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Role of 24-Epibrassinolide in Inducing Thermo-Tolerance in Plants

Mohsin Tanveer[1]

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Abstract

High-temperature stress (HT) is one of the most dramatic abiotic stresses, reducing crop yield significantly. Hormone application has been seen as one of most effective approaches in ameliorating HT stress-induced detrimental effects in plants. 24-Epibrassinolide (EBL) is an active by-product produced during brassinolide biosynthesis and can induce thermo-tolerance in plants by playing multiple roles in different metabolic processes. EBL application improves or protects plant growth and development under HT stress by improving the process of development and by protecting different plant growth stages from HT stress. Shortly, EBL improves plant growth and yield by improving germination, pollen development, pollen germination, biomass production and the source-to-sink relationship under HT stress. Moreover, EBL also enhances carbon assimilation rate, maintains positive redox potential and increases solute accumulation. EBL also increases the production of heat shock proteins (HSPs) to further cope with HT stress. In conclusion, EBL is a very impressive phyto-hormone, which can ameliorate HT stress-induced detrimental effects in plants. In this review article, potential mechanisms are discussed with respect to EBL-induced thermo-tolerance in plants.

Keywords 24-Epibrassinolide · Thermo-tolerance · Redox homeostasis · Proline · Heat shock proteins · Yield

Introduction

High-temperature/heat stress (HT) is one of most uncontrolled environmental setbacks, posing several devastating effects in plants (Wang et al. 2003; Teixeira et al. 2013). HT stress induces several detrimental effects on crop productivity by arresting numerous plant metabolic processes such as loss of turgor, carbon assimilation rate, leaf gas exchange and oxidative damage thereby leading to crop failure (Wahid et al. 2007; Bita and Gerats 2013). Plant responses to HT stress are very complex and depend on several factors such as severity and duration of HT stress and growth stage of plant, genetic potential of plant species and environmental factors (Angadi et al. 2000; Bita and Gerats 2013). HT stress alters enzymatic activity, leaf development, disruption of ion absorption, and ultimately causes losses in crop productivity (Kaplan et al. 2004; Wahid et al. 2007; Wahid 2007).

Numerous approaches and techniques have been described to ameliorate detrimental effects of HT stress in plants. Phyto-hormone application has been reported as the most effective and easily applicable approach to increase tolerance in plants under abiotic stress conditions (Anjum et al. 2011, 2016a; Singh et al. 2017; Chen et al. 2018). There is further evidence that exogenous application of plant growth regulators can enhance plant growth under different abiotic stresses such as heat stress, drought, heavy metal stress, as well as salt stress (Alcázar et al. 2010; Singh et al. 2017; Hussain et al. 2018). Brassinolides (BLs) are a very important class of phytohormones that play very crucial roles in plant metabolism (Kim et al. 2009; Mori and Yokota 2017). 24-epibrassinolide (EBL) is an active compound produced during BL biosynthesis and can stimulate different plant metabolic processes such as carbon assimilation, biosynthesis of nucleic acids, ROS metabolism and light harvesting (Bajguz 2000; Tanveer et al. 2018; Siddiqui et al. 2018b). In plants, EBL increases the activity of different enzymes required during photosynthesis (Wani et al. 2017). Besides its part in plant growth under normal conditions, EBL also exhibits stress relieving nature and helps plants to mitigate the adversities of abiotic stress conditions (Janeczko et al. 2011; Bajguz and Hayat 2009; Anjum et al. 2011; Yusuf et al. 2011; Shahzad et al. 2018; Tanveer et al. 2008).

✉ Mohsin Tanveer
Mohsin.tanveer@utas.edu.au

[1] School of Land and Food, University of Tasmania, Hobart, Australia

Under HT stress, EBL has showed very impressive results in enhancing growth and yield by playing an important role in plant metabolism; however, little information is available on the mechanism conferring EBL-induced thermo-tolerance in plants. In this review, the role of EBL in plant growth and yield, redox regulation, photosynthesis and chlorophyll fluorescence has been discussed. At the end, although little information is available, however, EBL-induced thermo-tolerance in plants by activating or stimulating heat shock proteins has also been discussed.

24-Epibrassinolide Biosynthesis

In plants, the exact mechanism of EBL biosynthesis has not been identified; however, EBL biosynthesis could be proposed via two pathways, including (1) the campestanol-dependent or (2) campestanol-independent pathway (reviewed in detail in Tanveer et al. 2018; Shimada et al. 2003; Fujioka et al. 2002; Kim et al. 2009). Briefly, in the campestanol-dependent pathway, campestanol is converted to castasterone either by the early C-6 oxidation pathway or late C-6 oxidation pathway. However, in the campestanol-independent pathway campestanol is converted into castasterone using 22α-hydroxycampesterol as substrate (Fig. 1). After castasterone production, it converts into brassinolide; however, it is unknown whether 24-brassinolide generates directly from castasterone or brassinolide. Future research is required to identify molecular or biochemical substrates for 24-epibrassinolide biosynthesis.

EBL Application and Plant Growth Response Under Heat Stress

Plant Growth and Yield

High temperature reduces plant growth and development significantly by reducing physical growth of plants. Major negative effects of high temperature in plants include scorching, delayed seed germination, retarded root growth, decreased pollen development and quality, which consequently reduce crop productivity (Vollenweider et al. 2005; Hasanuzzaman et al. 2013; Fahad et al. 2015). Moreover, HT stress decreases plant growth and development via altering the carbon assimilation rate, source-to-sink relationship and biomass production (Wahid et al. 2007). HT stress significantly reduces crop yield by reducing pollen viability, floret development, number of grains per spike, grain size and weight (Prasad et al. 2006; Wahid et al. 2007; Jagadish et al. 2009). Moreover Prasad et al. (2008) reported that HT stress delayed panicle emergence and decreased plant height, number of seeds per spike, seed yield and harvest index in sorghum.

High-temperature tolerance can be induced by exogenous application of EBL, as several previous studies indicated the potential role of EBL in alleviating different abiotic stresses (Yusuf et al. 2012, 2017; Sharma et al. 2013, 2015, 2017; Shahzad et al. 2018; Tanveer et al. 2018). EBL improves plant growth and yield under HT stress by improving numerous morphological and physiological traits (Fig. 2). EBL application significantly improves crop yield by improving

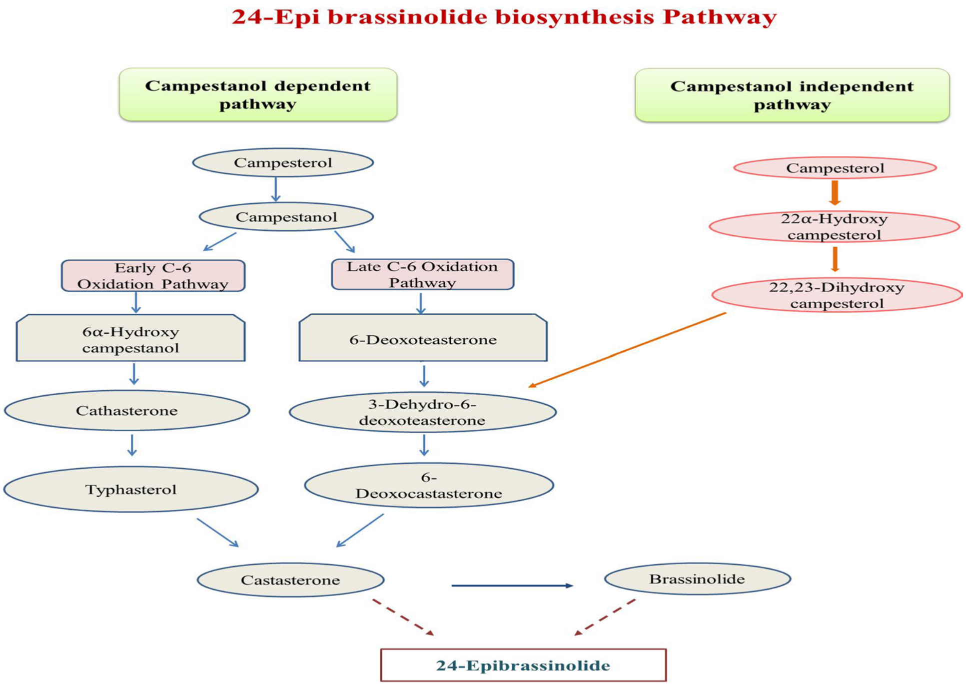

Fig. 1 Biosynthesis of EBL. It is still unknown whether the substrate for EBL is castasterone or brassinolide (dotted lines). However, it can be speculated from the above model that EBL might be produced by two pathways: (1) campestanol-dependent pathway or (2) campestanol-independent pathway (Kim et al. 2009; Tanveer et al. 2018)

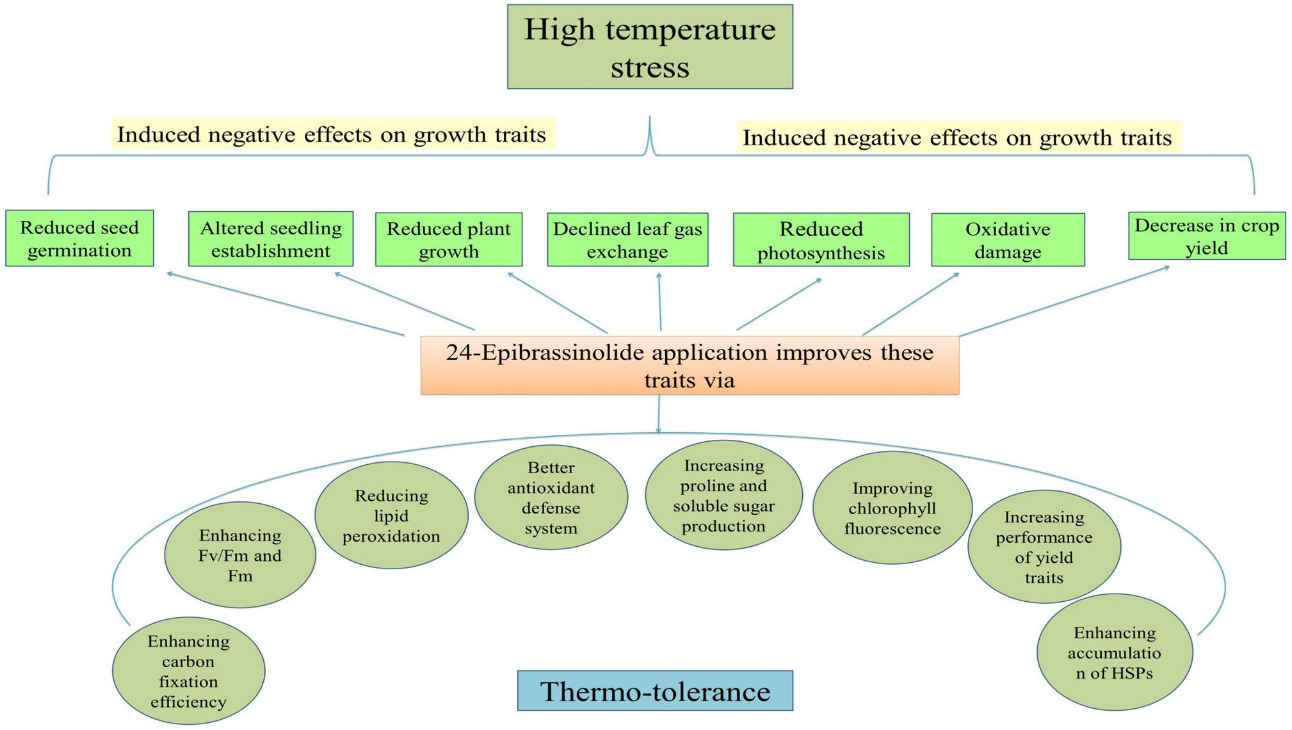

Fig. 2 24-Epibrassinolide application improves plant growth by improving the performance of numerous physiological traits

the development and performance of different yield-contributing traits. For instance, Wu et al. (2014) showed that under HT stress, growth and yield of egg plant was significantly reduced; however, EBL application improved plant height by 26%, stem diameter by 42% and root and shoot biomass by 43% and 55%, respectively. They further noted that improved growth of EBL-treated eggplant under HT stress was associated with higher photosynthesis and better photosynthetic apparatus. Thus, it can be suggested that EBL can improve plant growth under HT stress by improving the carbon assimilation process. Similarly, Zhang et al. (2013) showed that EBL application improved the fresh weight of shoots and roots in melon by improving the heat tolerance index (33–45%) and light harvesting and chlorophyll fluorescence. HT stress primarily reduces flowering and fruit setting in plants, and ultimately reduces crop yield (Wahid et al. 2007; Fahad et al. 2016). EBL application is found effective in improving fruit yield (160%) under HT stress Singh et al. 2005. Moreover, EBL-induced tomato yield enhancement was associated with better pollen germination, improved pollen tube growth with reduced pollen bursting and high number of fruits per plant under HT stress (Singh et al. 2005).

EBL also enhances plant growth under HT stress via enhancing the antioxidant defense system and accumulation of heat shock proteins. HT stress reduced the growth of rice; however, application of EBL induced thermo-tolerance in rice seedlings by improving antioxidant activity and by reducing lipid peroxidation (Cao and Hua 2008). Similar results have also been reported by Ogweno et al. (2008), who showed that EBL protects plants under HT stress by improving plant growth and the antioxidant defense system. Growth improvement due to EBL application could partially be associated with the role of BLs in the regulation of genes or enzymes important for cell wall enlargement, and the activities of sucrose synthase and cellulose synthase (Ashraf et al. 2010). Moreover, BLs are also involved in the modulation of the structure, plasticity and permeability of cell membranes under stress and non-stress conditions (Sasse 2003; Siddiqui et al. 2018a, b). Under osmotic stress, EBL improves seed germination and seedling growth (Vardhini and Rao 2003) and such improvement can also be associated with the role of EBL in cell elongation and division (Khripach et al. 2000; Catterou et al. 2001). Kartal et al. (2009) described a positive relationship between BL application and root growth via increased mitotic activity in *H. vulgare*. In conclusion, EBL application improves plant growth and yield by improving the carbon assimilation process and by protecting the carbon assimilation process from HT-induced oxidative damage.

Photosynthesis and Gas Exchange Traits

High-temperature (HT) stress significantly reduces the photosynthesis process by reducing leaf gas exchange and by decreasing the activity of different enzymes involved in photosynthesis. EBL on the other hand plays a very crucial role in protecting the carbon assimilation process from HT stress-induced detrimental effects (Table 1). Different studies documented different mechanisms behind EBL-induced enhancement in Pn under different abiotic stress conditions (Prasad et al. 2006; Lima and Lobato 2017; Shahzad et al. 2018; Tanveer et al. 2018); however, little information is available regarding EBL-induced improvement in Pn under HT stress. Singh et al. (2005) reported that under HT stress the carbon assimilation process was increased due to EBL-induced increase in Et and gs. Higher Et and gs due to EBL application might help in reducing the leaf temperature and performing different metabolic activities (Fariduddin et al. 2013). Numerous fatty acids and unsaturated lipids are also responsible for improving light harvesting in thylakoid membranes, thus improving the plant's ability to enhance photosynthesis under HT stress (Murakami et al. 2000). Loss of these compounds in the thylakoid membrane during HT stress results in the decline of Pn (Jajoo and Allakhverdiev 2017). Recently, it has been shown that by silencing the fatty acid desaturase gene, membrane stability and photosynthetic efficiency can be increased under heat stress (Hiremath et al. 2017). Moreover, reduction in Pn under HT stress is due to enhanced lipid desaturation, oxidation, acylation and damage of organelles (Djanaguiraman et al. 2018). EBL application can increase Pn by increasing the capacity of CO_2 assimilation in the Calvin cycle, and rubisco activity and by reducing ROS production (Yu et al. 2004).

In a study by Zhang et al. (2014), it was noted that EBL application increased Pn and gs but did not influence Ci, suggesting EBL improves Pn under HT stress only by reducing non-stomatal limitation to photosynthesis. However, under abiotic stresses such as salt stress, drought stress or heavy metal stress, EBL increased Pn by increasing both gs and Ci (Dubey 2005; Shahzad et al. 2018; Tanveer et al. 2018). Similarly, Xia et al. (2009) also reported that EBL application increased Pn but decreased Ci and thus suggesting that the CO_2 carboxylation capacity was a rate-limiting step in photosynthesis. Contrary to this, Wu et al. (2014) showed that EBL application at a low concentration (0.1 µM) increased gs and Ci; however, EBL application at higher concentrations (0.2 µM and 04 µM) decreased Ci only, and therefore it is not clear whether EBL improves Pn by increasing gs only or with Ci as well. Further studies are required to examine the dose-dependent response of EBL on these traits under HT stress. Plant species or other experimental conditions can also influence such responses; however, it would be more productive scientifically to identify molecular players for such responses.

In leaf mesophyll, there are six possible players that can influence photosynthesis under HT stress and EBL can improve them by interacting with (1) the availability of carbon metabolites, (2) photorespiration, (3) feedback control by carbohydrate metabolism, (4) improved efficiency of the photosynthetic carbon-fixation process and (5) scavenging of ROS via the activation of antioxidant activity, and (6) chlorophyll contents.

- *Availability of carbon metabolites* during Pn also governs the net assimilation rate (Paul and Pellny 2003). Under stress conditions, a significant reduction in these metabolites results in reduced Pn and plant productivity. EBL increases the accumulation of soluble sugars,

Table 1 Reported examples of EBL-mediated thermo-tolerance in plants by playing numerous roles in different physiological and biochemical processes

Effect of EBL on plant trait	Reported reasons how EBL influences these traits	References
Effects on photosynthesis and gas exchange		
	Enhanced rubisco activity	Xia et al. 2009; Wu et al. 2014; Zhang et al. 2013, 2014
Increase Pn	Up-regulation of genes responsible for enhanced photosynthesis	
Increase gs	Higher RCA transcript level	
Increase photosynthetic pigments	Higher gs	
	Higher chlorophyll content accumulation	
Effects on chlorophyll fluorescence		
	Higher Fv/Fm ratio	Li et al. 2009; Ogweno et al. 2008; Xia et al. 2009; Wu et al. 2014; Zhang et al. 2013, 2014
Better light quenching	Higher quantum yield of PSII	
Energy conversion	Higher photochemical quenching coefficient	
	Reduced non-photochemical quenching	
Effects on heath shock proteins		
Higher HSP production	EBL may signal to trigger HSP synthesis however mechanism is not known	Dhaubhadel et al. 2002; Singh and Shono 2005

starch or sucrose and improves Pn under stress and non-stress conditions (Yu et al. 2004; Xia et al. 2009). It is unknow how EBL interacts with the production or accumulation of these metabolites under HT stress.

- *Photorespiration*: Yu et al. (2004) observed Pn under photorespiratory conditions or non-photorespiratory conditions and found that EBR did not increase net photosynthetic rate by reducing photorespiration.
- *Feedback control*: One of the possibilities relating to EBL application and Pn improvement could be related to sugar-signal-induced feedback regulation (Paul and Foyer 2001). It is well reported that more Pn results in more translocation of carbohydrates and sugars to sink. Sink strength could be stimulated due to direct effects of enhanced substrate availability, and also through the stimulation of the expression of genes encoding enzymes involved in carbohydrate metabolism (Paul and Foyer 2001; Morris 2017). SchluÈter et al. (2002) compared the activity of the invertase enzyme and sucrose and starch contents in wild-type and mutant *Arabidopsis* and found that all these contents were lower in mutants as compared with wild type. Thus, it can be suggested that EBL may act as a signalling compound that gives feedback to plants to produce more sugar and carbohydrates under HT stress; however, the exact mechanism is still unknown.
- *Improved efficiency of photosynthetic carbon fixation*: EBL also enhances carbon-fixation efficiency by triggering the activities of enzymes involved in photosynthesis (Ali and Ashraf 2008; Ogweno et al. 2008). An extensive examination of numerous enzymes involved in carbon assimilation under HT stress was conducted and found that EBL induces positive effects on the activities of Rubisco, Rubisco carboxylation rates and total Rubisco activity (Xia et al. 2009). Moreover, EBL also up-regulates gene expression of different enzymes involved in ribulose 1,5 bisphosphate regeneration, thereby increasing the maximum carboxylation rate of Rubisco during the Calvin cycle (Xia et al. 2009). Rubisco activase (RCA) is involved in keeping RUBISCO in the active form. There are three subunits of RCA (38–39 kDa, 41–42 kDa, 45–46 kDa). The stability of the RCA structure depends on the interaction between different subunits, resulting in maintaining the initial Rubisco activity under a stressful environment in plants (Wang et al. 2010; Chen et al. 2015). Xia et al. (2009) showed that EBL increases the transcript levels of RCA and related subunits under HT stress and plays an important role in the regulation of the Rubisco activation state. In conclusion, EBL improves photosynthesis by improving the activities of numerous enzymes involved in the carboxylation reaction and metabolite accumulation.
- *ROS scavenging*: Under HT stress, production of reactive oxygen species can also reduce Pn by interfering with the activity of numerous enzymes. Nonetheless, EBL can help in scavenging ROS by activating the antioxidant defense system, thus increasing Pn under stress conditions (Tanveer et al. 2018). Ogweno et al. (2008) showed that EBL increased the activities of SOD, POD, CAT and APX and reduced MDA under HT stress. Such increment in antioxidant activity resulted in more protection of the carboxylation reaction under HT stress (Mazorra et al. 2002; Cao and Hua 2008)
- *Chlorophyll contents*: HT stress causes scorching in leaves and decreases total chlorophyll contents. Moreover, under severe HT stress conditions, production of ROS also damages the ultra-structure and biochemical composition of the photosynthetic apparatus, thus limiting Pn and plant productivity (Zhang et al. 2013, 2014; Tanveer et al. 2018). EBL has been reported as an effective stress reliever under HT stress as it somehow increases chlorophyll contents in plants. However, the exact molecular mechanism has not been identified for EBL-induced increases in chlorophyll contents in plants. According to Wu et al. (2014), EBL improves chlorophyll a, chlorophyll b and total chlorophyll contents by 17%, 27% and 20.08%, respectively. Similarly, Xia et al. (2009) reported that EBL application increased total chlorophyll contents under HT stress. Therefore, it can be suggested that EBL-induced increase in chlorophyll contents could be due to increased chlorophyll biosynthesis, which subsequently increases light harvesting and the carbon assimilation process. Several researchers who examined the effects of EBL on chlorophyll contents under different abiotic stress conditions (except HT stress) also suggested that increased chlorophyll contents due to EBL application could be/are associated with (1) down-regulation of the chlorophyllase encoding gene, (2) chlorophyll biosynthesis at transcriptional and translational levels, and (3) recovery of the shape and performance of chloroplasts (Mir et al. 2015a, b; Abd Allah et al. 2018; Dong et al. 2017; Gupta et al. 2017; Wani et al. 2017).

Chlorophyll Fluorescence

HT stress significantly reduces chlorophyll fluorescence by altering and disrupting light harvesting, energy conversion, and most importantly reduces the activity of PSII (Wahid et al. 2007; Allakhverdiev et al. 2008). EBL can improve chlorophyll fluorescence by acting in different ways (Table 1). Under HT stress, EBL reduces the negative effects of HT stress on Fv/Fm and Fm of plants (Zhang et al. 2014). Enhancement in Fv/Fm and Fm might be due to the positive effects of EBL on the PSII (reaction center) and reduction in the negative effects of photo-inhibition phenomenon

(Maxwell and Johnson 2000; Zhang et al. 2014). EBL is also involved in the improvement of ΦPSII, ETR and qP values in stress-treated plants (Hayat et al. 2011). Enhancement in qP and ETR is also important as these are involved in higher energy absorption of photons as well as enhanced energy flow, required for electron excitation needed by plastoquinone (Buonasera et al. 2011). EBL also enhances the harvesting of light energy by affecting the open PSII reaction centers (Li et al. 2015). Ribeiro et al. (2009) reported that in plants treated with EBL, there was a decline in the NPQ, EXC and ETR/Pn. This decline in these parameters was associated with less non-photochemical energy. Less quenching may also be due to the photorespiration and photo-reduction in response to EBL application (Silva et al. 2011; Barbosa et al. 2014). Moreover, EBL also affects gas exchange parameters and fluorescence of chlorophyll which may also cause decline in ETR/Pn values in plants (Lima and Lobato 2017). High light harvesting capacity of PSII after EBL application results in the reduction of NPQ as well as EXC values (Silva et al. 2012).

In another study, Hayat et al. (2010) suggested that EBL-induced increase in PSII activity might be associated with decline in the inhibition of electron flow at the oxidizing site of PS II. NPQ is closely linked with increasing extra energy dissipation via a non-radiative process, which ultimately protects the photosynthetic apparatus also regarded as photoprotection (Nama et al. 2018). EBL application decreases NPQ, which results in less dissipation of excitation energy in the PSII antennae under HT stress (Zhang et al. 2013). Thus, it can be suggested that EBL can protect PSII from over excitation and thylakoid membranes from HT-induced damage (Ogweno et al. 2008; Janeczko et al. 2011). Moreover, EBL-induced increase in PSII activity might also be associated with increased carboxylation efficiency resulting from a downstream regulating mechanism, and the increase in qP can be attributed to an increase in the rate of reduced ATP consumption during non-cyclic electron transport relative to the rate of excitation of open PSII reaction centers and increase in Fv/Fm to the less dissipation of excitation energy in the PSII antennae (Wu et al. 2014; Liu et al. 2009). Thus, it can be concluded that EBL increases PSII activity by improving quantum efficiency of PSII and photochemical quenching.

EBL Application and Redox Regulation in Plants Under HT Stress

EBL Application and Antioxidant Defense System

HT stress disturbs the balance between ROS accumulation and antioxidative defense system of plants causing oxidative damage and ultimately reducing crop yield (Wahid et al. 2007; Yu et al. 2004). These ROS generally include superoxide anions, hydroxyl ions and hydrogen peroxide, which cause lipid peroxidation and electrolyte leakage, resulting in the disturbance of normal cell function (Anjum et al. 2016b, 2017; Tanveer and Shabala 2018). To cope with these ROS, the plant antioxidant defense system effectively scavenges ROS and converts them into H_2O or O_2. Nonetheless, under severe stress conditions, enhanced activities of antioxidative enzymes alone are insufficient to protect plant cells from the negative effects of ROS generated under HT stress conditions (Talaat et al. 2015). In this context, the role of BLs has been extensively documented in triggering the antioxidant defense system and ROS scavenging under HT and other abiotic stress conditions (Lima and Lobato 2017; Shahzad et al. 2018; Sharma et al. 2018; Tanveer et al. 2018). EBL is an active brassinolide and plays a very crucial role in triggering the antioxidant defense system under HT stress. In eggplant, EBL application significantly increased the activity of SOD (30%), POD (103%), CAT (68%), and APX (22%) and decreased H_2O_2 by 42% and MDA by 15% (Wu et al. 2014). Moreover, Zhang et al. (2014) showed that EBL application increased SOD, POD, CAT and APX by 13%, 59%, 95% and 33%, respectively, under HT stress. This highlighted the lifesaving role of EBL in scavenging ROS and plant survival under HT stress. Moreover, it can also be suggested that EBL-induced high antioxidant activity might be due to higher de novo synthesis of enzymes, or the up-regulation of transcription and translation of stress-responsive genes (Bajguz 2000). It is however still unclear how EBL regulates the antioxidant defense system (Cao et al. 2008).

Since enhanced lipid peroxidation reduces the photosynthetic efficiency of plants (Ye et al. 2016), EBL application helps in the recovery of photosynthesis by reducing the MDA content (Lima and Lobato 2017; Ogweno et al. 2008). The reduction in the ROS like hydrogen peroxide after EBL application might be due to the BR-mediated regulation of the expression of the gene (*RBO*) involved in the production of hydrogen peroxide (Sharma et al. 2017). EBL downregulates the expression of *RBO* which may be another reason behind less production of hydrogen peroxide after EBL application (Sharma et al. 2017). Bajguz (2000) suggested that increase in the activities of various enzymatic antioxidants after EBL application is due to the BR-mediated transcription/translation of genes involved in the antioxidative defense system. Along with enzymatic antioxidants, EBL also increases the activity of some non-enzymatic antioxidants such as AsA and GSH (Wu et al. 2014). AsA converts superoxide anions and hydrogen peroxide into MDHA/DHA (De Gara et al. 2000). EBL regulates the activities of enzymes involved in the AsA-GSH cycle, resulting in maintaining the redox state of ascorbate and hence enhances HT stress tolerance in plants (Wu et al. 2014). GSH is also involved in scavenging of ROS via the AsA-GSH cycle

(Foyer and Noctor 2011). Under drought conditions, the GSH/GSSG ratio decreases but EBL positively regulates the GSH/GSSG ratio in plants grown in water-deficit conditions (Liu et al. 2009). They suggested that some amount of GSH might have been involved in maintaining the redox state and ultimately in helping the quenching of hydrogen peroxide, which results in boosting the cellular defense system.

EBL Application and Osmolyte Accumulation

Under HT stress conditions, various solutes like proline, glycine-betaine, sugars and phenolic compounds accumulate in plant cells to increase resistance in plants to cope with HT stress-induced detrimental effects (Farooq et al. 2009; Dobra et al. 2010; Chen et al. 2018). EBL can improve thermo-tolerance in plants by increasing osmolyte accumulation. Proline is known to help plants under stress conditions as it acts as an important membrane stabilizer as well as scavenger of harmful free radicals (Fariduddin et al. 2013). BL application triggers the synthesis of proline in plant cells under stress conditions (Farooq et al. 2009; Chen et al. 2018). It has been shown that BL application enhances the proline accumulation by stimulating Δ^1-Pyrroline-S-carboxylate synthase, which is the key enzyme of the proline biosynthetic pathway (Sharma et al. 2011). Proline is also involved in the protection of the cell membrane, structure of proteins and prevention of degradation of enzymes, accompanied by reduction in cell damage due to dehydration (Singh et al. 2018). Additionally, BL-regulated proline accumulation also plays an important role in maintaining water contents of plant tissues (Anjum et al. 2011). Wu et al. (2014) reported that EBL application increased proline by 87% and soluble sugars by 34% under HT stress. This is suggesting that EBL-induced increase in proline accumulation could be associated with reduced proline utilization, limited degradation of proline and increased proline biosynthesis (Shahid et al. 2011).

HT stress also has a negative impact on the protein biosynthesis of plants (Wahid et al. 2007) and this might be due to the reduction in energy supply resulting in the hindrance of photosynthetic efficiency and other biochemical pathways (Rahman et al. 2004). However, exogenous EBL application resulted in the recovery of protein content by 30% under HT stress (Wu et al. 2014). Phenolic compounds are also involved in the protection of plants under abiotic stress conditions by protecting non-photosynthetic membranes from harmful ROS (Blokhina et al. 2003; Wahid 2007). Glycine-betaine (GB) in plants under stressful conditions is involved in maintaining membrane structures, decreasing lipid peroxidation, scavenging of free radicals and maintaining cellular structures as well as cellular-redox-potentials (Ashraf and Foolad 2007; Kurepin et al. 2017). GB also enhances the plant resistance to HT stress and is involved in mechanisms that help in the prevention of water loss through osmotic adjustments. Moreover, EBL application also enhances the accumulation of GB by regulating the process of GB biosynthesis (Talaat et al. 2015). Sugars are also one of the most important osmolytes, involved in protection of plant cells from oxidative damage, and exogenous application of EBL further enhances sugar levels in plants under stress conditions, resulting in higher tolerance in plants under stress (Yu et al. 2004; Wu et al. 2014).

EBL Application and Heat Shock Proteins

Under HT stress, ROS along with acting as oxidizing agents also act as signalling compounds that may also signal plants to initiate the defense system. These ROS transduce heat signals and assist in the activation and expression of heat shock genes and heat shock proteins (Königshofer et al. 2008). HT stress causes mis-folding and denaturation of numerous proteins and enzymes. As a stress defense strategy, plants produce HSPs which not only control cellular signalling and protein synthesis but also play crucial roles in preventing proteins from denaturation and mis-folding. Under HT stress, plants significantly increase HSP production and accumulation to enhance thermo-tolerance (Nover et al. 2001); however, variations exist in HSP production among different plant species and under different experiment conditions.

Under HT stress, it has been shown that BL-induced thermo-tolerance in tomato and brassica was due to high expression and production of HSPs and such increases in HSPs were due to higher synthesis of HSPs (Dhaubhadel et al. 1999). Similarly, Singh et al. (2005) reported that EBL increased expression of HSPs under elevated temperature regime and these HSPs were responsible for improving photosynthesis and growth of tomato under HT stress. Dhaubhadel et al. (2002) showed that EBL application increased the accumulation of four major classes of HSPs under HT stress. They also noted enhanced accumulation of HSPs in EBL-treated seedlings, and this was due to higher HSP synthesis, even when the mRNA levels were lower in EBL-treated seedlings, which is suggesting that EBL can prevent the loss of the functionality of translational apparatus under HT stress, and also can increase the expression of some TFs from the translational machinery, which may correlate with a more rapid resumption of cellular protein synthesis process under HT stress. These results were verified by using BR-deficient *Arabidopsis* mutant EBL-treated plants accumulated high levels of HSPs and thus increases thermo-tolerance in *Arabidopsis* (Kagale et al. 2007).

Studies have shown that EBL has the ability to induce thermo-tolerance in plants (Table 1) by different ways but exact mechanisms have yet to be examined. Studies relating to EBL application under other abiotic stress tolerance are suggesting complex transcriptional and translational reprogramming occurs in EBL-treated plants under stress conditions; however, this has never been studied in HT stress. Therefore, future research should be focused on identifying EBL-mediated thermo-tolerance in plants at the molecular level.

Conclusion

Application of EBL can improve the thermo-tolerance in plants by playing different roles in different physiological and biochemical processes. Studies showed that EBL plays a crucial role as a heat protector and improves yield by improving the development and performance of different yield-contributing traits such as pollen development, pollen germination, root and shoot biomass production. Under HT stress, EBL application also protects plants from HT-induced oxidative damage by activating ROS scavenging enzymes and by increasing the accumulation of different compatible solutes (especially proline). Moreover, under HT stress, EBL application increases Pn by improving leaf gas exchange, chlorophyll contents and light harvesting. Beside all these, EBL also acts as a signalling molecule and signals plants to produce heat shock proteins as a defensive strategy to cope with HT stress. Future research is required to reveal the molecular players behind all EBL-mediated processes in plants under HT stress.

Compliance with Ethical Standards

Conflict of interest The author has no conflicts of interest to disclose.

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