

Synthesis of Brassinosteroid with Signaling and Response to Abiotic Stress: Review

Vipul G. Baldaniya^{1,*}, Ajay V. Narwade², Sagar K. Jadav³

Abstract

Brassinosteroids (BRs) are a group of plant steroid hormones with multiple roles in plant growth, development, and responses to stresses and signaling functions to promote cell expansion and cell division and plays a role in etiolation and reproduction. The entire synthetic pathway of sterol biosynthesis is brassinolide (BL) from the general campesterol synthesis pathway in Arabidopsis. Campesterol converts to BL in two different ways campesterol dependent or campesterol independent pathway. BRs are perceived by a plasma membrane-localized receptor and co-receptor complex including BRI1 and BAK1. The activated BRI1/BAK1 complex inactivates BIN2, which is one of the GSK3-like protein kinases and negatively regulates BR signaling, to promote the activity of two critical transcription factors, BES1 and BZR1 and BR responsive gene expression. In plants, BR deficiencies impair vital physiological processes and cause phenotypic abnormalities. A large number of studies show that BRs can positively influence plant responses to abiotic stresses such as heat, cold, drought, salinity, pesticides, and heavy metals.

Keywords: Hormone, Brassinolide, Synthesis, Signalling, Stress

INTRODUCTION

Hormones are required for all different physiological activities with growth and development regulation in plants at different stages. According to Pincus and Thimann plant hormones are defined as “organic substance produced naturally in the higher plants, controlling growth or other physiological function at a site remote its place of production and activity in minute amount”. In general, identified two different classes of plant hormones i) Growth promoters (Auxin, Gibberellin, and Cytokinin) ii) Growth inhibitors (Ethylene and Absciscic acid) but recently recognize the sixth class of plant hormone is known as Brassinosteroid (BRs) this is polyhydroxy steroids compound. In 1979,

the discovery of brassinolide (BL) and related 70 naturally occurring different compounds that is similar to brassinolide [1]. However, different three most bioactive BRs compound (Figure 1) are brassinolide, 24-epibrassinolide, and 28-homobrassinolide found in plants [2].

Steroid hormones have been studied first in animals and then after in plants. Estradiol, testosterone and progesterone those three steroid hormones found in animal and the adrenal cortex hormones (glucocorticoids and mineralocorticoids), mediating a wide range of pivotal developmental and physiological functions. BRs effect on growth and development processes in plants even stress condition also. The term brassinosteroid refers to naturally occurring

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steroids found in plants that are reported as free or with glucose and fatty acid conjunction. A substance first identifying from rape (*Brassica napus*) pollen was given the name brassin the first time and then after identified as brassinolide [3]. Brassinosteroids are widely distributed throughout the plant kingdom; and found in all plant organs (including pollen, anthers, flower, leaves, stem, and root) also in animals. Response of 24-Epibrassinolide is cell division and elongation in a shoot, fiber development in cotton, growth of pollen tube in flower, promotion of xylem differentiation, seed germination, and root growth [4, 5].

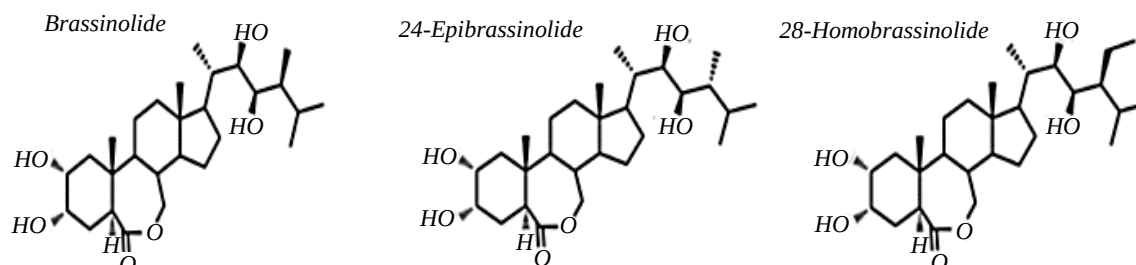


Figure 1. Structural diagram of three different common brassinosteroids compounds [3].

BIOSYNTHESIS OF BRASSINOSTEROIDS

The pathway of brassinosteroids biosynthesis is divided into two different parts. The first part is campesterol synthesis from cycloartenol and the second part is a synthesis of specific brassinosteroids compounds from campesterol [6]. The primary precursor for the synthesis of cholesterol is acetate. Here, three molecules of acetate combine to form a single five-carbon unit is isoprene. Cholesterol is a cyclization product of squalene, a 30-carbon polymer made up of six isoprene units. Squalene could readily be converted into cholesterol involving the synthesis of lanosterol through many steps. Formation of squalene mevalonate (MVA) from acetyl-CoA. In mevalonate production from bind three molecules of acetyl-CoA together and formation of farnesyl pyrophosphate via isopentenyl pyrophosphate and geranyl pyrophosphate, then after two molecules of farnesyl pyrophosphate are condensed to form squalene, which is then converted via squalene-2,3-oxide to cycloartenol [7].

In this pathway last produced isolated was campesterol and sitosterol via different compounds those are shown in below Figure 2. Then after produced 24-methylene cycloartenol from cycloartenol by adding a methyl at the 24 number carbon of the side chain using Sterol Methyltransferase 1 (SMT1) catalyzes enzyme [8]. 24-methylene cycloartenol is then converted to different compound like 4 α -methyl-5 α -ergosta-8,14,24(28)-trien-3 β -ol, 24-methylenelophenol, episterol, 5-dehydroepisterol, and last step produced is campesterol from 24-methlenecholesterol by DWF1 in parallel reactions [9,10] and last step in process is biosynthesis of brassinolide from campesterol via different step.

ISOLATION OF BRASSINOSTEROID

The invention of brassins, naturally occurring growth-promoting substances that are purified from pollen by the United States Department of Agriculture. To receive sufficient crude extract, about 225 kg of bee collected *Brassica napus* pollen was processed via a pilot size solvent extraction procedure and partially purified. Subsequently this emendation, crystals were acquired and subjected to X-ray crystallography to determine their structure.

Abscission and structural clarification of brassin chemical, this is potent plant growth-promoting activity and latter given name is Brassinosteroid (BRs). A highly plant-growth-promoting and more effective biological active steroid compound is brassinolide (BL) and its formula is $C_{28}H_{48}O_6$ with a molecular weight is 480.7 [11].

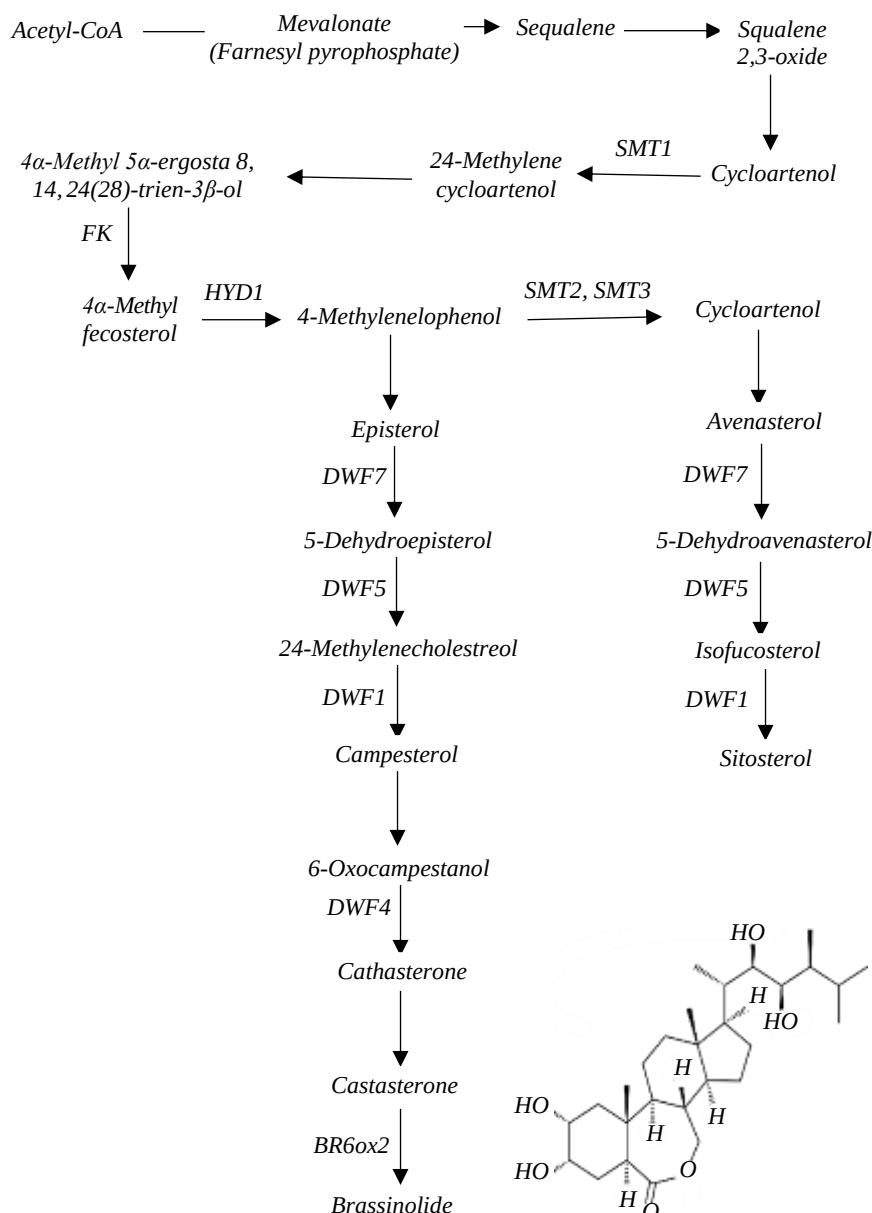


Figure 2. Brassinosteroid biosynthesis pathway. Synthesis of campesterol and sitosterol from acetyl-CoA via mevalonate and then after synthesis of brassinolide from campesterol using different enzymes in the pathway. (Fk–Fackel, Dwf–Dwarf, Hyd1–Hydra1, Smt1– Sterol Methyltransferase1) [6].

BRASSINOSTEROID SIGNALING PATHWAY

A simple model of the BRs signaling pathway is schematically shown below Figure 3. Brassinosteroid identification as a steroid hormone after started biochemical studies for signaling mechanism in *Arabidopsis*. The inception of brassinosteroid signaling is tightly mediated by a receptor-like kinase those are present on the plasma membrane, main receptor is a serine-threonine-kinase called Brassinosteroid Insensitive 1 (Bri1) and co-receptor kinase, Bri1-Associated Kinase (Bak1) [12]. BR binds with the extracellular receptor domain is BRI1, to the signaling pathway and regulation of transcription process, eventually inhibit, regulator Bri1 Kinase Inhibitor1 (Bki1) is dissociation and condenses a transphosphorylation between the kinase domains of BRI1 and BAK1. Phosphorylated BKI1 also interacts with the 14-3-3 family of phosphopeptide-binding proteins to promote brassinosteroid signaling [13].

After activation of BR signaling BRI1 will transmit BR signal to the downstream of the two kinds of protein Brassinosteroid Signaling Kinases 1 (Bsk1) and Constitutive Differential Growth Protein 1 (Cdg1). Bri1 phosphorylation promotes BSK1 and CDG1 binding to, and phosphorylation of, the phosphatase Bri1 Suppressor1 (Bsu1). Bsu1 inactivates the Glycogen Synthase Kinase 3 (Gsk3) Like Brassinosteroid Insensitive2 (Bin2) by dephosphorylating a conserved tyrosine residue [14]. There may be many proteins or transcription factors that are targeted BR signaling and BSU1 is a serine/threonine protein phosphatase with the N-terminal kelch-repeat domain, which leads to BIN2 dephosphorylation. BIN2 is restrained by KIB1 (Kik Suppressed In Bzr1-1d), which prevents the association of BINs with BZR1/BES1 and facilitates its ubiquitination. In the absence of BR, BIN2 is activated by auto-phosphorylation and directly phosphorylates BZR1 and BES1, leading to cytosolic accumulation through 14-3-3 binding and degradation by 26S-proteasome [15,16].

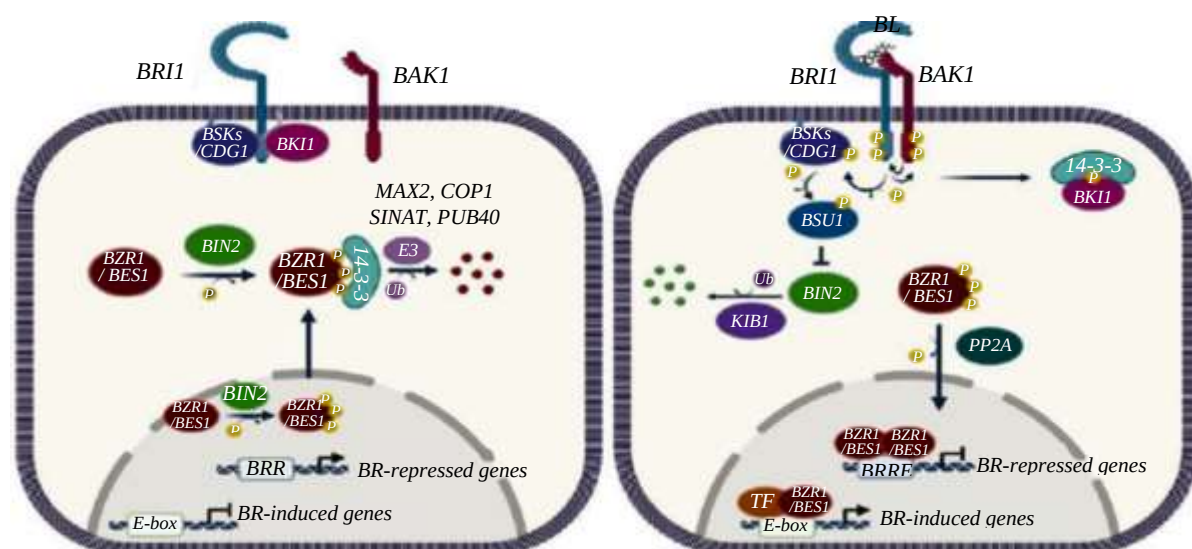


Figure 3. Brassinosteroid signaling pathway in Arabidopsis. Present first Figure when absent of BRs, So, BAK does not bind with BRI1 and BKI1 and signaling process cannot start and complex is inactive. Inactivation of BRI1 allows BIN2 to be constitutively active and to phosphorylate BZR1 and BES1 transcription factors. In turn, BZR1 and BES1 phosphorylation causes their cytoplasmic retention by interaction with 14-3-3 and abolishes their DNA-binding activity. BZR1 and BES1 degradation is mediated by different E3 ligases. Second, when BRs are present at the plasma membrane, BR binding with BAK1 and BRI1, making a single and triggers trans-phosphorylation between BRI1 and BAK1. Activated BRI1–BAK1 receptor complex transduces its signal to BSKs and CDG1 through direct phosphorylation. BSKs or CDG1 activate the BSU1 phosphatase. BSU1 then inactivates BIN2 by dephosphorylation, and the E3 ligase KIB1 mediates the BIN2 degradation. Meanwhile, PP2A activates BZR1 and BES1 via dephosphorylation and allows the transcription factors to enter the nucleus and bind DNA for BR responsive gene regulation [17].

ROLE OF BRS IN ABIOTIC STRESSES

Plants improve to different abiotic stress tolerance mechanisms due to brassinosteroids hormone improve and different environmental adaptions (Figure 4). Including some exceptions like as a BRs useful for plant improvement and change adaptions mechanism related to biotic and abiotic stresses, such as drought, salinity, high temperature, low temperature (Cold), heavy metals, pesticides, and organic pollutants [18,19].

Exogenous application of BRs enhances the transcript levels of autophagy-related genes and the production of autophagosomes. Enhances the production of autophagosomes and tolerance to nitrogen starvation conditions due to overexpression of the BZR1 gene. Nonetheless, exogenous application of BRs aggravates plant susceptibility to an iron deficiency that's are suggested BRs help in the plant

making to tolerance for nutrient deficiency [20]. Found results different numbers of experimental and then after that explicate BRs effects on plants under stress condition, most studies used pharmacological approaches where the exogenous application of BRs was used found a role of BRs in abiotic stress protection [21].

Different strategic use for applications of BRs such as pre-sowing seed treatment, pre-planting dipping of cuttings, post-emergence root treatment, foliar application, and so on have been used in multiple plant species [22, 23] and impact of BRs mostly depended on different factors including concentration, plant species, different growth stage, with or without stress condition, a loop of stress and other growth hormones, and signalling molecules [5]. BRs are members of the polyhydroxysteroids those are major role in a wide variety of morphological and physiological responses in plants such as cell elongation, cell division, stem elongation, activation of some enzymes, protein pump regulation present on the plasma membrane, protein production, regulation of photosynthesis activity, source to sink carbon distribution especially under various environmental stresses condition [24].

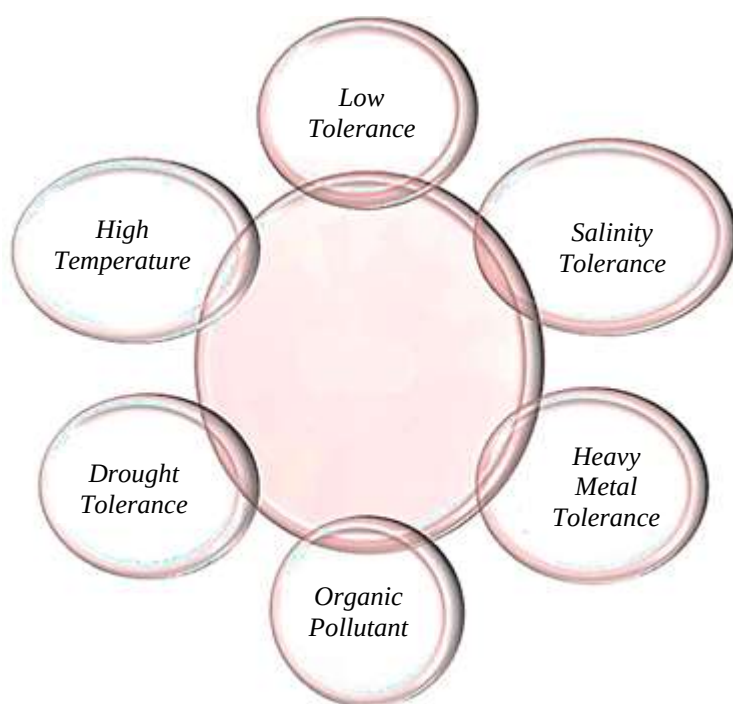


Figure 4. Brassinosteroids (BRs) improve plant tolerance to abiotic stresses. Different studies have reported roles of BRs treatment in enhancing plant tolerance to abiotic stresses, such as high and low temperature, drought, salinity, and heavy metals [21].

Drought

Water is the major raw material for plant growth and development throughout the life cycle so, drought conditions are serious issues for agriculture all over the world. Among all the other abiotic stresses, drought stress is considered one of the serious threats to crop production under arid and semiarid regions of the world limiting plant growth and productivity. In-plant show water deficit conditions can seriously reduce the rate of photosynthesis, degradation of chlorophyll contents, and damage membrane stability. When the application of BRs under water deficit conditions increases chlorophyll accumulation in the chloroplast, amylase activity, amino acid and protein contents, stomatal conductance, rate of photosynthesis, and membrane stability so, ultimately increases crop yield and productivity under drought condition. 24-epibrassinolide (EBL) increases or supports plant growth, development, and production increase by increasing the rate of carbon assimilation, maintaining level or concentration of ROS and antioxidants, increase solute storage and maintain

water potential in the plant cell. A different method of EBL application is important for increasing crop production like as a seed priming and foliar application are more productive as compared to root application. EBL is a very important phytohormone, which can ameliorate water stress-induced noxious effects in plants [24].

Exogenous treatment of BRs considerably reduced the effect of drought stress by increasing the rate of photosynthesis, pigments of photosynthesis, stomatal conductance, transpiration rate, antioxidants defense mechanism and also increase some osmolytes and antioxidants such as sugar, proline, glycine, betaine, and SOD, APX, catalase and peroxidase in *Brassica rapa* genotypes [25]. Foliar application of a higher concentration of 24-epibrassinolide helps to improve the drought stress tolerance in wheat concerning growth, biomass production, and yield production [26]. In barley crop exogenously application of brassinolide was significantly improved chlorophyll content, photosynthesis parameters, antioxidant enzyme activities, and reduced oxidative in leaves and root under water stress those are created using PEG [27].

High Temperature

In recent years, the biggest environmental problem is greenhouse gases and increases the environmental temperature in the world wild so; high-temperature stress is one of the major abiotic stresses problems in the world [5]. High temperature reduces crop yield all over the world. High-temperature stress symptoms include leaf burning, reduced flower numbers, increase leaf abscission, increase senescence, reduced plant growth, fruit scorching, and decreased yield [28]. At the molecular level, the accumulation of BES1 and BZR1 occurs under high temperatures, which promotes the levels of Phytochrome Interacting Factor4 (PIF4) [29]. The formation of PIF4-BES1 heterodimers facilitates BZR1 action on gene transcription, leading to thermogenic growth. On the other hand, a decreased accumulation of BRI1 under high temperatures affects BR signaling, resulting in increased root growth [30]. Notably, exogenous BR application can mitigate the deleterious effects of heat in plants [31].

BRs biosynthetic and signaling molecules found sensitive characteristics to heat stress as compared to wild type in *Arabidopsis thaliana*. Brassinosteroids have been observed to reduces the negative effects of high-temperature stress on the rate of photosynthesis, seed germination, and crops yield. Exogenous application of BRs shows two major patterns of gene regulation: (1) expression of developmental proteins that are suppressed under heat stress (2) Increase levels of protective proteins. BRs help to increase heat shock proteins (HSPs) under high-temperature stress in the cytosol and those are important for the production of proteins against irreversible heat-induced damage by preventing denaturation, stability of protein, and facilitating the refolding of proteins also BRs to maintain redox homeostasis under high temperatures stress by enhancing activities of enzymes involved in the ascorbate glutathione cycle including enzymes like as catalase, superoxide dismutase, APX, glutathione reductase, and monodehydro-ascorbate reductase.

A primary work of brassinosteroids under high temperature is found to protect the rate of leaf photosynthesis through improving the photosynthetic pigment contents (Chlorophyll, Xanthophyll, and Carotenoids), CO₂ bind with rubisco is increase, protection of PSI activity and maintain cell wall thermostability.

Low Temperature

Cold stress represents a substantial risk for plant growth and development and impacts on plant distribution and crop production. Low temperatures stress including chilling (>0°C) or freezing (<0°C) stress is the primary barrier for crop productivity in some areas of the world. Cold stress-induced cell membrane degradation and modification in plants due to high saturated fatty acid, alterations in macromolecules activities, reduces cell osmotic potential and also mechanical constraints [21]. Chilling or freezing stress also affects the photosynthetic pathway in plants which are

manifested by the reduction rate of CO₂ assimilation in the chloroplast, change in PSI and PSII due to photo-inhibitory effect, and decreased Benson–Calvin Cycle enzyme activity [32].

The positive effect was found when the application of 24-epibrassinolide (EBR) on gene expression and predicted functions in wucai (*Brassica campestris* L. ssp. *chinensis* var. *rosularis* Tsen) responding to low temperature stress. Significantly change in specific leaf area, membrane stability index, total soluble sugar, chlorophyll fluorescence parameters, and malondialdehyde under stress conditions through EBR in wucai [33].

Salinity or Salt Stress

Saline condition is a highly soluble salt concentration present in soil and EC of soil is more than 4 ds/m. Salt stress is one of the most negative effects or production limitation factors in agriculture yield. High salt concentration damage plant in a different way; reduces metabolic activity, reduced water absorption by root, impairment of chloroplast and mitochondria membrane, decrease photosynthesis activity, reduces protein synthesis and increase ions toxicity. The exogenous application of brassinosteroid increased chlorophyll contents, photosynthesis characters, increase activities of antioxidant enzymes, reduced reactive oxygen species (ROS), and MDA contents to mitigating the harmful effects of salinity stress also decreased ions toxicity and increased total amino acid in plants. Under salinity stress condition exogenous application of 24-epibrassinolide reduces Na⁺ content in leaves and membrane leakage and increase the net photosynthetic rate, stomatal conductance, transpiration rate, chlorophyll content, and maximum quantum efficiency of PSII [34].

Heavy Metal Stress

Earth's crust or layers are made up of different metals and nutrients so, many different heavy metals are present in the earth's crust, and sometimes those are metals create a negative effect for plants on growth and. Plants have an egregious ability to uptake and accumulate heavy metals. High concentrations of all heavy metals, including those that are essential or non-essential for plant growth and development, cause toxic effects on different metabolic activity pathway. The adversary effect of heavy metals in plants is: blocking functional groups of enzyme and amino acid, antagonist and decrease ions transportation and absorbed in a plant through the root, displacing essential nutrients in cell and imbalance of antioxidant enzymes. BR plays a major role in reduces the effect of heavy metal toxicity in cells and different organelle and increase growth and development in plants [18].

Brassinosteroid curtail the harmful impact of heavy metal stress on growth by preventing and increasing chlorophyll contents and photosynthetic activity and increasing synthesis of phytochelatins. Similarly, reported that BRs help to reduce the rate of the absorption of heavy metal ions through roots in plants. However, EBR application protected the Cr-induced damage to chloroplast and helped to maintain the organization of grana and thylakoids under Cr stress. Similar to the EBR, HBL also shows a stress-protective role in mitigating heavy metal stress. HBL treatment could alleviate the Cd-induced reduction of growth, photosynthesis, and the photochemistry of PSII in tomato seedlings [35].

CONCLUSION

In this review, discussed about role of brassinosteroid in abiotic stress with biosynthesis and signaling mechanism of hormone. Evaluation started simple to complex compound mechanism in plants and other organisms. In this continues process depending on different mechanism or hormones regulation in plants. Different plant hormones distribution in plant as per requirement at stages of plants. Brassinosteroids hormones recently identified in brassica plant and show that work on plant growth and the development of different stage. A wide range of BRs synthesis from steroid compound. Recently many work done on BRs effect on physiological process as well as prevents again different stress condition. Mechanism of BRs signaling pathway mainly depending on transcriptional factor (TF) and that is present on plasma membrane, and BES1 and BZR1 are two key transcription factors

present in cell. These two TF BES1/BZR1 proteins bind to their target promoters to control expression of thousands of genes important for plant growth, development, and stress tolerance. Since multiple stressors often occur under natural conditions, now a day face to climate changing day by day so, this condition BRs have important for proper plant growth, development and increase production under different stress condition.

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