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Brassinosteroids: Key Hormonal Regulators in Plant Stress Tolerance

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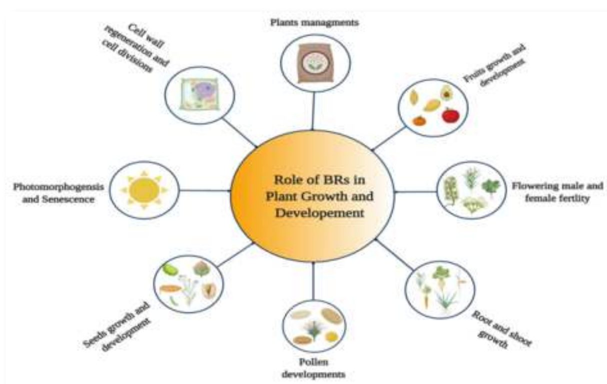
A class of plant steroid hormones known as brassinosteroids (BRs) plays a variety of functions in the growth, development, and stress-reaction of plants. Brassinosteroids (BRs) are recognized for their significant role in mitigating stress-induced disruptions in normal plant metabolism by activating various tolerance mechanisms. Global research efforts have increasingly focused on enhancing plant growth through the exogenous application of BRs, using methods such as foliar sprays, seed priming before sowing, and incorporation into the root growth medium. Numerous studies have demonstrated that applying BRs externally to stressed plants effectively enhances their stress tolerance mechanisms. Deficits in BR affect essential physiological functions in plants and result in aberrant phenotypes. Numerous investigations demonstrate that BRs can have a beneficial impact on how plants react to abiotic stressors such heat, cold, drought, salinity, pesticides, and heavy metals. However, little is known about the underlying processes of stress tolerance caused by BR. BR stimulate BRASSINAZOLE RESISTANCE 1 (BZR1)/BRI1-EMS SUPPRESSOR 1 (BES1), transcription factors that activate thousands of BR-targeted genes. Brassinosteroids (BRs) have been shown to enhance photosynthetic efficiency under stress conditions, significantly contributing to increased plant growth and biomass accumulation. Genetic studies generally support a positive link between endogenous BR levels



and abiotic stress tolerance; however, this relationship is sometimes contradicted by the stress responses observed in certain BR mutants. Importantly, plant responses to BRs vary widely depending on species, developmental stage, and environmental conditions. Moreover, interactions with other hormones and signaling molecules are crucial in modulating BR-mediated stress responses, further influencing plant adaptation under adverse conditions. They also strengthen the antioxidant defense system, elevate enzymatic activity, and upregulate stress-responsive genes such as superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), glutathione reductase (GR), and ascorbate peroxidase (APX) [17, 18]. The exogenous application of BRs has been shown to promote cucumber seedling growth under $Ca(NO_3)_2$-induced stress by improving photosynthetic capacity, reinforcing antioxidant defenses, and maintaining chloroplast ultrastructure [14]. Even under non-stress conditions, BR treatment stimulates plant growth, enhances net photosynthetic rate, and boosts antioxidant capacity, highlighting their multifunctional role in plant development. BR-insensitive mutants identified in model species such as *Arabidopsis* and *Brassica* exhibit various developmental abnormalities, including dwarfism, dark green leaves, delayed flowering, and male sterility.

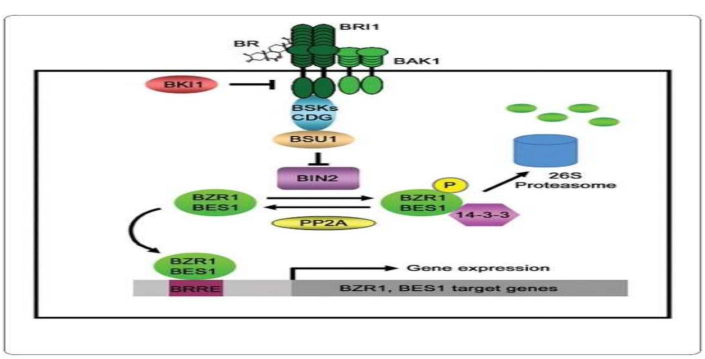


Fig 1 Structure of three common brassinosteroids

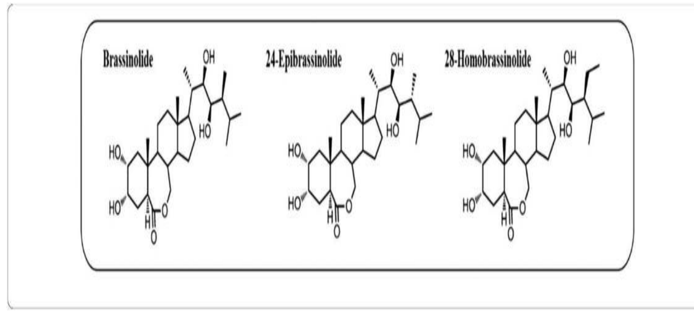


Fig :2- A model of brassinosteroid (BR) signaling in *Arabidopsis*.

Mechanisms of Brassinosteroid Action Under Stress Conditions

Cellular and molecular responses: Brassinolide, 24-epibrassinolide, and 28-homobrassinolide are among the most bioactive forms of brassinosteroids (BRs) and are commonly utilized in physiological and molecular studies . Early research has shown that BRs regulate a wide range of physiological and developmental processes across various plant species. These include cell elongation in stems and roots, leaf expansion, photomorphogenesis, flower development, male sterility, stomatal development, and enhanced resistance to environmental stress.

Regulation of gene expression

The signal transduction pathway begins with brassinosteroids (BRs) being recognized by the receptor kinase BRASSINOSTEROID INSENSITIVE 1 (BRI1) located on the cell surface, which activates the transcription factors BRASSINAZOLE RESISTANT 1 (BZR1) and BRI1-EMS SUPPRESSOR 1 (BES1) to promote stress tolerance. When BR is applied externally, it binds to BRI1, triggering its association with BRI1-ASSOCIATED RECEPTOR KINASE 1 (BAK1) and the dissociation of BRI1 KINASE INHIBITOR 1 (BKI1) . Activation of BRI1 requires sequential transphosphorylation with BAK1, which subsequently phosphorylates BR-SIGNALING KINASE 1 (BSK1) and enhances the activity of BRI1 SUPPRESSOR 1 (BSU1). Activated BSU1 inhibits BRASSINOSTEROID INSENSITIVE 2 (BIN2) by dephosphorylating a key phospho-tyrosine residue, allowing the accumulation of unphosphorylated BZR1 and BZR2/BES1 transcription factors. These dephosphorylated transcription factors then move into the nucleus, where they regulate BR-responsive genes that enhance plant stress tolerance by boosting antioxidant enzyme activity, modulating endogenous hormone levels, and upregulating thousands of target genes.

Role of Brassinosteroids in Enhancing Plant Stress Tolerance

Brassinosteroids (BRs) are plant steroid hormones that play a crucial role in regulating various physiological processes and enhancing plant adaptation to both abiotic and biotic stresses [15, 48]. Numerous studies have indicated that BRs influence the activity of defense-related enzymes and hormonal pathways during stress responses. This section highlights key physiological and molecular mechanisms through which BRs contribute to plant tolerance under different stress conditions.

Brassinosteroids and Abiotic Stress Tolerance

Chilling stress is a significant abiotic factor that adversely affects plant growth and development across many regions, disrupting various physiological processes. Exposure to low temperatures can halt plant growth, impair photosynthesis, reduce chlorophyll content, and cause flower bud abortion, ultimately leading to substantial yield and economic losses. To combat such environmental challenges, plants have evolved complex and overlapping regulatory mechanisms to respond to both abiotic and biotic stresses. Phytohormones such as brassinosteroids (BRs), salicylic acid (SA), jasmonic acid (JA), abscisic acid (ABA), and gibberellins (GA) play essential roles in stress signal transduction pathways and activation of plant defense mechanisms . Among these, BRs are particularly noted for their role in regulating plant growth and mediating a wide range of physiological responses to abiotic stresses, including both low and high temperature stress. Water availability, another critical factor for plant survival, is often inconsistent, especially in arid and semi-arid regions. Drought stress significantly hampers crop productivity by impairing antioxidant systems, reducing chlorophyll levels, affecting photosynthetic efficiency, and compromising membrane integrity . Studies have demonstrated the beneficial role of BRs in enhancing drought tolerance. For instance, in *Cicer arietinum* (chickpea), BR treatment under water deficit conditions led to notable improvements in fresh and dry biomass, tiller number, stem thickness, root activity, and nitrate reductase activity . Similarly, BR application in radish seedlings under drought conditions enhanced antioxidant enzyme activity and alleviated drought-induced damage , underscoring the protective role of BRs in water-stressed environments.

Brassinosteroids and Biotic Stress Resistance

In natural environments, plants encounter both biotic stresses, such as attacks from pathogens and pests, and abiotic stresses like extreme temperatures and salinity. To defend themselves, plants rely on an immune-like system composed of physical barriers and inducible defense mechanisms that are activated upon stress. These responses are regulated by complex signaling networks involving key plant hormones, including ABA, ethylene, jasmonic acid, salicylic acid, and brassinosteroids (BRs). BRs have been shown to improve plant growth, yield, and resistance to fungal and viral pathogens, with their effectiveness depending on the application method and timing. BRs also interact with transcription factors such as MYB30 and BES1 to regulate stress-responsive genes. In various studies, BR application has been linked to increased levels of stress-related hormones and antioxidants, particularly under conditions like chilling or pathogen attack. This indicates that BRs play a crucial role in enhancing biotic stress tolerance through hormonal crosstalk and gene regulation.

Conclusion

Brassinosteroids (BRs) are vital plant hormones that significantly contribute to growth, development, and stress adaptation. They enhance tolerance to a wide range of abiotic stresses, including drought, salinity, temperature extremes, and heavy metals, as well as biotic stresses like pathogens and pests. BRs function through complex signaling pathways, regulating key transcription factors such as BZR1 and BES1, which activate stress-responsive genes and antioxidant systems. Their interactions with other phytohormones further fine-tune plant defense responses. Both exogenous application and endogenous regulation of BRs have shown promising results in improving stress resilience and crop productivity. Overall, BRs represent a powerful tool for developing stress-tolerant crops and ensuring sustainable agricultural practices under changing environmental conditions.

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