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RESEARCH ARTICLE

AN OVERVIEW ON THE VARIOUS PHYSIOLOGICAL ROLES OF BRASSINOSTEROIDS IN THE PAST DECADE – A MINI REVIEW

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ABSTRACT

Brassinosteroids (BRs) are a novel group of plant growth regulators (PGRs) that exhibit pronounced growth promoting activities. Extensive reach on the role of BRs in positively modulating a wide range of processes, including source/sink relationship, seed germination, photosynthesis, senescence, photomorphogenesis, flowering and responses to abiotic and biotic stresses had been carried out in the past fourty years. The present mini- review highlights on various physiological roles of BRs in plants in the past decade.

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INTRODUCTION

Overview of Brassinosteroids (BRs)

Brassinosteroids (BRs) are well known as a novel type of polyhydroxy steroidal plant growth regulators exhibiting significant growth-promoting influence (Vardhini and Anjum, 2015). The initial discovery of BRs way back in the 1970s by Mitchell and his co-workers gave an insight in the existence of such growth promoting substances subsequently followed by its extraction from the pollen of *Brassica napus* L. paved the way for research of this wonderful PGR (Grove *et al.,* 1979). Vardhini (2013b) observed that BRs can be aptly classified as C_{27}, C_{28} or C_{29} BRs according to the number of carbons in their structure. Further, Vardhini (2013a) also observed that brassinolide (BL), 28-homobrassinolide (28-HomoBL) and 24-epibrassinolide (24-EpiBL) are the three bioactive BRs that are extensively used in most physiological and experimental research studies. Rao *et al.* (2002) stated that BRs are a new group of plant growth hormones that perform a variety of physiological roles like growth (Wang et al 2016), seed germination (Guo *et al.,* 2014), rhizogenesis (Vragovic *et al.,* 2015), senescence (Zhu *et al.,* 2015) etc. and also confer resistance to plants against various abiotic stresses and reported in most of the plants. Recently Tarkowska *et al.* (2016) reported that around 22 natural BRs could be determined in a minute sample of plant tissue.

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BRs are usually supplemented to plants at different stages of its life cycle viz., vegetative stage (Vardhini and Rao, 1998), flowering stage (Vardhini, 2013a), meiosis stage (Saka *et al.,* 2003), grain filling stage (Vardhini, 2013a), antheis stage (Liu *et al.,* 2006) etc. in the form of foliar spray (Vardhini *et al.,* 2012), seed treatment (Kartal *et al.,* 2009), root application (Song *et al.,* 2006) and even as shot gun approach (Hayat et al ., 2010). BRs are also reported to exhibit synergistic effects with other PGRs like ABA (Yang *et al.,* 2016), ethylene (Foo *et al.,* 2016; Zhu *et al.,* 2016), gibberellins (Foo *et al.,* 2016; Unterholzne *et al.,* 2016), auxins (Liu *et al.,* 2016b), cytokinins (Yuan *et al.,* 2015) salicylic acid (Litvinovskaya *et al.,* 2016), jasmonates (Peng *et al.* 2011) etc.

BRs and Germination of Seeds and Seedling Growth

BRs have known to play pivotal roles in regulating the process of seed germination as well as seedling growth of various crop plants. BRs were capable of enhancement of seed germination as well as seedling growth in *Leymus chinensis* (Guo *et al.,* 2014). Bukhari et al (2016) observed that the exogenous application of 24-epiBL mitigated chromium stress in tobacco seedlings by positively regulating various changes in ultrastructure and physicochemical traits. Ahammed *et al.,* (2012) found the efficacy of 24- epiEBL to improve seed germination and early development of tomato seedling grown under the phenanthrene stress. He *et al.* (2016) studied that application of epiBL conferred tolerance against zinc stress by regulating the antioxidative enzyme activities, contents of osmolytes as well as hormonal balance in *Solanum melongena* seedlings. Wu *et al.* (2015) reported that foliar spray application of 24-epiBL enhanced the rate of photosynthesis and anti-oxidant defense system in eggplant (*Solanum melongena* L.) seedlings subjected to chilling stress. Further, Wu *et al.* (2016) also reported that exogenous application of 24-epiBL alleviated the toxicity induced by Zinc metal in eggplant (*Solanum melongena* L.) seedlings by modulating the glutathione-ascorbate-dependent detoxification pathway which might be one of the regulatory mechanisms to increase seed germination as well as seedling growth.

BRs and Rhizogenesis

Wei and Li (2016) studied that supplementation of BRs positively regulated root growth, development and symbiosis. Foliar supplementaion of BRs to French bean plants exhibited improved growth of root epidermal cells (Cheng *et al.,* 2014). BL supplied in different concentrations increased root growth in potatoes by alleviating saline stress (Hu *et al.,* 2016). Vragovic *et al.* (2015) studied through translatome analyses that are capable to capture the opposing tissue specific to BR-signals to positively modulate the differentiation of root meristems.

BRs and Photomorphogenesis

Earlier research candidly showed that exogenous application of BRs resulted in expansion of *Arabidopsis thaliana* leaves (Zhiponova *et al.,* 2013), improvement of leaf nutrition in *Camellia oleifera* (Zhou *et al.,* 2013), closure of leaf stomata in *Solanum lycoperscion* (Xia *et al.,* 2014) and also development of leaf stomata (Kim *et al.,* 2012). Wang *et al.* (2016) studied that exogenous application of BL ameliorated chilling stress in *Leymus chinensis* (Trin.) Tzvel. by modulating morphological, physiological and biochemical traits., Foliar treatment of BL enhanced the various aspects of growth and anatomical features in leaves of dwarf pear cultured in *in vitro* conditions (Chen *et al.,* 2014) Exogenous application of BL altered the morphological and physiological traits of *Leymus chinensis* (Trin.) Tzvelev subjected to room and high temperatures (Niu *et al.,* 2016). Sun *et al.* (2015a) observed that BR- signaling positively regulated leaf erectness in *Oryza sativa* by controlling a very specific U-type of cyclin as well as proliferation of cells. Li *et al.* (2015) reported that supplementation of 24-BL elevated the different photosynthetic characteristics of cherry tomato. BR- signaling modulated the hyponastic growth in *Arabidopsis thaliana* caused due to submergence (Youn *et al.* 2016). Further, Tong and Chu (2016) reported that BRs regulated the processes of gibberellin synthesis to promote cell elongation in rice plants. Xu *et al.* (2015) reported that *BdBRD1*, a BR C-6 oxidase homolog in *Brachypodium distachyon* L. was essential for multiple organ development proving that BRs played a positive role in plant photomorphogenesis.

BRs and Photoperoidism and Flower Development

Application of BRs positively regulated the various aspects of photoperoidism and flower development in plants. Zhu *et al.* (2015) studied that exogenous treatment of BRs increased rice pollen grain development by triggering the expression of carbon starved anthers. Further, Ye *et al.* (2010) also reported that BRs controlled the male fertility in *Arabidopsis* by positively monitoring the expression of different key genes that are responsible in the development of anthers as well as pollens. Even, BRs played a pivotal role in controlling the sex expression and flower development of *Cucurbita pepo* (Manzano *et al.,* 2011). Application of BL improved the development of *Brassica napus* microspore-derived embryos (Belmonte *et al.,* 2011). Zhu *et al.* (2015) reported that supplementation of BRs promoted the development of rice pollen grains by triggering expression of carbon starved anther.

BRs and Photosynthesis

Application of BRs increased the survival rate of winter rye (*Secale cereale* L.) by enhancing its photosynthetic capacity and carbohydrate metabolism during the cold acclimation process (Pociecha *et al.,* 2016). Spraying of epiBL to pea plants 48 h prior to UV-B exposure alleviated its detrimental effects on chlorophyll ‘a’ and ‘b’, carotenoids and pheophytin (Dobrikova *et al.,* 2013). Filova *et al.* (2013) also reported that BRs eliminated the toxic effect of Cu in 6 sunflower cultivars (*Helianthus annuus* L. cv. Belinda, cv. Codiwer, cv. ESPrim, cv. MAS 95, cv. MAS 97 and cv. Spirov) by decreasing the metal stress and enhancing chlorophylls, proline and relative water content (RWC). The application of BRs resulted in retarding the rate of chlorophyll degradation of light-harvesting complexes in chloroplast thylakoid membranes (Hola, 2011). Further, Li et al (2016) reported that over expression of a BR-biosynthetic gene *Dwarf* markedly enhanced the photosynthetic capacity in tomato plants by the activation of Calvin cycle enzymes.

BRs and Nitrogen metabolism

The effect of BRs on the different pathways of nitrogen metabolism needs more ample of research. BRs were reported to enhance the uptake of ammonium ions that were required during the regulation of ammonium transporter and modulated the N-metabolism genes in *Arabidopsis* (Zhao *et al.,* 2016). It was also revealed that application of BRs enhanced the root nodulation and nitrogrenase activity in soya bean plants (Miao *et al.,* 2013).

BRs and Senescence

Supplementation of 24-EBL protected dopaminergic cells against apoptosis (Carange *et al.,* 2011). Zhu *et al.* (2010) reported that BRs promoted senescence of jujube fruit during the process of its storage. Further, it was reported that exogenous application of 24-epiBL during postharvest stages significantly enhanced the quality and resistance of Satsuma mandarin (*Citrus unshiu*). The ability of BRs in elevating the quality as well as ethylene synthesis during the postharvest time of tomato was observed by Zhu *et al.* (2015).

BRs and Biotic Stresses

The plants are adept to various stresses caused by the biotic beings like bacteria, fungi, insects, nematodes and viruses in their day to day life called as biotic stresses. The plants have evolved different defense mechanisms to increase their resistance and improve their potential growth and metabolism and supplementation of PGRs is one of the mechanisms employed by research scientists to mitigate these biotic stresses. BRs have played pivotal role in overcoming the variety of biotic stresses caused by fungi (Bitterlich *et al.,* 2014; Liu *et al.,* 2016a), bacteria (Canales *et al.,* 2016), viruses (Tao *et al.,* 2015; Deng *et al.,* 2016a; b), nematodes (Kaur *et al.,* 2013), and insects (Kaur *et al.* 2013; Miyaji *et al.,* 2014).

BRs on Abiotic Stresses

BRs are potential PGRs capable of mitigating the negative effect of stresses in plants caused by non-living matter of earth called as abiotic stresses. Du and Pooviah (2005) reported that BRs are plant-specific steroid hormones that have an important role in coupling environmental factors, especially light, with plant growth and development. BRs have been reported to alleviate various abiotic stresses in plants high temperature (Sonjaroon *et al.,* 2016; Niu *et al.,* 2016), low temperature in terms of chilling (Pociecha *et al.,* 2016; Wang *et al.,* 2016) as well as freezing (Eremina *et al.,* 2016), salt (Shu *et al.,* 2016; Zhu *et al.,* 2016), light (Li *et al.,* 2015; Wu and Lu, 2015; Cui *et al.,* 2016), darkness (Zhang *et al.,* 2015a), drought (Mahesh *et al.,* 2013; Xiong *et al.,* 2013), heavy metals (Surgun *et al.,* 2016; Yusuf *et al.* 2016), herbicides (Sun *et al.,* 2015b;c Zhang *et al.,* 2015b), pesticides (Wang *et al.,* 2015; Zhou *et al.,* 2015; Yin *et al.,* 2016; Sharma *et al.,* 2016b), insecticides (Xia *et al.,* 2011), organic pollutants (Sharma *et al.,* 2015), inorganic pollutants (An *et al.,* 2016; Li *et al.,* 2016b) etc. and the ability of overcoming these stresses may be by regulating the antioxidative defense mechanisms of the plants (Sharma *et al.,* 2016a)

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