

Review



Brassinosteroids: Relevant Evidence Related to Mitigation of Abiotic and Biotic Stresses in Plants

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Abstract: Extreme events of climate change are increasing, such as droughts and heat waves, causing limitations on growth and yield in relevant food crops, as well as threatening global food security. Brassinosteroids (BRs) are natural or synthetic steroids with significant properties that promote plant growth and development. In the current world scenario, research and solutions that can improve plant tolerance to climate change are strategic to ensure food security. The distinctiveness and novelty of this review lie in its comprehensive and detailed approach to the role of BRs in plants under biotic and abiotic stresses. We consolidate information on the action mechanisms on specific organs, providing detailed experimental conclusions of these plant growth regulators, including also commercial products and concentrations tested aiming to mitigate the adverse effects of the stresses. This practical approach highlights the potential of BRs in agriculture and plant protection against stresses. Additionally, our review presents results with plant models and essential food crops, focusing on multidisciplinary approaches and using physiological, biochemical, nutritional, anatomical and agronomic tools to explain the mechanisms of action of brassinosteroids in plants exposed to abiotic and biotic stresses.

Keywords: brassinosteroids; metabolic stimulation; plant steroid; protective molecule; stress tolerance mechanism

1. Introduction

On one of the first pages of the book *Phytohormones* [1], the authors cite an old lullaby: *Oats, peas, beans and barley grow, Oats, peas, beans and barley grow, Can you, or I, or anyone know how oats, peas, beans and barley grow?* How plants grow is a question that permeates the imagination of children and researchers. Much progress has been made since the knowledge that phytohormones were involved in several physiological processes related to growth, such as etiolation, elongation, germination, etc.

Plant growth regulators (PGRs) are signalling molecules involved in plant growth and development. The regulation of cellular and developmental processes can be determined by one or a combination of molecules [2]. The most studied and relevant PGRs in growth and development processes are auxin, cytokinin, ethylene, abscisic acid, gibberellin, brassinosteroid, salicylic acid, jasmonic acid, strigolactone and polyamines [3]. Robust equipment and new software for detecting and identifying molecules increase the accuracy, with new PGRs being studied in terms of plant \times molecule \times environment interaction. These molecules can be produced in plant organs and influence a specific physiological process when transferred to other parts. Thus, they are characterised as chemical messengers



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Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). responsible for coordinating certain physiological activities [1]. Among the main activities of PGRs are the regulation of developmental processes and signalling networks involved in plant responses to various biotic and abiotic stresses [4–6], such as diseases caused by fungi, bacteria, viruses and nematodes [7] and drought, thermal stress, salt stress and potentially toxic elements [8]. This review presents a comprehensive and detailed approach to the role of brassinosteroids (BRs) in plants under biotic and abiotic stresses. We consolidate information on the action mechanisms of specific organs, providing detailed experimental conclusions of these PGRs, including commercial products and concentrations tested that are aiming to mitigate the adverse effects of the stresses. This practical approach highlights the potential of brassinosteroids in agriculture and plant protection against stresses.

2. Brassinosteroids

BRs are considered PGRs. In 1970, Mitchell and collaborators published in *Nature* the paper "Brassins—a New Family of Plant Hormones from Rape Pollen". In this research, when testing an oily extract, "Brassin" of *Brassica Napus* pollen, on bean seedlings at deficient concentrations ($10 \mu g \text{ plant}^{-1}$), researchers observed the superior elongation of the internodes compared to the seedlings treated with controls, gibberellin and fractionated lanolin. The authors named these substances Brassins. Seedlings treated with these substances were histologically differentiated from those treated with the control. According to the chemical analyses, the authors suggested that Brassins would be a new family of PGRs, since they had a glyceride structure and differentiated action from gibberellin [9].

In 1979, the first brassinosteroid was isolated, brassinolide (BL), a lactone steroid, which is the most active [10]. In the 1990s, mutants that did not biosynthesise BRs in some species were identified. The isolation of the *Brassinosteroid Insensitive 1* (*BRI1*) gene, associated with molecular and biochemical studies, allowed the demonstration that *BRI1* is a ubiquitously expressed leucine-rich receptor kinase, which, through the phosphorylation of serine and threonine, acts in the signalling of BRs [11]. This receptor detects extracellular BRs and, as needed, triggers an intracellular signalling cascade [12]. These studies recognised these compounds as a new class of PGR. These substances gained attention from the scientific community, and many metabolic processes were understood. By 2017, 81 natural BRs, five conjugates, 137 analogues and eight metabolites isolated from 64 species, including angiosperms, gymnosperms, pteridophytes, bryophytes and algae, had already been characterised [13,14], whose division is, according to the B ring and the orientation of the hydroxyl, ketone and epoxide groups, at the C-1, C-2, C-3 and C-6 position on the A ring [15]. In addition to their chemical structure, these brassinosteroids differ in physiological activity [16].

BRs are found in small amounts in all plant organs. The concentration is higher in young tissues, varying between 1 and 100 ng g⁻¹ of fresh mass. However, mature tissues have a marked reduction between 0.01 and 0.1 ng g⁻¹ [17]. These hormones can act on metabolism, resulting in a greater tolerance to biotic and abiotic stresses, cell expansion and elongation, redox signalling and several other functions.

BRs are polyhydroxylated phytosterols synthesised from the sterols campesterol, sitosterol and cholesterol, which are metabolised in many intermediates in plant cells. Still, few of these metabolites have biological activity [15], BRs were defined as steroids with an oxygen fraction at C-3 and additional ones at one or more carbon atoms C-2, C-6, C-22 and C-23. All BRs can fall into three categories according to the carbon number of each steroid molecule: C27, C28 and C29. The biosynthesis of BRs (C27, C28 or C29) occurs through three biochemical pathways. The first phase, which results in the synthesis of sterols, can be the mevalonate or non-mevalonate pathway. Subsequently, follow cycloartenol and cycloartenol-dependent pathways. Various pathways lead to the synthesis of cholesterol and campesterol from cycloartenol, while sitosterol also can be synthesised from cycloartenol [18]. Campesterol and 24- β -methylcholesterol are precursors of C28 BRs, C27 BR's cholesterol and C29 BR's sitosterol [19]. Not all the biosynthetic compounds of all BRs have been deciphered, but there are already commercially available synthetic BRs.



BRs can act on metabolism, resulting in greater tolerance to biotic and abiotic stresses, cell expansion and elongation, redox signalling and several other functions (Figure 1).

Figure 1. Benefits induced by brassinosteroids in molecular, biochemical, physiological, anatomical, nutritional and morpho-agronomical aspects.

3. Abiotic Stresses

Similar metabolic processes may result from different stresses, causing equal cellular damage. Osmotic stress disrupts homeostasis and results in cellular electrolyte leakage (EL), whereas oxidative stress can denature functional and structural proteins. Both stresses generally activate similar signalling pathways and cellular responses, such as the production of stress proteins. When subjected to stress, the plant reacts with cellular biochemical changes to adapt to the new environmental condition, including new metabolic pathways and changes in the number of phytohormones [20].

Reactive oxygen species (ROS) play a key role in plant growth, development and interaction with biotic and abiotic stresses. ROS, constantly produced during photosynthesis and respiration, are essential regulatory and signalling elements in various cellular processes. Disruption of the protective mechanisms of redox homeostasis in the cell can cause oxidative stress, resulting in the increased production of ROS (O_2^- , H_2O_2 , -OH, NO), leading to oxidative damage and cell death. Water deficit, flooding, desiccation, salinisation, cooling, thermal shock, heavy metal poisoning, ultraviolet radiation, ozone, mechanical damage, nutritional deficit, the action of phytopathogenic microorganisms and excessive luminosity are stresses that cause disturbances in cellular homeostasis [21].

Antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX) and ascorbate peroxidase (APX) and non-enzymatic antioxidants like ascorbic acid, tocopherols, carotenoids, glutathione, etc. in plants under different stress conditions are modified by exogenous application of BRs. ROS interact directly or via enzymatic catalysis with vitamins C, E and glutathione, whereas carotenes inhibit intermediate forms of ROS [22–26].

The increased tolerance of plants under abiotic stresses (heat, cold, drought, salinity, metal toxicity, etc.) with the action of BRs has been proven using several phenotypic, anatomical, physiological, biochemical and molecular studies, which demonstrate how

these stresses cause damage and how BRs help plants in the dynamic defence response to such pressures (Table 1).

Table 1. Effects of exogenous application of brassinosteroids on different plant species and abiotic stresses.

Stress Conditions	Brassinosteroids and Concentration	Plant Species	BRs Application	Benefits Induced by BRs
Al [0–10 mM]	24-epiBL/28-homoBL [10 ⁻⁸ M]	Vigna radiata	Leaf	Biochemical [27]
Cd	EpiBL	Solanum nigrum		Biochemical [28]
Cd [0–12 mg.kg ⁻¹]	24-epiBL/28-homoBL [10 ⁻⁸ M]	Lycopersicon esculentum	Leaf	Physiological and biochemical [29]
Cd [1.0 mM]	24-epiBL [5 μM]	Phaseolus vulgaris	Leaf	Morphological and biochemical [30]
Cd [1.0 mM]	24-epiBL/28-homoBL [3.0 μM]	Raphanus sativus	Seed	Biochemical [31]
Cd [300 µM]	24-epiBL [100 nM]	Brassica Napus	Culture medium	Physiological [32]
Cd [1.0 µM]	BRs [0.01–10 μM]	Oryza sativa	Nutrient solution	Molecular [33]
Cu [100 mg.kg ⁻¹]	24-epiBL [0.01 μM]	Cucumis sativus	Leaf	Morphological, physiological and biochemical [34]
Cu [50–150 mg.kg ⁻¹]	28-HomoBL [10 ⁻¹⁰ -10 ⁻⁶ M]	Brassica juncea	Seed	Morphological, physiological and biochemical [35]
Fe [250–6250 µM]	24-epiBL [0–10 nM]	Oryza sativa	Root	Physiological [36]
Ni [0.0–0.6 mM]	24-epiBL [10 ⁻¹¹ –10 ⁻⁷ M]	Brassica juncea	Leaf	Biochemical [37]
Ni [50–100 μM]	28-homoBL [0.01 μM]	Triticum aestivum	Leaf	Morphological, physiological and biochemical [38]
Pb [0–200 μM]	24-epiBL [0–100 nM]	Oryza sativa	Leaf	Anatomical and biochemical [39]
Pb [3 mM]	24-epiBL [10 ⁻¹⁰ -10 ⁻⁶ M]	Brassica juncea	Seed	Biochemical [40]
Zn [0.0–2.0 mM]	24-epiBL [10 ⁻¹⁰ -10 ⁻⁶ M]	Brassica juncea	Seed	Morphological and biochemical [41]
Zn [1–10 mM]	28-homoBL [0.5–2 μM]	Raphanus sativus	Seed	Biochemical [42,43]
Drought	EpiBL/HomoBL [1–5 µM]	Phaseolus vulgaris	Leaf	Morpho-agronomical [44]
Drought	24-epiBL $[0.01 \text{ mg.L}^{-1}]$	Capsicum annuum	Leaf	Physiological [45]
Drought	24-epiBL [1 μg.L ⁻¹]	Cucumis sativus	Root	Physiological and biochemical [46]
Drought	24-epiBL [0.01–1 μM]	Lycopersicon esculentum	Leaf	Biochemical [47]
Drought	24-epiBL/28-homoBL [0.5–2 μM]	Raphanus sativus	Seed	Biochemical [43]
Drought	24-epiBL [1.0 μM]	Capsicum annum	Leaf	Physiological and biochemical [48]
Drought	24-epiBL [0.1 μM]	Carthamus tinctorius	Leaf	Biochemical [49]
Drought	24-epiBL [0–100 nM]	Glycine max	Seed	Morphological and biochemical [50]
Drought	24-epiBL [0.4 μM]	Triticum aestivum	Seed	Biochemical, hormonal and anatomical [51]

Table 1. Cont.

Stress Conditions	Brassinosteroids and Concentration	Plant Species	BRs Application	Benefits Induced by BRs
Drought	24-epiBL [0.10 μM]	Vitis vinifera	Leaf	Hormonal and biochemical [52]
Drought	28-homoBL [0.01 μM]	Brassica juncea	Leaf	Biochemical [34]
Drought	BL [1 mg.L $^{-1}$]	Arachis hypogaea	Seed	Biochemical [53]
Drought	BL [0.1 mg.L ⁻¹]	Glycine max	Leaf	Biochemical and physiological [54]
Drought	BL [0–0.4 mg.L ⁻¹]	Robinia pseudoacacia	Leaf	Morphological and biochemical [55]
Drought	BL [0–0.4mg.L ⁻¹]	Xanthoceras sorbifolia	Root	Morphological [56]
Drought	Biobras16 TM [16–0.1 mg. L^{-1}]	Carica papaya	Leaf	Morphological and biochemical [57]
Drought	BR analogue [10% w/v]	Passiflora edulis f. edulis	Substrate	Morphological [58]
Flooding	BL [1.0 mM]	Zea mays	Leaf	Biochemical and physiological [59]
High temperature	24-epiBL $[0.2 \text{ mg.L}^{-1}]$	Camellia sinensis	Leaf	Biochemical [60]
High temperature	BL [10 ⁻⁶ M]	Brassica Napus	Leaf	Hormonal [61]
High temperature	24-epiBL [0.01–1.0 mg.L ⁻¹]	Lycopersicon esculentum	Leaf	Physiological and biochemical [62]
Low temperature	BL [1–9 μM]	Solanum lycopersicum	Fruit	Biochemical [63]
Low temperature	24-epiBL [0.1 μM]	Cucumis sativus	Leaf	Biochemical, physiological and morphological [64]
Low temperature	28-homoBL [10 ⁻⁸ –10 ⁻⁶ μM]	Cucumis sativus	Leaf	Biochemical, physiological and morphological [35]
Low temperature	24-epiBL [10 μM]	Vigna radiata	Leaf	Biochemical and anatomical [65]
Low temperature	24-epiBL [1.00 μM]	Brassica Napus	Leaf	Biochemical [66]
Low temperature	24-epiBL [0.1 μM]	Capsicum annuum	Leaf	Biochemical, physiological and nutritional [37]
Low temperature	24-epiBL [0.5 μM]	Vitis vinifera	Seedling	Biochemical, physiological and molecular [67]
NaCl	BRs [0–0.2 mg.L ⁻¹]	Cucumis sativus	Root and leaf	Biochemical [68]
CaSO ₄ [5 t.ha ⁻¹]	BL [0–0.3 mg.L ⁻¹]	Trifolium alexandrinum	Leaf	Biochemical and morpho-agronomical [69]
Imidacloprid [0.01–0.02%]	24-epiBL [10 ⁻¹¹ -10 ⁻⁷ M]	Oryza sativa	Seed	Biochemical [70,71]
NaCl	24-epiBL	Capsicum annuum		Biochemical and nutritional [71]
NaCl [0-150mM]	24-epiBL [0–0.2 mg.L ⁻¹]	Lycopersicon esculentum		Biochemical [72]

Stress Conditions	Brassinosteroids and	Plant Species	BRs Application	Benefits Induced by BRs
	Concentration	T failt Species	DRS Application	Denents induced by DKs
NaCl [0-150 mM]	24-epiBL [0–2.5 mg.L ⁻¹]	Mentha piperita	Leaf	Biochemical and morphological [73]
NaCl [0-250mM]	24-epiBL [0–50 nM]	Eucalyptus urophylla	Leaf	Physiological and nutritional [74]
NaCl [0.3-0.4 M]	24-epiBL [3 μM]	Hordeum vulgare	Seed	Anatomical and genetics [75]
NaCl [0–100 mM]	24-epiBL [0–3 μM]	Lactuca sativa	Seed and leaf	Morphological, anatomical and nutritional [76]
NaCl [0-100 mM]	24-epiBL [10 ⁻⁴ −1 μM]; 28-homoBL [10 ⁻⁴ −1 μM]	Zea mays	Seed	Biochemical and nutritional [77]
NaCl [0–100 mM]	BL $[0.25 \text{ mg}.\text{L}^{-1}]$	Zea mays	Seed and leaf	Biochemical [78]
NaCl [100 mM]	24-epiBL [0–100 mM]	Glycine max	Seed	Nutritional [79]
NaCl [13.6 dS/m]	BL [5 μM]	Medicago sativa	Seed	Morphological and biochemical [80]
NaCl [150 mM]	24-epiBL [0.01 μM]	Cucumis sativus	Leaf	Morphological, physiological and biochemical [35]
NaCl [150 mM]	24-epiBL [0.013–0.038 mg.L ⁻¹]	Triticum aestivum	Leaf	Morphological, physiological and biochemical [81]
NaCl [2%]	24-epiBL [0.4 μM]	Triticum aestivum	Seed	Hormonal [82]
NaCl [200 mM]	BL $[0.005-0.05 \text{ mg.L}^{-1}]$	Cucumis sativus	Root and leaf	Biochemical, physiological and morphological [83]
NaCl [250 mM]	24-epiBL [0–10 μM]	Cucumis sativus	Seed	Biochemical and molecular [84]
NaCl [25–100 mM]	28-homoBL [10 ⁻¹¹ –10 ⁻⁷ M]	Zea mays	Seed	Morphological and biochemical [85]
NaCl [25–150 mM]	BL $[0.05 \text{ mg.L}^{-1}]$	Vigna unguiculata	Leaf	Biochemical [86]
NaCl [35 mM]	24-epiBL [0–1 μM]	Fragaria x ananassa	Leaf	Nutritional, physiological and biochemical [87]
NaCl [400 mM]	24-epiBL [10 ⁻⁷ -0.5×10 ⁻⁹ M]	Cajanus cajan	Substrate	Biochemical, physiological, anatomical and nutritional [88]
NaCl [50-150 mM]	28-HomoBL [10 ⁻¹⁰ -10 ⁻⁶ M]	Brassica juncea	Leaf	Morpho-agronomical [89]
NaCl [75–150 mM]	24-epiBL [1–100 nM]	Pisum sativum		Morphological and biochemical [90]
NaCl [90 mM]	24-epiBL [0–0.2 mg.L ⁻¹]	Solanum melongena	Leaf	Morphological, biochemical and nutritional [91]
NaCl, CaCl ₂ , MgSO ₄ [4.7–9.4 dS/m]	24-epiBL [0–0.1 mg.L ⁻¹]	Triticum aestivum	Leaf	Nutritional and biochemical [92]
NaCl [500 mM]	24-epiBL [0–2.0 μM]	Kandelia obovata	Root	Biochemical [93]
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Table 1. Cont.

24-epiBL = 24-epibrassinolide; 28-HomoBL = 28-homobrassinolide; BL = brassinolide; BRs = brassinosteroids.

For each type of response, factors such as time, BR concentration, plant species, application method and type of stress may vary. Biochemical reactions are faster than phenotypic responses, for example. BRs respond to all stresses. However, they are susceptible to injuries and wounds, implying application methods without mechanical damage, such as seed soaking, substrate application, root or fruit immersion and foliar spraying (Table 1). According to [94], providing BRS between 14 and 21 days before exposure to stress via roots is the method that generates the most reproducible results.

3.1. Thermal Stress

With the effects of climate change, the use of substances that increase stress tolerance to extreme temperatures is increasingly necessary. Temperature stress comprises extreme values of both low and high temperatures. BRs most studied in increasing tolerance to heat stress are 24-epibrassinolide (24-epiBL), 28-Homobrassinolide (28-homoBL) and BL (Table 1). The concentrations of the tested BR solutions vary between 0.01 and 10 μ M. Different modes of application of BRs are reported, for example, needleless foliar injection, foliar spraying and fruit immersion, in at least six studied species (Camellia sinensis, B. napus, Solanum lycopersicum, Capsicum annuum, Vigna radiata and Cucumis sativus). Some of the described effects of BRs on thermotolerance are increased carboxylation efficiency and improved antioxidant enzyme systems in leaves [62], increase in the endogenous concentration of abscisic acid (ABA) in leaves of B. napus [61], protective effect against membrane leakage and degradation of photosynthetic pigments [66]; increased levels of partial free amino acids (proline, arginine, aspartic acid and glycine) [37]; increased nitrate reductase (NR), glutamine synthase (GS), glutamate synthase (GOGAT) and glutamate dehydrogenase (GDH) activities in sweet pepper seedling leaves and reduced $H_2O_2 e O_2^{-}$. accumulation [37]; reduced electrolyte leakage (EL) and malondialdehyde (MDA) leakage content and increased proline content [63] (Table 1).

BRs increase thermotolerance by reducing, for example, the effects of cold stress, such as photoinhibition caused by damage to chloroplast thylakoid membranes and the inactivation of enzymes involved in CO₂ assimilation [95], which indirectly leads to oxidative damage to DNA, proteins and lipids [96]. In addition, BRs alter the physicochemical properties of the membrane, regulate the expression of stress-responsive genes, and have indirect effects on metabolism through other hormones or signalling molecules (such as H_2O_2) [16].

Cold and drought stress response genes (*COR47* and *COR78*) and heat (*HSP83*, *HSP70*, *HSF3*, *Hsc70-3* and *Hsc70-G7*), related to oxidative stress that encodes monodehydroascorbate reductase and thioredoxin, were identified in mutant plants of BR-deficient Arabidopsis streated with BR [97]. The BR-biosynthetic gene DWARF4 from transgenic Arabidopsis seeds evidences the role of BRs in cold stress tolerance [98]. Photoprotective pathways and hormone regulation can be regulated by H_2O_2 in the apoplast acting as a signalling molecule, and photoinhibition was probably reduced in tomato due to the abundance of D1 protein, derived from the application of EBR (0.2 μ M) [95]. The photosystem II reaction centre (PSII) comprises proteins D1 and D2, because the damage caused by ROS on D1 and D2 proteins reduce carbon fixation and oxygen evolution and disrupts the flow of electrons [95,99].

In *A. thaliana*, cold tolerance and freezing mediated by BRs have already been studied in cell suspension [100] and seedling spraying before exposure to low temperatures [101,102], as well as the immersion of eggplant (*Solanum melongena*) fruits in BR solution before cold storage [103]. Grape seedlings sprayed with 0.5 μ M 24-epiBL and subsequently subjected to cold (0 °C/36 h) had lower relative EL and higher maximum quantum yield of photosystem II—PSII (Fv/Fm) [67]. Seedlings of *B. napus* and *A. thaliana* were cultured in Murashige and Skoog (MS) medium containing one μ mol/L of 24-epiBL for 14 or 21 days before being subjected to heat stress (45 °C) [98]. Pre-treatment with BR increased the relative survival rate, the accumulation of heat shock proteins (HSPs) in *B. napus* [104] and the level of ABA compared to untreated *A. thaliana* seedlings [105]. Positive effects on damage caused by stress at high temperatures by the application of BRs have already been

detected in grass (*Bromus inermis*) subjected to 40–45 °C [106], in *C. sinensis* at 35 °C [106], in *B. napus* at 45 °C [61] and tomato in a 12 h photoperiod at 40–30 °C [62]. In tomatoes under high temperatures (40 °C), applying 24-epiBL on leaf discs increased the activity of CAT, peroxidase—POD and SOD [107]. The benefits of using BRs under cold stress have also been proven for *Oryza sativa* [108,109], *Z. mays* [110], *C. sativus* [111] and *Musa paradisiaca* [112].

3.2. Drought

Water, and consequently the hydric balance, is essential for the survival and development of the plant since more than 90% of its green mass is made up of water [113]. Gas exchange, photosynthesis, absorption, and transport of nutrients are some factors that water mediates. Water stress causes biochemical, anatomical and physiological changes. BRs 24-epiBL, 28-homoBL, BL, and Spirostanic analogue of brassinosteroid (BB16) showed positive responses when applied at doses ranging from 0.01 to $5 \,\mu$ mol/L in cultures of S. lycopersicum, Phaseolus vulgaris, B. napus, C. annuum, C. sativus, Raphanus sativus, Carthamus tinctorius, Glycine max, Triticum aestivum, Vitis vinifera, Brassica juncea, Arabidopsis, Sorghum vulgare, Arachis hypogaea, Robinia pseudoacacia, Carica papaya and Xanthoceras sorbifolia. Among the effects of BRs that alleviate water stress are greater CO_2 assimilation, reduced photoinhibition, increased efficiency in light utilisation and dissipation of excitation energy in PSII in leaves, increased concentration of ABA and antioxidant enzymes, carotenoids and proline (Table 1). Lower net photosynthetic rates and lower accumulation of osmoprotectants were detected in barley allelic mutants (Hordeum vulgare) with deficient enzymatic activity (BR-biosynthetic C6-oxidase) related to drought tolerance [114]. The exogenous use of BL increased the activities of SOD, CAT, APX, and the levels of vitamin C and carotenoids in corn seedlings under water deficit [22].

Waterlogging stress limits gas exchange and subjects the root system to low oxygen (O₂) conditions. These define the functions and growth of the roots and consequently affect the entire development of all organs, which can lead to the death of the plant. Corn seedlings subjected to waterlogging stress, previously treated with BL, showed an improvement in the antioxidant system, regulating the formation of aerenchyma, with consequent maintenance of the general vital system of the plant [59,115] induced the condition of hypoxia in mutants of *A. thaliana det2*, blocked the synthesis of BRs, and observed anatomical changes, such as thicker layers of the cuticle; however, when adding BL, the anatomical characteristics were similar to the control (Cv. Columbia). The authors presume that BRs can mediate plant developmental responses under hypoxic conditions because BRs, in their biosynthesis, require molecular oxygen in several steps.

3.3. Salt Stress

Salt stress is one of the most severe and essential stresses. In 2002, FAO estimated that 1 to 2% of the arable land on the planet would be unfeasible for agriculture per year due to salinity or sodicity [116]. Approximately half of the irrigated area in the world has or has a problem with salinisation and soil saturation [117]. The exogenous application or endogenous stimulation of BRs minimises the effects of salinity on plants in these soils and their respective consequences, including the prevention of secondary problems such as diseases (Table 1).

Most articles focused on studying the effect of BRs on salinity tolerance, but the induction of salt stress is mainly due to sodium chloride (NaCl) (Table 1). However, MgSO₄ and CaCl₂ have also been reported. In the literature, exogenous applications of BRs (24-epiBL; 28-homoBL and BL) are reported to mitigate salt stress with concentrations of 10^{-11} to 10^{-1} M. The main effects of the application of these hormones by different methods, such as seed soaking, foliar spraying and substrate application, were: higher levels of nutrients in the tissues [74,87,92], higher levels of photosynthetic pigments and photochemical efficiency [74,81]; more excellent activity of enzymes and antioxidant compounds (CAT, POD, SOD) and non-toxic osmoprotectors, such as proline, glycine, betaine, mannitol and trehalose [35,74,81]; increased activity of the ROS elimination system; reduction in

MDA content [70]; improvement in anatomical attributes [71]; removal of electrolyte leakage [118,119], among others. It is worth mentioning that different effects were observed for the maturation stages of the plant, for the cultivars of the same species, for the salt concentration and for the attention and form of application of the BRs. These data were analysed for 23 plant species (Table 1). CAT, SOD and glutathione reductase (GR) activities increased in rice seedlings subjected to salt stress (NaCl) and treated with the BB16 analogue [23]. Seedlings of salinity-sensitive varieties treated with 24-epiBL had partial and short-term improvement in salinity tolerance due to a sustained higher activity of APX under these conditions [24].

3.4. Potentially Toxic Elements

Potentially toxic elements (PTEs) can cause stress in the metabolic pathways of plants, although some cultivars are used for bioremediation. High concentrations of PTM can cause changes in the chemical structure of molecules, such as the blocking of functional groups (-OH, -COOH, -C=O) or displacement or replacement of essential ions, which can lead to regulatory changes such as chlorosis and nutritional imbalance [120].

The BRs most used in studies of attenuation of the effects of intoxication by PTM are 24-epiBL, 28-homoBL and epiBL with concentrations from 0.01 nM to 5 μ M. The most studied metal regarding the interaction with BRs was cadmium. Other metals are mentioned, such as Al, Cu, Fe, Ni, Pb and Zn, in 11 plant species (*R. sativus, Solanum nigrum, S. lycopersicum, C. sativus, O. sativa, Triticum aestivum, Vigna radiata, B. juncea, B. napus, Cicer arietinum, Phaseolus vulgaris*) (Table 1). In these studies, the BRs were applied in a culture medium by foliar spraying, seed imbibition and application in the root whose effects were: 24-epiBL and 28-homoBL caused additional stimulation of antioxidant enzymes and proline content, elevation of the proline level in association with the antioxidant system that, at least in part, was responsible for the improvement of Al stress in mung bean (*V. radiata*) seedlings [27]. Antioxidant enzyme activities (CAT, POD and SOD) and proline contents increased in control, regardless of treatment [121]. The analogue 24-epiBL reduced the toxic effect of Cd on photochemical processes, decreasing damage to reaction centres and O₂ evolving photochemical centres and maintaining efficient photosynthetic electron transport [32].

3.5. Abiotic Disorders

One of the central abiotic diseases is blossom-end rot (BER), which affects several crops, mainly Solanaceae. The low Ca^{2+} content in the distal tissue of the fruit is the main trigger for this physiological disorder. The imbalance of this ion leads to membrane rupture, accumulation of ROS and cell death, serving as a gateway to secondary diseases. In the 'BRS Montese' tomato, the application of 24-epiBL (0.01 μ M) reduced the incidence of BER by 44.2% and increased fruit mass and size. Fruits showed physiological improvement by increasing the concentration of ascorbic acid, the activity of antioxidant enzymes (APX, CAT and SOD) and the concentration of soluble Ca^{2+} , necessary for the structure and stability of the membrane, resulting in increased tolerance to BER [26]. Calcium is also essential in the defence induced by BRs.

3.6. Crosstalk between Brassinosteroids and Other Plant Growth Regulators

The regulation of plant development against biotic and abiotic factors is made possible by the interaction between PGRs and biochemical pathways triggered by external stimulation. The connections between the signalling pathways are integrated by a network whose products are BRs, auxin, ethylene, jasmonic acid (JA) and salicylic acid (SA). There are synergistic effects of BRs with other PGRs, such as increased ethylene production in mung bean epicotyl segments [122] and with auxin on stem segment elongation [123,124]. Brassinosteroids enhanced expression proteins (BEE1, BEE2 and BEE3), and the opposite effect was observed; when BEE1 was overexpressed, there was a reduction in ABA accumulation, suggesting that this protein may function as a signalling intermediary in multiple pathways. In sorghum (*Sorghum vulgare*), ABA and BR synergistic effects on increasing drought tolerance were observed [125]. There is a potential interaction between BR and JA biosynthesis, reinforcing the role of BRs in mitigating the effects caused by abiotic and biotic stresses [59,115].

The synergistic effects of BRs and the BR-INSENSITIVE 2 (*BIN2*) inhibitor bikinin lead to increased physiological responses mediated by SA, such as resistance to *Pseudomonas syringae* pv. *tomato* DC3000 in Arabidopsis. SA is an elicitor that regulates several immune responses in plants, including pathogen-associated molecular pattern (PAMP)—triggered immunity (PTI), effector-triggered immunity (ETI) and systemic acquired resistance (SAR). Brassinosteroids enhance SA-mediated immune responses in Arabidopsis by inactivating *BIN2*, which inhibits clade I TGACG motif-binding transcription factors (TGAs). Only TGA1 and TGA4 interact with *BIN2*, resulting in changes. In TGA4, *BIN2* phosphorylates serine at position 202, suppressing the redox-dependent interaction between the non-expressor of pathogenesis-related genes (NPRs) and TGA4 and destabilising the latter. Plant defence responses are regulated by BRs, not exclusively via crosstalk with the PTI signature but also with hormonal interaction with SA [126]. Gibberellic acid inhibitor proteins (DELLA) and the BR-regulated transcription factor BZR1 are central hubs for crosstalk and signal integration, playing ambivalent roles in plant innate immunity, microbial virulence, and disease resistance [127].

4. Biotic Stresses

Phytopathogenic microorganisms penetrate plants through natural openings (stomata, lenticels and hydathodes) or lesions (artificial, natural and by the action of fungi). Phytopathogenic bacteria and viruses do not have active structures that allow penetration into plants by mechanical force. Insects and mites usually spread viruses by pores that extend along the cell wall. Phytopathogenic fungi may have different structures that also allow direct penetration into the host, including direct penetration at the subcuticular level and the cellular level (with haustoria, intercellular mycelium, intercellular mycelium with haustoria or appressorium and intracellular mycelium) [128].

In the interaction process between plant and pathogen, there is bidirectional communication. Plants can recognise foreign organisms and activate their defence mechanisms. On the other hand, the pathogen can manipulate the plant's biology to create an ideal environment for its growth and development by avoiding a plant defence response. In this relationship of attack and defence, the pathogen and the host can produce a series of toxic chemical compounds. The symptoms resulting from the interference of these compounds in the host physiology are indicators of its susceptibility or resistance. Structural and biochemical mechanisms, both pre-formed (passive or constitutive) and post-formed (active or induced), are the means of plant defence against the attempted infection and colonisation of the pathogen [129].

Structural mechanisms are physical barriers that inhibit or hinder the pathogen's penetration and/or colonisation. Constitutive physical barriers include cuticles (waxes and cutin), cell walls, trichomes, stomata, etc. Induced physical barriers include cellular defence structures, lignification, papillae, halos, cork layers, abscission layers, tyloses and glycoproteins rich in the amino acids hydroxyproline and glycine. Biochemical processes involve substances that can inhibit the development of the pathogen or generate adverse conditions for its survival in the tissues of the survivor. The constitutive biochemical apparatus includes phenolic compounds, saponins, unsaturated lactones, glycosides, phytotoxins, antimicrobial proteins related to pathogenesis (PR), which can also pre-exist in the plant [130]. In recent decades, phytohormones have stood out in plant–pathogen interactions as a biochemical defence. Plant responses to pathogen infection are coordinated through integrated signalling, communication and response systems. The transmission of signals between cells is essential for the life of an organism, as it provides the control by which cells perceive, recognise and respond to external stimuli [131].

The main chemical mechanisms of pathogen attacks on the host are enzymes, toxins, and hormones. The pathogen secretes these chemical weapons to penetrate, colonise and/or provide nutrients in the host cell. Enzymes are essential in all these stages of pathogenesis and act in the disintegration of cellular components and substances present in host cells. Toxins are highly mobile molecules, active at deficient concentrations $(10^{-6} \text{ to } 10^{-8} \text{ M})$, capable of causing physiological, metabolic or structural changes. Their sites of action are the plasma membrane, mitochondria, chloroplasts and enzymes, which are essential for host defence. Some phytopathogenic agents synthesise hormones in the same way as those of the host and other different hormones. This pathogen attack mechanism causes a hormonal imbalance, resulting in irregular growth and development and accelerating plant tissue senescence [132].

Salicylic and jasmonic acids and ethylene are the main hormones involved in the response of plants under biotic stress [133]. Abscisic acid, auxin, gibberellic acid, cytokinin, brassinosteroids and peptide hormones also act in plant defence signalling pathways in different pathosystems [134]. Depending on the type of plant–pathogen interaction, various hormones play positive roles (when the hormone can act against the disease), negative (when the occurrence of the disease is favoured) or neutral (when there is no influence of the hormone). In mango fruits, it was observed that resistance to *Colletotrichum gloeosporioides* resulted from the involvement of the up-regulation of ET, BRs and phenylpropanoid pathways [135].

The reprogramming of host metabolism, gene expression, and modulation of plant defence responses against pathogen attacks can occur through treatment with plant hormones. BRs regulate other hormones and are involved in plant–pathogen interactions, regardless of whether they are biotrophic, hemibiotrophic or necrotrophic [134]. When applied exogenously, they play an essential role in the innate immunity of plants [127].

4.1. Oomycetes, Bacteria, Fungi and Virus

BR concentrations, modes of application, and plant development stages must be welldefined to control diseases efficiently using these hormones. Inadequate concentrations, for example, can stimulate the growth of the pathogen and, consequently, the progression of the disease [136]. The root oomycete *Pythium graminicola*, which causes root rot in rice, uses BRs as virulence factors to cause disease; in this case, BRs favour the pathogen, causing greater plant susceptibility [137]

Treatments with 24-epiBL and a formulation based on a brassinosteroid analogue DI-31 (BB16) activated the innate immunity of strawberry plants (*Fragaria* spp.) in response to infection by *Colletotrichum acutatum*. Both steroids were more effective in inducing the resistance response at the lowest concentration (0.1 mg/L), with the BB16 analogue causing a more substantial effect than 24-epiBL. Defence biochemical markers showed an increase in the production of H_2O_2 , O_2^{-} , NO, calcium oxalate crystals and greater callose and lignin deposition in plants treated with 24-epiBL and BB16 compared to control plants. It was also observed that in plants treated with BB16, 40% of the stomata closed six hours after treatment, while 24-epiBL did not cause any change in stomata opening [138].

The ability of BRs to induce resistance to more than one disease has been observed in rice and tobacco plants. In rice plants, BL treatment induced resistance to rice blast, caused by the fungus *Magnaporthe grisea*, and bacterial blight, caused by *Xanthomonas oryzae* pv. *oryzae*. BL provided excellent resistance to the tobacco mosaic virus (TMV) and *Pseudomonas syringae* pv. *tabaci* in tobacco (bacteria) and *Oidium* sp. (fungus). Resistance triggered by BL occurred differently from systemic acquired resistance and resistance to disease induced by wounds; there was no induction of SA biosynthesis or acidic or basic pathogenesis-related (PR) gene expression [27].

BRs have also been effective pretreatments for postharvest diseases. Grape bunches, submitted to exogenous application of 24-EpiBR (0.4 and 0.8 mg L⁻¹), stored at 0 ± 1 °C, without *B. cinerea* inoculation, evaluated in 15, 30 and 60 days, greater firmness and less deterioration, fall and weight loss of the berries were observed. In the fungus inoculation

treatment, bunches were previously immersed in 1L of solution with 24-EpiBR and, after six h, artificially inoculated with *B. cinerea* and stored at 25 ± 2 °C and 95% relative humidity. There was an increase in resistance to grey mould with a reduction of oxidising substances (OO⁻² and MDA) and an increase in the activities of defence-related enzymes (SOD, POD, CAT and PAL) in berries pretreated with BRs [139]. Similar results were observed in the *Rosa hybrida–Botrytis cinerea* pathosystem. Potential defence elicitors against grey mould in cut roses indicated that BR at a concentration of 1 µmol/L provided disease inhibition and increased anthocyanin and water content, the vase life of cut flowers (~four days), of SOD and CAT activities and relative fresh mass [140].

In addition to increasing thermotolerance, BRs also increased the resistance of *C. sinensis* seedlings to *C. gloeosporioides* and significantly suppressed the spread of this fungus. The use of exogenous 24-epiBL reduced H₂O₂ accumulation in tea leaves. It markedly increased the PAL activity of leaves from 48.74% 24 h after inoculation with *C. gloeosporioides* to 71.21% when leaves received the combined treatment (24-epiBL and fungus suspension). This response is correlated with increased levels of transcription of genes involved in the phenylpropanoid pathway *CsPAL*, *CsC4H* and *Cs4CL*. There was an increase in the relative expression of the pathogenesis-related gene 1 (*CsPR1*), indicating that 24-epiBL activates the systemic defence response. However, there was a reduction in the face of the lipoxygenase 1 (*CsLOX1*) gene with this BR [141]. Failure to activate the lipoxygenase pathway can suppress JA biosynthesis, which is related to defence against pathogens [142].

In mango fruits, resistance against anthracnose (*C. gloeosporioides*) was improved by the exogenous use of 24-epiBL (ideal concentration of one μ mol/L). The reduction in the severity and incidence of anthracnose in mango fruits treated with 24-epiBL was mainly due to the activation of defence-related enzymes (PAL, chitinase—CHT, cinnamate-4-hydroxylase—C4H, β -1,3-glucanase—GLU and 4-hydroxycinnamate CoA ligase—4CL), increased levels of total phenolics, flavonoids, lignin and prospecting, suppression of pectin hydrolases and regulation of ROS levels and antioxidant enzyme activities (CAT, APX, SOD and POD). There was no direct action of this BR to inhibit the growth of *C. gloeosporioides* in vitro [143]. On the other hand, fungistatic activity against *Helminthosporium teres*, which causes net blotch in barley (*H. vulgare*), was observed in vitro experiments, with 50% of the growth suppressed with the mechanical mixture of 24-epicastasterone and succinic acid. In the field, this combination (25 to 50 mg/ha) increased resistance to leaf spot and productivity with a 34% increase in seed mass per ear [144].

4.2. Nematodes

BRs can induce favourable or unfavourable host responses. In rice, we are applying epibrassinolide against root-knot nematode (*Meloidogyne graminicola*)-induced root susceptibility, favouring the nematodes. The mutual antagonistic effect on the signalling pathways between BR and JA is a critical factor in the interaction between *Oryza sativa–M. graminicola*. Jasmonic acid activates PR genes that result in the expression of resistance. However, low concentrations of BR inhibit the expression of *OsAOS2* (JA biosynthesis) and *OsJAmyb* (JA response) genes [145]. On the other hand, the exogenous application of BR in *Solanum lycopersicum* resulted in resistance to *M. incognita*. BR induced H₂O₂ production in the apoplast and activated MPK1/2/3 (mitogen-activated protein kinase 1/2/3), associated with induced systemic resistance (ISR) against root-knot nematodes. Plants with BR-deficient roots decreased the accumulation of apoplastic ROS, the transcription of *Respiratory Burst Oxidase Homolog1* (*RBOH1*) and *Whitefly Induced1* (*WFI1*), and the activation of MPK1/2 and MPK3. BR-induced activation of MPK1/2 is dependent on RBOH1. In this case, BR-induced systemic resistance is probably against the JA (ISR) and SA (SAR) independent nematodes [146].

4.3. Pests

In *B. napus* mutants, beneficial pleiotropic effects of the BR biosynthetic gene *AtDWF4* were observed, resulting in antifungal action (*Leptosphaeria maculans* and *Sclerotinia sclero*-

tiorum), increased branching, silica and seed formation, more remarkable sprouting and root system, increased tolerance to drought and basal thermotolerance of the seedlings (at 45 °C/3–4 h, recovered at 20 °C, with the accumulation of heat shock protein, *Hsp101* and *Hsp90*). These effects may result from three main mechanisms, in which BRs act as modulators of cell structure and functions, acting mainly on protein synthesis, increasing stress responses and under stress conditions, mobilising resources for growth regulation. Although the transgenic lines AtDWF4, BL35 and BL16 showed more excellent resistance to fungi, they were 50% and 100% more attractive to spider mites than wild-type plants [147].

The negative interaction of BR with the JA pathway has been associated with the formation of anti-herbivory characteristics (glandular trichomes, synthesis of allelochemicals and expression of enzymes, such as proteinase and polyphenol oxidase inhibitors) in tomatoes. Trichome density and allelochemical content are directly affected by BRs and JA. However, on the contrary, BR deficiency increases pubescence, whereas JA deficiency favours the reduction of trichomes. The double mutant with the genes that cause a lack of both hormones ($dpy \times jai-1$) demonstrates an epistatic effect between these genes, indicating the action of BR in the JA signalling pathway. The interaction of these hormones in the defence against *Spodoptera frugiperda* and *Tuta absoluta* was confirmed through the density of trichomes since plants with the dpy gene had high densities of trichomes compared to plants that contained only one of the genes. Plants with dpy, deficient in BRs, express proteinase inhibitor I (PI-I) and produce 4.5 times the content of zingiberene (zgb), an allelochemical with an anti-herbivory effect [148].

The plant–BR–insect interaction is little studied, but it could contribute to the control of insects in plantations. Rice plants' susceptibility to brown plant hopper (BPH, *Nilaparvata lugens*) was increased when treated with 24-epiBL, and there is a suppression of the BRs' pathway when there is BPH infestation and activation of the SA and JA pathways. This is confirmed with BR-deficient mutants, which increase resistance to this insect [149].

5. Commercial Products of BRs

In the early 1980s, the usefulness of BRs as agrochemicals was confirmed by studies carried out in Japan and the former Soviet Union [150–152]. Since then, numerous reports worldwide have appeared, and many potential practical uses have been patented [153]. Despite the vast importance of BRs, the amount present in plants could be higher, limiting their practical application in crops. One way to overcome this obstacle is using synthetic compounds called brassinosteroids analogues (Table 2), which play a physiological role similar to the natural one. These analogues have certain structural groups in natural BRs [154].

Table 2. Brassinosteroids and	l analogues applied	l in crops, with	ι respective co	ncentrations and	effects.
		*	*		

Commercial Name	Brassinosteroids/ Analogue	Concentration	Effects
¹ Brassinolide ² Biobras-16 [®]	Brassinolide Spirostanic analogue of castasterone	0.5 – 1.0 mg L^{-1} 0.4 mg L^{-1}	Higher rice yield (10%) Increased seed yield (68%)
³ CIDEF-4	(80% steroid compound)	0.3 mg L^{-1}	Higher yield in fertile maize hybrids (2.5 times more)
⁴ DI-31 (BB16)	Spirostane BR analogues	$30~\mathrm{mg}~\mathrm{ha}^{-1}$	Increase in lettuce production (25.93%)
⁴ DI-100	Spirostane BR analogues	$30 { m mg} { m ha}^{-1}$	Increase in lettuce production (31.08%)
⁵ Brassinazole	Triazole compound	5.0 µM	Increased firmness and cellulose content in persimmon fruits
⁶ 24-eBL (Phyto Technology Laboratories, US).	24-epibrassinolide	$0.2 \text{ mg } \mathrm{L}^{-1}$	Increased yield per vine, berry weight, cluster weight and specific gravity

Source: ¹ [111]; ² [155]; ³ [156]; ⁴ [157]; ⁵ [158]; ⁶ [159]. Adapted from [154].

In soybean cultivars under water stress, a single foliar application of the functional analogue of BR DI31 (BB16) was able to promote stability in the canopy and efficient use of water from the first days of stress. There was also an improvement in the response antioxidant, nitrogen homeostasis, and attenuation of nodular senescence in roots. Finally, there was a 9% increase in productivity when applications were spaced at 21 days [160].

Foliar application of 1 μ M of 24-epiBL in strawberries increased fruit growth rate, fruit mass, water, phenolic and anthocyanin contents, and carbohydrate metabolism [161]. The 24-epiBL steroid is one of the most active and studied forms of BRs, as it is organic, biodegradable and regulates several biochemical and physiological processes in plants [162].

BRs can influence the quantity produced and the quality of what is produced. The exogenous application of BRs at doses of 10 and 20 mg.ha⁻¹ in potato plants promoted a 20% increase in productivity, reduced nitrate content in tubers and increased starch and vitamin C content [163]. The application of 28-homoBL directly to the roots of tomato seedlings 20 days after germination resulted in increased production of fruits with higher lycopene and β -carotene contents compared to the control treatment [72].

Horticultural products (fruits, vegetables and greens) are highly perishable, requiring various post-harvest care to prolong the shelf life of these products. The BRs induce the ripening of the fruits; a solution for this is inhibiting their synthesis. Brassinazole (BZ), a BR inhibitor, increased the shelf life of fruits and vegetables [164]. The application of 5 μ M of BZ in persimmon fruits (immersion for 30 min) delayed ripening, increased fruit firmness and cellulose content, decreased ethylene biosynthesis, the activity of enzymes that act in the degradation of the cell wall and the expression of genes related to ethylene biosynthesis [158]. The application of BL can accelerate fruit ripening by up to five days. With the application of BZ in strawberries, ripening was delayed by seven days compared to the control treatment [165].

In addition to the benefits promoted in crop yield and quality, BR's analogues are environmentally friendly, as they are non-toxic and are a sustainable and low-cost tool for use in agriculture. Current research has been directed towards improving the understanding of the fundamental mechanisms of action of exogenously applied BRs and investigating the ideal stage of growth and development of plants so that their use is more efficient in the production and improvement of crops [153].

6. Conclusions

With global warming, the recurrence of abiotic and biotic stresses and the infeasibility of arable soils due to salinity or contamination by toxic metals, the search for new sustainable strategies is necessary. BRs are promising PGRs that act against biotic and abiotic stresses. However, not all BR biosynthesis pathways have been fully elucidated, which leads to a low number of synthetic BRs available on the market. Furthermore, endogenous BR synthesis is little explored and limited information is found in the literature.

BRs are involved in several processes in plant metabolism, including those associated with expressing epistatic and pleiotropic genes, increasing tolerance and/or resistance to abiotic and biotic stresses, and improvement of agronomical characteristics. Thus, the studies available in the literature (molecular, anatomical, biochemical, physiological, nutritional, morpho-agronomical, etc.) can generate opportunities to utilize these PGRs in agriculture and plant biology, maximizing the tolerance to stress. Additionally, interactions (synergistic and antagonistic) and crosstalk between BRs and other phytohormones also can be exciting strategies to control pests and diseases, being environmentally friendly and durable in various agricultural ecosystems [127].

In this review, we described several studies with abiotic stress, mainly focused on the action mechanisms of BRs in situations where plants are exposed to drought, salinity, and potentially toxic elements. With biotic stresses, our review provided recent research demonstrating the possibilities of BRs to mitigate adverse impacts occasioned by oomycetes, bacteria, fungi and viruses. However, nematodes and pests are critical biotic stresses whose interaction with BRs has not been explored.

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