and preservatives (Hu et al., 2014).

Hereunder, recent reports on the role of BRs (and associated compounds) in the modulation of both enzymatic and non-enzymatic components of antioxidant defense system in abiotic stressed plants are critically appraised. The discussion will consider primarily metals/metalloids followed by temperature regimes (high and low), drought, salinity and other major abiotic stresses.

METAL/METALLOID STRESS

Foliar application of homoBL was reported to improve Cd-tolerance in *Brassica juncea* through increasing activity of antioxidative enzymes (such as CAT, POD, SOD) and the content of osmolyte (such as proline) (Hayat et al., 2007). Improved Cd-tolerance in *Phaseolus vulgaris* was possible as a result of 24-epiBL (5 μM)-mediated increased activity of antioxidative enzymes, and proline content and subsequent improvements in the membrane stability index (MSI), relative leaf water content (RLWC) (Rady, 2011). Nullification of the damaging effect of Cd was reported in totamato cultivars (K-25 and Sarvodya) as a result of 28-homoBL/24-epiBL ($10(^{-8}$) M)-mediated improvement in photosynthetic machinery and antioxidant defense system (Hasan et al., 2011). Application of BRs (10^{-8} M) to Cd (3.0, 6.0, 9.0, and 12 mg kg^{-1}) stressed *Solanum lycopersicum* plants enhanced antioxidant system activity and improved fruit yield and quality (Hayat et al., 2012). Cd-impact-ameliorative role of 24-epiBL and 28-homoBL (3.0 μM) was evidenced in *Raphanus sativus*, where these BRs enhanced levels of free proline, antioxidant enzymes CAT, SOD, APX, GPX, and also reduced the activity of POD and AAO (Anuradha and Rao, 2007b). In Cd (0.5, 1.0, and 1.5 mM)-exposed *Raphanus sativus*, a diminished oxidative stress via 24-epiBL (10^{-7}, 10^{-9}, and 10^{-11} M)-supplementation-mediated elevation in the activity of GST and PPO enzymes was reported (Sharma et al., 2012). Earlier, these authors evidenced 28-homoBL (10^{-11}, 10^{-9}, and 10^{-7} M)-assisted amelioration of Cd (0.5, 1.0, and 1.5 mM) impacts in *Raphanus sativus*, where improved biomass and seedling growth was argued as a result of 28-homoBL-mediated regulation of the activity of APX, CAT, GR, POD, and SOD (Sharma et al., 2010). Hasan et al. (2008) also reported 28- homoBL-mediated elevated activity of CAT, POD, and SOD and the protection of *Cicer arietinum* against Cd (50, 100, or 150 μM).

Application of 24-epiBL ameliorated Ni-stress in *Brassica juncea* by enhancing mainly the activity of antioxidant enzymes (Kanwar et al., 2013). Earlier, these authors reported BRs (24-EpiBL, CS, dolicholide and typhasterole)-mediated significant

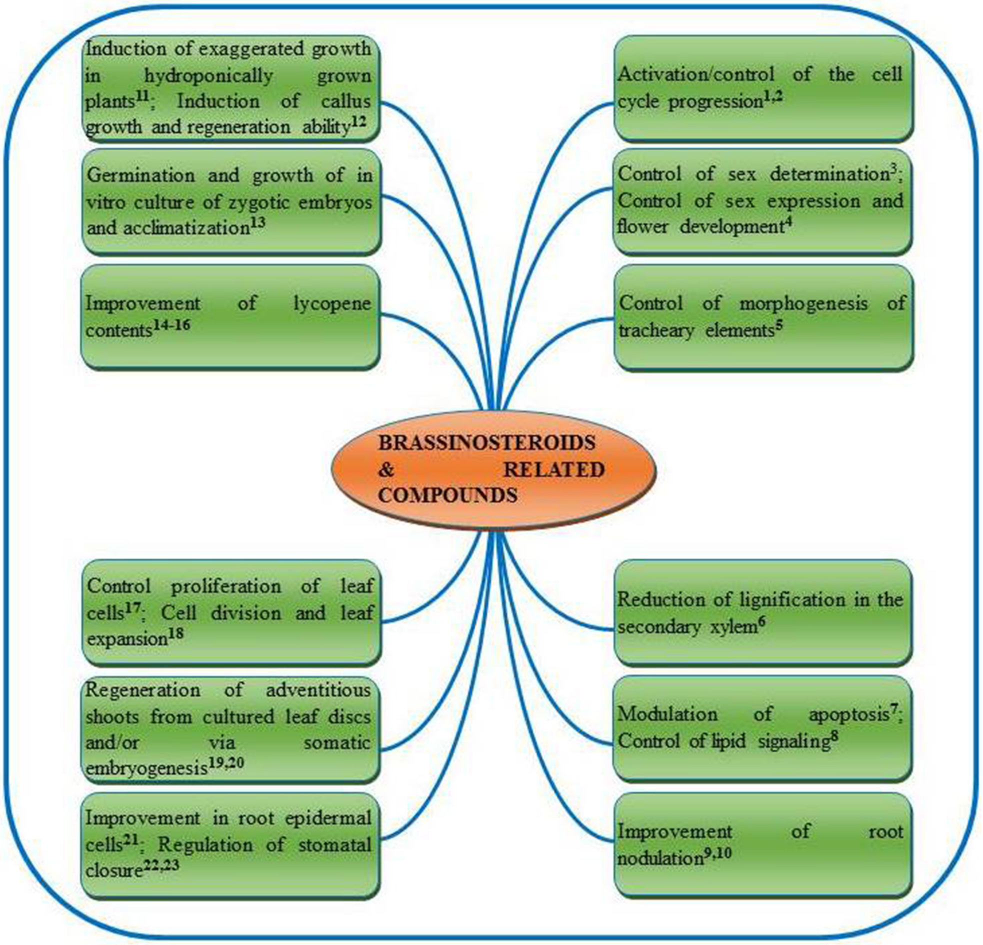

FIGURE 3 | Summarized roles of brassinosteroids and related compounds reported in plants. [1]Zadvornova et al., 2005; [2]González-Garcia et al., 2011; [3]Hartwig et al., 2011; [4]Manzano et al., 2011; [5]Yamamoto et al., 2001; [6]Jin et al., 2014; [7]Carange et al., 2011; [8]Pokotylo et al., 2014; [9]Vardhini and Rao, 1999; [10]Upreti and Murti, 2004; [11]Arteca and Arteca, 2001; [12]Lu et al., 2003; [13]Borcioni and Bonato-Negrelle, 2012; [14]Vardhini and Rao, 2002; [15]Weng et al., 2007; [16]Vogler et al., 2014; [17]Nakaya et al., 2002; [18]Zhiponova et al., 2013; [19]Malabadi and Nataraja, 2007; [20]Aydin et al., 2006; [21]Cheng et al., 2014; [22]Haubrick et al., 2006; [23]Xia et al., 2014.

mitigation of Ni (0.2, 0.4, and 0.6 mM)-stress in *Brassica juncea* plants by elevating the activity of ROS-metabolizing enzymes (and also via lowering the metal uptake) (Kanwar et al., 2012). Significantly elevated activity of antioxidant enzymes (such as GPX, CAT, GR, APX, and SOD) in *Brassica juncea* seedlings emerged from the homoBL (0.01, 1.0,and 100 nM)-treated seeds was argued to provide tolerance of this plant to Ni concentrations (25, 50, and 100 mg dm^{-3}) (Sharma et al., 2008). In *Brassica juncea*, the spraying of homoBL was evidenced to partially neutralize the toxic effect of 50 or 100 μM Ni, where elevated activity of POD and CAT, and content of proline was observed in leaves and roots (Alam et al., 2007). Spraying of 24-epiBL (1.0 μM) to Ni-exposed *Brassica juncea* was reported to detoxify Ni-impacts (Ali et al., 2008a). Elevated CAT, POD, and SOD activity via the spray of 0.01 μM of 28-homoBL was argued to protect five wheat (*Triticum aestivum*) cultivars (PBW-373, UP-2338, DL-LOK-01, DL-373, and HD-2338) against Ni concentrations (50 and 100 μM) (Yusuf et al., 2011b). *Raphanus sativus* seedlings emerged from seeds pre-soaked in 24-epiBL, exhibited elevated activity of APX, SOD, CAT, GPX, MDHAR, DHAR, and GR; that eventually resulted in reducing lipid peroxidation, enhanced proline and protein contents, and improved enhancing the root/shoot length, fresh biomass under Ni exposure (Sharma et al., 2011a). Application of 10^{-6} M 24-epiBL as shotgun approach (pre-sowing seed soaking) to the Ni-stressed T-44 (Ni-tolerant) and PDM-139 (Ni-sensitive) varieties of *Vigna radiata* plants improved biological yield, number of nodules, leghemoglobin content, and the activity of CAT, POD, and SOD enzymes. The 24-epiBL-mediated up-regulation of antioxidant enzyme activity and the elevated level of proline (osmolyte) were argued to confer Ni-tolerance and improve growth, nodulation and yield attributes (Yusuf et al., 2012). Recently, these authors reported BRs-mediated improved antioxidant defense (and also nitrogen metabolism) in two contrasting cultivars of *Vigna radiata* under different levels of Ni (Yusuf et al., 2014).

The role of BRs and associated compounds in the mitigation of elevated levels of Cu has also been reported in plants. To this end, treatment of *Brassica juncea* seedlings with 10^{-10}, 10^{-8}, and

10^{-6} M homoBL improved growth and photosynthetic traits via decreased H_2O_2 and elevated activity of CAT, POD, and SOD (Fariduddin et al., 2009b). Recently, these authors reported an improved growth of NaCl+Cu (100 mg kg^{-1}) stressed *Cucumis sativus* via epiBL-mediated enhancements in the activity of CAT, POD, and SOD (Fariduddin et al., 2013a). Supplemantation of 10^{-7}, 10^{-9}, and 10^{-11} M 24-epiBL to *Raphanus sativus* ameliorated the oxidative stress caused by Hg (0.5, 1.0, and 1.5 mM) by enhancing the activity of ROS-metabolizing enzymes such as GST and PPO (Sharma et al., 2012). Recently, 24-epiBL (10^{-7}, 10^{-9}, 10^{-11} M)-mediated increased activity of antioxidative enzymes such as SOD, CAT, APOX, GPX, GR, MDHAR and DHAR, and also the contents of GSH were argued to help radish plants to counteract the consequences of Hg (Kapoor et al., 2014).

Supplementation of 24-epiBL reduced Pb toxicity and enhanced the growth in radish (*Raphanus sativus* L.) seedlings by increasing the activities of antioxidant enzymes like CAT, APX, GPX, SOD and reducing POD activity (Anuradha and Rao, 2007a). Mitigation of the consequences of Pb (100 or 200 μM) was reported in tomato plants as a result of 24-epiBL-mediated increases in the activities of SOD, CAT, APX and GR, and the contents of AsA and GSH (Rady and Osman, 2012). 24-epiBL ameliorated Cr (VI) stress in 7-d old *Raphanus sativus* L. cv. "Pusa chetki" seedlings by enhancing the pools of reduced GSH and AsA, the activity of GR, SOD, and APX enzymes, and also the contents of phytochelatins, proline, and glycinebetaine (Choudhary et al., 2011). Co-application of epiBL and spermidine (polyamine) was also evidenced to remarkably enhance the titers of antioxidants (GSH, AsA, proline, glycine betaine and total phenols) and the activity of GPX, SOD, and GR) in Cr-stressed *Raphanus sativus* (Choudhary et al., 2011). Seed pre-soaking treatment of 28-homoBL at $10^{(-7)}$ M was effective in ameliorating Cr(VI) stress in *Raphanus sativus* L. (Pusa Chetaki), where an increased activity of antioxidative enzymes (except GPX) and the contents of proline and proteins but reduced lipid peroxidation were evidenced (Sharma et al., 2011b). 24-EpiBL-mediated diminution of Cr-toxicity in *Brassica juncea* was reported, where increased activity of GPX, CAT, GR, APX, SOD, MDHAR, and DHAR was argued to improve plant health (Arora et al., 2010b). Amelioration of Al-impacts was evidenced through epiBL or homoBL spraying to mung bean (*Vigna radiata*), where these BRs increased RLWC, water use efficiency, photosynthetic rate via enhancing the activity of antioxidative enzymes such as CAT, POD, and SOD in leaves (Ali et al., 2008b). Plant tolerance to Pb (and also to Cu and Cr) is possible via BL-mediated significant activation of enzymes (such as SOD, CAT, APX, and GR) and non-enzymes (such as reduced GSH, total AsA) (Bajguz, 2010) (**Table 1**).

Least reports are available on the role of BRs in plants under Zn, Bo, Co, Mn, and As stress. Supplementation of 28-homoBL to *Raphanus sativus* seedlings was reported to help this plant to tolerate Zn toxicity by enhancing antioxidative enzyme activities, strengthening GSH metabolism and redox status, and improving the contents of non-enzymatic antioxidants and proteins (Ramakrishna and Rao, 2013). The role of 28-homoBL (Arora et al., 2008b) and that of 24-epiBL (Arora et al., 2010a) was reported respectively in *Zea mays* and *Brassica juncea* under Zn stress. In the previous studies, increased activity of SOD, CAT, APOX, GPX, GR, MDHAR and DHAR and the contents of GSH were reported to control Zn-accrued lipid peroxidation. Application of 28-homoBL ($10^{(-8)}$ M) to Bo (0.50, 1.0, and 2.0 mM)-exposed *Vigna radiata* improved the growth, water relations, photosynthesis by enhancing antioxidant enzymes (such as CAT, POD and SOD) (Yusuf et al., 2011a). Foliar spray treatment with 24-epiBL (0, 10^{-10}, 10^{-8}, and 10^{-6} M) alleviated the stress generated by Co (0, 5×10^{-4}, 10^{-3}, 1.5×10^{-3}, and 2×10^{-3} M) ion in *Brassica juncea* through significantly improving the activities of SOD, CAT, POD, GR, APOX, MDHAR, and DHAR enzymes (Arora et al., 2012). Under elevated lelevs of Mn, epiBL application was reported to enhance the activities of SOD, POD, CAT, APX, DHAR, and GR, and the contents of AsA, and GSH that eventually controlled lipid peroxidation and metabolized superoxide radical and H_2O_2 in *Zea mays* (Wang et al., 2009). Recently, Raghu et al. (2014) reported BRs-mediated improved As-tolerance in *Raphanus sativus* as a result of increased activity of SOD and CAT.

TEMPERATURE REGIMES

BRs and associated compounds have been extensively reported to modulate different components of antioxidant defense system and to play a positive role in the mitigation of the consequences in different plants exposed to both high (Mazorra et al., 2002, 2011; Zhou et al., 2004; Cao and Zhao, 2007; Ogweno et al., 2008; Hayat et al., 2010b) and low (Janeczko et al., 2007; Liu et al., 2009; Kumar et al., 2010; Aghdam et al., 2012; Wang et al., 2012; Hu et al., 2013; Xi et al., 2013; Aghdam and Mohammadkhani, 2014) temperatures (**Table 1**).

Young seedlings of two Indica rice (*Oryza sativa*) cultivars namely *Xieqingzao* B (heat-sensitive) and 082 (heat-tolerant), subjected to high temperature; sprayed with 0.005 mg L^{-1} of BR exhibited significant enhancement in activities of POD and SOD isozyme expression levels, reduction in MDA level and leakage of leaf electrolytes (Cao and Zhao, 2007). Supplementation with 28-homoBL to *Vigna radiata* c.v. T-44 plants detoxified the stress generated by high temperature by improving the membrane stability index (MSI), leaf water potential (ψ) via increased the activities of antioxidative enzymes and the level of proline (Hayat et al., 2010b). Pre-treatment of 24-epiBL to *Lycopersicon esculentum* Mill. cv. 9021 plants exposed to high temperature (40/30°C; for 8 days) significantly alleviated high-temperature-caused inhibition of photosynthesis by increasing the activities of SOD, APX, GPX, and CAT, and reducing total H_2O_2 and MDA contents (Ogweno et al., 2008). Pre-incubation of tomato leaf discs with 24-epiBL or MH_5 (polyhydroxylated spirostanic analog of BR) (for 24 h) stimulated the activities of CAT, POD and SOD, controlled cell damage under heat stress (40°C) (Mazorra et al., 2002). EpiBL-induced tolerance to heat shock (HS) in tomato seedlings (BR-deficient mutant, *extreme dwarf d(x)*), a partially BR-insensitive mutant *curl*$_3$(-abs) allele (*curl*$_3$ altered brassinolide sensitivity; and a line overexpressing the dwarf, BR-biosynthesis gene, 35SD) was argued as a result of reduced ion leakage, lipid peroxidation through enhanced activities of antioxidative enzymes (Mazorra et al., 2011).

Table 1 | Summary of representative studies on brassinosteroids (BRs) and related compounds in the mitigation of major abiotic stress-impacts in different plant species.

Brassinosteroids and related compounds	Abiotic stresses	Plant species	References
BRs	Cd	*Raphanus sativus*	Anuradha and Rao, 2007b
		Brassica juncea	Hayat et al., 2007
		Lycopersicon esculentum	Hayat et al., 2010a
		Lycopersicon esculentum	Hasan et al., 2011
		Triticum aestivum	Kroutil et al., 2010
		Solanum lycopersicum	Hayat et al., 2012
		Helianthus annuus	Filova et al., 2013
		Helianthus tuberosus	Gao et al., 2013
		Solatium nigrum	Zhao et al., 2013
	Al	*Vigna radiata*	Ali et al., 2008b
		Glycine max	Dong et al., 2008
	Ni	*Brassica juncea*	Kanwar et al., 2012
24-epiBL	Cd	*Brassica napus*	Janeczko et al., 2005
		Raphanus sativus	Anuradha and Rao, 2009
		Phaseolus vulgaris	Rady, 2011
	Ni	*Brassica juncea*	Kanwar et al., 2013
		Raphanus sativus	Sharma et al., 2011a
	Cu	*Cucumis sativus*	Fariduddin et al., 2013a
	Co	*Brassica juncea*	Arora et al., 2012
	Zn	*Brassica juncea*	Arora et al., 2010a
	Pb	*Raphanus sativus*	Anuradha and Rao, 2007a
24-EpiBL and 28-HomoBL	Ni	*Brassica juncea*	Ali et al., 2008a; Sharma et al., 2008
28-HomoBL	Cd	*Cicer arietinum*	Hasan et al., 2008
		Raphanus sativus	Sharma et al., 2010
	Cu	*Brassica juncea*	Fariduddin et al., 2009b
	Cr	*Raphanus sativus*	Sharma et al., 2011b
	Bo	*Raphanus sativus*	Yusuf et al., 2011a
	Zn	*Raphanus sativus*	Ramakrishna and Rao, 2013
BRs	High temperature	*Lycopersicon esculentum*	Ogweno et al., 2008
	Low temperature	*Vigna radiata*	Huang et al., 2006
		Brassica napus	Janeczko et al., 2007
		Solanum lycopersicum	Aghdam et al., 2012
		Cucumis sativus	Jiang et al., 2013
		Brassica napus	Ma et al., 2009
24-epiBL	High temperature	*Solanum lycopersicum*	Singh and Shono, 2005
		Hordeum vulgare	Janeczko et al., 2011
		Cucumis melo	Zhang et al., 2013
	Low temperature	*Cucumis sativus*	Hu et al., 2010
		Brassica juncea	Kumar et al., 2010
		Vitis vinifera	Xi et al., 2013
28-HomoBL		*Cucumis sativus*	Fariduddin et al., 2011
BL	Low temp	*Campsicum annum*	Wang et al., 2012
		Solanum lycopersicum	Aghdam and Mohammadkhani, 2014
		Oryza sativa	Wang et al., 2014
	High temp	*Brassica napus*	Kurepin et al., 2008

(Continued)

Table 1 | Continued

Brassinosteroids and related compounds	Abiotic stresses	Plant species	References
BRs	Drought	*Phaseolus vulgaris*	Upreti and Murti, 2004
		Sorghum vulgare	Vardhini and Rao, 2005
		Lycopersicon esculentum	Behnamnia et al., 2009
		Solanum lycopersicum	Yuan et al., 2010
		Carica papaya	Gomes et al., 2013
		Raphanus sativus	Mahesh et al., 2013
	Flooding	*Brassica napus*	Liang and Liang, 2009
BL	Drought	*Robinia pseudoacacia*	Li et al., 2008
		Glycine max	Zhang et al., 2008
		Xanthoceras sorbifolia	Li and Feng, 2011
		Arachis hypogaea	Savaliya et al., 2013
	Flooding	*Cucumis sativus*	
		Glycine max	Lu et al., 2006
24-EpiBL	Drought	*Capsicum annuum*	Hu et al., 2013
		Brassica napus	Mousavi et al., 2009
		Cucumis sativus	Kang et al., 2009
28-homoBL	Drought	*Brassica juncea*	Fariduddin et al., 2009a
BRs	Salinity	*Lycopersicon esculentum*	Ali et al., 2006
		Cucumis sativus seedlings	Shang et al., 2006
		Cucumber seedlings	Song et al., 2006
		Triticum aestivum	Shahbaz and Ashraf, 2007
		Cucumber	Wang et al., 2011
		Trifolium alexandrinum	Daur and Tatar, 2013
		Oryza sativa	Sharma et al., 2013b
BL	Salinity	*Medicago sativa*	Zhang et al., 2007
		Zea mays	El-Khallal et al., 2009
		Vigna unguiculata	El-Mashad and Mohamed, 2012
		Oryza sativa	Das et al., 2013
		Cucumis sativus	Lu and Yang, 2013
24-EpiBL	Salinity	*Triticum aestivum*	Talaat and Shawky, 2013
		Pisum sativum	Fedina, 2013
		Cucumis sativus	Fariduddin et al., 2013a
		Cajanus cajan	Dalio et al., 2013
		Capsicum annuum	Abbas et al., 2013
		Lactuca sativa	Ekinci et al., 2012
		Solanum melongena	Ding et al., 2012
		Phaseolus vulgaris	Rady, 2011
		Pisum sativum	Shahid et al., 2011
		Cajanus cajan	Durigan et al., 2011
		Fragaria x ananassa	Karlidag et al., 2011
		Triticum aestivum	Avalbaev et al., 2010
		Hordeum vulgare	Tabur and Demir, 2009
		Triticum aestivum	Shahbaz et al., 2008
28-HomoBL	Salinity	*Cicer arietinum*	Ali et al., 2007
		Zea mays	Arora et al., 2008a
		Vigna radiata	Hayat et al., 2010b
		Triticum aestivum	Yusuf et al., 2011b
		Brassica juncea	Alyemeni et al., 2013

Literature is full also on the role of BRs in plants under low temperature stress. BR infiltration prior to cold treatment can reduce the ion leakage in chilling-exposed rape plants (Janeczko et al., 2007); whereas, 24-epiBL can increase the antioxidant defense (and also osmoregulation) in chilling stressed young grapevines (Xi et al., 2013). Application of 24-EpiBL to suspension cultured cells of low temperature (4 and 0°C)-exposed *Chorispora bungeana* alleviated oxidative damage through enhancing the activity of ROS-metabolizing enzymes such as APX, CAT, POD and SOD and the content of AsA (Liu et al., 2009). In chilling (4°C) exposed *Brassica juncea* seedlings, exogeniously applied 24-epiBL alleviated the toxic effect of H_2O_2 through increasing the activities of various enzymes involved in antioxidant defense system like CAT, APX, and SOD (Kumar et al., 2010). Hu et al. (2010) reported that exogenous application of 24-epiBL alleviated the 12/8°C chilling-induced inhibition of photosynthesis in cucumber (*Cucumis sativus*) by reducing ROS generation and accumulation through increasing the activities of SOD, APX. In another study on cucumber pretreated with 24-epiBL (0.3 and 1.0 $\text{mmol}\cdot\text{L}^{-1}$ chlorpyrifos) and exposed to chilling stress, these authors reported elevations in the activities of APX, GR, CAT, and GPX that eventually alleviated the chilling-accrued phytotoxicity (Hu et al., 2013). 28-homoBL (10^{-8}, or 10^{-6} M)-mediated significantly increased activities of antioxidant enzymes like CAT, POD, and SOD (and also the elevated content of proline) in cucumber (*Cucumis sativus*) were reported to improve tolerance of this plant to chilling temperatures (10/8°C, 5/3°C) (Fariduddin et al., 2011; BRs 5, 10, and 15 μM) effectively reduced chilling injury of pepper fruit during 18-day storage at 3°C by reducing the electrolyte leakage, MDA content; increasing the activities of antioxidant enzymes including CAT, POD, APX, and GR (Wang et al., 2012). Aghdam et al. (2012) reported that treatments with 3.0 and 6.0 μM BRs to tomato fruits stored at 1°C for 21 days reduced the chilling injury, electrolyte leakage, MDA content; enhanced proline, total phenol contents, phenylalanine ammonia-lyase (PAL) activity and maintained membrane integrity. In a recent work, these authors reported that application of 0, 3 and 6 μM BL to tomato fruits subjected to 1°C chilling stress can inhibit the activities of phospholipase D (PLD) and lipoxygenase (LOX), major causes of chilling injury induction in tomato fruits (Aghdam and Mohammadkhani, 2014). BRs protected the photosynthetic apparatus from cold-induced damage in *Cucumis sativus* plants by activating the enzymes of Calvin cycle and increasing the antioxidant capacity, which in turn mitigated the photo-oxidative stress and plant growth inhibition during the recovery of chilling injury (Jiang et al., 2013).

DROUGHT STRESS

Reports are extensive on the role of BRs and related compounds in plant drought tolerance (Li and Van Staden, 1998a,b; Li et al., 1998, 2008, 2012b; El-Khallal, 2002; Vardhini and Rao, 2003a,b, 2005; Zhang et al., 2008; Behnamnia et al., 2009; Fariduddin et al., 2009a; Farooq et al., 2010; Yuan et al., 2010; Anjum et al., 2011; Mahesh et al., 2013). Field and pot experiments of 0.2 mg L^{-1} BL application to 1-year-old *Robinia pseudoacacia* seedlings grown under drought stress increased the activity of SOD, POD and CAT, and the contents of soluble sugars and free proline (Li et al., 2008). Application of 0.1 μM 24-epiBL increased the resistance in drought-stressed *Chorispora bungeana* by reducing the lipid peroxidation (measured in terms of MDA content), membrane permeability as a result of increased activities of antioxidative enzymes and the pools of non-enzymatic antioxidants such as AsA and GSH (Li et al., 2012b). BL ameliortaed the negative effect water stress (Poly Ethylene Glycol:PEG for 24 h) on callus tissues of drought-resistant (PAN 6043) and drought-sensitive (SC 701) cultivars of *Zea mays* by enhancing the activities of SOD, CAT, APX, POD, and GR (Li and Van Staden, 1998a,b). Earlier also, BL was reported to increase the activities of SOD, CAT, and APX eznymes, and the contents of AsA and total carotenoids in seedlings of drought-resistant (PAN 6043) and drought-sensitive (SC 701) cultivars of *Zea mays* under water stress (−1.0 MPa PEG 6000) (Li et al., 1998). Exogenous application of BL alleviated the detrimental effects of drought in *Zea mays* by enhancing enzymatic antioxidant enzyme activities and the contents of proteins, relative leaf water and proline (Anjum et al., 2011). 28-HomoBL and 24-epiBL ameliorated the negative impact of PEG-imposed osmotic/water stress in CSH-14, ICSV (Vardhini and Rao, 2003a) and CSH-15 (Vardhini and Rao, 2005) varieties of *Sorghum vulgare* seedlings by increasing the activity of CAT and the contents of free proline and nucleic acids. Seedlings of *Triticum* cultivars Sakha 69 (drought-resistant) and Giza 164 (drought-sensitive) subjected to water stress (by soaking the roots for 48 h in 30% PEG 6000; −0.9 MPa) and BR treatment, exhibited higher RWLC, MSI, proline, regulation of expression of water stress-inducible proteins as well as induced *de-novo* synthesis of specific polypeptides (El-Khallal, 2002). Exogenously applied 24-epiBL (0.01 μM) improved the drought tolerance in rice (*Oryza sativa*) cultivar *Super-Basmati* which was sturdily associated with the greater tissue water potential, increased synthesis of metabolites and enhanced capacity of antioxidant system (Farooq et al., 2010). Spraying with HBL (0.01 μM) to 30-day stage seedlings of *Brassica juncea* subjected to drought stress (for 7 days at the 8–14 (DS_1)/15–21 (DS_2) days stage of growth) improved the activities of antioxidant enzymes such as CAT, POD and SOD, and the content of proline (Fariduddin et al., 2009a). Foliar application of BRs elevated the activities of POD and SOD, increased the concentrations of soluble sugars and proline that eventualy resulted into decreased MDA concentration and electrical conductivity in the leaves of drought exposed *Glycine max* (Zhang et al., 2008). *Lycopersicon esculentum*, subjected to drought stress and pretreated with BR showed increased activities of POD, SOD, CAT and APX, and the contents of non-enzymatic antioxidants such as AsA and proline (Behnamnia et al., 2009). Yuan et al. (2010) also reported that 1.0 μM 24-epiBL treatment significantly alleviated water stress and increased the activities of antioxidant enzymes such as CAT, APX, and SOD that decresaed the levels of H_2O_2 and MDA in two *Lycopersicon esculentum* genotypes viz., Mill. cv. Ailsa Craig (AC) and its ABA-deficient mutant notabilis (not). 24-epiBL and 28-homoBL-mediated reduction in the inhibitory effect of water stress on seed germination and seedling growth of radish (*Raphanus sativus*) subjected to water stress (imposed by 15% (w/v) PEG) was a result of elevated levels of SOD, CAT and APX and the free proline content (Mahesh et al., 2013) (**Table 1**).

SALINITY STRESS

Modulation of various components of antioxidant defense system via BRs and associated compounds in salinity exposed plants has been extensively reported (Nunez et al., 2003; Özdemir et al., 2004; Song et al., 2006; Shahbaz and Ashraf, 2007; Zhang et al., 2007; Ali et al., 2008b; Arora et al., 2008a; El-Khallal et al., 2009; Hayat et al., 2010b; Rady, 2011; Vardhini, 2011; Ding et al., 2012; El-Mashad and Mohamed, 2012; Abbas et al., 2013; Fariduddin et al., 2013b; Lu and Yang, 2013; Sharma et al., 2013b) (**Table 1**). BL mitigated the negative impact of salt stress in *Zea mays* by inducing the activities of different antioxidant enzymes (El-Khallal et al., 2009). Application of 28-homoBL (10^{-7}, 10^{-9}, and 10^{-11} M) for 7 days improved seedling growth, lipid peroxidation via elevating antioxidative enzyme activities (SOD, CAT, GR, APX, and GPX) in the seedlings of *Zea mays* (var. Partap-1) subjected to salt (25, 50, 75, and 100 mM NaCl) stress (Arora et al., 2008a). 24-EpiBL applied as a foliar spray could alleviate the adverse effects of salt on two hexaploid wheat (*Triticum aestivum*) cultivars, S-24 (salt tolerant) and MH-97 (moderately salt sensitive), grown in saline conditions (150 mM of NaCl) by enhancing the activity of POD and CAT (Shahbaz and Ashraf, 2007). BL treatment increased the activities of CAT, SOD and GR; reduced the activities of POD and PPO of two varieties of sorghum plants ("CSH-5" and "CSH-6") grown in two saline experimental sites of Karaikal (Varchikudy and Mallavur), thus indicating its ability to counteract the negative impact of saline stress (Vardhini, 2011). Exogenous BL (0. 01 mg × L $^{(-1)}$) markedly decreased the salt stress index, mortality rate, MDA, electrolyte leakage via enhancing the activities of SOD, POD, and CAT in *Cucumis sativus* seedlings (Song et al., 2006). Exogenous BR (0.005, 0.01, 0.05, 0.1, and 0.2 mg/L^{-1}) protected *Cucumis sativus* seedlings against salt stress by elevating the activity of SOD, POD and CAT, and that in turn distinctly lowered the salt injured index (40.2%) and increased the contents of free-proline, soluble sugars (Shang et al., 2006). Application of epiBL to salinity-exposed *Cucumis sativus* seedlings decreased leaf superoxide anion production rate, H_2O_2, MDA, cell membrane permeability, improved seedlings growth as a result of increased the activities of SOD, POD, CAT (Lu and Yang, 2013). Application of epiBL to the Cu+NaCl (150 mM) stressed seeds of two cultivars (Rocket and Jumbo) of *Cucumis sativus* plant enhanced the activities of various antioxidant enzymes viz., CAT, POD, SOD, that eventually improved growth, carbonic anhydrase activity, photosynthetic efficiency (Fariduddin et al., 2013b). Seed priming with 5.0 μM L^{-1} BL was reported to improve the seed germination and seedling growth of 3 lucerne (*Medicago sativa* L.) varieties, viz., *Victoria*, *Golden Empress*, and *Victor* by significantly increasing the activities of POD, SOD, and CAT under salt stress (13.6 dS/m NaCl solution) (Zhang et al., 2007).

In salinity (120 mM NaCl) exposed IR-28 *Oryza sativa* seedlings, 24-EpiBL considerably alleviated oxidative damage and improved seedling growth by increasing APX activity and reducing lipid peroxidation (Özdemir et al., 2004). A polyhydroxylated spirostanic brassinosteroid analog (BB-16; 0.001 or 0.01 mg dm^{-3}) application to salinity (75 m NaCl)-exposed *O. sativa* seedlings showed significant increases in the activities of CAT, SOD, and GR (Nunez et al., 2003). Exogenous application of 24-epiBL to *Oryza sativa* var *Pusa Basmati-1*, grown under salt stress conditions exhibited improvement in growth, levels of protein, proline contents and antioxidant enzymes activities through expression of various BRs (OsBRI1, OsDWF4) and salt (SalT) responsive genes (Sharma et al., 2013b). Eggplant seedlings, when exposed to 90 mM NaCl with 0, 0.025, 0.05, 0.10, and 0.20 mg dm^{-3} of epiBL for 10 days exhibited decreased electrolyte leakage, superoxide production, MDA, H_2O_2 probably as a result of increased activities of SOD, GPX, CAT and APX enzymes and the contents of non-enzymatic antioxidants such as AsA and GSH (Ding et al., 2012). 24-epiBL decreased the adverse effects of salinity stress on two varieties of pepper (*Capsicum annuum*) arguably by increasing the activities of antioxidative enzymes and the contents of proline, total anthocyanins and minerals (Abbas et al., 2013). Spraying of 1.0 μM of 24-epiBL to NaCl-exposed *Brassica juncea*detoxified the stress generated by NaCl by enhancing antioxidative enzymes and the level of proline (Ali et al., 2008b). Supplementation of *Vigna radiata* c.v. T-44 plants with 28-homoBL detoxified the stress generated by NaCl by elevating the activities of antioxidative enzymes and the proline content that in turn improved the MSI, leaf water potential (ψ) (Hayat et al., 2010b). In a similar study, Rady (2011) reported that spraying 5 μM of 24-epiBL to NaCl-exposed *Phaseolus vulgaris* improved the MSI, RLWC as a result of significant elevations in the activities of antioxidative enzymes and proline content. Imbibition with 24-epiBL to pea (*Pisum sativum* L.) cv. climax seeds, subjected to sodium chloride stress significantly elevated the activity of SOD, POD, and CAT enzymes the helped plants to improve fresh and dry biomass, seedling height, photosynthetic rate, stomatal conductance, and the total chlorophyll content (Shahid et al., 2011). Treatment with 0.05 ppm BL as foliar spray mitigated salt stress-impacts in cowpea (*Vigna sinensis*) by inducing the activities of antioxidant enzymes such as SOD, POD, PPO and GR and the contents of AsA (El-Mashad and Mohamed, 2012).

OTHER ABIOTIC STRESSES

Apart from the discussed above major abiotic factors, BRs and associated compounds can also play significant roles in plants under a range of other abiotic stress factors such as photoinhibition/light stress, waterlogging/flooding stress, pesticides, neonicotinoid insecticide, imidacloprid (IMI) etc. (Kang et al., 2006, 2009; Lu et al., 2006; Xia et al., 2006, 2009a,b; Liang and Liang, 2009; Hayat et al., 2010c; Ogweno et al., 2010; Ahammed et al., 2012c; Lu and Guo, 2013; Sharma et al., 2013a,b). 24-BL (0.01 mg l^{-1}) has been benefitted tomato (*Lycopersicon esculentum* Mill.) to maintain net photosynthetic rate (Pn), quantum efficiency of PSII (Φ_{PSII}) and photochemical quenching (qP) under photoinhibition/light stress by decreasing lipid peroxidation as a result of efficient ROS-metabolism via enhanced activity of SOD, GPX, CAT, and APX enzymes (Ogweno et al., 2010). In another study, exogenous application of 24-epiBL was reported to enhance the tolerance of elite Indica *O. sativa* variety (*Pusa Basmati-1* seedlings) to stress generated by neonicotinoid insecticide, imidacloprid (IMI) by elevating the activity of antioxidative enzyme such as SOD, APX, CAT, GR and MDHAR, upregulating the expression of most of the genes like Cu/Zn-SOD, Fe-SOD, Mn-SOD, APX, CAT and GR, and decreasing lipid peroxidation (Sharma et al., 2013a). In 80 mM $Ca(NO_3)_2$-exposed *Cucumis sativus* cv. Jinyou No. 4, EpiBL (0.1 μM) protected the photosynthetic membrane system by up-regulating the ROS-scavenging capacity of the antioxidant system (Yuan et al., 2012). Folair spray of epiBL or homoBL to *Lycopersicon esculentum* Mill. cv. K-21 showed lowered sodium nitroprusside (SNP) concentration (10^{-5} M) and improved growth and the content of pigment contents via strengthning antioxidant system (Hayat et al., 2010c). Application of 24-epiBL-mediated increased H_2O_2-metabolism and decreased lipid peroxidation via enhanced activity of GST and the content of GSH were argued to help *Solanum lycopersicum* seedlings to counteract three-ringed PAH (phenanthrene-PHE)-accrued consequences (Ahammed et al., 2012a,c). Alleviation of impacts caused by phenanthrene and pyrene phytotoxicity in tomato plants has been evidenced as a result of 24-epiBL-mediated increased activities of GPX, CAT, APX and GR and decreased content of MDA) (Ahammed et al., 2012b). Recently, these authors reported that 24-epiBL (100 μM) can alleviate PCB (polychlorinated biphenyls)-induced oxidative stress in tomato plants by enhancing the activities of antioxidant enzymes, and maintaining photochemical efficiency of PSII Fv/Fm), the quantum efficiency of PSII photochemistry [Φ(PSII)] and photochemical quenching coefficient (Pq) (Ahammed et al., 2013b). The 24-epiBL-mediated strengthning of antioxidant defense system and eventually decreased membrane lipid peroxidation was reported in plants exposed to phenanthrene + Cd co-contamination (Ahammed et al., 2013a). Pretreatment of *Cucumis sativus* with 24-epiBL alleviated the phytotoxicities of nine pesticides (paraquat, fluazifop-p-butyl, haloxyfop, flusilazole, cuproxat, cyazofamid, imidacloprid, chlorpyrifos, and abamectin) by increasing the activities of antioxidant enzymes, and CO_2 assimilation capacity (Xia et al., 2006). Significant role of 24-epiBL was also reported in plants exposed to Chlorpyrifos (a widely used insecticide), where elevated activity of GST, POD, and GR was argued to regulate net photosynthetic rate and quantum yield of PSII [Phi(PSII)] (Xia et al., 2009a). BRs and associated compounds were reported to provide tolerance to waterlogging/flooding stress in different crops including soybean (Lu et al., 2006), cucumber (Kang et al., 2006, 2009; Lu and Guo, 2013) and oilseed rape (Liang and Liang, 2009) mainly as a result of decreased oxidative damage via enhanced activities of SOD and POD.

CONCLUSION AND FUTURE PROSPECTS

It is a well-established fact that environmental stresses are the primary cause of crop loss worldwide, reducing average yields for most major crop plants adversely affecting the global crop production and the adverse impacts are getting more serious in the past few decades. Environmental stresses induce the production of ROS, alter the activity of antioxidant system and adversely affect the process of photosynthesis. The crop physiologists and scientists have employed strategies to mitigate the elevated ROS (and their reaction products)-accrued oxidative stresses/damages via strengthening antioxidant defense system in plants exposed to various abiotic/stress factors. In this regard, the use of different plant growth regulators (PGRs) has been considered as a better sustainable alternative, and also as a technically simpler approach (Khan et al., 2012; Iqbal et al., 2013; Asgher et al., 2014). To this end, in addition to playing significant roles under general plant growth, development and metabolism, BRs and associated compounds have been extensively reported to counteract consequences of various abiotic stresses including temperature (heat, chilling, and freezing), water (drought, water logging), salt, heavy metals, light (intense and weak) and radiation (UV-A/B). Though much has been achieved in the current context, integrated approach is required to investigate more insights into molecular-genetic mechanisms of BRs and associated compounds-mediated modulation of various components of antioxidant defense system and subsequently the control of abiotic stress-consequences in plants.

ACKNOWLEDGMENTS

Financial support to B. V. Vardhini from University Grants Commission (UGC), New Delhi [MRP-655/05 (UGC-SERO); Link No 1655.0] India is gratefully acknowledged. Naser A. Anjum gratefully acknowledges the partial financial support received from Portuguese Foundation for Science and Technology (FCT) through post-doctoral research grants (SFRH/BPD/64690/2009; SFRH/BPD/84671/2012), and the Aveiro University Research Institute/Centre for Environmental and Marine Studies (CESAM).

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 30 November 2014; accepted: 19 December 2014; published online: 12 January 2015.

Citation: Vardhini BV and Anjum NA (2015) Brassinosteroids make plant life easier under abiotic stresses mainly by modulating major components of antioxidant defense system. Front. Environ. Sci. ***2****:67. doi: 10.3389/fenvs.2014.00067*

This article was submitted to Environmental Toxicology, a section of the journal Frontiers in Environmental Science.