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## SOIL & CROP SCIENCES | REVIEW ARTICLE

# Brassinosteroid-mediated pesticide detoxification in plants: A mini-review

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**Abstract:** To protect crops from pests, pesticides are used. Pesticides also cause toxicity to crop plants and persist in plant parts in the form of pesticide residues. Brassinosteroids (BRs) are known for their protective role in plants under various abiotic stresses like heavy metal, drought, temperature, pesticide etc. BRs ameliorate pesticide toxicity in intact plants by activating the antioxidative defence system. BRs also enhance the degradation of pesticides that leads to reduction in pesticide residues in plant parts. Present review gives an updated information about the protective roles of BRs in plants and the underlying mechanisms under pesticide stress.

**Subjects:** Agriculture & Environmental Sciences; Botany; Plant Biology

**Keywords:** brassinosteroids; pesticide detoxification; pesticide residues; oxidative stress; antioxidative defence system

### 1. Introduction

Plants are attacked by various pests, resulting in reduction of yield as well as the quality of crops, and to check these pests, various pesticides are utilized (Goh, Yiu, Wong, & Rajan, 2011). However, the extensive use of pesticides may cause toxicity to plants which may impair the plant metabolism and may persist in plant parts in the form of pesticide residues (Table 1, Sharma, Bhardwaj, Kumar, & Thukral, 2016; Xia et al., 2009; Zhou et al., 2015). Plants detoxify pesticides by enzyme mediated three phased detoxification system (Cherian & Oliveira, 2005; Coleman, Blake-Kalff, & Davies, 1997). First of all the activation of pesticides is catalysed by enzymes P450 monooxygenase, peroxidase and carboxylesterase. After this, conjugation of activated pesticides to glutathione and glucose is catalysed by glutathione-S-transferase and UDP-glycosyltransferase respectively. Finally less toxic pesticide metabolites are stored in the vacuoles/apoplast.

Brassinosteroids (BRs) are plant polyhydroxysteroids which were discovered by Grove et al. (1979). BRs are distributed throughout the plant kingdom and are present in small concentrations in young plant parts including the pollens (Clouse & Sasse, 1998; Gupta, Bhardwaj, Nagar, & Kaur, 2004; Kanwar, Poonam, & Bhardwaj, 2015). Approximately sixty types of BRs have been identified (Haubrick & Assmann, 2006), out of which 24-epibrassinolide (EBR,  $C_{28}H_{48}O_6$ , Figure 1) and

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Anket Sharma is working as an assistant professor in DAV University, Jalandhar, India. He has done his MSc, MPhil, and PhD in Botany from Guru Nanak Dev University, Amritsar, India. His area of research is plant stress physiology and has expertise in GC-MS and statistical analysis. He has more than 50 articles/chapters in journals/books of national and international repute.

### PUBLIC INTEREST STATEMENT

Pesticides are used all over the world to protect crops from pests. However pesticides also cause toxicity to plants and accumulate in plant parts in form of pesticide residues. Brassinosteroids are plant hormones which help in protection of plants from pesticide toxicity and reducing the harmful pesticide residues. Present review describes how exogenous application of brassinosteroids reduces pesticide toxicity and residues in plants.

**Table 1.** Persistence of pesticides in various plant parts

Pesticide	Plant	Application mode	Concentration (pesticide applied)	Plant part analyzed	Time after treatment (Days)	Residues detected (mg Kg <sup>-1</sup> )	References	
Acetamiprid	<i>Brassica juncea</i> L.	Spray	40 g ai ha <sup>-1</sup>	Young plant	1	0.42	Pramanik, Bhattacharya, Dutta, Dey, and Bhattacharyya (2006)	
					7	0.01		
Atrazine	<i>Capsicum annuum</i> L.	Spray	40 g ai ha <sup>-1</sup>	Fruits	1	0.03	Sanyal, Chakma, and Alam (2008)	
					7	0.009		
					2	2.94	Zhang, Lu, Zhang, Tan, and Yang (2014)	
						6		4.26
β-Cyfluthrin	<i>Cajanus cajan</i> L.	Spray	25 g ai ha <sup>-1</sup>	Green pods	1	13.73	Mukherjee, Gopal, and Mathur (2007)	
					10	3.45		
					1	5.98		
					10	1.22		
					1	0.57		Chahil, Mandal, Sahoo, Battu, and Singh (2014)
					5	0.06		
Chlorpyrifos	<i>Solanum melongena</i> L.	Spray	36 g ai ha <sup>-1</sup>	Leaves	1	0.26	Sinha and Gopal (2002)	
					5	0.10		
					1	0.23		
					7	0.11		
					1	0.08		Mandal, Chahil, Sahoo, Battu, and Singh (2010)
					5	0.01		
Cypermethrin	<i>Capsicum annuum</i> L.	Spray	1,000 g ai ha <sup>-1</sup>	Fruits	1	1.30	Jyot, Mandal, Battu, and Singh (2013)	
					7	0.47		
Deltamethrin	<i>Brassica oleracea</i> L. var. Snowball 16	Spray	100 g ai ha <sup>-1</sup>	Heads	1	0.86	Singh, Singh, and Battu (1990)	
					3	0.08		
					1	0.35		
					3	0.08		
Deltamethrin	<i>C. annuum</i> L.	Spray	100 g ai ha <sup>-1</sup>	Fruits	1	0.28	Jyot et al. (2013)	
					7	0.12		
					1	0.13		Singh et al. (1990)
					2	0.06		
Deltamethrin	<i>B. oleracea</i> L. var. Snowball 16	Spray	24 g ai ha <sup>-1</sup>	Heads	1	0.09	Singh et al. (1990)	
					2	0.04		

(Continued)

**Table 1. (Continued)**

Pesticide	Plant	Application mode	Concentration (pesticide applied)	Plant part analyzed	Time after treatment (Days)	Residues detected (mg Kg <sup>-1</sup> )	References
Fenvalerate	<i>B. oleracea</i> L. var. Snowball 16	Spray	100 g ai ha <sup>-1</sup>	Heads	1	1.07	Singh et al. (1990)
				Leaves	3	0.25	
				Leaves	1	0.25	
Flubendiamide	<i>Abelmoschus esculentus</i> L.	Spray	48 g ai ha <sup>-1</sup>	Fruits	3	0.03	Das, Mukherjee, and Das (2012)
				Fruits	1	0.41	
				Fruits	5	0.21	
Fipronil	<i>Brassica oleracea</i> L.	Spray	48 g ai ha <sup>-1</sup>	Head	1	0.41	Mohapatra et al. (2010)
				Leaves	7	0.19	
				Leaves	1	0.86	
Imidacloprid	<i>Cicer arietinum</i> L.	Spray	96 g ai ha <sup>-1</sup>	Leaves	5	0.22	Singh et al. (2011)
				Pods	1	0.61	
				Pods	5	0.10	
Fipronil	<i>Cucumis anguria</i> L.	Spray	120 g ai ha <sup>-1</sup>	Fruits	1	1.03	Paramasivam, Selvi, and Chandrasekaran (2014)
				Fruits	7	0.15	
				Fruits	1	0.31	
Fipronil	<i>Lycopersicon esculentum</i> L.	Spray	100 g ai ha <sup>-1</sup>	Fruits	5	0.10	Paramasivam and Banerjee (2012)
				Fruits	1	0.08	
				Fruits	3	0.02	
Fipronil	<i>C. annuum</i> L.	Spray	80 g ai ha <sup>-1</sup>	Fruits	1	1.01	Kooner, Sahoo, Singh, and Battu (2010)
				Fruits	7	0.50	
				Fruits	1	0.02	
Imidacloprid	<i>Saccharum officinarum</i> L.	Seed	300 g ai ha <sup>-1</sup>	Leaves	1	0.66	Mandal and Singh (2014)
				Leaves	7	0.16	
				Leaves	45	0.16	
Imidacloprid	<i>Beta vulgaris altissima</i> D.	Seed	900 µg <sup>-1</sup> seed	Leaves	21	15.2	Westwood, Bean, Dewar, Bromilow, and Chamberlain (1998)
				Leaves	97	0.5	
				Leaves	49	1.3	
Imidacloprid	<i>Brassica campestris</i> L.	Spray	40 g ai ha <sup>-1</sup>	Herbage	97	0.08	Kumar and Dikshit (2001)
				Herbage	1	1.86	
				Herbage	15	0.17	
Imidacloprid	<i>Brassica campestris</i> L.	Seed	10 g ai Kg <sup>-1</sup> seed	Herbage	30	5.39	Kumar and Dikshit (2001)
				Herbage	82	0.33	
				Herbage	82	0.33	

(Continued)

**Table 1. (Continued)**

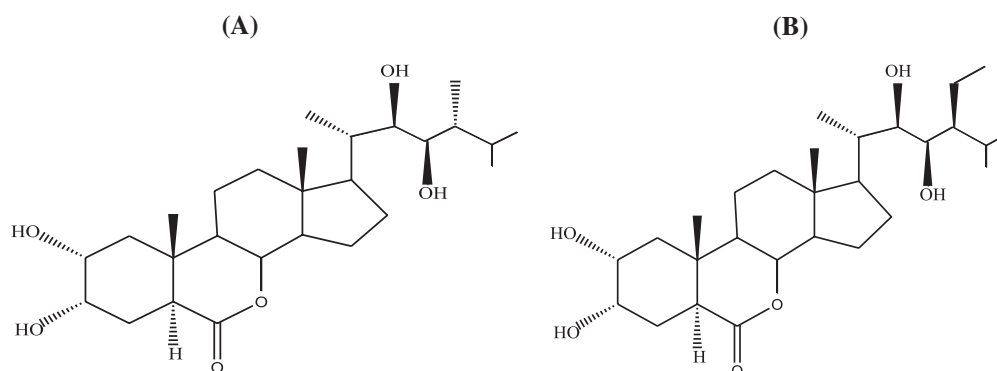
Pesticide	Plant	Application mode	Concentration (pesticide applied)	Plant part analyzed	Time after treatment (Days)	Residues detected (mg Kg <sup>-1</sup> )	References
	<i>B. juncea</i> L.	Spray	40 g ai ha <sup>-1</sup>	Leaves	1	2.98	Mukherjee and Gopal (2000)
					10	0.90	
	<i>B. oleracea</i> L. var. capitata	Spray	40 g ai ha <sup>-1</sup>	Leaves	1	6.14	
					10	0.97	
	<i>B. oleracea</i> L. var. Golden acre	Spray	40 g ai ha <sup>-1</sup>	Leaves	2	0.18	Gajbiye, Gupta, and Gupta (2004)
					5	0.03	
	<i>B. oleracea</i> L. var. Ketki	Spray	40 g ai ha <sup>-1</sup>	Leaves	2	0.32	
					5	0.03	
	<i>C. aretium</i> L.	Spray	84 g ai ha <sup>-1</sup>	Curd	2	0.57	
					5	0.12	
		Spray		Leaves	1	0.72	Chahil et al. (2014)
					5	0.34	
		Spray		Pods	1	0.30	
					5	0.07	
	<i>Cucumis sativus</i> L.	Spray	60 g ai ha <sup>-1</sup>	Fruits	1	2.54	Hassanzadeh, Esmaili Sari, and Bahramifar (2012)
					7	1.01	
		Spray	125 g ai ha <sup>-1</sup>	Fruits	1d	0.37	Nasr, Abbassy, Marzouk, and Mansy (2014)
					15	0.03	
	<i>L. esculentum</i> L.	Spray	100 g ai fe <sup>-1</sup>	Leaves	1	2.35	Romeh, Mekky, Ramadan, and Hendawi (2009)
					7	0.76	
		Spray		Fruits	1	0.58	
					7	0.25	
	<i>Oryza sativa</i> L.	Spray	80 g ai ha <sup>-1</sup>	Leaves	7	9.40	Akoiyam and Singh (2014)
					45	0.59	
	<i>Punica granatum</i> L.	Spray	54 g ai ha <sup>-1</sup>	Peel	1	0.33	Kadam, Deore, and Umate (2014)
					7	0.11	
		Spray		Whole fruit	1	0.25	
					7	0.05	

(Continued)

**Table 1. (Continued)**

Pesticide	Plant	Application mode	Concentration (pesticide applied)	Plant part analyzed	Time after treatment (Days)	Residues detected (mg Kg <sup>-1</sup> )	References
Penconazole	<i>Saccharum officinarum</i> L.	Soil	80 g ai ha <sup>-1</sup>	Leaves	7	12.99	Sharma and Singh (2014)
					45	2.37	
	<i>Solanum melongena</i> L.	Spray	84 g ai ha <sup>-1</sup>	Fruits	1	0.25	Mandal et al. (2010)
					5	0.13	
					1	2.37	
	<i>Vitis vinifera</i> L.	Spray	160 g ai ha <sup>-1</sup>	Fruit	10	0.37	Mukherjee and Gopal (2000)
					1	1.02	
	<i>Zea mays</i> L.	Seed	1.0 mg <sup>-1</sup> seed	Roots	45	0.29	Mohapatra et al. (2011) Donnarumma et al. (2011)
					60	0.12	
					45	0.013	
60					0.005		
45					0.008		
Profenofos	<i>Lycopersicon esculentum</i> L.	Spray	10 g ai fe <sup>-1</sup>	Leaves	60	0.006	Romeh et al. (2009)
					1	1.22	
					7	0.50	
					1	0.17	
					7	0.12	
					1	26.06	
Tetraconazol	<i>L. esculentum</i> L.	Spray	540 g ai fe <sup>-1</sup>	Leaves	7	0.33	Romeh et al. (2009)
					1	3.47	
					7	1.28	
					1	0.10	
Thiocloprid	<i>Cucumis sativus</i> L.	Spray	50 g ai ha <sup>-1</sup>	Fruits	11	0.002	Nasr et al. (2014)
					1	0.14	
					3	0.05	

**Figure 1. Structure of 24-epibrassinolide (A) and 28-homobrassinolide (B).**



28-homobrassinolide (HBR,  $C_{29}H_{50}O_6$ , Figure 1) have been widely used for physiological studies (Vardhini & Anjum, 2015). BRs are reported to play an important role for the recovery of plants under abiotic stress conditions like salts, heavy metals and pesticides by activating the antioxidative defence system of the plants (Bajguz, 2009; Krishna, 2003; Shahzad et al., 2018; Sharma, Bhardwaj, & Pati, 2015; Sharma, Kumar, Thukral, & Bhardwaj, 2016). Additionally, exogenous application of BRs has also been observed to enhance the activities of enzymes involved in three phased pesticide detoxification system mentioned above (Xia et al., 2009; Zhou et al., 2015). BRs also modulate the expression of genes involved in pigment and secondary metabolite biosynthesis under pesticide stress (Sharma, Thakur, et al., 2016). Keeping in mind about the role of BRs in pesticide stress management, the present review explains BR-regulated pesticide detoxification in plants.

## 2. Climatic/environmental factors and BRs

The main factor which is an integral part of climate change is the  $CO_2$  concentration in the environment. It is believed that  $CO_2$  interacts with BRs, resulting in the regulation of plant growth. Interaction between  $CO_2$  and BRs increase the plant growth, sugar and starch contents, and regulates various the activities of enzymes involved in various photosynthetic and Benson-Calvin cycle by regulating the genes encoding them in cucumber. These genes encodes various enzymes include ribulose-1,5-bisphosphate carboxylase/oxygenase, ribulose-1,5-bisphosphate carboxylase/oxygenase activase, sedoheptulose-1,7-bisphosphatase), ribulose-5-phosphate kinase, triose-3-phosphate isomerase, glycerate-3-phosphate kinase, fructose-1,6-bisphosphatase (Jiang et al., 2012). Environmental factors like light and temperature are involved in the regulation of gene expression in tobacco plants after interacting with BRs. There exist a direct interaction between BR-activated transcript factor (BZR1), and dark and heat transcription factor i.e. phytochrome interacting factor 4 (PIF4). This interaction after perceiving environmental signals is responsible for the regulation of various genes involved in modulation of plant metabolism to regulate these climatic factors (Oh, Zhu, & Wang, 2012). It has been noticed that BRs produced under Ni heavy metal stress, further enhanced the resistance of mustard plants. They regulated the antioxidative defense system of plants to counter-attack the toxicity of heavy metals (Kanwar et al., 2012). Arsenic toxicity has also been reported to regulate the biosynthesis of BRs in mustard plants (Kanwar et al., 2015). Under other climatic conditions like drought, BRs interact with other plant growth regulators (PGRs) to regulate biochemical processes of plants (Yuan et al., 2010). Moreover, crosstalk of BRs with other PGRs like auxins, abscisic acid, cytokinins, ethylene, gibberellins, salicylic acid etc. is also responsible for BR-mediated regulation of various plant metabolic processes (Choudhary, Yu, Yamaguchi-Shinozaki, Shinozaki, & Tran, 2012).

Pesticides are absorbed by plants through roots or leaf surface. There are many environmental factors like temperature, precipitation and physiochemical characteristics of soil, which affect the uptake of pesticides and their metabolism in plants (Finlayson & MacCarthy, 1973). These absorbed pesticides may get metabolized by the internal detoxification system of plants or they get accumulated in various plant parts resulting in pesticide bio-magnification (Mwevura, 2000). Since BRs are known to protect plants from various environmental factors like temperature, drought, soil-salt

toxicity, soil-metal toxicity (El-Mashad & Mohamed, 2012; Farooq, Wahid, & Basra, 2009; Kanwar et al., 2012; Khan, Fariduddin, & Yusuf, 2015), it may be attributed that BRs can provide resistance to plants under pesticide stress accompanied by various other environmental factors.

### 3. Pesticide toxicity in plants

Pesticides cause toxicity to plants by means of chlorosis, necrosis and vein discoloration, leading to retarded growth and development by reducing photosynthetic efficiency, nitrogen and carbon metabolism (Kaňa et al., 2004). Pesticide application was also reported to inhibit photosynthesis by negatively affecting the plant photosystems (Xia et al., 2006). In rice seedlings, imidacloprid and chlorpyrifos were reported to reduce the root length, shoot length, fresh weight and protein content. These pesticides were also reported to degrade the chlorophyll pigment (Sharma, Bhardwaj, & Pati, 2012, 2013). Sharma et al. (2015) reported that imidacloprid and chlorpyrifos cause oxidative stress to rice seedlings by generating reactive oxygen species (ROS) like superoxide anions and hydrogen peroxide ( $H_2O_2$ ). In tomato plants, Zhou et al. (2015) also reported the enhanced levels of  $H_2O_2$  after the application of chlorothalonil pesticide. Moreover, NADPH oxidases are involved in the production of reactive oxygen species (Kaur, Sharma, Guruprasad, & Pati, 2014). Additionally, *RBOH1* (respiratory burst oxidase homologue 1) has been reported to regulate the levels of  $H_2O_2$  in tomato plants under pesticide stress (Zhou et al., 2015). In cucumber plants, phytotoxic effects of various pesticides were studied by Xia et al. (2006). They observed that application of pesticides negatively affects the photosynthetic machinery of cucumber plants, resulting in reduced photosynthetic rate ( $P_n$ ), stomatal conductance ( $G_s$ ) and intercellular  $CO_2$  ( $C_i$ ). These researchers also reported the inhibitory effects of pesticides on quantum efficiency ( $F_v/F_m$ ) as well as quantum efficiency ( $\Phi$ ) of PS II. Siddiqui and Ahmed (2006) studied the effect of six different pesticides (topsin-M, demacron, benlate, cypermethrin, dimethrithide and chlorosulfuron) on soybean plants. They found that at higher concentrations (0.5 and 0.75 g  $L^{-1}$ ), these pesticides cause declined relative growth rate and crop growth rate. Reduced total phenol and ascorbic acid contents in potatoes were observed after the application of imidacloprid pesticide (Chauhan, Agrawal, & Srivastava, 2013). Application of pesticides (mancozeb, flusilazol, dithianon, pirimicarb) on apple tree was reported to inhibit the photosynthesis (Untiedt & Blanke, 2004). In mustard plants reduction in photosynthesis was noticed by Sharma, Kumar, Singh, Thukral and Bhardwaj (2016) after imidacloprid insecticide application. In *Saccharina japonica*, application of diuron pesticide resulted in retarded growth, decreased carotenoid and chlorophyll content, optimal quantum yield and maximum electron transport rate (Kumar, Choo, Yea, Seo, & Han, 2010). Studies carried out by Sharma, Kumar, Kohli, Thukral, and Bhardwaj (2015a), Sharma, Kumar, Singh, Thukral, and Bhardwaj (2015b) reported the decreased levels of various phytochemicals after the application of imidacloprid pesticide in *Brassica juncea* plants. In response to pesticide toxicity, plants have the mechanism to detoxify pesticides, discussed already in introduction. Additionally, recent studies carried out by Huang, Lu, Zhang, Luo, and Yang (2016) demonstrated that laccase encoding genes in rice were involved in the degradation of atrazine and isoproturon. They also reported that laccase activity was increased in pesticide treated plants, in comparison to control plants, which confirmed the possible role of laccases in pesticide detoxification. Lu et al. (2016) reported the role of DNA methylation in the detoxification of atrazine in rice by regulating the genes like *CYP70IA8*.

### 4. Physiological and abiotic stress protecting roles of BRs

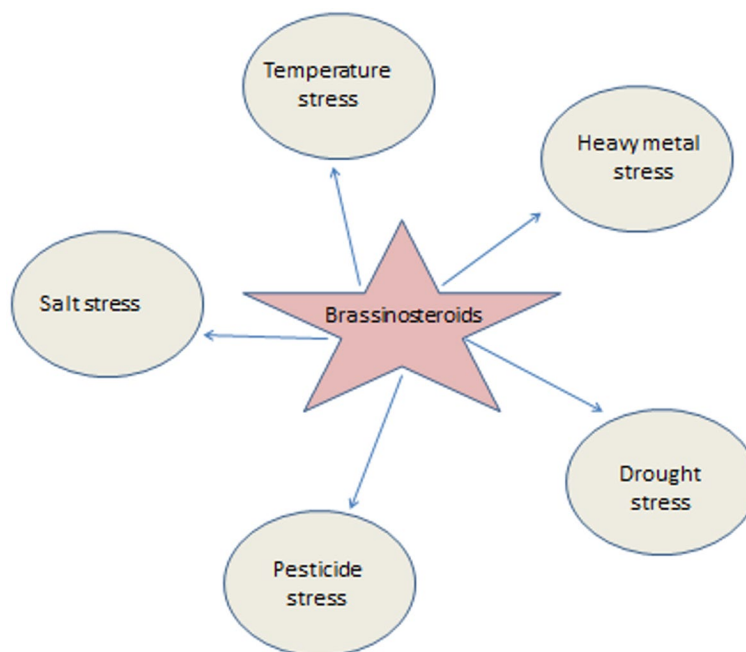
Important roles played by BRs in physiology of plants include process of cell elongation and differentiation, development of pollen tube, differentiation of vascular bundles, reassembling of nucleic acids resulting in protein formation, activation of antioxidative defense system of plants and regulation of photosynthesis (Sasse, 2003; Sharma et al., 2015; Xia et al., 2006; Yu et al., 2004). In dicots, BRs are reported to enhance the elongation of epicotyles, hypocotyls and peduncles, whereas in monocots, they increase the elongation of coleoptiles and mesocotyls (Clouse, 1996; Mandava, 1988).

BRs like EBR and HBR have been observed to play an important role in promotion of seed germination (Sasse, Smith, & Hudson, 1995; Sharma & Bhardwaj, 2007). The percentage of germination was observed to increase in *Cicer arietinum* and *Triticum aestivum* after seed application of HBR (Ali, Hayat, & Ahmad, 2005; Hayat & Ahmad, 2003). Increase in yield, carbonic anhydrase activity and net photosynthetic rate was observed when HBR was applied exogenously to *B. juncea* plants (Hayat, Ahmad, Mobin, Hussain, & Fariduddin, 2000). The net photosynthetic rate was reported to be enhanced by the application of BRs in various plant species including *B. juncea*, *C. sativus*, *G. max*, *O. sativa* and *V. radiata* (Fariduddin, Ahmad, & Hayat, 2003; Farooq et al., 2009; Hayat, Ali, Aiman Hasan, & Ahmad, 2007; Sharma, Kumar, Singh, Thukral, Bhardwaj, 2016; Xia et al., 2006; Zhang, Zhai, Tian, Duan, & Li, 2008).

BRs also play a role in stimulation of flowering in *Arabidopsis thaliana* (Domagalska, Sarnowska, Nagy, & Davis, 2010). Deluc et al. (2007) found significant role of brassinosteroids in fruit ripening. Pilati et al. (2007) concluded that accumulation of BRs during the process of fruit development can lead to the ripening of fleshy fruits. Many researchers have also reported the enhanced ripening of cucumber, grapes, rice, tomato and yellow passion fruit after the application of BRs (Fu et al., 2008; Fujii & Saka, 2001; Gomes et al., 2006; Symons et al., 2006; Vardhini & Rao, 2002).

BRs are also reported to affect the expression of other genes that plays important role in plant defense as well as biosynthesis of other plant growth regulators (Bari & Jones, 2009). Several studies have documented their important role in protecting plants from adverse environmental stress conditions like drought, heavy metals, pesticides, salinity and viruses (Krishna, 2003; Kanwar et al., 2012, 2013; Özdemir, Bor, Demiral, & Türkan, 2004; Sharma, Thakur, et al., 2016; Wachsman, López, Ramirez, Galagovsky, & Coto, 2000). Recent studies carried out by Derevyanchuk, Litvinovskaya, Khripach, Martinec, and Kravets (2015) have demonstrated the role of EBR in modulation of respiration in *A. thaliana* under salt stress. BRs help in amelioration of the toxic effects of various abiotic stress conditions in plants by activating the antioxidative defense system (Vardhini & Anjum, 2015). Moreover, physiological roles of BRs in plants have also been extensively reviewed by Clouse (2015). Figure 2 shows various abiotic stresses which are regulated by BRs.

**Figure 2. Brassinosteroids modulate plant responses under different abiotic stresses.**



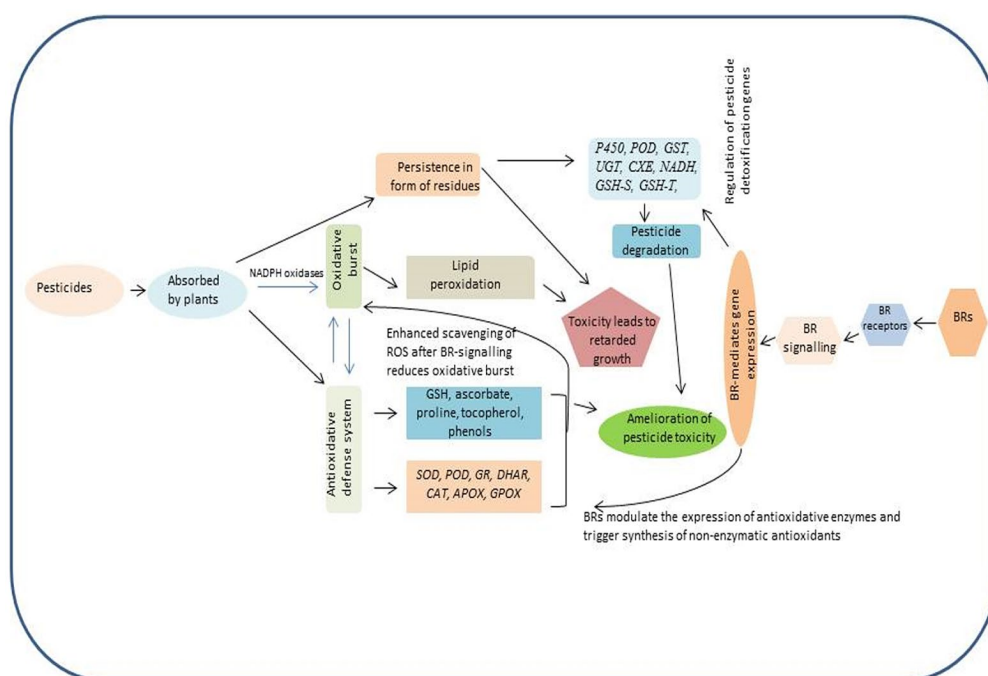


### 5. Amelioration of pesticide toxicity by BRs in plant systems

As a consequence of pesticide toxicity, plant growth and development are negatively affected due to generation of reactive oxygen species. However, in response to this pesticide stress, plants internal defence system (antioxidative defence system) gets activated to cope up with pesticide toxicity. Moreover, BR application further triggers this antioxidative defence system of plant, resulting in enhancing resistance of plants to pesticide toxicity (Figure 3). In cucumber plants, exogenous application of 24-EBL resulted in increased photosynthetic rate and stomatal conductance, which were earlier negatively affected by pesticide application (Xia et al., 2006). They reported that 0.48 g L<sup>-1</sup> chlorpyrifos application decreased photosynthetic rate and stomatal conductance by 81.01 and 71.97% respectively when compared to control plants. However the application of 24-EBL enhanced photosynthetic rate and stomatal conductance by 395 and 277% respectively when compared to chlorpyrifos treated plants. These researchers also observed that application of 24-EBL significantly increased the quantum efficiency of PSII and phytochemical quenching co-efficient. Sharma, Kumar, Singh, Thukral, Bhardwaj (2016) also observed the recovery of growth and photosynthetic parameters in *B. juncea* plants raised from 24-EBL treated seeds and grown under imidacloprid toxicity. Antioxidative defence system of plants gets activated under pesticide stress (Sharma et al., 2012, 2013, 2015; Xia et al., 2009; Zhou et al., 2015). 24-EBL and 28-HBL were reported to enhance the activities of antioxidative enzymes like superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione peroxidase (GPOX), glutathione reductase (GR), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), and contents of protein, proline, under chlorpyrifos (CPF) and imidacloprid (IMI) pesticide stress in rice seedlings (Sharma et al., 2012, 2013, 2015). They also noticed the stimulatory effect of 24-EBL and 28-HBL on overall growth of rice seedlings under CPF and IMI toxicity. Expression and activities of enzymes involved in enzyme mediated pesticide detoxification system were reported to enhance after the application of BRs (Xia et al., 2009; Zhou et al., 2015). Seed treatment of 24-EBL (before sowing) has been also reported to significantly enhance the levels of various phytochemicals which were earlier decreased by the application of IMI pesticide in *Brassica juncea* plants (Sharma et al., 2015a, 2015b). Contents of non-enzymatic antioxidants like polyphenols, ascorbic acid, tocopherol and glutathione were also observed to enhance in *Brassica juncea* plants raised from seeds soaked in 100 nM 24-EBL before sowing in IMI (250, 300 and 350 mg IMI Kg<sup>-1</sup> soil) supplemented soils (Sharma, Kumar, Thukral, Bhardwaj, 2016b). Recent studies carried out by Sharma, Thakur, et al. (2016), Sharma, Kumar, Kanwar, Thukral, and Bhardwaj (2017) has reported that exogenous applied EBR enhanced the contents of organic acids

**Figure 3. Overview and mechanism of plant responses to pesticide stress and BRs.**

Notes: ROS = reactive oxygen species, BRs = brassinosteroids, SOD = superoxide dismutase, GPX = glutathione peroxidase, CAT = catalase, POD = guaiacol peroxidase, GR = glutathione reductase, APX = ascorbate peroxidase, GST = glutathione-S-transferase, DHAR = dehydroascorbate reductase, MDHAR = monodehydroascorbate reductase.



(citric, fumaric, malic, and succinic acid) by modulating the expression of genes involved in their metabolism (*CS*-citrate synthase, *FH*-fumarate hydratase, *SUCLG1*-succinyl Co-A ligase, *SDH*-succinate dehydrogenase, and *MS*-malate synthase) in *B. juncea* seedlings under pesticide toxicity. Moreover, expression of *PAL* (phenylalanine ammonia-lyase) was also observed to be regulated by the application of EBR under pesticide stress. BRs are also known to recover the elemental composition of Indian mustard plants under IMI toxicity (Sharma, Kumar, Kanwar, Thukral, & Bhardwaj, 2016). Recently, recovery in amino acid and protein content was reported by Sharma, Kumar, Thukral, and Bhardwaj (2017) in the green leaves of Indian mustard plants which were germinated from seeds treated with 24-EBL and grown in soil containing IMI.

### 6. Role of BRs in reducing pesticide residues

Exogenous application of BRs can significantly reduce the pesticide residues in intact plants (Sharma, Bhardwaj, Kumar, Thukral, 2016; Sharma, Kumar, Bhardwaj, & Thukral, 2017; Sharma, Thakur, et al., 2017; Zhou et al., 2015). This might be due to the BR-regulated expression of various genes encoding key enzymes involved in pesticide detoxification including GST, P450 monooxygenase, POD and carboxylesterase (Sharma, Thakur, Kumar, Kesavan, Thukral, & Bhardwaj 2017; Xia et al., 2009). A significant decline in IMI residues were seen in seedlings, green leaves and pods of *Brassica juncea* after the seed pre-sowing treatment with 24-EBL and grown in solutions/soils amended with IMI (Sharma, Bhardwaj, Kumar, Thukral, 2016; Sharma, Kumar, Bhardwaj, & Thukral, 2017; Sharma, Thakur, Kumar, Kesavan, Thukral, & Bhardwaj 2017). Reduction in CHT residues in tomato plants and grapevine were observed by Zhou et al. (2015) and Wang et al. (2017) after the exogenous application of 24-EBL. Xia et al. (2009) studied that, 24-EBL application reduced the pesticide residues (chlorpyrifos, carbendazim, cypermethrin and chlorothalonil) in cucumber plants by more than 30%. They further reported that reduced pesticide residues were accompanied by the enhanced activity of antioxidative enzymes including peroxidase (POD), glutathione-S-transferase (GST) and glutathione reductase (GR). These researchers also observed that exogenous 24-EBL application significantly enhanced the expression of *P450* (P450 monooxygenase), *GST* and *MRP* (Multidrug resistance associated protein) genes responsible for pesticide detoxification in plants. BRs triggered the pesticide degradation in intact plants by 34 to 71% (chlorpyrifos in cucumber, tea, rice, broccoli and chinese cabbage, phoxim in tea and chinese chives, chlorothalonil in tomato, celery, strawberry and asparagus, omethoate in cucumber, cypermethrin in cucumber, tea, chinese cabbage and broccoli, carbofuran in garlic and chinese chives, and 3-hydroxycarbofuran in chinese chives) (Zhou et al., 2015). They also reported that 24-EBL enhanced the expression of genes under chlorothalonil (CHT) pesticide stress in tomato plants. Recently, it has been reported that mitogen activated protein kinase (MAPK) and nitric oxide (NO) play an important role in BR-mediated pesticide detoxification (Yin et al., 2016). They also demonstrated that *SIMP1* and *SIMP2* were regulated by EBR resulting in the metabolism of CHT pesticide. EBR was also noticed to regulate the activities of GST, nitrate reductase, S-nitrosogluthathione reductase and contents of S-nitrosothiol and glutathione accompanied with the reduction of CHT residues in tomato plants.

### 7. Conclusions and future prospects

On the basis of various reports explaining the role of BRs in pesticide detoxification and amelioration of toxicity, it is concluded that BRs hold strong future prospects in crop protection and can decrease the levels of pesticide residues in food crops. Additionally, total transcriptome sequencing/genome wide expression studies after the application of BRs in plants under pesticide toxicity can add new information to better understanding the protective roles of BRs. Moreover, studying important secondary metabolites and stress signalling pathways can help to understand the exact mechanism behind the responses of plants to pesticide stress. Further, crosstalk studies among different plant growth regulators under pesticide stress can add more information to pesticide stress management in plants.

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