Brassinolide-Mediated Stress Management: Multifaceted Approach to Plant Protection

Harshita Saini[1], Suresh Chand Mali[2], Anita Dhaka[3],
Sheetal Sharma[4], Rohini Trivedi[5]

[1,3,4,5]Laboratory of Plant Pathology, Department of Botany, University College of Science, Mohanlal Sukhadia University, Udaipur, 313001, Rajasthan, India
[2]Assistant Professor of Botany, Veena Memorial PG College Karauli (Rajasthan) India

[5]Corresponding author: Rohini Trivedi
Assistant Professor, Laboratory of Plant Pathology, Department of Botany, University College of Science, Mohanlal Sukhadia University, Udaipur, 313001
E-mail:rohini.l.trivedi@gmail.com

Abstract:
Plants are constantly challenged by a variety of phytopathogens, including fungi, bacteria, and viruses, which can significantly impact crop productivity. To counter these biotic stresses, plants have evolved a complex innate immune system that involves both preformed barriers and inducible defence mechanisms. Brassinolide (BL), a bioactive brassinosteroid (BR), has emerged as a key regulator in enhancing plant immunity. Recent advances in plant physiology and molecular biology have shown that BL modulates defence responses by inducing the expression of pathogenesis-related genes, promoting the biosynthesis of antimicrobial compounds, and strengthening structural barriers, such as cell walls. Additionally, BL interacts synergistically or antagonistically with other phytohormones such as salicylic acid, jasmonic acid, and ethylene to fine-tune the immune response depending on the type of invading pathogen. BL also boosts transient H_2O_2 accumulation and the activities of POD, APX, GST, and GPX (antioxidant system). This review consolidates current knowledge on BL-mediated defence signalling pathways and explores its potential application in integrated disease management strategies to reduce chemical pesticide usage and promote sustainable agriculture.

Keywords: Brassinolide, defence responses, pathogenesis-related genes, antioxidant system.

1. Introduction

Plant diseases caused by various pathogens, including fungi, bacteria, viruses, and nematodes, pose significant threats to global food security, leading to substantial yield losses estimated at 10-40% each year worldwide(Venbrux *et al.*, 2023). With a growing global population and changing climate patterns, improving plant disease resistance has become essential for sustainable agriculture. Traditional disease management methods, such as chemical pesticides, often raise environmental and health concerns, emphasising the need for alternative strategies.

BR were first discovered in the 1970s when Mitchell and colleagues isolated BL from pollen of *Brassica napus* (Grove *et al.*, 1979). These steroidal plant hormones have since been recognised as essential regulators of various physiological processes, including cell elongation, vascular differentiation, photomorphogenesis, and stress responses(Li & He, 2020). Among the over 70 BR compounds identified till date, BL is the most bioactive form.

Plants have evolved sophisticated innate immune systems to defend against pathogens. Unlike mammals, plants lack adaptive immunity and depend entirely on innate defences. Plant innate immunity functions through a two layered system: pattern-triggered immunity (PTI) and effector-triggered immunity (ETI)(Yu *et al.*, 2021). PTI is activated when pattern recognition receptors (PRRs) detect pathogen associated molecular patterns (PAMPs), while ETI is initiated when plant resistance proteins recognise pathogen effectors (Yu *et al.*, 2024; Yu *et al.*, 2021). This detection triggers various defence responses, including the production of reactive oxygen species (ROS), activation of mitogen-activated protein kinase (MAPK) cascades, the buildup of callose, and the expression of pathogenesis-related (PR) genes (Kumar *et al.*, 2018). These hormones are known to influence plants during stress, such as pathogen infection. They promote growth, alter protein synthesis, and modulate the expression of stress-related genes, as well as activate antioxidant enzymes and compounds. All these responses help reduce the effects of stress, maintaining or boosting plant performance. Stress responses both biotic and abiotic are mediated by BL-induced genes, including those that detoxify ROS and defence genes activated under abiotic stress.

While the role of BL in plant growth and development has been extensively studied, their involvement in regulating plant immunity has gained significant attention only in the past two decades. Early studies indicated that exogenous application of BL could induce disease resistance in various plant species. This has led to extensive research into the mechanisms underlying BL-mediated immunity and the potential applications in crop protection.

1.1. Structure of Brassinolide: -

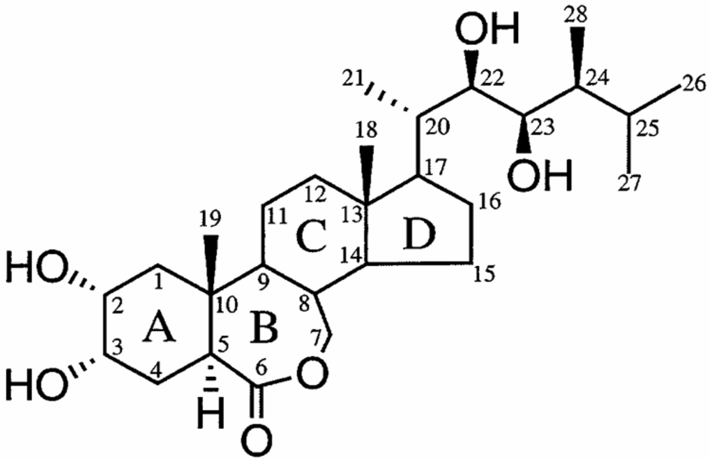

Figure 1: Structure of Brassinolide (Fujioka & Yokota, 2003)

Currently, over 40 BR have been identified to occur naturally. Their structural variation stems from different substituents in the A/B-rings and the side chain, which are produced by oxidation and reduction reactions during biosynthesis. BR with either an α-hydroxyl, β-hydroxyl or ketone at position C3 in the A-ring are precursors of BR carrying 2α,3α-vicinal hydroxyls; those with 2α,3β-, 2β,3α-, or 2β, 3β-vicinal hydroxyls may be metabolites of 2α,3α-vicinal hydroxyls. With respect to the substituent in the B-ring, BR are classed as either 6-deoxo, 6-oxo (ketone) or 6-oxo-7-oxa (lactone). In the side chain, BR have a-oriented vicinal hydroxyls at positions C22 and C23 (in the side chain stereochemistry of steroids, groups in front of the plane are defined as a-oriented T). Cathasterone, with a single hydroxyl at C22, is a precursor of BR with a 22,23-vicinal diol. ((Yokota, 1997)

Table 1: Brassinosteroids isolated for the first time in plants

No.	Common Name	Chemical Name	Plant	Reference
1	BL	(22R,23R,24S)-2α,3α,22,23-tetrahydroxy-24-methyl-B-homo-7-oxa-5α-cholestan-6-one)	*Brassica napus* L.	Grove *et al.*, 1979
2	Castasterone	(22R,23R,24S)-2α,3α,22,23-tetrahydroxy-24-methyal-5α-cholestan-6-one	*Castanea crenata Sieb. et Zucc.*	Yokota *et al.*, 1982
3	28-	(22R,23R,24S) -2α,3α,22,23-tetr	*Brassica*	Abe *et al.*,

	Homocastasterone	ahydroxy-24-ethyl-5α-cholestan-6-one	*campestris var. pekinensis*	1983
4	28-Homobarssinolide	(22R,23R)-2α,3α,22,23-tetrahydroxy-24-ethyl-B-homo-7-oxa-5α-cholestan-6-one	*Brassica campestris var. pekinensis* L.	Ikekawa *et al.*, 1984
5	24-Epicastasterone	(22R,23R,24R)-2α,3α,22,23-tetrahydroxy-24-methyl-5α-cholestan-6-one	*Hydrodictyon reticulatum* (L.) *Lager*.	Yokota *et al.*, 1987
6	24-Epibrassinolide	(22R,23R,24R)-2α,3α,22,23-tetrahydroxy-24-ethyl-B-homo-7-oxa-5α-cholestan-6-one	*Vicia faba* L.	IKEKAWA *et al.*, 1988
7	Typha sterol	(3α,5α,22R,23R,24S) -3,22,23-trihydroxyergostan-6-one	*Arabidopsis thaliana* (shoot)	Fujioka *et al.*, 1996
8	6-deoxotyphasterol	(3β,5α,22R,23R,24S)-3,22,23-trihydroxy-24-methyl-5α-cholest-7-en-6-one	*Arabidopsis thaliana* (shoot)	Fujioka *et al.*, 1996

2. BRASSINOLIDE: BIOSYNTHESIS AND SIGNALLING

2.1. Biosynthetic Pathway

BL are synthesised in ER membranes, as the enzymes involved in BL synthesis are localised in the ER membranes(Symons *et al.*, 2008; Wang *et al.*, 2023). The precursor for the biosynthetic pathway is campesterol (CR), which is first converted into campestenol (CN). The biosynthesis is generally divided into CN-dependent and CN-independent pathways. CN-dependent pathways include early and late C-6 oxidation pathways (Fujioka & Sakurai, 1997), while CN-independent pathways include C-22 and C-23 hydroxylation pathways (Fujioka & Yokota, 2003). In the early C-6 pathway, CN is oxidised to form 6-oxocampestanol (6-oxoCN), and then, through a series of catalytic reactions, castasterone (CS) is formed. In the late C-6 oxidation pathway, CN is first hydroxylated to form 6-deoxocathasterone (6-deoxoCT), the non-oxidised form of CT, then undergoes a catalytic reaction, similar to the early C6 oxidation pathway, and forms CS in the final step, which is finally converted into BL. The enzymes involved in CR catalysis to form BL are DWF4 (Dwarf 4), CPD (Constitutive photomorphogenesis and dwarfism), DET2 (De-etiolated 2), ROT3/CYP90D1 (Rotundifolia 3/Cytochrome P450 90D1), and CYP85A1/2 (Cytochrome P450 85A1/Cytochrome P450 85A2 (Kour *et al.*, 2021; Fujioka & Yokota, 2003; Fujioka & Sakurai, 1997).

2.2. BL Perception and Signalling Mechanism

BRASSINOSTEROID INSENSITIVE1 (BRI1), a leucine-rich repeat receptor kinase, plays a key role in BL signal transduction. In the absence of BL, BRI1 is inactive due to its interaction with inhibitory proteins like BRI1 KINASE INHIBITOR1 (BKI1) or BOTRYTIS-INDUCED KINASE1 (BIK1). BRASSINOSTEROID INSENSITIVE2 (BIN2) is a negative regulator of the BRs signalling pathway. BIN2 phosphorylates two critical transcription factors, BRASSINAZOLE-RESISTANT1 (BZR1) and BRI1-EMS SUPPRESSOR1 (BES1), which are essential for the regulation of BL-responsive gene expression (Wang *et al.*, 2002). This phosphorylation inhibits the BL signalling cascade. However, in the presence of BL BRI1 phosphorylates BKI1 and dissociates from BKI1. BRI1 then interacts with its co-receptor, BRI1-ASSOCIATED RECEPTOR KINASE1 (BAK1), also known as SOMATIC EMBRYOGENESIS RECEPTOR-LIKE KINASE 3 (SERK3), resulting in trans-phosphorylation between BRI1 and the other SERK family members (SERK1, SERK2, and BKK1), activating the receptor complex (She *et al.*, 2011). Plasma membrane-associated copine proteins, specifically BONZAI (BON), ensure efficient BRI1-SERK complex formation and transphosphorylation(Jing *et al.*, 2024). Now, the activated BRI1-SERK receptor complex directly phosphorylates BL SIGNALING KINASES (BSKs) and CONSTITUTIVE DIFFERENTIAL GROWTH1 (CDG1), which, in turn, activates BRI1 SUPPRESSOR1 (BSU1) phosphatase. BSU1 dephosphorylates and inactivates BIN2. Thus, in the presence of BL, BIN2 is deactivated, and BZR1 and BES1 are dephosphorylated. Then, BZR1 and BES1 are released, translocated into the nucleus, and allow the expression of BL-target genes essential for growth and development (Kim *et al.*, 2009; Wang *et al.*, 2002). Hormone homeostasis is critical for normal plant growth and development (Wang *et al.*, 2023; Zhang *et al.*, 2023; He *et al.*, 2005). BZR1 and BES1 regulate multiple BL-biosynthesis genes through a negative feedback loop that adjusts BL synthesis based on the levels of active BRs (He *et al.*, 2005). Thus, BZR1 has dual biological functions. When the BL signal is activated, the BZR1 is unphosphorylated and accumulates in the nucleus, activating the gene expression for growth while inhibiting the expression of biosynthesis genes (Zhao & Li, 2012)

3. BRASSINOLIDE ROLE IN ABIOTIC STRESS

BL, an essential BR, significantly boosts plant resilience to abiotic stresses by regulating physiological, biochemical, and molecular processes. Its use has demonstrated promising improvements in stress tolerance in key crops such as wheat, rice, maize, and horticultural plants.

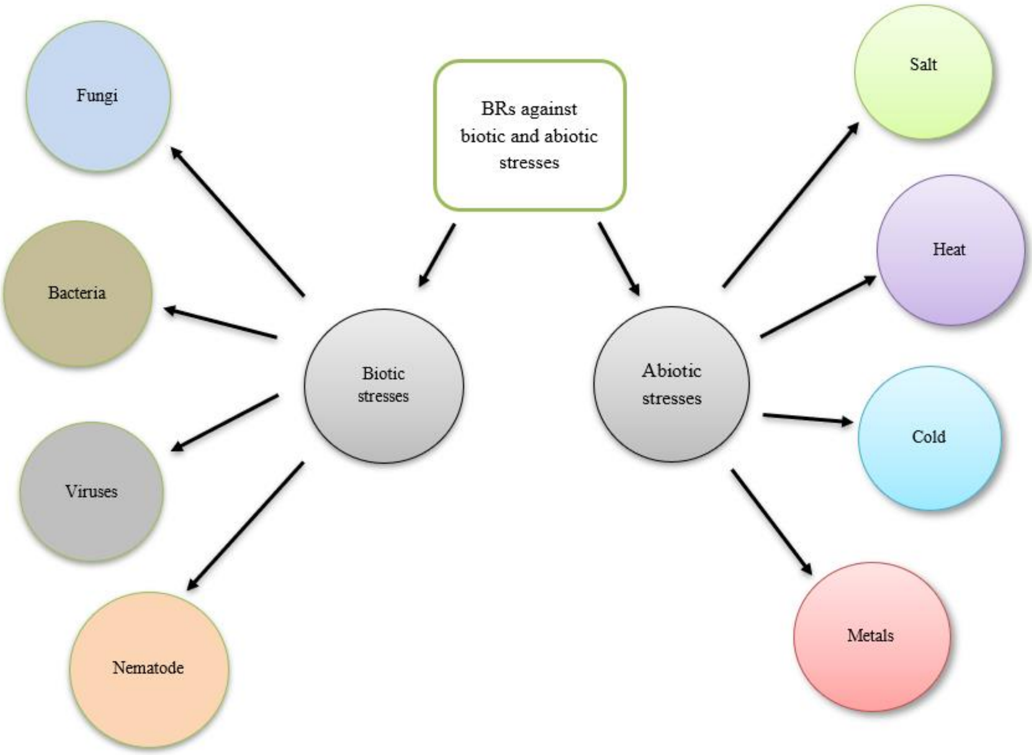

Figure 2. Role of BL against different biotic and abiotic stresses in plants

3.1. BL Response to Cold Stresses

Table 2. BL response to various kinds of cold stresses

S. No.	Stress	Crops	Effect	Reference
1	Temperature stress	*Brassica*	BL significantly reduces the negative effect and protects the cell membrane by increasing proline contents and antioxidant enzyme activity to enhance stress resistance	Kumar & Manish, 2013
2	Chilling stress	Cucumber	BL is involved in ethylene biosynthesis to regulate the plant defence system, to resist abiotic (chilling) stress	Wei *et al.*, 2015

3	Freezing stress	*Arabidopsis*	BL is a basic helix-loop-helix transcriptional factor that regulates cold stress resistance genes	Eremina *et al.*, 2016
4	Chilling stress	Pepper	BL regulates thousands of genes in response to chilling stress	Li *et al.*, 2016
5	Chilling stress	Pepper	BL regulates thousands of genes in response to chilling stress	Li *et al.*, 2016

3.2. BL Response to Temperature Stresses

Table 3. BL response to various kinds of high-temperature stresses

S. No.	**Stress**	**Crop**	**Effect**	**Reference**
1	Heat stress	Tomato	BL increase basic thermos tolerance of germinating pollen	Singh & Shono, 2005
2	Thermo-tolerance	Tomato	BL significantly increase photosynthesis, chlorophyll, pollen germination % and bursting % yield and related parameters under heat stress	Mazorra *et al.*, 2011
3	High temperature	*Brassica*	Decreased lipid peroxidation, increased proline contents, and protected cell membrane by BL	Kumar & Manish, 2013
4	Heat stress	Rice	BL increase pollen fertility, germination rate and reduces the effect of heat stress	Fahad *et al.*, 2016
5	Heat drought	Wheat	BL increase photosynthetic capacity significantly by increasing RCA subunit and Rubisco activity under drought and heat stress	Zhao *et al.*, 2017

3.3. BL Response to Salt and Saline Stresses

Table 4. BL response to various kinds of salt and saline stresses

S, No.	**Stress**	**Plant**	**Effect**	**Reference**
1	Salinity	Mung bean	Increase plant growth parameters, membrane stability index, relative water contents, NR, CA activities, EC, H_2O_2 and chlorophyll SPAD by BL treatment under stress conditions	Hayat *et al.*, 2010
2	NaCl	Cucumber	BL reduce NaCl stress effect and increases germination, ACS and ACO gene expression (ethylene biosynthesis), and ACO activity	Wang *et al.*, 2011
3	Saline	Pigeon pea	BL increase NR activity, amino acid, protein contents, nutrient contents, and	Dalio *et al.*, 2013

			increases defence system	
4	Salinity	Potato	BL significantly enhance *in vitro* potato adventitious root growth, root length, root number, biomass, root activity, maintaining K^+/Na^+ homeostasis and antioxidant capacity	Hu *et al.,* 2016
5	Salinity	*Brassica juncea*	BL protect plants from salinity stress and enhances nitrogen, proline and ABA metabolism	Gupta *et al.,* 2017

3.4. BL Response to Heavy Metal Stresses

Table 5. BL response to various kinds of heavy metal stresses

S. No.	**Stress**	**Crop**	**Effect**	**Reference**
1	Cadmium	Tomato	BL play a protective role against Cadmium stress by increasing plant defense system and activating enzymes	Hasan *et al.,* 2011
2	Nikal	Wheat	BL enhance wheat seedling growth and related parameters, photosynthesis, chlorophyll, antioxidant enzymes capacity and activates enzymes	Yusuf *et al.,* 2011
3	Iron deficiency	Cucumber	BL regulate cucumber growth, stimulates ferric reductase activity (FRO), FRO1 and IRT1 (Fe transporters) gene expression and reduces Fe translocation from roots to shoots, reducing Fe deficiency effect	Wang *et al.,* 2012
4	Heavy metal	Maize	BL have a stimulating effect on seed germination and seedling growth. It reduces heavy metal-induced electrolyte leakage from maize cells	Lukatkin *et al.,* 2013
5	Lead	Fenugreek	BL improve plant growth, biomass, photosynthetic pigment, and reduces Pb toxic effect	Swamy *et al.,* 2014

4. BL MEDIATED BIOTIC STRESS MANAGEMENT

BL plays a pivotal role in enhancing plant immunity against a wide spectrum of biotic stressors, including fungi, bacteria, viruses, and insect pests. It acts as a hormonal priming agent, activating defence pathways and modulating gene expression to strengthen plant resilience. Recent reviews highlight BL's capacity to induce systemic resistance, regulate hormonal crosstalk, and promote structural and biochemical defences.

4.1 BL Response to Biotic Stresses

Table 5. BL Response to various kinds of Biotic Stresses

S. No.	**Pathogen**	**Crop**	**Effect**	**Reference**
1	*Fusarium oxysporum* (fungi)	*Cucumis sativus*	BL induced systemic resistance via ROS and defence gene expression	Xia *et al.,* 2011
2	*Fusarium culmorum* (Fungi)	Barely	BL reduced symptoms and enhanced antioxidant defence	Ali *et al.,* 2013
3	TMV (Tobacco mosaic virus)	*Nicotiana benthamiana*	BL receptor (NbBRI1) promotes defence, but overactivation of BES1 reduces resistance	Deng *et al.,* 2016
4	*Meloidogyne*	Tomato	BL signalling mutants were more	Kyndt *et al.,*

	incognita (Root-knot nematode)		susceptible	2017
5	Rice black-streaked dwarf virus (RBSDV)	Rice	BL-deficient mutants were more resistant	He *et al.*, 2020

5. BRASSINOLIDE IN PLANT GROWTH AND DEVELOPMENT

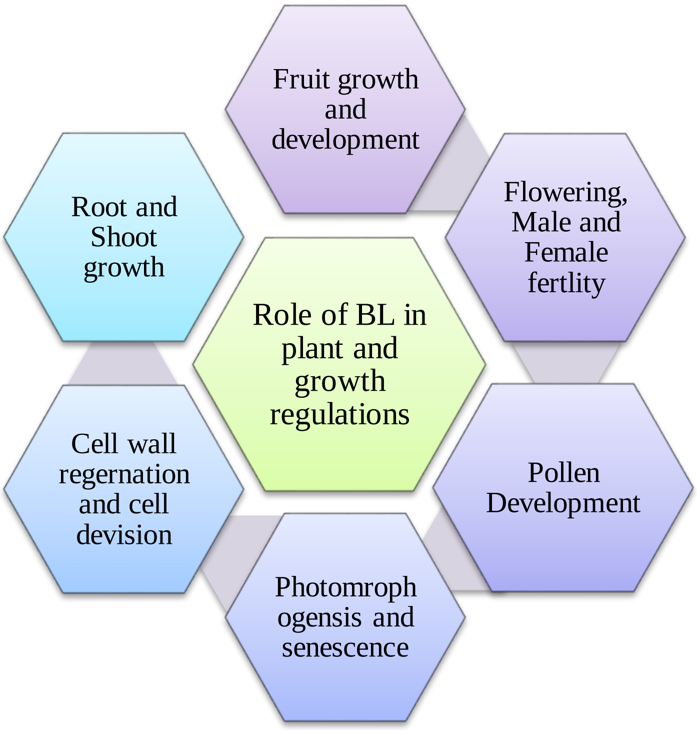

Figure 3. Role of BL in growth and development of plants.

BL are steroid hormones that play various roles in the growth and development of plants (Zhang *et al.*, 2023; Zhao & Li, 2012; He *et al.*, 2005). BL regulate various developmental and physiological processes in plants, such as expansion, cell division, stem cell maintenance, vascular development, elongation of different cell types, and floral transition (Wang *et al.*, 2020; Lv *et al.*, 2018; Singh & Savaldi-Goldstein, 2015; Fàbregas & Caño-Delgado, 2014). Moreover, they play diverse roles in hypocotyl elongation (Oh *et al.*, 2014), root growth (Planas-Riverola *et al.*, 2019; Hacham *et al.*, 2011), shoot growth (Bajguz *et al.*, 2020), stomata patterning (Khan *et al.*, 2013; Kim *et al.*, 2012), pollen tube growth, seed germination, and pollen germination and development (Vogler *et al.*, 2014), treachery element differentiation (Yamamoto *et al.*, 2001), xylem formation (Lee *et al.*, 2019; Saito *et al.*, 2018), xylem differentiation, photomorphogenesis and plant reproduction (Ahammed *et al.*, 2020; Nolan *et al.*, 2020), and senescence (Yin *et al.*, 2002). BL can activate the cell cycle during seed germination (Zadvornova *et al.*, 2005), regulate cell cycle progression (González-García *et al.*, 2011), control leaf cells' proliferation (Nakaya *et al.*, 2002), and induce excessive growth in hydroponically grown plants (Arteca & Arteca, 2001). BL also regulate the abiotic and biotic stress responses and stomata development (Ackerman & Goldstein, 2020; Lin, 2020; Riverola *et al.*, 2019). Moreover, BL plays a vital role in regulating male and female fertility in crops (Makarevitch *et al.*, 2012; Hartwig *et al.*, 2011). BL plays a role in etiolation and promotes the elongation of stigma (Li & He, 2020), plant architecture, thermos tolerance, proton transport, tiller number, leaf angle, and leaf size (Zhu *et al.*, 2015; Jaillais & Vert, 2012). In addition, the exogenous application of BL or alteration in their biosynthesis and signalling could improve crop yields (Jaiswal *et al.*, 2020; Divi & Krishna, 2009).

Priming of lucerne seeds with BL considerably increased length, vigour, and fresh and dry shoot and root weights (Zhang *et al.*, 2007). The application of BL promoted the ripening of grape berry (Xu *et al.*, 2015).

Treatment with BL was observed to substantially increase sucrose synthase (sucrolytic) and soluble sugar content in berries(Zhu *et al.*, 2015). Treatment with BL helped in reducing the decay of jujube fruits, likely due to its ability to postpone senescence and induce disease resistance (Zhu *et al.*, 2010). Additionally, in potato tubers, the BL have been shown to promote apical meristem growth (Meudt *et al.*, 1983), accelerating the cell division rate in isolated protoplasts of *Petunia hybrida* (Oh, 2003). In *Pharbitisnil*, CS and BL treatments inhibit flowering in combination with the inductive photoperiod, implying that BL works in tandem with environmental cues to ensure the proper reproductive transition (Li & He, 2020; Kęsy *et al.*, 2003).

BL can participate in physiological processes in response to stress by tuning plant growth and improving plant performance by interacting with plant growth regulators or other plant hormones (Trevisan *et al.*, 2020; Ahammed *et al.*, 2015). The disruption of BL signalling affects several developmental processes, including seed development (Jiang *et al.*, 2013), pollen development (Ye *et al.*, 2010), and flowering time (Domagalska *et al.*, 2010). Plants with BL deficiency are dwarf (Li *et al.*, 1996) and exhibit altered stomatal development (Gudesblat *et al.*, 2012; Kim *et al.*, 2012), reduced male fertility, shortened hypocotyls, petioles and internodes, downward curled leaves, and delayed flowering (Ye *et al.*, 2010). Moreover, BL deficient plants also have a compact plant structure because of the reduced lamina inclination. However, BL deficiency can reduce grain size, seed fertility and tiller number (Tong & Chu, 2018), improper stomatal distribution, and reduce seed germination (Zhu *et al.*, 2013). BR-insensitive and -deficient mutants are often referred to as late flowering due to their retarded growth (Zhao & Li, 2012; Clouse, 2008). In contrast, plants over accumulating BRs display elongation of petioles and hypocotyls and increased height (Rozhon *et al.*, 2019).

6. REGULATION OF DIFFERENT STRESS-RELATED GENES BY BL

Several studies have reported that BL regulate the expression of many genes in response to different stresses in various crops. Earlier studies have shown that BL play a positive role in drought tolerance in *Brassica napus*, *Arabidopsis thaliana*, and wheat (*Triticum aestivum* L.). (Kagale *et al.*, 2007). For example, overexpression of *A. thaliana* BR biosynthetic AtDWARF4 gene in *B. napus* increased drought resistance (Sahni *et al.*, 2016). In barley, the leaf disease at the tillering phase caused by *Helminthosporium teres* Sacc was reduced using 24 EBL (Hussain *et al.*, 2020). The application of BL has the potential to induce tolerance against various plant diseases caused by the Tobacco mosaic virus (TMV) in tobacco and *Xanthomonas oryzae* and *Maganoprothe grisea* in rice (Hussain *et al.*, 2020; Nakashita *et al.*, 2003). The use of BL has the potential to enhance defence against plant virus response by inducing several resistance genes and activating various vital antioxidant enzymes. BL signalling is required for BL-induced resistance to plant viruses. In response to Cucumber mosaic virus (CMV) infection, BL signalling can induce the expression of several resistance genes (Zhang *et al.*, 2015). Furthermore, in response to chilling stress in tomato, the BL regulate the NBR1-dependent selective autophagy in a BZR1-dependent manner (Chi *et al.*, 2020). The exogenous application of EBR and 28-homobrassinolide (HBL) has been shown to mitigate the harmful effects of heavy metals on plants (Zhou *et al.*, 2018; Soares *et al.*, 2016). Moreover, Exogenous application of BL was observed to increase pepper tolerance against low-temperature stress (Huang *et al.*, 2016).

Table 6: Regulation of different stress-related genes by BL.

S. No.	Gene	Function of gene	Crop	Stress	Reference
1.	*DREB*	Involved in regulating various cold stress-responsive genes	Rice	Cold stress	Kagale *et al.*, 2007; Xiao *et al.*, 2009
2.	Proline-5-caryboxylate synthetase 1 (*P5CS1*)	Involved in the proline biosynthesis	*Arabidopsis thaliana*	Salt stress	Zeng *et al.*, 2010
3.	Respiratory	Involved in ROS	Tomato	Heat	Zhou *et al.*,

	burst oxidase homolog 1 (*RBOH1*)	generation		tolerance	2014
4.	*bes1-D*	BRI1 EMS SUPRESSOR 1	*Arabidopsis thaliana*	*Cucumber mosaic virus* (CMV)	Zhang *et al.,* 2015
5.	*WRKY*	Involved in regulating various stress-responsive genes	*Arabidopsis thaliana*	Drought stress	Chen *et al.*, 2017

7. CROSSTALK BETWEEN BL AND OTHER HORMONES

BL are a group of polyhydroxylated phytosterols that play essential roles in regulating plant growth and development as well as stress adaptation. It is worth noting that BL do not function alone, but rather they crosstalk with other endogenous signalling molecules, including the phytohormones Auxin, Cytokinins, Gibberellins, Abscisic acid, Ethylene, Jasmonates, Salicylic acid and Strigolactones, forming elaborate signalling networks to modulate plant growth and development.

7.1. Crosstalk between BL and Auxin

Auxin is a growth-promoting phytohormone that plays essential roles throughout the life cycle of a plant (Zhang *et al*., 2022). The interaction between BL and auxin in plant growth and stress adaptations is complex, involving synergistic or antagonistic regulatory mechanisms (Hirano *et al*., 2017; Chaiwanon & Wang, 2015). BL can regulate the biosynthesis, polar transport or signalling pathway of auxin (Bao *et al.*, 2004; Nakamura *et al.*, 2003). Under mild nitrogen (N) deficiency, increased BL signalling induces expression of auxin biosynthesis genes, including TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS 1 (TAA1) and YUCCA5/7/8 (YUC5/7/8) via BZR1, further promoting the higher accumulation of auxin in the apical meristem of lateral roots (LRs) to modulate LR elongation (Jia *et al.*, 2021). Interestingly, BL have dual effects on auxin in the same tissue; they can increase auxin levels by upregulating the expression of auxin biosynthesis genes, such as YUC9, and simultaneously inhibit auxin signal output in the root apical meristem(Ackerman-Lavert *et al.*, 2021).

BL modulate late auxin accumulation in a site-specific manner. For example, BL signalling in the epidermis of root meristem zone elevates the expression levels of several auxin biosynthesis genes, such as YUC3, YUC9 and TAA1, causing higher auxin accumulation. Conversely, BL signalling in the stele of meristem zone represses the expression of auxin biosynthesis genes (Vragović *et al.*, 2015). Exogenous application of BL promotes the expression of RHO-RELATED PROTEIN FROM PLANTS 2 (ROP2), leading to the accumulation of PIN-FORMED 2 (PIN2) that mediates polar auxin transport (Li *et al.*, 2005).

7.2. Crosstalk between BL and Cytokinin

Cytokinin (CKs) play essential roles in almost every aspect of plant growth and development, including cell division and differentiation, organogenesis, leaf senescence, nutrient uptake and stress responses (Lin *et al.*, 2021; Kieber & Schaller, 2018). Exogenous application of 24-epibrassinolide (EBL) increases the accumulation of CKs by inhibiting the transcription levels of CYTOKININ OXIDASE 3 (CKX3) gene, which is responsible for CK degradation (Yuldashev *et al*., 2012). PROTEIN PHOSPHATASE WITH KELCH-LIKE DOMAINS 1 (PPKL1), which is considered a regulatory component of the BL signalling, competes with OsARR21 for the interaction with OsAHP2, hence inhibiting the OsAHP2-to-OsARR21 phosphorelay and attenuating the CK responses (Liu *et al.*, 2022). Additional interactions between BL and CKs have not been well elucidated, possibly due to the high redundancy of CK signalling components.

7.3. Crosstalk between BL and Gibberellic acid

Gibberellic acid (GAs) plays a fundamental role in a wide range of developmental processes, such as seed germination, stem elongation, pollen maturation and leaf and flower development. (Achard & Genschik, 2009). BL and GAs synergistically function in a series of physiological processes such as seed germination, apical hook development and resistance to zinc toxicity (Ren *et al*., 2023; Xiong *et al*., 2022; Zhao *et al.*, 2021). Under normal growth conditions, BL enhance the expression of GAs biosynthesis genes such as GIBBERELLIN 20-OXIDASE 1 (GA20ox1) and GA3ox2 via BES1/BZR1, resulting in higher accumulation of GAs (Tong *et al*., 2014; Unterholzner *et al*., 2015).

In rice, however, BL reduce GAs levels by increasing its metabolism via GA2ox3 activation and reducing its biosynthesis via GA20ox3 repression, in response to the root oomycete *Pythium graminicola* (Vleesschauwer *et al.*, 2012). Additionally, BL negatively regulate GA biosynthesis by inhibiting the expression of SlGA20ox1 in tomato ovaries (BarroTrastoy *et al.*, 2020). BL regulated transcription factors, CESTA (AtCES) in *Arabidopsis* and SlCES in *Solanum lycopersicum*, can also induce GA catabolism (Albertos *et al.*, 2022; Shuai *et al.*, 2022).

7.4. Crosstalk between BL and Abscisic acid

Abscisic acid (ABA) is widely considered a plant stress hormone as it plays a pivotal role in orchestrating growth and adaptation to stress conditions (Yang *et al.*, 2022). Under normal conditions, BL antagonistically interact with ABA. Exogenous BL treatment can reduce ABA levels by downregulating the transcription of ABA biosynthesis genes (Ha *et al.*, 2018). For instance, BZR1 binds to the promoter of ABA-DEFICIENT 2 (ABA2) to hamper its expression and downregulate ABA accumulation (Moon *et al.*, 2021). By contrast, BIN2 phosphorylates and activates SnRK2s, including SnRK2.2 and SnRK2.3, to promote ABA responses (Cai *et al.*, 2014). Moreover, BIN2 phosphorylates and stabilises ABA-responsive factor ABA INSENSITIVE 5 (ABI5) to amplify ABA signalling (Hu & Yu, 2014).

7.5. Crosstalk between BL and Ethylene

Ethylene (ET) is a simple gaseous hormone that not only modulates many vital cellular processes, including seed germination, fruit ripening and senescence, but also enhances plant tolerance to heavy metals, drought and flood (Fatma *et al*., 2022). BL influence ethylene biosynthesis in a concentration-dependent manner (Lv *et al*., 2018). Exogenous application of high levels of BL can induce higher formation of ET by increasing the stability and activity of 1-AMINOCYCLOPROPANE 1-CARBOXYLATE (ACC) SYNTHASES (ACSs) and ACC OXIDASES (ACOs), both of which are the key enzymes in the ethylene biosynthetic pathway (Wei *et al.*, 2015; Wang *et al.*, 2011; Hansen *et al.*, 2009). Similarly, overexpression of the BL receptor SlBRI1 can also enhance the transcript abundance of SlACSs and SlACOs in *S. lycopersicum*, promoting ET production (Nie *et al.*, 2017). Consistently, ACS expression is repressed in the BR-deficient mutant det2, resulting in lower accumulation of ET (Li & He, 2016). However, exogenous treatment with a low concentration of BL attenuates the biosynthesis of ET (Ma *et al*., 2021; Lv *et al.*, 2018). BL-activated BZR1 directly binds to the promoter of ACSs and ACOs to inhibit their transcription, resulting in decreased ET production (Guo *et al.*, 2019; Lv *et al.*, 2018).

ET also influences BL signalling by modulating the expression of key enzymes in the BL biosynthetic pathway. Exogenous application of ACC, the precursor of ET, upregulates the transcription of the BL biosynthesis gene CPD, resulting in an accumulation of BL and enhanced BL signalling (De Grauwe *et al.*, 2005).

7.6. Crosstalk between BL and Jasmonic acid

Jasmonic acid (JAs) are a class of key lipid-derived phytohormones, regulating various developmental processes including apical hook formation, root growth and seedling photomorphogenesis, as well as defence responses such as pathogen resistance, insect defence and mechanical wounding (Hu *et al.*, 2023; Zhang *et al.*, 2023). A mutually antagonistic interaction occurs between BL and JAs by repressing one another's biosynthesis and signal transduction. BL-activated BES1 inhibits the JA signalling pathway by interacting with JA-induced transcription factors MYB34, MYB51 and MYB122 (Liao *et al.*, 2020). A rice GSK3-like kinase, OsGSK2, a key suppressor of BL signalling, activates JA responses by phosphorylating and degrading OsJAZ4, a key negative regulator of JA signalling (He *et al.*, 2020). However, BL interact synergistically with JAs in response to virus infection. After rice stripe virus (RSV) infection, accumulated OsGSK2 directly interacts with MYC2 to trigger its degradation, reducing the JA mediated RSV resistance response (Hu *et al*., 2020).

In rice, exogenous application of MeJA, a derivative of JAs, significantly decreases the transcript abundance of BL-related genes, including D11, OsDWARF4, D2, OsCPDs, OsBRI1 and OsBAK1 in an OsCOI1-dependent manner (He *et al*., 2017).

7.7. Crosstalk between BL and Strigolactone

Strigolactone (SLs) are a group of terpenoid phytohormones responsible for a wide range of developmental processes, especially the branching of shoots, and responses to stresses (Korek & Marzec, 2023). BL and SLs function antagonistically to govern many physiological processes. BES1/BZR1 mediates the interplay between BL and SLs via direct protein–protein interactions. For example, OsBZR1 directly interacts with

D53 to synergistically inhibit FC1 expression, thereby facilitating tillering in rice (Fang *et al.*, 2020). MAX2 directly interacts with BES1 and triggers its degradation, downregulating BL signalling. This process is promoted by GR24, a synthetic analogue of SLs (Wang *et al.*, 2013).

7.8. Crosstalk between BL and Salicylic acid

Salicylic acid (SA) is a major plant hormone responsible for activating immune responses against pathogens and for mediating systemic acquired resistance (Park *et al.*, 2007; Shigenaga *et al.*, 2017). Accumulating evidence indicates that BL antagonise SA action in defence responses. BL decrease SA concentrations by reducing transcript levels of SA biosynthesis genes, such as ISOCHORISMATE SYNTHASE 1 (OsICS1) and PHENYLALANINE AMMONIA LYASE (OsPAL) (Pan *et al.*, 2018). BL interfere with SA signalling by downregulating the expression of the master SA regulators OsNPR1 and OsWRKY45 in rice (Vleesschauwer *et al.*, 2012). Recent study suggested that BL cooperatively regulate the protein stability of key SA signalling components such as TGA4. BIN2 phosphorylates and destabilises TGA4, interfering with the formation of active complexes of NPR1 and TGA4, thereby decreasing SA responses (Kim *et al.*, 2022).

Table 7- Crosstalk Interactions of BL with Other Hormones

S. No.	**Type of hormone that interacts with BL**	**Interaction type**	**Functional outcome**	**Reference**
1.	Auxin	synergistic or antagonistic regulatory mechanisms	plant growth, development, and environmental adaptation.	Bao *et al.*, 2004; Nakamura *et al.*, 2003
2.	Cytokinin	synergistic, antagonistic, or context-dependent	plant growth, organ development, meristem activity, and stress responses.	Kieber & Schaller, 2018; Lin *et al.*, 2021
3.	Gibberellic acid	synergistic, context-dependent	positive regulators of cell elongation and expansion	Ren *et al.*, 2023; Xiong *et al.*, 2022; N. Zhao *et al.*, 2021
4.	Abscisic acid	antagonistic	growth regulation and stress response	Yang *et al.*, 2022
5.	Ethylene	context-dependent	Plant growth, development, senescence, and stress responses	Fatma *et al.*, 2022
6	Jasmonic acid	antagonistic	growth–defense balance, development, and stress responses.	Hu *et al.*, 2023; Zhang *et al.*, 2023
7	Strigolactone	antagonistic, but it can also be context-dependent, based	shoot branching, root architecture, developmental plasticity, and stress responses	Korek & Marzec, 2023
8	Salicylic acid	antagonistic	defence against biotrophic pathogens, stress tolerance.	Park *et al.*, 2007; Shigenaga *et al.*, 2017.

CONCLUSION

BL, an essential member of the BR class of plant hormones, plays a complex and integrated role in boosting plant resilience under various abiotic and biotic stresses. Its capacity to adjust physiological, biochemical, and molecular responses gives plants a strong defence system to reduce stress-related damage. Applying BL externally has been demonstrated to improve photosynthesis, enhance antioxidant enzyme activities, increase osmolyte levels, and activate stress-responsive genes, thereby supporting overall plant health and yield in stressful conditions. Additionally, BL works synergistically with other hormones and signalling pathways, strengthening its key role in stress signal networks. As climate change and environmental stresses threaten global agriculture, using BL strategically in crop management offers a promising route for sustainable farming. Future studies should aim to understand its specific signalling mechanisms, optimal doses, and how different plant varieties respond, to maximise its effectiveness across various agricultural systems.

CRediT authorship contribution statement

Harshita Saini: Writing–original draft, Visualization, Validation. Suresh Chand Mali: Writing–original draft, Visualization, Validation, Resources, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. Anita Dhaka and Sheetal Sharma: Investigation, Data curation, Conceptualization. Rohini Trivedi: Investigation, editing, Writing–original draft, Validation administration, Conceptualization.

REFERENCES:

1. Abe, H., Morishita, T., Uchiyama, M., Takatsuto, S., Ikekawa, N., Ikeda, M., Sassa, T., Kitsuwa, T., & Marumo, S. (1983). Occurrence of three new brassinosteroids: brassinone, (24S)-24-ethylbrassinone and 28-norbrassinolide, in higher plants. *Experientia*, *39*(4), 351–353.
2. Achard, P., & Genschik, P. (2009). Releasing the brakes of plant growth: how GAs shut down DELLA proteins. *Journal of Experimental Botany*, *60*(4), 1085–1092.
3. Ackerman-Lavert, M., Fridman, Y., Matosevich, R., Khandal, H., Friedlander-Shani, L., Vragović, K., El, R. Ben, Horev, G., Tarkowská, D., & Efroni, I. (2021). Auxin requirements for a meristematic state in roots depend on a dual brassinosteroid function. *Current Biology*, *31*(20), 4462–4472.
4. Ackerman-Lavert, M., & Savaldi-Goldstein, S. (2020). Growth models from a brassinosteroid perspective. *Current Opinion in Plant Biology*, *53*, 90–97.
5. Ahammed, G. J., Li, X., Liu, A., & Chen, S. (2020). Brassinosteroids in plant tolerance to abiotic stress. *Journal of Plant Growth Regulation*, *39*(4), 1451–1464.
6. Ahammed, G. J., Li, X., Xia, X.-J., Shi, K., Zhou, Y.-H., & Yu, J.-Q. (2015). Enhanced photosynthetic capacity and antioxidant potential mediate brassinosteroid-induced phenanthrene stress tolerance in tomato. *Environmental Pollution*, *201*, 58–66.
7. Albertos, P., Wlk, T., Griffiths, J., Pimenta Lange, M. J., Unterholzner, S. J., Rozhon, W., Lange, T., Jones, A. M., & Poppenberger, B. (2022). Brassinosteroid-regulated bHLH transcription factor CESTA induces the gibberellin 2-oxidase GA2ox7. *Plant Physiology*, *188*(4), 2012–2025.
8. Ali, S. S., Kumar, G. B. S., Khan, M., & Doohan, F. M. (2013). Brassinosteroid enhances resistance to *fusarium* diseases of barley. *Phytopathology*, *103*(12), 1260–1267.
9. Arteca, J. M., & Arteca, R. N. (2001). Brassinosteroid-induced exaggerated growth in hydroponically grown Arabidopsis plants. *Physiologia Plantarum*, *112*(1), 104–112.
10. Bajguz, A., Chmur, M., & Gruszka, D. (2020). Comprehensive overview of the brassinosteroid biosynthesis pathways: substrates, products, inhibitors, and connections. *Frontiers in Plant Science*, *11*, 1034.
11. Bao, F., Shen, J., Brady, S. R., Muday, G. K., Asami, T., & Yang, Z. (2004). Brassinosteroids interact with auxin to promote lateral root development in Arabidopsis. *Plant Physiology*, *134*(4), 1624–1631.
12. Barro-Trastoy, D., Carrera, E., Baños, J., Palau-Rodríguez, J., Ruiz-Rivero, O., Tornero, P., Alonso, J. M., López-Díaz, I., Gómez, M. D., & Pérez-Amador, M. A. (2020). Regulation of

ovule initiation by gibberellins and brassinosteroids in tomato and Arabidopsis: two plant species, two molecular mechanisms. *The Plant Journal*, *102*(5), 1026–1041.

13. Cai, Z., Liu, J., Wang, H., Yang, C., Chen, Y., Li, Y., Pan, S., Dong, R., Tang, G., & Barajas-Lopez, J. de D. (2014). GSK3-like kinases positively modulate abscisic acid signalling through phosphorylating subgroup III SnRK2s in Arabidopsis. *Proceedings of the National Academy of Sciences*, *111*(26), 9651–9656.
14. Chaiwanon, J., & Wang, Z.-Y. (2015). Spatiotemporal brassinosteroid signalling and antagonism with auxin pattern stem cell dynamics in Arabidopsis roots. *Current Biology*, *25*(8), 1031–1042.
15. Chen, J., Nolan, T. M., Ye, H., Zhang, M., Tong, H., Xin, P., Chu, J., Chu, C., Li, Z., & Yin, Y. (2017). Arabidopsis WRKY46, WRKY54, and WRKY70 transcription factors are involved in brassinosteroid-regulated plant growth and drought responses. *The Plant Cell*, *29*(6), 1425–1439.
16. Chi, C., Li, X., Fang, P., Xia, X., Shi, K., Zhou, Y., Zhou, J., & Yu, J. (2020). Brassinosteroids act as a positive regulator of NBR1-dependent selective autophagy in response to chilling stress in tomato. *Journal of Experimental Botany*, *71*(3), 1092–1106.
17. Clouse, S. D. (2008). The molecular intersection of brassinosteroid-regulated growth and flowering in Arabidopsis. *Proceedings of the National Academy of Sciences*, *105*(21), 7345–7346.
18. Dalio, R. J. D., Pinheiro, H. P., Sodek, L., & Haddad, C. R. B. (2013). 24-epibrassinolide restores nitrogen metabolism of pigeon pea under saline stress. *Botanical Studies*, *54*(1), 9.
19. De Grauwe, L., Vandenbussche, F., Tietz, O., Palme, K., & Van Der Straeten, D. (2005). Auxin, ethylene and brassinosteroids: tripartite control of growth in the Arabidopsis hypocotyl. *Plant and Cell Physiology*, *46*(6), 827–836.
20. De Vleesschauwer, D., Van Buyten, E., Satoh, K., Balidion, J., Mauleon, R., Choi, I.-R., Vera-Cruz, C., Kikuchi, S., & Höfte, M. (2012). Brassinosteroids antagonise gibberellin-and salicylate-mediated root immunity in rice. *Plant Physiology*, *158*(4), 1833–1846.
21. Deng, X.-G., Zhu, T., Peng, X.-J., Xi, D.-H., Guo, H., Yin, Y., Zhang, D.-W., & Lin, H.-H. (2016). Role of brassinosteroid signalling in modulating Tobacco mosaic virus resistance in *Nicotiana benthamiana*. *Scientific Reports*, *6*(1), 20579.
22. Divi, U. K., & Krishna, P. (2009). Brassinosteroid: a biotechnological target for enhancing crop yield and stress tolerance. *New Biotechnology*, *26*(3–4), 131–136.
23. Domagalska, M. A., Sarnowska, E., Nagy, F., & Davis, S. J. (2010). Genetic analyses of interactions among gibberellin, abscisic acid, and brassinosteroids in the control of flowering time in *Arabidopsis thaliana*. *PloS One*, *5*(11), e14012.
24. Eremina, M., Unterholzner, S. J., Rathnayake, A. I., Castellanos, M., Khan, M., Kugler, K. G., May, S. T., Mayer, K. F. X., Rozhon, W., & Poppenberger, B. (2016). Brassinosteroids participate in the control of basal and acquired freezing tolerance of plants. *Proceedings of the National Academy of Sciences*, *113*(40), E5982–E5991.
25. Fàbregas, N., & Caño-Delgado, A. I. (2014). Turning on the microscope turret: a new view for the study of brassinosteroid signalling in plant development. *Physiologia Plantarum*, *151*(2), 172–183.
26. Fahad, S., Hussain, S., Saud, S., Khan, F., Hassan, S., Amanullah, Nasim, W., Arif, M., Wang, F., & Huang, J. (2016). Exogenously applied plant growth regulators affect heat-stressed rice pollens. *Journal of Agronomy and Crop Science*, *202*(2), 139–150.
27. Fang, Z., Ji, Y., Hu, J., Guo, R., Sun, S., & Wang, X. (2020). Strigolactones and brassinosteroids antagonistically regulate the stability of the D53–OsBZR1 complex to determine FC1 expression in rice tillering. *Molecular Plant*, *13*(4), 586–597.
28. Fatma, M., Asgher, M., Iqbal, N., Rasheed, F., Sehar, Z., Sofo, A., & Khan, N. A. (2022). Ethylene signalling under stressful environments: analysing collaborative knowledge. *Plants*, *11*(17), 2211.
29. Fujioka, S., Choi, Y.-H., Takatsuto, S., Yokota, T., Li, J., Chory, J., & Sakurai, A. (1996a). Identification of castasterone, 6-deoxocastasterone, typhasterol and 6-deoxotyphasterol from the shoots of *Arabidopsis thaliana*. *Plant and Cell Physiology*, *37*(8), 1201–1203.

30. Fujioka, S., & Sakurai, A. (1997). Brassinosteroids. *Natural Product Reports*, *14*(1), 1–10.
31. Fujioka, S., & Yokota, T. (2003). Biosynthesis and metabolism of brassinosteroids. *Annual Review of Plant Biology*, *54*(1), 137–164.
32. González-García, M.-P., Vilarrasa-Blasi, J., Zhiponova, M., Divol, F., Mora-García, S., Russinova, E., & Caño-Delgado, A. I. (2011). Brassinosteroids control meristem size by promoting cell cycle progression in Arabidopsis roots. *Development*, *138*(5), 849–859.
33. Grove, M. D., Spencer, G. F., Rohwedder, W. K., Mandava, N., Worley, J. F., Warthen Jr, J. D., Steffens, G. L., Flippen-Anderson, J. L., & Cook Jr, J. C. (1979). Brassinolide, a plant growth-promoting steroid isolated from *Brassica napus* pollen. *Nature*, *281*(5728), 216–217.
34. Gudesblat, G. E., Schneider-Pizoń, J., Betti, C., Mayerhofer, J., Vanhoutte, I., Van Dongen, W., Boeren, S., Zhiponova, M., De Vries, S., & Jonak, C. (2012). SPEECHLESS integrates brassinosteroid and stomata signalling pathways. *Nature Cell Biology*, *14*(5), 548–554.
35. Guo, Y., Shan, W., Liang, S., Wu, C., Wei, W., Chen, J., Lu, W., & Kuang, J. (2019). MaBZR1/2 act as transcriptional repressors of ethylene biosynthetic genes in banana fruit. *Physiologia Plantarum*, *165*(3), 555–568.
36. Gupta, P., Srivastava, S., & Seth, C. S. (2017). 24-Epibrassinolide and sodium nitroprusside alleviate the salinity stress in *Brassica juncea* L. cv. Varuna through cross-talk among proline, nitrogen metabolism and abscisic acid. *Plant and Soil*, *411*(1), 483–498.
37. Ha, Y. M., Shang, Y., Yang, D., & Nam, K. H. (2018). Brassinosteroid reduces ABA accumulation, leading to the inhibition of ABA-induced stomatal closure. *Biochemical and Biophysical Research Communications*, *504*(1), 143–148.
38. Hacham, Y., Holland, N., Butterfield, C., Ubeda-Tomas, S., Bennett, M. J., Chory, J., & Savaldi-Goldstein, S. (2011). Brassinosteroid perception in the epidermis controls root meristem size. *Development*, *138*(5), 839–848.
39. Hansen, M., Chae, H. S., & Kieber, J. J. (2009). Regulation of ACS protein stability by cytokinin and brassinosteroid. *The Plant Journal*, *57*(4), 606–614.
40. Hartwig, T., Chuck, G. S., Fujioka, S., Klempien, A., Weizbauer, R., Potluri, D. P. V, Choe, S., Johal, G. S., & Schulz, B. (2011). Brassinosteroid control of sex determination in maize. *Proceedings of the National Academy of Sciences*, *108*(49), 19814–19819.
41. Hasan, S. A., Hayat, S., & Ahmad, A. (2011). Brassinosteroids protect photosynthetic machinery against the cadmium-induced oxidative stress in two tomato cultivars. *Chemosphere, 84*(10), 1446–1451.
42. Hayat, S., Hasan, S. A., Yusuf, M., Hayat, Q., & Ahmad, A. (2010). Effect of 28-homobrassinolide on photosynthesis, fluorescence and antioxidant system in the presence or absence of salinity and temperature in *Vigna radiata. Environmental and Experimental Botany*, *69*(2), 105–112.
43. He, J.-X., Gendron, J. M., Sun, Y., Gampala, S. S. L., Gendron, N., Sun, C. Q., & Wang, Z.-Y. (2005). BZR1 is a transcriptional repressor with dual roles in brassinosteroid homeostasis and growth responses. *Science*, *307*(5715), 1634–1638.
44. He, L., Chen, X., Yang, J., Zhang, T., Li, J., Zhang, S., Zhong, K., Zhang, H., Chen, J., & Yang, J. (2020). Rice black-streaked dwarf virus-encoded P5-1 regulates the ubiquitination activity of SCF E3 ligases and inhibits jasmonate signalling to benefit its infection in rice. *New Phytologist*, *225*(2), 896–912.
45. He, Y., Hong, G., Zhang, H., Tan, X., Li, L., Kong, Y., Sang, T., Xie, K., Wei, J., & Li, J. (2020). The OsGSK2 kinase integrates brassinosteroid and jasmonic acid signalling by interacting with OsJAZ4. *Plant Cell*, *32*(9), 2806–2822.
46. He, Y., Zhang, H., Sun, Z., Li, J., Hong, G., Zhu, Q., Zhou, X., MacFarlane, S., Yan, F., & Chen, J. (2017). Jasmonic acid-mediated defence suppresses brassinosteroid-mediated susceptibility to Rice black streaked dwarf virus infection in rice. *New Phytologist*, *214*(1), 388–399.
47. Hirano, K., Yoshida, H., Aya, K., Kawamura, M., Hayashi, M., Hobo, T., Sato-Izawa, K., Kitano, H., Ueguchi-Tanaka, M., & Matsuoka, M. (2017). SMALL ORGAN SIZE 1 and

SMALL ORGAN SIZE 2/DWARF AND LOW-TILLERING form a complex to integrate auxin and brassinosteroid signalling in rice. *Molecular Plant*, *10*(4), 590–604.

48. Hu, J., Huang, J., Xu, H., Wang, Y., Li, C., Wen, P., You, X., Zhang, X., Pan, G., & Li, Q. (2020). Rice stripe virus suppresses jasmonic acid-mediated resistance by hijacking brassinosteroid signalling pathway in rice. *PLoS Pathogens*, *16*(8), e1008801.
49. Hu, S., Yu, K., Yan, J., Shan, X., & Xie, D. (2023). Jasmonate perception: ligand–receptor interaction, regulation, and evolution. *Molecular Plant*, *16*(1), 23–42.
50. Hu, Y., Xia, S., Su, Y., Wang, H., Luo, W., Su, S., & Xiao, L. (2016). Brassinolide increases potato root growth in vitro in a dose-dependent way and alleviates salinity stress. *BioMed Research International*, *2016*(1), 8231873.
51. Hu, Y., & Yu, D. (2014). BRASSINOSTEROID INSENSITIVE2 interacts with ABSCISIC ACID INSENSITIVE5 to mediate the antagonism of brassinosteroids to abscisic acid during seed germination in Arabidopsis. *The Plant Cell*, *26*(11), 4394–4408.
52. Huang, Y., Zhao, L., Kong, Q., Cheng, F., Niu, M., Xie, J., Nawaz, M. A., & Bie, Z. (2016). Comprehensive mineral nutrition analysis of watermelon grafted onto two different rootstocks. *Horticultural Plant Journal*, *2*(2), 105–113.
53. Hussain, M. A., Fahad, S., Sharif, R., Jan, M. F., Mujtaba, M., Ali, Q., Ahmad, A., Ahmad, H., Amin, N., & Ajayo, B. S. (2020). Multifunctional role of brassinosteroid and its analogues in plants. *Plant Growth Regulation*, *92*(2), 141–156.
54. IKEKAWA, N., NISHIYAMA, F., & FUJIMOTO, Y. (1988). Identification of 24-epibrassinolide in bee pollen of the broad bean, *Vicia faba* L. *Chemical and Pharmaceutical Bulletin*, *36*(1), 405–407.
55. Ikekawa, N., Takatsuto, S., Kitsuwa, T., Saito, H., Morishita, T., & Abe, H. (1984). Analysis of natural brassinosteroids by gas chromatography and gas chromatography—mass spectrometry. *Journal of Chromatography A*, *290*, 289–302.
56. Jaillais, Y., & Vert, G. (2012). Brassinosteroids, gibberellins and light-mediated signalling are the three-way controls of plant sprouting. *Nature Cell Biology*, *14*(8), 788–790.
57. Jaiswal, S., Båga, M., & Chibbar, R. N. (2020). Brassinosteroid receptor mutation influences starch granule size distribution in barley grains. *Plant Physiology and Biochemistry*, *154*, 369–378.
58. Jia, Z., Giehl, R. F. H., & von Wirén, N. (2021). Local auxin biosynthesis acts downstream of brassinosteroids to trigger root foraging for nitrogen. *Nature Communications*, *12*(1), 5437.
59. Jiang, W.-B., Huang, H.-Y., Hu, Y.-W., Zhu, S.-W., Wang, Z.-Y., & Lin, W.-H. (2013). Brassinosteroid regulates seed size and shape in Arabidopsis. *Plant Physiology*, *162*(4), 1965–1977.
60. Jing, T., Wu, Y., Yu, Y., Li, J., Mu, X., Xu, L., Wang, X., Qi, G., Tang, J., & Wang, D. (2024). Copine proteins are required for brassinosteroid signalling in maize and Arabidopsis. *Nature Communications*, *15*(1), 2028.
61. Kagale, S., Divi, U. K., Krochko, J. E., Keller, W. A., & Krishna, P. (2007). Brassinosteroid confers tolerance in *Arabidopsis thaliana* and *Brassica napus* to a range of abiotic stresses. *Planta*, *225*(2), 353–364.
62. Kęsy, J., Trzaskalska, A., Galoch, E., & Kopcewicz, J. (2003). Inhibitory effect of brassinosteroids on the flowering of the short-day plant *Pharbitis nil*. *Biologia Plantarum*, *47*(4), 597–600.
63. Khan, M., Rozhon, W., Bigeard, J., Pflieger, D., Husar, S., Pitzschke, A., Teige, M., Jonak, C., Hirt, H., & Poppenberger, B. (2013). Brassinosteroid-regulated GSK3/Shaggy-like kinases phosphorylate mitogen-activated protein (MAP) kinase kinases, which control stomata development in *Arabidopsis thaliana*. *Journal of Biological Chemistry*, *288*(11), 7519–7527.
64. Kieber, J. J., & Schaller, G. E. (2018). Cytokinin signalling in plant development. *Development*, *145*(4), dev149344.
65. Kim, T.-W., Guan, S., Sun, Y., Deng, Z., Tang, W., Shang, J.-X., Sun, Y., Burlingame, A. L., & Wang, Z.-Y. (2009). Brassinosteroid signal transduction from cell-surface receptor kinases to nuclear transcription factors. *Nature Cell Biology*, *11*(10), 1254–1260.

66. Kim, T.-W., Michniewicz, M., Bergmann, D. C., & Wang, Z.-Y. (2012). Brassinosteroid regulates stomatal development by GSK3-mediated inhibition of a MAPK pathway. *Nature*, *482*(7385), 419–422.
67. Kim, Y.-W., Youn, J.-H., Roh, J., Kim, J.-M., Kim, S.-K., & Kim, T.-W. (2022). Brassinosteroids enhance salicylic acid-mediated immune responses by inhibiting BIN2 phosphorylation of clade I TGA transcription factors in Arabidopsis. *Molecular Plant*, *15*(6), 991–1007.
68. Korek, M., & Marzec, M. (2023). Strigolactones and abscisic acid interactions affect plant development and response to abiotic stresses. *BMC Plant Biology*, *23*(1), 314.
69. Kour, J., Kohli, S. K., Khanna, K., Bakshi, P., Sharma, P., Singh, A. D., Ibrahim, M., Devi, K., Sharma, N., & Ohri, P. (2021). Brassinosteroid signalling, crosstalk and physiological functions in plants under heavy metal stress. *Frontiers in Plant Science*, *12*, 608061.
70. Kumar, P. S., & Manish, K. (2013). Effect of 24-Epibrassinolide on lipid peroxidation and proline in three *Brassica* species under temperature stress. *Journal of Stress Physiology & Biochemistry*, *9*(3), 376–384.
71. Kyndt, T., Zemene, H. Y., Haeck, A., Singh, R., De Vleesschauwer, D., Denil, S., De Meyer, T., Höfte, M., Demeestere, K., & Gheysen, G. (2017). Below-ground attack by the root knot nematode *Meloidogyne graminicola* predisposes rice to blast disease. *Molecular Plant-Microbe Interactions*, *30*(3), 255–266.
72. Lee, J., Han, S., Lee, H.-Y., Jeong, B., Heo, T.-Y., Hyun, T. K., Kim, K., Je, B. Il, Lee, H., & Shim, D. (2019). Brassinosteroids facilitate xylem differentiation and wood formation in tomato. *Planta*, *249*(5), 1391–1403.
73. Li, J., Nagpal, P., Vitart, V., McMorris, T. C., & Chory, J. (1996). A role for brassinosteroids in light-dependent development of Arabidopsis. *Science*, *272*(5260), 398–401.
74. Li, J., Yang, P., Kang, J., Gan, Y., Yu, J., Calderón-Urrea, A., Lyu, J., Zhang, G., Feng, Z., & Xie, J. (2016). Transcriptome analysis of pepper (*Capsicum annuum*) revealed a role of 24-epibrassinolide in response to chilling. *Frontiers in Plant Science*, *7*, 1281.
75. Li, L., Xu, J., Xu, Z.-H., & Xue, H.-W. (2005). Brassinosteroids stimulate plant tropisms through modulation of polar auxin transport in *Brassica* and *Arabidopsis*. *The Plant Cell*, *17*(10), 2738–2753.
76. Li, Q.-F., & He, J.-X. (2016). BZR1 interacts with HY5 to mediate brassinosteroid-and light-regulated cotyledon opening in Arabidopsis in darkness. *Molecular Plant*, *9*(1), 113–125.
77. Li, Z., & He, Y. (2020a). Roles of brassinosteroids in plant reproduction. *International Journal of Molecular Sciences*, *21*(3), 872.
78. Li, Z., & He, Y. (2020b). Roles of brassinosteroids in plant reproduction. *International Journal of Molecular Sciences*, *21*(3), 872.
79. Liao, K., Peng, Y.-J., Yuan, L.-B., Dai, Y.-S., Chen, Q.-F., Yu, L.-J., Bai, M.-Y., Zhang, W.-Q., Xie, L.-J., & Xiao, S. (2020). Brassinosteroids antagonise jasmonate-activated plant defence responses through BRI1-EMS-SUPPRESSOR1 (BES1). *Plant Physiology*, *182*(2), 1066–1082.
80. Lin, W., Zhou, X., Tang, W., Takahashi, K., Pan, X., Dai, J., Ren, H., Zhu, X., Pan, S., & Zheng, H. (2021). TMK-based cell-surface auxin signalling activates cell-wall acidification. *Nature*, *599*(7884), 278–282.
81. Lin, W.-H. (2020). Designed manipulation of the brassinosteroid signal to enhance crop yield. *Frontiers in Plant Science*, *11*, 854.
82. Liu, D., Zhao, H., Xiao, Y., Zhang, G., Cao, S., Yin, W., Qian, Y., Yin, Y., Zhang, J., & Chen, S. (2022). A cryptic inhibitor of cytokinin phosphorelay controls rice grain size. *Molecular Plant*, *15*(2), 293–307.
83. Lukatkin, A. S., Kashtanova, N. N., & Duchovskis, P. (2013). Changes in maize seedlings growth and membrane permeability under the effect of epibrassinolide and heavy metals. *Russian Agricultural Sciences*, *39*(4), 307–310.
84. Lv, B., Tian, H., Zhang, F., Liu, J., Lu, S., Bai, M., Li, C., & Ding, Z. (2018). Brassinosteroids regulate root growth by controlling reactive oxygen species homeostasis and dual effect on ethylene synthesis in Arabidopsis. *PLoS Genetics*, *14*(1), e1007144.

85. Ma, X., Yuan, Y., Li, C., Wu, Q., He, Z., Li, J., & Zhao, M. (2021). Brassinosteroids suppress ethylene-induced fruitlet abscission through LcBZR1/2-mediated transcriptional repression of LcACS1/4 and LcACO2/3 in litchi. *Horticulture Research*, *8*.
86. Makarevitch, I., Thompson, A., Muehlbauer, G. J., & Springer, N. M. (2012). Brd1 gene in maize encodes a brassinosteroid C-6 oxidase. *PloS One*, *7*(1), e30798.
87. Manghwar, H., Hussain, A., Ali, Q., & Liu, F. (2022). Brassinosteroids (BRs) role in plant development and coping with different stresses. *International Journal of Molecular Sciences*, *23*(3), 1012.
88. Mazorra, L. M., Holton, N., Bishop, G. J., & Núñez, M. (2011). Heat shock response in tomato brassinosteroid mutants indicates that thermos tolerance is independent of brassinosteroid homeostasis. *Plant Physiology and Biochemistry*, *49*(12), 1420–1428.
89. Meudt, W. J., Thompson, M. J., & Bennett, H. W. (1983). Investigations on the mechanism of the brassinosteroid response. III. Techniques for potential enhancement of crop production [Barley, bean]. *Proceedings Annual Meeting Plant Growth Regulator Society of America*.
90. Moon, J., Park, C.-H., Son, S.-H., Youn, J.-H., & Kim, S.-K. (2021). Endogenous level of abscisic acid down-regulated by brassinosteroid signalling via BZR1 to control the growth of *Arabidopsis thaliana*. *Plant Signaling & Behavior*, *16*(9), 1926130.
91. Nakamura, A., Higuchi, K., Goda, H., Fujiwara, M. T., Sawa, S., Koshiba, T., Shimada, Y., & Yoshida, S. (2003). Brassinolide induces IAA5, IAA19, and DR5, a synthetic auxin response element in Arabidopsis, implying a crosstalk point of brassinosteroid and auxin signalling. *Plant Physiology*, *133*(4), 1843–1853.
92. Nakashita, H., Yasuda, M., Nitta, T., Asami, T., Fujioka, S., Arai, Y., Sekimata, K., Takatsuto, S., Yamaguchi, I., & Yoshida, S. (2003). Brassinosteroid functions in a broad range of disease resistance in tobacco and rice. *The Plant Journal*, *33*(5), 887–898.
93. Nakaya, M., Tsukaya, H., Murakami, N., & Kato, M. (2002). Brassinosteroids control the proliferation of leaf cells of Arabidopsis thaliana. *Plant and Cell Physiology*, *43*(2), 239–244.
94. Nie, S., Huang, S., Wang, S., Cheng, D., Liu, J., Lv, S., Li, Q., & Wang, X. (2017). Enhancing brassinosteroid signalling via overexpression of tomato (*Solanum lycopersicum*) SlBRI1 improves major agronomic traits. *Frontiers in Plant Science*, *8*, 1386.
95. Nolan, T. M., Vukašinović, N., Liu, D., Russinova, E., & Yin, Y. (2020). Brassinosteroids: multidimensional regulators of plant growth, development, and stress responses. *The Plant Cell*, *32*(2), 295–318.
96. Oh, E., Zhu, J.-Y., Bai, M.-Y., Arenhart, R. A., Sun, Y., & Wang, Z.-Y. (2014). Cell elongation is regulated through a central circuit of interacting transcription factors in the Arabidopsis hypocotyl. *Elife*, *3*, e03031.
97. Oh, M. H. (2003). Secondary Metabolite/Biochemistry Metabolic Engineering; Brassinosteroids Accelerate the Rate of Cell Division in Isolated Petal Protoplasts of *Petunia hybrida*. *JOURNAL OF PLANT BIOTECHNOLOGY*, *5*(1), 69–77.
98. Pan, G., Liu, Y., Ji, L., Zhang, X., He, J., Huang, J., Qiu, Z., Liu, D., Sun, Z., & Xu, T. (2018). Brassinosteroids mediate susceptibility to brown planthopper by integrating with the salicylic acid and jasmonic acid pathways in rice. *Journal of Experimental Botany*, *69*(18), 4433–4442.
99. Park, S.-W., Kaimoyo, E., Kumar, D., Mosher, S., & Klessig, D. F. (2007). Methyl salicylate is a critical mobile signal for plant systemic acquired resistance. *Science*, *318*(5847), 113–116.
100. Planas-Riverola, A., Gupta, A., Betegón-Putze, I., Bosch, N., Ibañes, M., & Caño-Delgado, A. I. (2019). Brassinosteroid signaling in plant development and adaptation to stress. *Development*, *146*(5), dev151894.
101. Ren, Y., Li, X., Liang, J., Wang, S., Wang, Z., Chen, H., & Tang, M. (2023). Brassinosteroids and gibberellic acid actively regulate the zinc detoxification mechanism of *Medicago sativa* L. seedlings. *BMC Plant Biology*, *23*(1), 75.
102. Rozhon, W., Akter, S., Fernandez, A., & Poppenberger, B. (2019). Inhibitors of brassinosteroid biosynthesis and signal transduction. *Molecules*, *24*(23), 4372.

103. Sahni, S., Prasad, B. D., Liu, Q., Grbic, V., Sharpe, A., Singh, S. P., & Krishna, P. (2016). Overexpression of the brassinosteroid biosynthetic gene DWF4 in *Brassica napus* simultaneously increases seed yield and stress tolerance. *Scientific Reports*, *6*(1), 28298.
104. Saito, M., Kondo, Y., & Fukuda, H. (2018). BES1 and BZR1 redundantly promote phloem and xylem differentiation. *Plant and Cell Physiology*, *59*(3), 590–600.
105. She, J., Han, Z., Kim, T.-W., Wang, J., Cheng, W., Chang, J., Shi, S., Wang, J., Yang, M., & Wang, Z.-Y. (2011). Structural insight into brassinosteroid perception by BRI1. *Nature*, *474*(7352), 472–476.
106. Shigenaga, A. M., Berens, M. L., Tsuda, K., & Argueso, C. T. (2017). Towards engineering of hormonal crosstalk in plant immunity. *Current Opinion in Plant Biology*, *38*, 164–172.
107. Shu, S., Tang, Y., Yuan, Y., Sun, J., Zhong, M., & Guo, S. (2016). The role of 24-epibrassinolide in the regulation of photosynthetic characteristics and nitrogen metabolism of tomato seedlings under a combined low temperature and weak light stress. *Plant Physiology and Biochemistry*, *107*, 344–353.
108. Shuai, H., Chen, T., Wlk, T., Rozhon, W., Pimenta Lange, M. J., Sieberer, T., Lange, T., & Poppenberger, B. (2022). SlCESTA is a brassinosteroid-regulated bHLH transcription factor of tomato that promotes chilling tolerance and fruit growth when overexpressed. *Frontiers in Plant Science*, *13*, 930805.
109. Singh, A. P., & Savaldi-Goldstein, S. (2015). Growth control: brassinosteroid activity gets context. *Journal of Experimental Botany*, *66*(4), 1123–1132.
110. Singh, I., & Shono, M. (2005). Physiological and molecular effects of 24-epibrassinolide, a brassinosteroid, on thermotolerance of tomato. *Plant Growth Regulation*, *47*(2), 111–119.
111. Soares, C., de Sousa, A., Pinto, A., Azenha, M., Teixeira, J., Azevedo, R. A., & Fidalgo, F. (2016). Effect of 24-epibrassinolide on ROS content, antioxidant system, lipid peroxidation and Ni uptake in *Solanum nigrum* L. under Ni stress. *Environmental and Experimental Botany*, *122*, 115–125.
112. Swamy, K. N., Vardhini, B. V, Ramakrishna, B., Anuradha, S., Siddulu, N., & Rao, S. S. R. (2014). Role of 28-homobrassinolide on growth biochemical parameters of *Trigonella foenu-graecum* L. plants subjected to lead toxicity. *International Journal of Multidisciplinary and Current Research*, *2*, 317–321.
113. Symons, G. M., Ross, J. J., Jager, C. E., & Reid, J. B. (2008). Brassinosteroid transport. *Journal of Experimental Botany*, *59*(1), 17–24.
114. Thulasi Devendrakumar, K., Li, X., & Zhang, Y. (2018). MAP kinase signalling: interplays between plant PAMP-and effector-triggered immunity. *Cellular and Molecular Life Sciences*, *75*(16), 2981–2989.
115. Tong, H., & Chu, C. (2018). Functional specificities of brassinosteroid and potential utilization for crop improvement. *Trends in Plant Science*, *23*(11), 1016–1028.
116. Tong, H., Xiao, Y., Liu, D., Gao, S., Liu, L., Yin, Y., Jin, Y., Qian, Q., & Chu, C. (2014). Brassinosteroid regulates cell elongation by modulating gibberellin metabolism in rice. *The Plant Cell*, *26*(11), 4376–4393.
117. Trevisan, S., Forestan, C., Brojanigo, S., Quaggiotti, S., & Varotto, S. (2020). Brassinosteroid application affects the growth and gravitropic response of maize by regulating gene expression in the roots, shoots and leaves. *Plant Growth Regulation*, *92*(1), 117–130.
118. Unterholzner, S. J., Rozhon, W., Papacek, M., Ciomas, J., Lange, T., Kugler, K. G., Mayer, K. F., Sieberer, T., & Poppenberger, B. (2015). Brassinosteroids are master regulators of gibberellin biosynthesis in Arabidopsis. *The Plant Cell*, *27*(8), 2261–2272.
119. Venbrux, M., Crauwels, S., & Rediers, H. (2023). Current and emerging trends in techniques for plant pathogen detection. *Frontiers in Plant Science*, *14*, 1120968.
120. Vogler, F., Schmalzl, C., Englhart, M., Bircheneder, M., & Sprunck, S. (2014). Brassinosteroids promote Arabidopsis pollen germination and growth. *Plant Reproduction*, *27*(3), 153–167.
121. Vragović, K., Sela, A., Friedlander-Shani, L., Fridman, Y., Hacham, Y., Holland, N., Bartom, E., Mockler, T. C., & Savaldi-Goldstein, S. (2015). Translatome analyses capture of opposing

tissue-specific brassinosteroid signals orchestrating root meristem differentiation. *Proceedings of the National Academy of Sciences*, *112*(3), 923–928.

122. Wang, B., Li, Y., & Zhang, W.-H. (2012). Brassinosteroids are involved in response of cucumber (*Cucumis sativus*) to iron deficiency. *Annals of Botany*, *110*(3), 681–688.
123. Wang, B., Zhang, J., Xia, X., & Zhang, W.-H. (2011a). Ameliorative effect of brassinosteroid and ethylene on germination of cucumber seeds in the presence of sodium chloride. *Plant Growth Regulation*, *65*(2), 407–413.
124. Wang, B., Zhang, J., Xia, X., & Zhang, W.-H. (2011b). Ameliorative effect of brassinosteroid and ethylene on germination of cucumber seeds in the presence of sodium chloride. *Plant Growth Regulation*, *65*(2), 407–413.
125. Wang, Q., Yu, F., & Xie, Q. (2020). Balancing growth and adaptation to stress: Crosstalk between brassinosteroid and abscisic acid signalling. *Plant, Cell & Environment*, *43*(10), 2325–2335.
126. Wang, Y., Perez-Sancho, J., Platre, M. P., Callebaut, B., Smokvarska, M., Ferrer, K., Luo, Y., Nolan, T. M., Sato, T., & Busch, W. (2023). Plasmodesmata mediate cell-to-cell transport of brassinosteroid hormones. *Nature Chemical Biology*, *19*(11), 1331–1341.
127. Wang, Y., Sun, S., Zhu, W., Jia, K., Yang, H., & Wang, X. (2013). Strigolactone/MAX2-induced degradation of brassinosteroid transcriptional effector BES1 regulates shoot branching. *Developmental Cell*, *27*(6), 681–688.
128. Wang, Z.-Y., Nakano, T., Gendron, J., He, J., Chen, M., Vafeados, D., Yang, Y., Fujioka, S., Yoshida, S., & Asami, T. (2002). Nuclear-localised BZR1 mediates brassinosteroid-induced growth and feedback suppression of brassinosteroid biosynthesis. *Developmental Cell*, *2*(4), 505–513.
129. Wei, L.-J., Deng, X.-G., Zhu, T., Zheng, T., Li, P.-X., Wu, J.-Q., Zhang, D.-W., & Lin, H.-H. (2015a). Ethylene is involved in brassinosteroid-induced alternative respiratory pathway in cucumber (*Cucumis sativus* L.) seedlings response to abiotic stress. *Frontiers in Plant Science*, *6*, 982.
130. Xia, X., Zhou, Y., Ding, J., Shi, K., Asami, T., Chen, Z., & Yu, J. (2011). Induction of systemic stress tolerance by brassinosteroid in Cucumis sativus. *New Phytologist*, *191*(3), 706–720.
131. Xiao, B.-Z., Chen, X., Xiang, C.-B., Tang, N., Zhang, Q.-F., & Xiong, L.-Z. (2009). Evaluation of seven function-known candidate genes for their effects on improving drought resistance of transgenic rice under field conditions. *Molecular Plant*, *2*(1), 73–83.
132. Xiong, M., Yu, J., Wang, J., Gao, Q., Huang, L., Chen, C., Zhang, C., Fan, X., Zhao, D., & Liu, Q.-Q. (2022). Brassinosteroids regulate rice seed germination through the BZR1-RAmy3D transcriptional module. *Plant Physiology*, *189*(1), 402–418.
133. Xu, F., Xi, Z., Zhang, H., Zhang, C., & Zhang, Z. (2015). Brassinosteroids are involved in controlling sugar unloading in *Vitis vinifera* 'Cabernet Sauvignon'berries during véraison. *Plant Physiology and Biochemistry*, *94*, 197–208.
134. Yamamoto, R., Fujioka, S., Demura, T., Takatsuto, S., Yoshida, S., & Fukuda, H. (2001). Brassinosteroid levels increase drastically prior to morphogenesis of tracheary elements. *Plant Physiology*, *125*(2), 556–563.
135. Yang, X., Jia, Z., Pu, Q., Tian, Y., Zhu, F., & Liu, Y. (2022). ABA mediates plant development and abiotic stress via alternative splicing. *International Journal of Molecular Sciences*, *23*(7), 3796.
136. Ye, Q., Zhu, W., Li, L., Zhang, S., Yin, Y., Ma, H., & Wang, X. (2010). Brassinosteroids control male fertility by regulating the expression of key genes involved in Arabidopsis anther and pollen development. *Proceedings of the National Academy of Sciences*, *107*(13), 6100–6105.
137. Yin, Y., Wang, Z.-Y., Mora-Garcia, S., Li, J., Yoshida, S., Asami, T., & Chory, J. (2002). BES1 accumulates in the nucleus in response to brassinosteroids to regulate gene expression and promote stem elongation. *Cell*, *109*(2), 181–191.
138. Yokota, T. (1997). The structure, biosynthesis and function of brassinosteroids. *Trends in Plant Science*, *2*(4), 137–143.

139. Yokota, T., Arima, M., & Takahashi, N. (1982). Castasterone, a new phytosterol with plant-hormone potency, from chestnut insect gall. *Tetrahedron Letters*, *23*(12), 1275–1278.
140. Yokota, T., Kim, S. K., Fukui, Y., Takahashi, N., Takeuchi, Y., & Takematsu, T. (1987). Brassinosteroids and sterols from a green alga, *Hydrodictyon reticulatum*: configuration at C-24. *Phytochemistry*, *26*(2), 503–506.
141. Yu, T.-Y., Sun, M.-K., & Liang, L.-K. (2021). Receptors in the induction of the plant innate immunity. *Molecular Plant-Microbe Interactions*, *34*(6), 587–601.
142. Yu, X., Niu, H., Liu, C., Wang, H., Yin, W., & Xia, X. (2024). PTI-ETI synergistic signal mechanisms in plant immunity. *Plant Biotechnology Journal*, *22*(8), 2113–2128.
143. Yuldashev, R., Avalbaev, A., Bezrukova, M., Vysotskaya, L., Khripach, V., & Shakirova, F. (2012). Cytokinin oxidase is involved in the regulation of cytokinin content by 24-epibrassinolide in wheat seedlings. *Plant Physiology and Biochemistry*, *55*, 1–6.
144. Yusuf, M., Fariduddin, Q., Hayat, S., Hasan, S. A., & Ahmad, A. (2011). Protective response of 28-homobrassinolide in cultivars of *Triticum aestivum* with different levels of nickel. *Archives of Environmental Contamination and Toxicology*, *60*(1), 68–76.
145. Zadvornova, Y. V, Alekseichuk, G. N., Laman, N. A., Khripach, V. A., & Grut, S. (2005). Effect of brassinosteroids on activation of the cell cycle during germination of *Brassica oleracea* L. seeds. *Doklady Natsional'noi Akademii Nauk Belarusi*, *49*, 70–73.
146. Zeng, H., Tang, Q., & Hua, X. (2010). Arabidopsis brassinosteroid mutants det2-1 and bin2-1 display altered salt tolerance. *Journal of Plant Growth Regulation*, *29*(1), 44–52.
147. Zhang, D.-W., Deng, X.-G., Fu, F.-Q., & Lin, H.-H. (2015). Induction of plant virus defense response by brassinosteroids and brassinosteroid signaling in *Arabidopsis thaliana*. *Planta*, *241*(4), 875–885.
148. Zhang, J., Chen, W., Li, X., Shi, H., Lv, M., He, L., Bai, W., Cheng, S., Chu, J., & He, K. (2023). Jasmonates regulate apical hook development by repressing brassinosteroid biosynthesis and signaling. *Plant Physiology*, *193*(2), 1561–1579.
149. Zhang, S., Hu, J., Zhang, Y., Xie, X. J., & Knapp, A. (2007). Seed priming with brassinolide improves lucerne (*Medicago sativa* L.) seed germination and seedling growth in relation to physiological changes under salinity stress. *Australian Journal of Agricultural Research*, *58*(8), 811–815.
150. Zhang, Y., Berman, A., & Shani, E. (2023). Plant hormone transport and localization: signaling molecules on the move. *Annual Review of Plant Biology*, *74*(1), 453–479.
151. Zhang, Y., Yu, J., Xu, X., Wang, R., Liu, Y., Huang, S., Wei, H., & Wei, Z. (2022). Molecular mechanisms of diverse auxin responses during plant growth and development. *International Journal of Molecular Sciences*, *23*(20), 12495.
152. Zhao, B., & Li, J. (2012a). Regulation of brassinosteroid biosynthesis and inactivation F. *Journal of Integrative Plant Biology*, *54*(10), 746–759.
153. Zhao, B., & Li, J. (2012b). Regulation of brassinosteroid biosynthesis and inactivation F. *Journal of Integrative Plant Biology*, *54*(10), 746–759.
154. Zhao, G., Xu, H., Zhang, P., Su, X., & Zhao, H. (2017). Effects of 2, 4-epibrassinolide on photosynthesis and Rubisco activase gene expression in *Triticum aestivum* L. seedlings under a combination of drought and heat stress. *Plant Growth Regulation*, *81*(3), 377–384.
155. Zhao, N., Zhao, M., Tian, Y., Wang, Y., Han, C., Fan, M., Guo, H., & Bai, M. (2021). Interaction between BZR1 and EIN3 mediates signalling crosstalk between brassinosteroids and ethylene. *New Phytologist*, *232*(6), 2308–2323.
156. Zhou, J., Wang, J., Li, X., Xia, X.-J., Zhou, Y.-H., Shi, K., Chen, Z., & Yu, J.-Q. (2014). H2O2 mediates the crosstalk of brassinosteroid and abscisic acid in tomato responses to heat and oxidative stresses. *Journal of Experimental Botany*, *65*(15), 4371–4383.
157. Zhou, Y., Huo, S., Wang, L., Meng, J., Zhang, Z., & Xi, Z. (2018). Exogenous 24-Epibrassinolide alleviates oxidative damage from copper stress in grape (*Vitis vinifera* L.) cuttings. *Plant Physiology and Biochemistry*, *130*, 555–565.
158. Zhu, J.-Y., Sae-Seaw, J., & Wang, Z.-Y. (2013). Brassinosteroid signalling. *Development*, *140*(8), 1615–1620.

159. Zhu, X., Liang, W., Cui, X., Chen, M., Yin, C., Luo, Z., Zhu, J., Lucas, W. J., Wang, Z., & Zhang, D. (2015). Brassinosteroids promote development of rice pollen grains and seeds by triggering expression of Carbon Starved Anther, a MYB domain protein. *The Plant Journal*, *82*(4), 570–581.
160. Zhu, Z., Zhang, Z., Qin, G., & Tian, S. (2010). Effects of brassinosteroids on postharvest disease and senescence of jujube fruit in storage. *Postharvest Biology and Technology*, *56*(1), 50–55.