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REVIEW

Significance of brassinosteroids and their derivatives in the development and protection of plants under abiotic stress

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Abstract

Brassinosteroids have been identified as polyhydroxylated steroidal plant hormones which are known for their response against stress and development processes like flowering, germination and crop production. Because of their multiple properties, brassinosteroids occupy a significant place among hormones. These naturally occurring plant hormones induce tolerance against abiotic and biotic stresses such as temperature variation (extreme cold/hot), salinity, water scarcity or drought, injury, fungal infection and metal toxicity. As a result of these stresses free radicals, like superoxide ions and peroxide are produced which cause damage to the plant system. Exogenous application of brassinosteroids at appropriate time can save plants from oxidative stresses. Brassinosteroids enhance carbon dioxide assimilation capacity, chlorophyll contents, antioxidants including ascorbate, carotenoids and proline under adverse environmental conditions. Besides inducing resistance against stresses, brassinosteroids also regulate growth, increase seed germination and ripening of fruits. It has been also noticed that the brassinazole-resistant-dependent brassinosteroid signaling up-regulates the expression of autophagy-related genes and autophagosome formation under stress. We have summarized, in this review, the information available until 2021, the impact of BRs application on plant growth and development under abiotic stress.

Keywords Abiotic stress · Antioxidant · Brassinosteroids · Gene expression · Metal toxicity

Introduction

All stresses experienced by the agricultural crops/plants result in decreased grain yield and reduced plant growth. Under biotic and abiotic stresses, the plants are forced to make adaptation to combat with the environmental changes which lead to changes in their physiological, metabolic and molecular functions (Cramer et al. 2011; Husen et al. 2014; Jeandroz and Lamotte 2017; Yurchenko et al. 2018; Chi et al. 2019; Wang 2020). Hormones are known to protect and improve the physical development of plants under water scarcity, soil salinity, temperature variation and metal toxicity (Kagale et al. 2007; Bajguz and Hayat 2009; Divi and Krishna 2009; Siddiqi and Husen 2017, 2019; Podlešáková et al. 2019; Heidari et al. 2020; Nolan et al. 2020) (Fig. 1).

Brassinosteroids (BRs) and their derivatives occupy a prominent place among plant steroidal hormones owing to their multifunctional role in the development and protection of plants. Bajguz and Tretyn (2003) have reported over 69 different BRs and their derivatives in various plants. They are produced by the plants themselves under abiotic/biotic stress in order to survive and maintain normal life cycle (Hussain et al. 2020). These hormones are not toxic and hence they can be safely used to increase resistance and crop yield even under abnormal weather conditions**.** Grove et al. (1979) first purified the most active brassinolide (BL) from rapeseed (*Brassica napus*) pollen and its structure was determined by x-ray analysis. They are effective at very low concentration and widely distributed in lower as well as higher plants (Bajguz and Hayat 2009). They have been classified as per the presence of number of carbons in their structure such as C27, C28 or C29 BRs. The frequently used BRs in experimental investigation under abiotic stress in various plant species are 28-homobrassinolide (28-HBL), 24-epibrassinolide (24-EBL)

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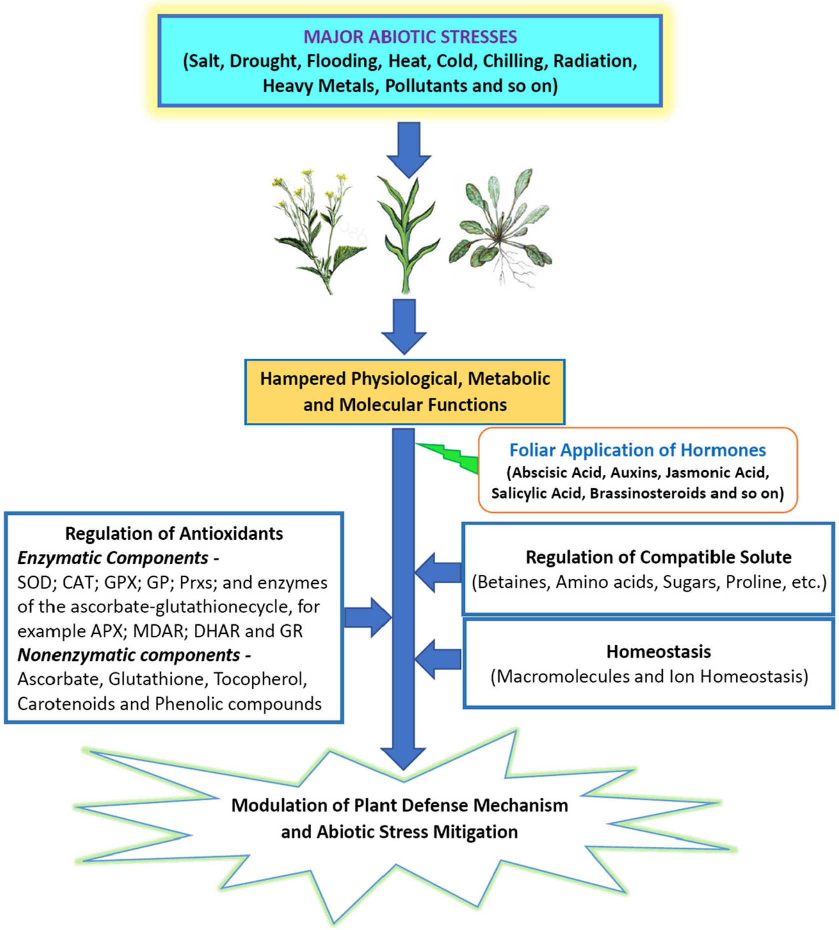
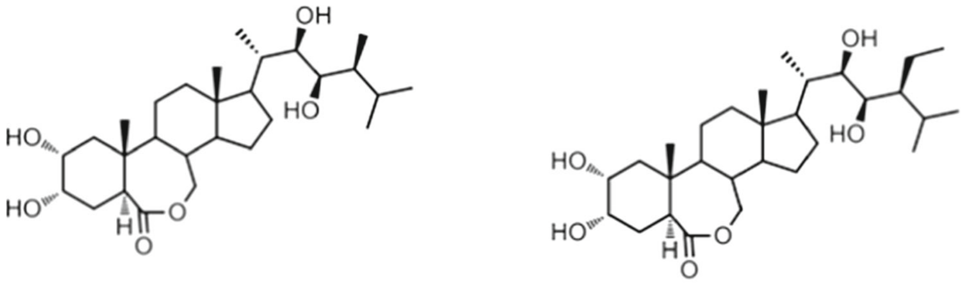


Fig. 1 Role of plant hormones under major abiotic stresses, their consequences and the components of plant defense system. SOD – Superoxide dismutase; CAT – Catalase; GPX – Glutathione peroxidase; GP – Guaiacol peroxidase; Prxs – Peroxiredoxins; APX – ascorbate peroxidase; MDAR – monodehydroascorbate reductase; DHAR – dehydroascorbate reductase; and GR – glutathione reductase

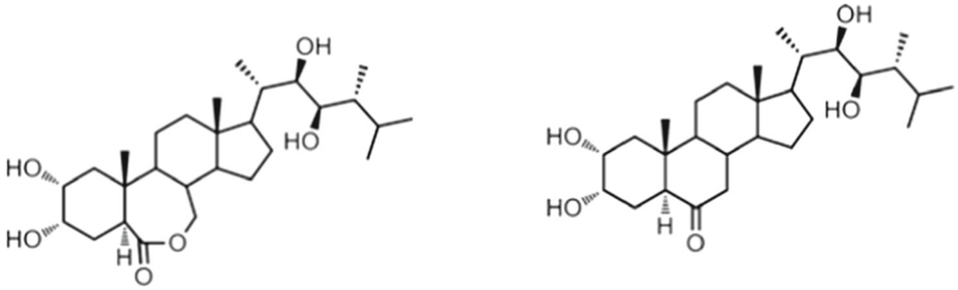
and 24-epicasterone (Fig. 2 and Table 1). They alone promote the growth of plants but in combination with other growth promoting hormones the effect is enhanced manifold (Clouse et al. 1992; Sun et al. 2010; Bai et al. 2012). Plants are sensitive to stresses and respond to them quickly (Getnet et al. 2015; Embiale et al. 2016; Husen et al. 2016, 2017). Even though, BRs respond to all stresses, they are very sensitive to injury and wounds. Plants with BR deficiency exhibit stunted growth, short and dark green leaves, delayed flowering, and improper development of reproductive organs and fertilization (Sasse 2002). Adaptation against stresses increase crop yield followed by changes in plant morphology, physiology and overall development strategies (Bohnert et al. 1995). As a consequence of adaptation to stresses, many substances such as polyols, sugars, proline and betaines get accumulated (Munns and Tester 2008; Iqbal et al. 2011).

Like other BR analogs, castasterone is also widely distributed in plants. It was first isolated from the insect gall of the chestnut tree (Yokota et al. 1982). Kanwar et al. (2012) have investigated the role of BRs under heavy metal stress, for instance nickel on *Brassica juncea* plants. They have found that exposure to nickel accelerates the BRs biosynthesis such as castasterone, typhasterol, EBL and dolicholide in *Brassica juncea*.

Several attempts have been made to understand how BRs modulate overall plant growth, development and adaptation under changing environmental conditions (Bajguz and Hayat 2009; Nolan et al. 2020; Hwang et al. 2021; Kothari and Lachowiec 2021). BR biosynthesis and signaling pathways in which numerous genes are involved have also been reported (Wang et al. 2006; Guo et al. 2013; Wang et al. 2014; Belkhadir and Jaillais 2015; Nolan et al. 2017). Sahni et al. (2016) have observed that the BR-related genes are key targets for enhancing the plant productivity under abiotic and biotic stresses. Recently, Zhang et al. (2021) have reported that the exogenous EBL treatment of plants increased the leaf size and expansion by promoting the cell expansion and division via BR modulation, auxin, and gibberellin contents and the up-regulation of cell growth-related genes in tobacco seedlings. It has been also reported that BR regulated the transcript expression of nitrate transporter genes to promote nitrogen uptake in maize plants. In addition to BRs biosynthetic pathway, other associated plant growth and developmental processes have also been discussed. The major objective of this review is to



Brassinolide 28-homobrassinolide



24-epibrassinolide 24-epicasterone

Fig. 2 Most frequently used brassinosteroids

explore the impact of exogenous application of BRs on crops and plants under different stresses.

BRs biosynthetic pathway, plant growth and development processes

Sakurai and Fujioka et al. (1997) initially reported the BR biosynthetic pathways in vivo using *Catharanthus roseus* cell lines. They were analyzed by the endogenous levels of BRs in BR-deficient mutants by several researchers (Fujioka et al. 1997; Choe et al. 1999a; Choe et al. 1999b; Klahre et al. 1998). There are a number of proteins and enzymes involved in signaling process which are interdependent and are activated only in presence of BRs. Generally, BR regulated genes are involved in synthesis of hormones and plant development (Vert et al. 2005). Major work on the mechanistic pathway has been done on *Arabidopsis*, rice and tomato (Noguchi et al. 2000). A diagrammatic representation for BR synthesis (Fig. 3) clearly indicates two pathways (Noguchi et al. 2000; Ohnishi et al. 2006; Divi and Krishna 2009) where oxidation involving cytochrome P450 facilitates the biosynthesis. Further, Chung and Choe (2013) illustrated the BRs biosynthetic pathway in *Arabidopsis*, with campesterol as the key precursor of the three BR biosynthetic pathways, two derived from the conversion of campesterol to campestanol and the third one is a campestanol-independent pathway. They have reported that conversion of BRs biosynthetic pathways are mainly mediated by ROTUNDIFOLIA 3 (ROT3), CYP85A1 and CYP85A2.

BRs regulate many biological functions and development in plants. Exogenous application of BR leads to molecular changes, in order to save the plant from multiple stresses by activating antioxidant enzymes. Crops give better yield under stress perhaps due to enhanced activity of hormones, photosynthesis and gene expression in response to adverse conditions (Vert et al. 2005). As a consequence of a number of physical and chemical stresses plants are forced to produce excessive reactive oxygen species (ROS) which oxidize many essential phytochemicals in cells and damage them. In response to these damaging effects of ROS plants produce antioxidants as a secondary metabolite such as phenols, lignin and BRs. Oxidation reduction reactions occur and accumulation of ROS is prevented to a greater extent. Bartwal et al. (2013) have stated that water molecule is oxidized by photosystem II complex producing molecular oxygen which can be reduced to superoxide radical. It is true that plants produce oxygen during photosynthesis after a series of complicated chemical reactions but molecular oxygen released is never reduced to superoxide ion or superoxide radical. The following reactions show the mechanism of the formation of molecular oxygen by the splitting of water molecule.

$$H_2O \rightarrow H^+ + OH^- \quad (1)$$

$$OH^- \rightarrow OH + 1e- \quad (2)$$

$$2OH \rightarrow H_2O + O \quad (3)$$

Table 1 Some of the studies associated with the impact of different types of brassinosteroids on different plant species in abiotic stress conditions

Stress conditions	Type of brassinosteroids	Plant species	Key references
Salinity	Brassinosteroids	*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)
		Trifoliumalexandrinum	Daur and Tatar (2013)
		Oryza sativa	Sharma et al. (2013)
		Mentha piperita	Çoban and Baydar (2016)
	Brassinolide	*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)
	24-Epibrassinolide	*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)
		Eucalyptus urophylla	de Oliveira et al. (2019)
		Zea mays	Rattan et al. (2020)
		Glycine max	Soliman et al. (2020)
	28-Homobrassinolide	*Cicer arietinum*	Ali et al. (2007)
		Zea mays	Arora et al. (2008)
		Vigna radiata	Hayat et al. (2010b)
		Triticum aestivum	Yusuf et al. (2011)
		Brassica juncea	Alyemeni et al. (2013)
		Zea mays	Rattan et al. (2020)
Drought/Water stress	Brassinosteroids	*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)
	Brassinolide	*Robinia pseudoacacia*	Li et al. (2008)
		Glycine max	Zhang et al. (2008)
		Xanthoceras sorbifolia	Li and Feng (2011)
		Arachis hypogaea	Savaliya et al. (2013)
	24-Epibrassinolide	*Capsicum annuum*	Hu et al. (2013)
		Brassica napus	Mousavi et al. (2009)
		Cucumis sativus	Kang et al. (2009)
		Glycine max	dos Santos Ribeiro et al. (2019) & Pereira et al. (2019)
		Capsicum annum	Kaya et al. (2019)
		Vitis vinifera	Wang et al. (2019)
		Triticum aestivum	Avalbaev et al. (2020)
		Carthamus tinctorius	Zafari et al. (2020)
	28-Homobrassinolide	*Brassica juncea*	Fariduddin et al. (2009a)
Flooding	Brassinolide	*Cucumis sativus*	Liu et al. (2006)
		Glycine max	
High temperature	Brassinosteroids	*Lycopersicon esculentum*	Ogweno et al. (2008)

Table 1 (continued)

Stress conditions	**Type of brassinosteroids**	**Plant species**	**Key references**
Low temperature		*Vigna radiata* *Brassica napus* *Solanum lycopersicum* *Cucumis sativus*	Huang et al. (2006) Janeczko et al. (2007) Aghdam et al. (2012) Jiang et al. (2013)
	28-Homobrassinolide	*Cucumis sativus*	Fariduddin et al. (2011)
Low temperature	Brassinolide	*Campsicum annum* *Solanum lycopersicum* *Oryza sativa*	Wang et al. (2012) Aghdam and Mohammadkhani (2014) Wang et al. (2014)
High temperature		*Brassica napus*	Kurepin et al. (2008)
	24-Epibrassinolide	*Camellia sinensis*	Li et al. (2018)
Low temperature		*Capsicum annuum*	Yang et al. (2019)
Cd	Brassinosteroids	*Raphanussativus* *Brassica juncea* *Lycopersicon esculentum Triticum aestivum* *Solanum lycopersicum* *Helianthus tuberosus* *Solatium nigrum*	Anuradha and Rao (2007) Hayat et al. (2007) Hayat et al. (2010a) & Hasan et al. (2011) Kroutil et al. (2010) Hayat et al. (2012) Gao et al. (2013) Zhao et al. (2013)
	24-Epibrassinolide	*Brassica napus* *Raphanus sativus* *Phaseolus vulgaris*	Janeczko et al. (2005) Anuradha and Rao (2009) Rady (2011)
	28-Homobrassinolide	*Cicer arietinum* *Raphanus sativus*	Hasan et al. (2008) Sharma et al. (2010)
Al	Brassinosteroids	*Vigna radiata*	Ali et al. (2008b)
Ni	Brassinosteroids	*Brassica juncea*	Kanwar et al. (2012)
	24-Epibrassinolide	*Brassica juncea* *Raphanus sativus*	Kanwar et al. (2013) Sharma et al. (2011b)
Cu		*Cucumis sativus*	Fariduddin et al. (2013a)
	28-Homobrassinolide	*Brassica juncea*	Fariduddin et al. (2009b)
Zn	24-Epibrassinolide	*Brassica juncea* *Raphanus sativus*	Arora et al. (2010) Ramakrishna and Rao (2013)
	28-Homobrassinolide	*Raphanus sativus*	Ramakrishna and Rao (2013)
Pb	24-Epibrassinolide	***Brassica juncea***	Soares et al. (2020)
Fe		*Oryza sativa*	Guedes et al. (2021)
		Oryza sativa	Tadaiesky et al. (2021)
Zinc oxide nanoparticles induced toxicity	24-Epibrassinolide	*Solanum lycopersicum*	Li et al. (2016)

$$2O \rightarrow O_2 \quad (4)$$

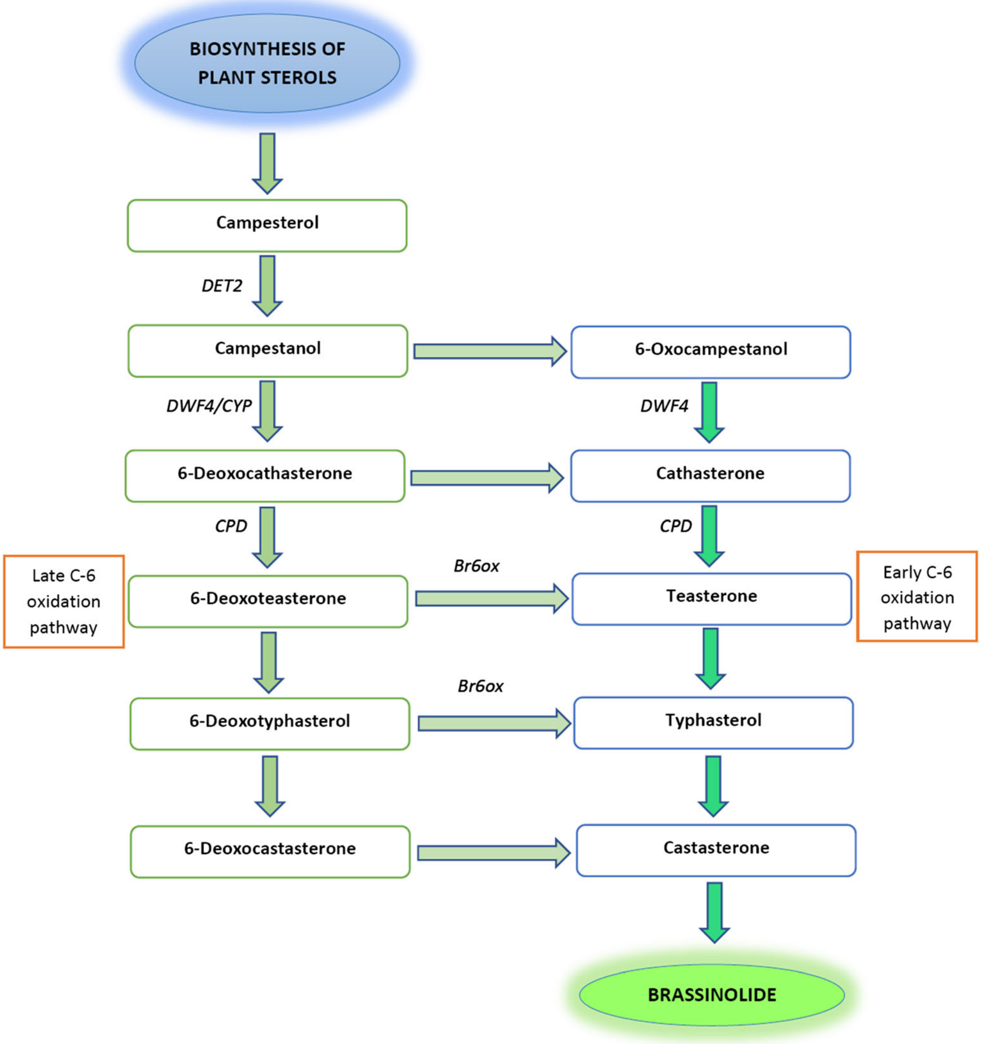
$$2H^+ + 2e^- \rightarrow H_2 \quad (5)$$

The overall reaction can be shown as:

$$2H_2O \rightarrow 2H_2 + O_2 \quad (6)$$

Hydrogen, thus produced represents the reducing power (not the free hydrogen molecule) which is used in the reduction of carbon dioxide in presence of sunlight during photosynthesis producing starch or carbohydrate. Experimentally, oxygen can be trapped in vitro but hydrogen is utilized and does not escape. If a plant produces superoxide radical/ion it will damage the system before it is removed. The O^{2-} is commonly formed because it has s^2p^4 configuration and can accept two electrons into its half-filled p orbital to complete its octet. However, all these electronic transfers are made during complex formation. Free singlet oxygen or free superoxide ions are not easily available as they are highly reactive. However, enzymes and hormones minimize the damaging effect of ROS which are produced as a consequence of environmental variation. It has also been reported that during stressed condition ROS and Ca^{2+} are released more quickly in absence of BRs than in its presence (Gilroy et al. 2014).

Fig. 3 The biosynthesis pathway of brassinosteroids. *CPD – constitutive photomorphogenesis and dwarfism*; *DET2 – deetiolated2; DWF4 – DWARF4;* CYP – Cytochrome P450; *Br6ox – Br-6-oxidase* (adopted from Divi and Krishna 2009)



Plants use defensive mechanism against stresses and activate a number of enzymes, for instance superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaiacolperoxidase (GP) glutathione peroxidase (GPX) (Ruley et al. 2004; Simonovicova et al. 2004; Sarker and Oba 2018; Nikoleta-Kleio et al. 2020; Kumar et al. 2021) and many non-enzymatic antioxidants (Özdemir et al. 2004; Sarker and Oba 2020). After a series of redox reactions, the ROS are converted to non-toxic compounds which are harmless to plants. BRs actually modify the pathway of enzymes when plants are exposed to stress. Li et al. (1998) have demonstrated that maize seedlings treated with BR and placed under water stress had shown an increase in SOD, APX and CAT activities. Obviously, the activity of some of the enzymes is enhanced and in others it is decreased. Oxidation and reduction occur simultaneously, but only one pathway is followed so that oxidizing species are reduced and subsequently removed as harmless substances. Similar results were obtained by Vardhini and Rao (2003) in case of sorghum. Under salinity, BR exposure to rice seedlings also exhibits an increased SOD, CAT, GR and APX activities (Nunez et al. 2003). It has been reported that EBL seed priming and optimal nitrogen supply improves salt tolerance in soybean (Soliman et al. 2020). Chakma et al. (2021) primed cotton seeds with EBL alone or in combination with other hormones and examined for germination and early seedling growth. They have noticed that the EBL promoted germination under control as well as under salinity and heat stress. However, other tested hormones were found to be ineffective under stress conditions. They have also found that the EBL promoted cotyledon opening and the development of lateral roots in germinated seedlings. Further, Liu et al. (2020a) have found that EBL at certain concentration worked as an active BR, and promoted the tolerance of canola under high-salt stress, nonetheless the same concentration was disadvantageous under low-salt stress. In a recent experiment, it was found that the BR-mediated lignin accumulation plays an important role in garlic adaption to salt stress (Kong et al. 2021). BRs generally enhance the activity of enzymes of plants under stress. Studies on *Chlorella* *vulgaris* and tomato support the above results (Bajguz and Hayat 2009; Mazorra et al. 2002). Peroxidases are calcium ion dependent enzymes because the activity depends on their equilibrium (Hu et al. 2007; Bhattacharjee 2008) which is induced by BR. They increase the yield of seeds and biomass as a whole and regulate the expression of genes.

BRs application (presoaking at 10^{-8} or 10^{-10} M) has enhanced the percentage of seed germination in *Brassica juncea*, *Orobanche minor* and *Cicer arietinum* seeds (Takeuchi et al. 1995; Ali et al. 2008a; Sirhindi et al. 2009). They also enhance the activity of pigments which in turn, increase the rate of photosynthesis that depends on the type and quantity of chlorophyll pigments. For instance, plants devoid of green pigments such as croton plant, showed decreased rate of photosynthesis. Thus, there is a relationship between the activity, rate of photosynthesis and the chlorophyll pigments (Gomez 2011). Bjornson et al. (2016) have shown that while BRs signaling not only causes an increase in oxylipin synthesis but it also causes changes in the jasmonates response transcription factors (Müssig et al. 2000). Under extreme stress conditions, plants slow down the transpiration by closing the stomata to prevent the loss of water. They also produce amino acids, polyols and some proteins which prevent the oxidation of cellular components such as nucleic acid (Rontein et al. 2002). BRs are activated at this stage and upregulate defensive genes (Kwak et al. 2006) nevertheless the enzymes and hormones are universally known to be more active against salinity stress. Major function of these responsive genes is to help scavenge ROS and relieve the plant from additinal stress. It has been noticed that the opening and closing of stomata in leaves and their development is controlled by BR although, abscisic acid (ABA) and auxins are also involved in this activity (Kim et al. 2012; Le et al. 2014). They have been found to suppress the development of stomata in *Arabidopsis* plant leaves (Kim et al. 2012; Tanaka et al. 2013) but Gudesblat et al. (2012) have observed negligible effect on the development of stomata in cotyledons. There is a close relationship between BRs and sugar signaling (Zhang and He 2015). Sugar level and expression level of BRs related genes in many plants are linked to each other. BR contents are linked to the increase/decrease of sugar concentration in *Arabidopsis* (Schröder et al. 2014).

$$[\mathrm{BR}] \quad \rightarrow \quad \mathrm{Sucrose} \quad \rightarrow \quad \mathrm{Flowering} \tag{7}$$

Both, sugar and BR are required for flowering in *Arabidopsis* (Schröder et al. 2014). It has been found that BR deficient plants flower late but when they are treated with BR, flowering occurs in time (Laxmi et al. 2004). Specific type of BR (BZR1 and BZR2) transcription factors are involved in signaling (Matsoukas 2014) pathways which also interact with sugars. It has been noted that shoots are more efficiently involved in the synthesis of BR than other parts of the plant. Synthetic BRs are quite expensive, and possibly their application in agriculture to boost crop yield may not be economical. It is therefore essential to modify biosynthetic pathway to produce its own BR derivatives to improve the quality of grain and increase the crop production. Like gibberellins modification to increase rice and wheat production, BR activity can also be enhanced through modification of genes involved in the BR synthesis (Choe et al. 2001). BRs have been found to increase not only crop yield of gram but also increase florescence, plant biomass and plant length. As a result of enhanced activity of BRs, the rate of is also increased which produce more glucose/starch in plants. However, BRs accelerate photosynthesis and overall productivity in many plant species.

Clouse (2016) have reported that ABA acts as antagonist of BR in rice and inhibits their vegetative growth. Some *A. thaliana* mutants have been found to be insensitive to BRs, although a variety of plants respond to BR even under stress (Sasse 1991). Since BRs regulate gene expression, the mutants are rescued by their exogenous application (Evans 1988). In a detailed experiment on *Cucumis sativus*, Yu et al. (2004) have shown that besides other progresses and developments, absorption and complete assimilation of carbon dioxide leading to increased photosynthesis occurs when the plant was sprayed with 24-EBL. Different concentrations of BR were tested but maximum increase of 210%, in photosynthesis was observed at a concentration of 0.1 mg/L after which the rate declined which suggests that BR concentrations above 0.1 mg/L has no beneficial effect. Accordingly, an upsurge in sucrose, sugars, starch and many enzymes also occur. Similar treatment of BR on *Arabidopsis* mutants did not show any positive result perhaps due to defective genes. Zhu et al. (2015) have thoroughly examined the effect of BL on tomato ripening and ethylene production. Ethylene regulates fruit ripening, and any substance that catalyses the generation of ethylene can also accelerate the ripening of fruits by influencing many enzymes (Hamilton et al. 1990; Oeller et al. 1991). Application of BR to tomato fruit increased the evolution of ethylene and lycopene with a consequent lowering of chlorophyll pigments (Liu et al. 2014). BR regulates the biosynthesis of ethylene and lycopene via ACS and ACO enzymes (Barry et al. 2000; Klee and Giovannoni 2011) which help in ripening of tomato with the reduction of chlorophyll after they were plucked green and stored at 25 °C. BRs also increase the synthesis of jasmonates (Müssig et al. 2000) besides providing tolerance against biotic/abiotic stresses to plant species (Koca and Karaman 2015). Application of naturally occurring BRs also decrease the quantity of pesticides in fruits and vegetables by degrading them to harmless residues (Zhou et al. 2015).

Plant response to BRs application under abiotic stress

Application of BRs enhanced plant production during stress and abrupt environmental changes, although they are useful even under normal conditions. Any deviation from normal condition is felt by the plants and reflected from their biochemical changes which are connected to their growth and development. These responses are triggered in plants as a signal similar to reflex action in mammals. The changes in antioxidants, up-regulation and down-regulation of proteins cause changes in protein pathways. The harsh environmental conditions force the plants to make adaptations in order to survive (Smirnoff 1995; Fujita et al. 2006). BRs application in plants and their response under changing environment have been discussed under the following subheadings.

Salinity stress

Phytohormones are synthesized to enhance the yield of fruits, cereals, crops and regulate the biological function of plants (Iqbal et al. 2014) during salinity stress. BRs under normal conditions are engaged almost in all physical and chemical activities but under stress they protect the plants to maintain their normal functioning. BL treatment of Lucerne seed under salinity has been shown to enhance the dry weight and antioxidant activity (Zhang et al. 2007b). It has been observed by Tanaka et al. (2003) that BRs increased the growth of hypocotyls and cotyledonous leaf-blades in a dose-dependent manner. BRs also catalyse the efficiency of other hormones (gibberellins and auxin) and plant growth promoters (Tanaka et al. 2003). Increased salinity or water scarcity produces oxidative stress which in turn, reduces the crop production, photosynthesis, protein synthesis, respiration and overall growth of many plant species (Xiong and Zhu 2002; Hussain et al. 2013; Husen et al. 2016, 2017). Substantial quantity of ROS is produced due to salinity stress. Thus, superoxide anion O_2^-, hydrogen peroxide H_2O_2 and hydroxyl radicals $OH^•$ are generated (Mittler 2002; Masood et al. 2006). In order to prevent the damage by these species, plants produce enzymes namely SOD, APX and GRX in defense (Munns and Tester 2008) which act as antidote against them. Besides BRs, there are many more hormones which control several functions of the plant. These phytohormones are produced by rhizobacteria (Ahmad et al. 2005; Babaloa 2010) under adverse situation of salinity, high temperature or excess of water together with antibiotics to protect plants from pathogenic microbes. Phytohormones are produced to sustain the harsh environmental conditions so that the normal functioning of the plant continues. Exogenous application of BR on sorghum cultivars and sugar beet plants under stress showed positive effect in terms of increased root length, biomass and germination (Vardhini and Rao 2003). Unlike drought stress, salinity disturbs the exchange and translocation of cations and anions in the plant system. In order to reduce the concentration of the ions either the intake of salt is minimized or the common ions are exchanged with another ion which is essential for the plant. For instance, Ca^{2+} ions may be replaced by Mg^{2+} ions as their exchange is chemically favored since they both are divalent metal ions and belong to the same group of elements. Similarly, Na^+ ion may be replaced by K^+ ion, the concentration of which is relatively lower than that of Na^+ ion. Under salinity stress, EBL treatment decreased proline accumulation to prevent the damage of seedlings (cv IR-28 rice) and thus allows normal growth (Özdemir et al. 2004). Conflicting results have been reported about accumulation of proline and enhanced activity of antioxidant enzymes in salt sensitive plants/crops (Ali et al. 2007; Hayat et al. 2007). However, degradation of proline and plant growth is the main focus of study. There is however, consensus on the ameliorating effect of EBL on salt stressed plants. These results are supported by work done on *Cicer arietinum* (Ali et al. 2007) *Vigna radiata* (Hayat et al. 2010b) and *A. thaliana* (Kagale et al. 2007). BR application in salt stressed rice plant increases the activity of nitrate reductase, which in turn, increases the crop production. Since ROS damage the plant metabolites, the plants modify mechanistic pathway to scavenge the ROS so that the plants grow and produce fruit/ crop in usual manner (Vardhini and Anjum 2015). It has been observed almost in all salt stressed crops that BL application improves germination and growth of seedlings (El-Khallal et al. 2009; Shahbaz and Ashraf 2007). The stress produced by a combination of two substances (copper and sodium chloride) has been reported to be mitigated by epi-BL application in two varieties of *Cucumis sativus* (Fariduddin et al. 2013b). Besides increasing the activity of antioxidant enzymes, the rate of photosynthesis was also enhanced. It may be a good effort to explore the combined effect of two substances on plant development but an appropriate reason for doing such experiment is required. The other metals of copper group (silver and gold) have altogether different chemical behavior which has not been tested. Application of BR analog, DI-31 showed improvement in growth in lettuce plant under salt stress (Serna et al. 2015). Salinity is known to decrease plant growth and increase ethylene production (Siddikee et al. 2012). Increased ethylene production causes more stress which reduces plant growth. The BR analog treated lettuce plant showed tolerance to salinity in terms of fresh weight (Zeng et al. 2010; Shahid et al. 2014). The rate of respiration in roots and shoots of lettuce increased under salinity stress (Zapata et al. 2007) to overcome the effect of stress. This is a defensive response of the plant. Since NaCl is completely dissociated as Na^+ and Cl^- ions they have higher mobility than other essential ions. They block the passage for them which cause deficiency of essential ions as a result of which the plants have to respire more rapidly than usual. BR application normalizes the respiration. K^+ ion treatment of saline stressed plants showed reduction in ethylene emission

(Amjad et al. 2014). The BRs increase the growth of the plant but K^+ alone responds to tolerance against stress. The K^+ ion is relatively larger than Na^+ ion and hence its mobility is lower than that of Na^+. Perhaps it can make up for the loss of essential nutrients in plants. If a combination of K^+ and BR is applied to the plant/crop the rate of vegetative growth may be enhanced several fold. All adverse effects produced by NaCl stress are directly proportional to its concentration. Initially, the aerial parts of the plants show a decrease in growth, and at a reasonably higher concentration of NaCl the plant dies if appropriate measures are not taken.

Effect of NaCl and BRs concentration on peppermint (*Mentha piperita*) revealed that salinity is the main cause of plants to perish. In the beginning, yellowing of leaves occurs, as a result of which, quantity of chlorophyll pigments decreases which reduces the rate of photosynthesis. Weight of aerial parts of the plant significantly decreased. There was a marked reduction in essential oil production of mentha and an increase in lipid peroxidation, phenols and antioxidant enzymes with increasing NaCl concentration (Khorasaninejad et al. 2010; Çoban and Baydar 2016). Salinity causes overall reduction in growth of plants. BR application reduces the salinity stress and prevents the damage. In tomato and geranium, BR treatment enhanced their growth (Hayat et al. 2010b; Hayat et al. 2010c; Swamy and Rao 2009). Çoban and Baydar (2016) have reported that, under saline condition NaCl ionizes to produce free Na^+ and Cl^- ions which are deposited on the surface of cell membrane. They further reported that it decreases the pH of the cell surface as a consequence of which the protein breaks down. The acidic medium damages the plant. This proposal is hypothetical and chemically impossible. NaCl is a salt of strong acid (HCl) and a strong base (NaOH) which is completely ionized in aqueous medium. The sodium ions are always in equilibrium with chloride ions and their recombination will give neutral NaCl salt and hence the pH of the medium will never change. Ionization of NaCl and reaction of Na and Cl ions are shown below:

$$\mathrm{NaCl} \quad \rightarrow \quad \mathrm{Na}^{+} + \mathrm{C1}^{-} \quad \text{Ionization} \tag{8}$$

$$\mathrm{Na}^{+} + \mathrm{H{-}OH} \quad \rightarrow \quad \mathrm{NaOH} \quad \text{Combination of Na ion with OH of water} \tag{9}$$

$$\mathrm{Cl}^{-} + \mathrm{H}^{+} \quad \rightarrow \quad \mathrm{HC1} \quad \text{Combination of Cl ion with H}^{+}\text{of water} \tag{10}$$

Assuming damage of cell membrane by lowering the pH due to free Cl ions producing HCl, is improbable. Ion leakage may be due to excessive accumulation of Na and Cl ions around the cell membrane. Excess sodium ions are toxic to all living beings because they trigger the impulses through Na^+/K^+ pump. Chloride ions have bleaching effect and gradually damage the chlorophyll pigments. A NaCl solution in aqueous medium is neutral and all such assumptions that it produces acidity and damages the crop are baseless. Large excess of NaCl is harmful to plants due to toxicity of Na^+ ions. They are transferred from intracellular fluids to extracellular fluids through carrier proteins. Conversely, K^+ ions are transferred from extracellular fluids to intracellular fluids. During salinity, excess Na^+ ions are transferred to extracellular fluid which produces a charge gradient on one hand and concentration gradient on the other, across the cell membrane. This potential difference accounts for the trigger of impulses in plants and mobility of ions through osmosis. Sodium and potassium pump also maintains the volume of the cells without which volume increases uncontrollably and the cell bursts. Excess of Na ions during salinity also causes imbalance between Na and K ions which disturbs the metabolism.

It has been reported that salt stressed *Oryza sativa* treated with BR exhibited increased growth and development (Anuradha and Ram Rao 2003). Also, it induced the activity of nitrate reductase in salt stressed rice crop. BRs regulate the activity of antioxidant enzymes, chlorophyll pigments, rate of photosynthesis and carbohydrate metabolism to upsurge plant growth under stress. Exogenous application of BR enhances the biosynthesis of endogenous hormones and regulates signal transduction pathways to different stresses (Anwar et al. 2018). Salinity is also increased by the presence of other alkali metals (Li, Na, K) and alkaline earth metals (Be, Mg, Ca) chlorides, bicarbonates and sulfates in the soil. BRs provide tolerance against all stresses and improve the quality of fruits and grains by increasing the photosynthesis and enzyme activity (Anwar et al. 2018).

BR application has shown tolerance against salt stress in *Eucalyptus urophylla*. ROS is produced due to large quantity of Na ions deposited which decreases chlorophyll pigments as a consequence of which rate of photosynthesis is decreased (Kim et al. 2016). K^+/Na^+ pump balances the ionic concentration of these ions within the cells in plants through symport and antiport but extremely large excess of sodium ions during salt stress causes imbalance. At this point foliar application of EBR improves overall development in *E. urophylla* (de Oliveira et al. 2019) and reduces salt stress. K^+/Na^+ equilibrium was maintained which led to an increase in CAT and APX enzymes. Very recently, Liu et al. (2020b) have shown the impact of EBR/EBL application on plants under different stages of development increasing their tolerance against salt stress. It has been noticed that all concentrations of hormones are not equally effective in mitigating the influence of salinity, drought or extreme temperature variation. At low level of salinity, a certain BR concentration was effective, however with increase in salinity the same BR concentration does not work. Therefore, emphasis must be given to prevent excessive sodium ion accumulation, because it induces the ROS production. *Zea mays* under salinity stress, exposed to 28-HBL and 24-EBL have shown to withstand the abrasive effect of NaCl (Rattan et al. 2020). In this experiment, the quantity of saline solution added has not been mentioned which could measure the amount of salt. Further, the equilibrium between K+/Na+, antioxidant enzymes and phytochemicals were measured in maize plants. The sodium ions were decreased with a consequent increase in potassium ion concentration. In fact, it is the concentration gradient that accelerates the mobility of Na ions out and K ions inside the cell maintaining the normal functioning of K^+/Na^+ pump. Thus, antioxidant enzyme activity enhanced with a consequent decrease in malondialdehyde accumulation. With the removal of free radicals, the enzyme activity is enhanced which maintains the normal functioning of plants under salt stress. Treatment of soybean with EBL coupled with nitrogen, further enhances the tolerance of plant by NaCl stress (Soliman et al. 2020). Nitrogen acts as a nutrient which synergises the photosynthesis in plants.

Water/drought stress

Photosynthesis is essential for a plant to survive even under different stresses. Water, carbon dioxide, sunlight and moderate temperature are required for chlorophyll to produce carbohydrate/sugar. During drought or water scarcity the process of photosynthesis is retarded or even completely arrested. It is a general phenomenon for all plants to slow down metabolic processes. The stomata remain closed to prevent the loss of water as the growth of the plant as a whole is retarded. It has been observed that when *Arabidopsis* and *Brassica napus* seedlings were grown in very dilute solution of EBL (1 μM) and placed under artificial drought for 96 and 60 h respectively, their tolerance for drought was increased (Kagale et al. 2007). In response to EBL application some modification in the activity of antioxidant enzymes and defense genes occurs which stimulates the normal functioning of plants (Li et al. 2012). It has also been found that BR treated *Cucumis sativus* increases the reduction process of carbon dioxide in presence of glutathione which was indirectly involved in activating the process (Jiang et al. 2012). However, HBL treatment of mustard plant under drought enhanced CAT, POX, SOD activities and proline content. BRs and BL have also been found to increase the biomass and crop yield in soybean and mustard (Zhang et al. 2008; Fariduddin et al. 2009a). It has been reported (dos Santos Ribeiro et al. 2019) that water scarcity diminishes seed germination, biomass and root growth in soybean plants which can be ameliorated by 24-EBL application. Under water stress the oxidative damage is prevented through antioxidants (SOD, CAT, APX and POX) before it damages the plant morphology (Cruz de Carvalho 2008). Drought like condition is inversely proportional to the production of RO. The increased amount of antioxidants produced more tolerance in plants toward water deficiency. Water stressed plants showed improvement in growth after they were treated with BR. However, this effect was synergized by endogenous application of NO specifically in *Capsicum annum* (Kaya et al. 2019). Pereira et al. (2019) examined the role of 24-EBL on soybean plants under water deficiency and observed that quantum yield of PSII photochemistry, electron transport and net photosynthetic rates were reduced. However, exogenous application of EBR (at 100 nM) has mitigated the negative effect of water stress on the studied features. The EBR also decreased the superoxide and hydrogen peroxide and prevented cell membrane damage.

It has been noticed that the ABA controls a wide range of RAB (responsive to ABA) genes coding for the proteins concerned to the cell protection against dehydration injuries in *Manihot esculenta* (Feng et al. 2019). Avalbaev et al. (2020) have shown the ability of 24-EBL to stimulate additional synthesis of wheat germ agglutin under normal conditions. Severe water scarcity partially damages the aerial parts which is clearly visible. It has been reported in the case of grapevine (*Vitis vinifera*) under drought condition that, the production of H_2O_2 and superoxide radicals is enhanced with a consequent reduction in ascorbic acid and glutathione (Wang et al. 2019). After the exogenous BR application these symptoms were reversed, viz., the production of H_2O_2 and O^{2-} were decreased and those of ascorbic acid and antioxidants were enhanced. It has been shown that there is a close relationship between ABA and drought stress. BRs reduce the adverse symptoms and increase the tolerance of grapevine to drought. All antioxidants and genes related to their production are activated by BR application. Activity of enzymes and proteins increased after EBL was sprayed on *Echinacea purpurea* under severe drought condition (Hosseinpour et al. 2020). Despite substantial increase in total protein, SOD, CAT, POX, proline and H_2O_2 a large reduction in plant biomass was observed. It is interesting that the substances needed for plant development were increased which suggests tolerance of *E. purpurea* to drought. A slight deviation from normal behavior of plant and an increase in ROS is an indication of abiotic stress.

Temperature stress

Both, extremely low and high temperature disturb the normal functioning of plants. At very high temperature the loss of water and increased permeability of plasma membrane decrease the rate of photosynthesis which is vital for all green plants. It has been found that when the plants under temperature stress are treated with EBL the proteins responsible for heat shock protect the plant as a result of which the photosynthesis efficiency is enhanced as has been found in tomato plant (Singh and Shono 2005). Plants/seedlings treated with EBL prior to exposure to high temperature for few hours (1–4 h) showed delayed adverse symptoms relative to untreated ones (Kagale et al. 2007). This is quite obvious but such short time exposure does not show any meaningful result which may be generalized because plants can recover such losses by their own immune system. High temperature and chilling cold also have damaging effect on plants which are clearly visible. For instance, reduced growth, yield (Sheehy et al. 2005) shortening and wilting of leaves, necrosis and reduction in development of reproductive organs occur (Kang and Saltveit 2002).

Photosynthesis is always hampered at abnormally low temperature, particularly when sudden change occurs (for instance, snowfall). Absorption of carbon dioxide, enzyme activities and osmosis are reduced to minimum. EBL treatment at this stage helps to recover the loss in dicots (Huang et al. 2006). However, a slight variation in temperature (20 ± 5 °C) does not show any noticeable change in treated/untreated plant (Kagale et al. 2007). BR treated wheat leaves under thermal stress (43 °C) showed normal development indicating normal protein synthesis. The untreated ones had shown a nearly threefold (Kulaeva et al. 1991) fall in the process. BRs and indole acetic acid (IAA) separately induce the plant growth under temperature stress. This effect is synergized if a combination of BRs and IAA is applied to plants. BR increases the rate of germination in seasonal crops (He et al. 1991). Some BR derivatives protect the plants even at 7 °C while others do the same at abnormally high temperature (González-Olmedo et al. 2005). BR (24 epi-BL) application shows very low tolerance to *Bromus inermis* development at low temperature (3–5 °C), but at high temperature (40–45 °C) the tolerance is appreciably high (González-Olmedo et al. 2005). BRs also increase the fruit yield in tomato under heat stress (Singh and Shono 2005).

Yang et al. (2019) have studied the chilling effect in BR pretreated and control pepper seedlings. Foliar spray of EBR on pepper leaves showed an increase in plant growth, rate of photosynthesis, maximum quantum efficiency and photochemical quenching coefficient. Plants also showed an increase in free amino acids and enzyme activity (glutamine synthase, nitrate reductase, glutamate synthase etc.) which enhanced nitrogen metabolism in leaves. Chilling stress produces ROS but treatment with EBR reduces the accumulation of H_2O_2 and superoxide anion showing increasing tolerance toward falling temperature below normal. In recent years, it has been noticed that the autophagy process is important for the degradation of dysfunctional cellular components at some stage of development under negative environmental situations (Qin et al. 2007; Liu and Bassham 2012). So far, more than thirty autophagy-related genes (ATGs) have been recognized (Yoshimoto 2012; Marshall and Vierstra 2018). In plant system, the role of autophagy has been investigated under numerous abiotic stresses (Guiboileau et al. 2013; Wang et al. 2015a, 2015b; Zhai et al. 2016). BRs worked as a positive regulator of NBR1-dependent selective autophagy in tomato plants (Chi et al. 2020). They have verified that low temperature and BRs together induced the BRASSINAZOLE-RESISTANT1 (BZR1) stability, which up-regulates ATG2, ATG6, NEIGHBOR OF BRCA1(NBR1a) and (NBR1b) expression by binding to their promoters. The upsurge in autophagy and the selective autophagy receptor NBR1 increased photoprotection via higher accumulation of functional proteins (PsbS, VDE and D1) leading to increased tolerance to cold (Fig. 4).

The effect of BL on rice under chilling stress has shown improvement in activity of enzymes (SOD and Peroxidases) sugars and proteins (Wang et al. 2020). Other toxic substances such as malondialdehyde were reduced. Minerals/inorganic ions like N, P and K were enhanced when rice plants were exposed to BR. In fact, these nutrients are already there but owing to low temperature their release and transportation was delayed or arrested.BR treatment induces the release of nutrients and activate the enzymes which is termed tolerance. The plants recover from cold stress when temperature becomes normal and all activities are restored even in absence of BR/EBL. However, these hormones induce the activity of antioxidants and reduce ROS under all types of stresses. Recently, Chen et al. (2021) have also suggested that BRs mediated the impact of high temperature stress on pistil activity during antithesis and increased antioxidants and suppressed ROS generation in photo-thermosensitive genetic male-sterile rice lines.

Heavy metal toxicity

Radioactive metals and toxic metals accumulated in plant parts were reduced by the application of BRs. Perhaps, metal ions forming soluble complexes with the donor groups of BRs are prevented from their deposition in cells. In tobacco seedlings, biomass accumulation was drastically reduced under cadmium stress (Ahammed et al. 2013). However, it has been noticed that the exogenous EBR application at 0.1 μM increases plant biomass by augmenting carbon dioxide assimilation capacity, chlorophyll fluorescence and photosynthetic pigment. They also suggested that the foliar application of EBR reduces cadmium uptake in roots and its translocation to tobacco leaves. In another experiment, BR (24-EBL and 24-

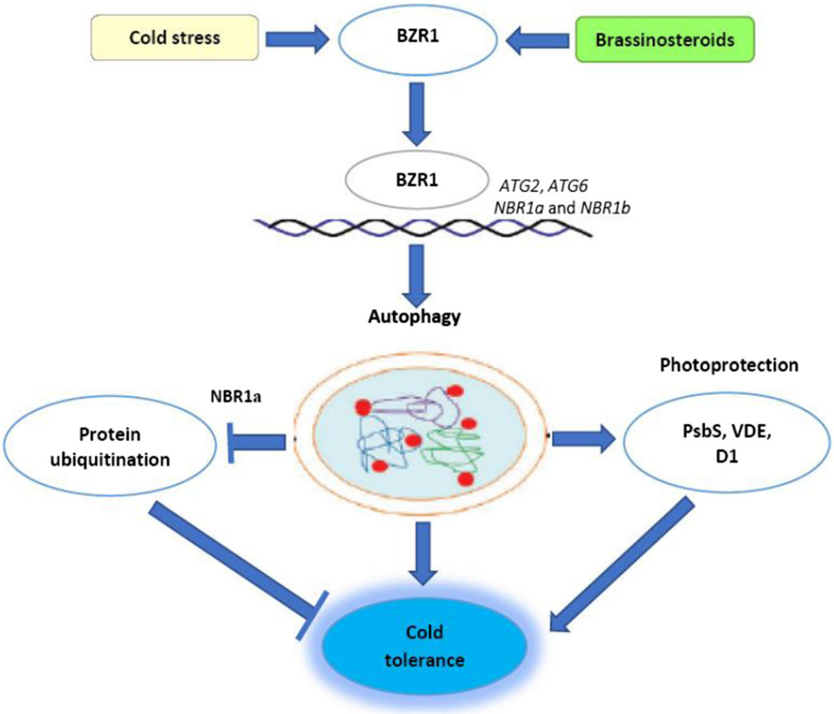


Fig. 4 Projected mechanism of BZR1 induced cold tolerance by the autophagy activation in tomato plants. Cold and BRs induced BZR1 stability; and turn on the transcription of autophagy genes (ATG2, ATG6, NBR1a, and NBR1b) by their promoters binding, thereafter increasing the autophagy. Autophagy facilitates photoprotection by functional proteins accumulation namely, PsbS, VDE, and D1; and enhances the degradation of stress-damaged insoluble ubiquitinated protein aggregates through selective autophagy receptor NBR1. Arrows in the illustration showed the positive control; while the bar ends exhibit the negative control (adopted from Chi et al. 2020). BZR1 – brassinazole resistant 1; BRs – Brassinosteroids; ATG2 & ATG6 – Autophagy *genes;* NBR1 – neighbor of brca1; and PsbS, VDE & D1 – functional proteins

epicasterone and 4154) treatments were found to decrease the uptake of heavy-metal (lead and cadmium) in spring wheat plants (Kroutil et al. 2010). Bukhari et al. (2016) have described that the tobacco leaf mesophyll cells (cell wall, cell membrane, and dilated thylakoid) were distorted under chromium exposure. 24-EBL application had protected the chromium-induced damage to chloroplast. In tomato seedlings, Singh and Prasad (2017) have also reported that application of 28-homobrassinoloid improved the chromium-induced decrease in growth, photosynthesis and the photochemistry of PSII. Further, Hasan et al. (2008) have reported that 28-HBL protects chickpea from cadmium toxicity by stimulating the levels of enzymatic and non-enzymatic antioxidants. Song et al. (2016) have suggested that ROS generation is increased due to heavy metal exposure and adversely influenced the overall plant metabolism, triggering oxidative injury to proteins, lipids and nucleic acids. However, Kanwar et al. (2012) have found that exposure of nickel accelerates the BRs biosynthesis such as castasterone, typhasterol, EBL and dolicholide in *Brassica juncea*.

Ali et al. (2008b) have investigated the function of BRs in the reduction of aluminum toxicity in mung bean (*Vigna radiata*) seedlings. The seedlings were exposed to various concentrations of aluminum (0.0, 1.0 or 10.0 mM) at 1-week-old stage and were sprayed with 10^{-8} M of 24-EBLor 28-HBL at 14-day stage. After three weeks, carbonic anhydrase activity, chlorophyll content and the rate of photosynthesis were found to decrease. However, leaf antioxidative enzyme activities (CAT, SOD, peroxidase) and proline in leaves and roots enhanced in these seedlings. Further, foliar spray of 24-EBL or 28-HBL, in absence of aluminum strongly improved the above parameters and also accelerated their growth. Radish plant growth by foliar application of BR (24-EBL or 28-HBL at 0.5, 1.0, or 2.0 μM) in zinc toxicity alleviation has been carried out by Ramakrishna and Rao (2013). Zinc stress was found to reduce growth parameters and photosynthetic pigments but BRs exposure improved these traits. BRs application however, decreased H_2O_2 level, lipid peroxidation, electrolyte leakage and enhanced the water absorbing capacity of leaf under stress. Foliar application of 24-EBL was more effective than 28-EBL in zinc stress mitigation. Several other findings have also revealed that application of BRs can modify antioxidant activities in maize, mustard, radish, wheat and rice under metal stress (Sharma et al. 2007, 2010, 2011a, 2016; Ramakrishna and Rao, 2015). It has also been suggested that BRs under metal stress may inhibit lipid degradation and accelerate the antioxidative enzyme activities (Sudo et al. 2008; Soares et al. 2016). Phytochelatins (PCs) syntheses are another important mechanism of metal detoxification; and BRs are known to stimulate PCs syntheses in cells treated with lead (Rajewska et al. 2016). A possible mechanism of BRs regulation of heavy metal stress tolerance in plants is illustrated in Fig. 5.

A recent study of *Brassica juncea* has shown that lead (Pb) tolerance can be diminished by BR application before or after seed germination (Soares et al. 2020). If the

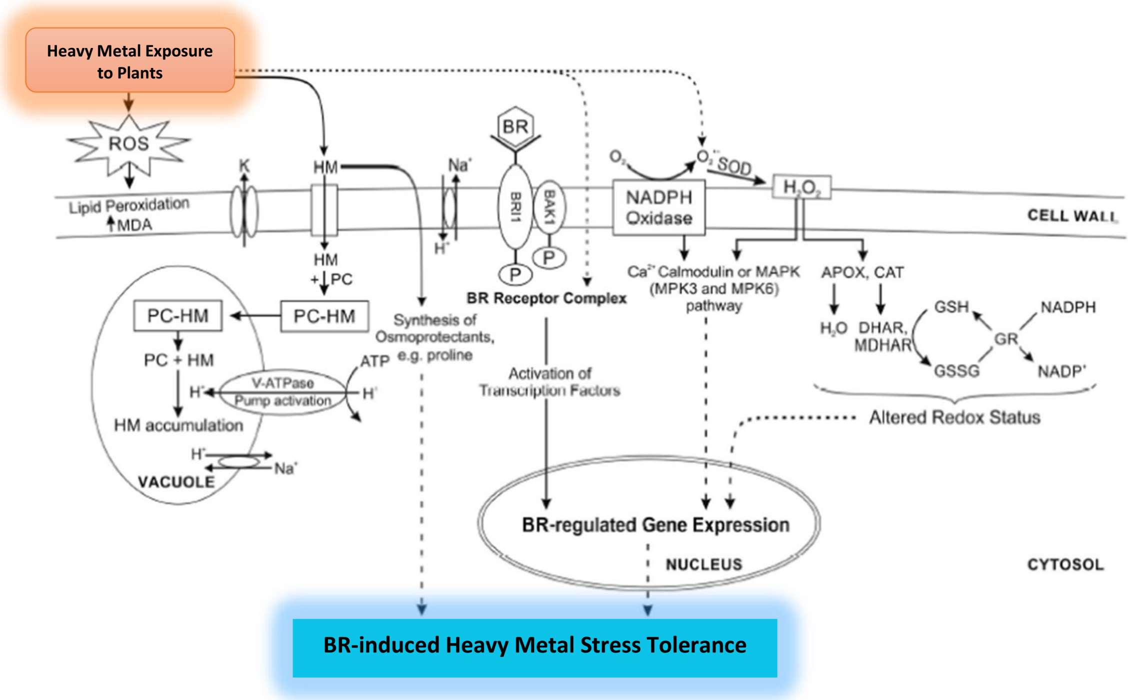


Fig. 5 Proposed possible mechanism (dotted lines) of BRs regulation of heavy metal tolerance in plants. APOX – ascorbate peroxidase; BAK1 – BRI1-associated kinase1; BRI1 – brassinosteroid insensitive1; CAT – catalase; DHAR – dehydroascorbate reductase; GR – glutathione reductase; GSH – glutathione; GSSG – glutathione disulphide; HM – heavy metal; K – potassium; MAPK – mitogen activated protein kinases; MDA – malondialdehyde; MDHAR – monodehydroascorbate reductase; P – phosphate; PC – phytochelatins; ROS – reactive oxygen species; V-ATPase; and vacuolar H+ − ATPase (adopted from Rajewska et al. 2016; re-drawn based on Sharma et al. 2011a)

soil is contaminated with lead it is absorbed by the plant through its roots. Of all the lead salts only lead chloride and lead nitrate are slightly soluble (not more than 1 g/100 ml in water at 25 °C) and therefore, chances of lead toxicity are rare. However, lead is known to be a cumulative poison as it accumulates in different parts of the plant and produces lesion. Exogenous application of EBL (10^{-8} M) was highly effective against lead stress in *B. juncea*. It accelerated the activity CAT and POX which prevented the damage by lead. The extent of injury depends on the concentration of the toxic metal and the stage of plant development. In a very recent study, Tadaiesky et al. (2021) have reported that EBR decreased iron toxicity in rice plants modulating the parenchyma area, contributing to the formation of an oxidative barrier and Fe immobilization at the root surface. Similarly, Guedes et al. (2021) have shown that lead produces toxicity in rice plants but EBR treatment alleviated the adverse effects of lead.

Conclusion

BRs are a group of naturally occurring plant hormones comprising of BL, castasetrone and their derivatives which regulate plant growth and development. Over 69 BRs have been isolated from different parts of plants. These steroidal hormones are timely produced and utilized by plants. They are synthesized in response to salinity, drought, extremely cold/hot temperature, injury or pathogenic attack to maintain the normal functioning of plants and enhance fruits and crop yield. In future BRs and BL would be the key hormones to increase the yield of fruits, vegetables and agri-products. Their application would also protect the plant/crops from pests, insects and physical stresses.

Abbreviations 24-EBL, 24-epibrassinolide; 28-HBL, 28-homobrassinolide; ABA, Abscisic acid; APX/APOX, Ascorbate peroxidase; ATGs, Autophagy-related gene; BL, Brassinolide; BR, Brassinosteroid; BZR1, BRASSINAZOLE RESISTANT 1; BAK1, brassinosteroids associated kinase1; BRI1, brassinosteroid insensitive1; $CaCl_2$, Calcium chloride; $CaSO_4$, Calcium sulfate; CAT, Catalase; DHAR, Dehydroascorbate reductase; GP, Guaiacol peroxidase; GSH, Glutathione; GSSG, Glutathione disulphide; GPX, Glutathione peroxidase; GR, Glutathione reductase; H_2O_2, Hydrogen peroxide; HCl, Hydrogen chloride; HM, Heavy Metal; IAA, Indole acetic acid; NBR1, next-to-BRCA1; KCl, Potassium chloride; MDA, Malondialdehyde; MAPK, Mitogen-activated protein kinases; MDHAR, Monodehydroascorbate reductase; K, Potassium; P, Phosphate; NaCl, Sodium chloride; NaOH, Sodium hydroxide; PC, Phytochelatin; Prxs, Peroxiredoxins; ROS, Reactive oxygen species; RWC, Relative water content; SOD, Superoxide dismutase; V-ATPase, vacuolar H^+-ATPase

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Declaration

Conflict of interest The authors declare that they have no conflict of interest.

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