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Brassinosteroids: Orchestrating Resilience and Growth in Modern Fruit Production

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Abstract

Plant growth regulators control various physiological processes in plants, including growth and development. Among these regulators, brassinosteroids (BRs) have emerged as important phytohormones with diverse roles in crop development and metabolism. They influence processes like cell division, elongation, reproduction, flowering, vascular differentiation, fruit ripening, root formation, and responses to both biotic and abiotic stressors. Additionally, BRs enhance tolerance and resilience to these stressors. Their impact on fruit trees' defense mechanisms holds significant potential for the fruit industry. This review focuses on the wide-ranging physiological and economic importance of BRs in modern fruit production, highlighting their applications and implications through conceptual research and development efforts.

Keywords

Brassinosteroids; development; growth; post-harvest; yield

Introduction

Plant Growth Regulators (PGRs) have significantly transformed and advanced agricultural practices globally. These are chemical compounds that modulate growth, development, and various physiological processes by either enhancing or inhibiting specific components. PGRs can originate naturally or be synthetically produced. They exert control over one or more physiological mechanisms within plants. Different PGRs exhibit distinct sites of action and effects in various plant species. PGRs are categorized into two groups based on their historical usage in the field of horticulture. While some PGRs are widely adopted and integrated by farmers, others remain underutilized at the grassroots level due to technological gaps and inadequate information regarding their impact on fruit crops. Prominent PGRs such as Gibberellins, Abscisic acid, Ethylene, Auxins, and Cytokinin have been effectively employed. In addition to these, certain PGRs, such as Jasmonic acid (JA), Brassinosteroids (BR), N-(2-chloro-4-pyridyl)-N′-phenylurea (CPPU), and Salicylic acid (SA), demonstrate established efficacy and efficiency but have yet to be fully harnessed due to existing knowledge gaps and technological limitations.

Brassinosteroid (BR) application proves beneficial in mitigating fruit abortion and premature fruit drop. Furthermore, BR application enhances pollen tube growth and fertilization processes. By preventing fruit abscission, BRs play a role in maintaining fruit retention. Additionally, BRs exert control over defense-related enzyme activity, thereby facilitating the establishment of robust defense mechanisms against a diverse array of pathogens. Manipulating endogenous BR levels has shown promise in enhancing fruit quality (1, 2). Notably, the structural variation at the C-24 position leads to the classification of the identified 70 BRs from different plant sources into C27, C28, or C29 categories (3) (see Fig. 1). These polyhydroxy steroidal plant hormones exhibit widespread distribution within the plant system, governing various aspects of plant growth. These functions include stimulating stem elongation, facilitating pollen tube expansion, promoting xylem development, inducing leaf epinasty, influencing ethylene production, activating proton pumps, modulating gene expression and photosynthesis, directing gravitropism, and orchestrating adaptive responses to environmental stress (4)

This review focuses on the discovery of a novel class of PGRs known as BRs. These BRs exhibit remarkable capabilities in influencing various plant development functions, even at exceptionally low doses. As advancements in agricultural and horticultural technologies persist and scientific research unveils novel approaches to enhance conventional crop production methods, the significance of understanding how to regulate growth processes through external factors becomes increasingly pivotal. This knowledge is essential for harnessing the full potential of these adaptable resources, thereby augmenting agricultural productivity and quality. This becomes particularly crucial given the challenges posed by shifting agroclimatic conditions.

Brassinosteroids Signalling

BRs (brassinosteroids) aid plants in adapting to diverse environmental stressors. A plant's resilience to challenges like temperature fluctuations, water scarcity, or soil salinity hinges on its ability to toggle between growth promotion and inhibition during unfavourable conditions (5, 6). BRs play a vital role in balancing normal growth and safeguarding against environmental stressors, achieved through collaboration with the Abscisic acid (ABA) pathway or independently. Several mechanisms have been proposed to elucidate how BR signaling facilitates stress adaptation. These include modifying stress-responsive gene expression machinery (7), initiating antioxidant systems (8, 9, 10), and promoting osmoprotectant synthesis (11).

The signaling pathway of abscisic acid (ABA) plays a pivotal role in modulating responses to environmental stressors (12, 13). At a comparable level to BRASSINOSTEROID -INSENSITIVE 2 (BIN2) and BRASSINAZOLE RESISTANT 1 (BZR1), BRs and ABA generally elicit opposing physiological effects (14, 15). BIN2 acts as a suppressor of BR signaling while augmenting ABA-triggered stress responses through phosphorylation of SNF1-RELATED PROTEIN KINASE 2 (SnRK2), consequently activating ABA-responsive genes (14). Moreover, exogenous application of BR suppresses the activation of RD26 (RESPONSIVE TO DESICCATION 26), a gene encoding a transcriptional regulator of stress-responsive genes mediated by ABA (16). The interplay between transcription factors in the BR signaling and ABA-response pathways, leading to reciprocal antagonism, critically regulates plant growth and drought resistance. Recent revelations highlight that the interaction of BR signaling via BIN2 and autophagy pathways significantly contributes to plant growth regulation and survival during periods of drought stress and nutrient deprivation (17).

BR signaling also plays a role in the adaptation of plants to varying temperatures. Specifically, it impacts the process of cold acclimation through the modulation of a transcription factor called BR-ENHANCED EXPRESSION 1 (BEE1). BEE1 indirectly influences the transcription of components within the MYB-bHLH-WD40 complex (18), which is pivotal in this process. At higher temperatures, BZR1 primarily accumulates in the nucleus and initiates the transcription of genes that facilitate growth. BZR1 can

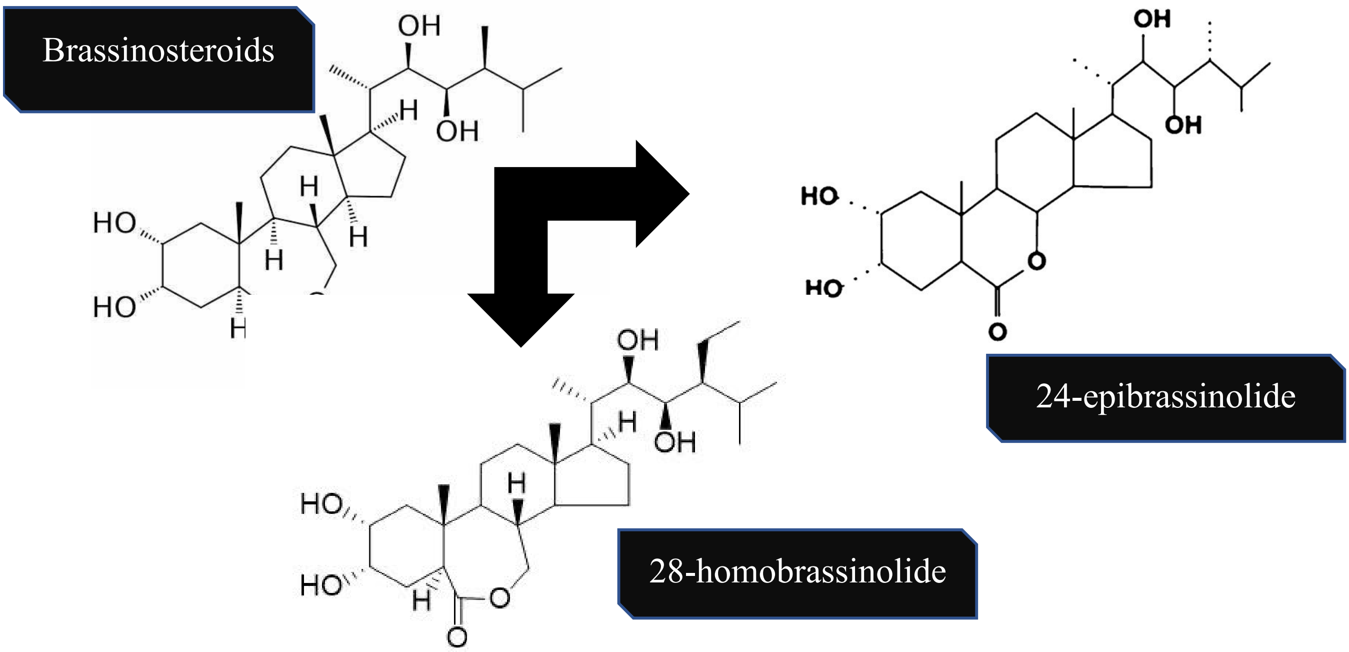

Fig 1. Chemical structure of two of the most common Brassinosteroids, 24-epibrassinolide (Epi-BL) and 28-homobrassinolide (HBL).

directly bind to certain gene promoters or associate with the promoter of PHYTOCHROME INTERACTING FACTOR 4 (PIF4) to orchestrate thermally-induced morphogenesis (19, 20). The study has demonstrated that elevated temperatures result in heightened levels of active PIF4, leading to a reshaping of nuclear protein complexes from BES1 (BRI1-EMS-SUPPRESSOR 1) homodimers to BES1-PIF heterodimers (21).

BR signalling plays a pivotal role in enhancing salt tolerance by regulating both the synthesis and transmission of ethylene signals. When plants encounter salinity stress, pretreatment with BR amplifies the activity of 1-aminocyclopropane-1-carboxylate synthase (ACS), an enzyme crucial for ethylene synthesis. This amplification leads to an augmentation in ethylene production and signaling (22, 23). The involvement of a membrane-associated signaling complex called BRASSINOSTEROID INSENSITIVE 1 (BRI1) during saline conditions implies BRI1's potential role in modulating salt stress tolerance. This notion gains support from findings indicating that partially inhibiting the endoplasmic reticulum-associated protein degradation system mitigates the heightened salt sensitivity observed in bri1-9 mutants (24).

Through a multi-omics approach, recent research has revealed that the activation of BR signaling in vascular cells plays a crucial role in regulating drought adaptation during various developmental stages in both root and shoot organs (11). The study demonstrated that disrupting four receptors of BR (bri1, brl1, brl3, bak1) leads to enhanced drought tolerance; however, this improvement comes at the expense of overall plant growth. Conversely, overexpressing BRL3 (BRASSINOSTEROID INSENSITIVE 1-ETHYL METHANESULFONATE-SUPPRESSOR 1 (BRI1 EMS-SUPPRESSOR 1)-LIKE 3) receptors specifically in vascular tissues results in significantly enhanced drought tolerance without adversely affecting plant growth.

In both regular and water-deprived scenarios, the existence of BRL3 receptors within vascular tissues triggers the activation of genes associated with responses to water stress and the metabolism of osmoprotectants. Metabolomic assessments revealed elevated levels of osmoprotectant sugars and amino acids in roots exhibiting BRL3 overexpression. Furthermore, transcriptome analysis demonstrated an enrichment of genes engaged in abiotic stress responses within these roots (11).

Brassinosteroids (BRs)

BRs are a class of phytohormones in plants that bear structural similarities to animal steroid hormones. They play a crucial role in regulating various physiological processes, including plant growth, development, and defense mechanisms. BRs can be categorized based on their alkyl-substitution patterns as C27, C28, or C29. Active BRs typically feature a trans-fused A/B ring system with a 6 -ketone or 7-oxa-6-ketone moiety in ring B and two hydroxyl groups in ring A. One specific BR, brassinolide, has a chemical structure denoted as ((22R, 23R, 24S)-2α, 3α, 22, 23-tetrahydroxy-24-methyl-B-homo-7-oxa-5α-cholestan-6-one) (25). The application of BRs has demonstrated a significant positive impact on the growth, yield, and quality of various fruit crops. For instance, the foliar spray of BRs on fruits before harvest has been shown to extend shelf life and preserve quality. Exogenous application of BRs through an aqueous solution has led to remarkable enhancements in grape cluster diameter, weight, as well as berry length, diameter, and weight. Additionally, BRs have been found to slow the breakdown of soluble solids and titratable acidity, thereby preserving peel color even during cold storage (26). The augmentation of osmo-protectants, such as proline and glycine betaine, under stress conditions has been revealed to exhibit heightened efficacy. These steroidal compounds can be exogenously administered either during seed germination or via foliar application (27). Through exogenous application of BRs on grapevines, researchers achieved a reduction in berry drop, an increase in fruit firmness, a decrease in ethylene production rates and respiration during storage, and a decline in berry decay (28). Vergara et al. (29) demonstrated that the application of BRs via spraying on grapes elevated their soluble solids, coloration, and anthocyanin content. In concurrence, Chervin et al. (30) and Symons et al. (31) illustrated that external administration of BR inhibitors can effectively modulate grape berry ripening by modifying BR levels, leading to significant delays or advancements in the ripening process. Furthermore, Luan et al. (32) reported that a concentration of 0.4 mg L^{-1} of BRs increased the overall anthocyanin content in grapes compared to control fruits.

Chinese ber (*Ziziphus jujuba* cv. Huping) fruits that were addressed with BR had much lower storage ethylene levels than untreated fruits (33). In fruit crops, one of the crucial physiological reactions of BRs is thought to be the facilitation of the ripening process of fruit by promoting ethylene production. The only way these compounds could increase fruit ripening was through the exogenous application; however, any change in the endogenous level of BRs had little to no noticeable effects on climacteric fruit ripening like mango (34).

According to Zaharah and Singh (35), the postharvest application of Epibrassinolide (Epi-BL) accelerated mango fruit ripening by influencing the climacteric peak and improved fruit quality by enhancing color development and softening. The increase in mango peel coloration due to Epi-BL treatment could be attributed to enzymatic breakdown of chlorophyll or accumulation of carotenoids. Chai et al. (36) investigated the involvement of Brassinosteroids (BRs) in different fruit development phases, finding that BRs enhanced strawberry fruit cell division. They also observed that the BR receptor FaBRI-1's expression significantly increased during strawberry fruit's transition from early red to white stages, indicating a link between BRs and ripening. Ayub et al. (37) explored the impact of Epi-BL on FaBRI1 receptor expression and signaling pathways in Camino Real strawberries, suggesting that perception pathways and signal transduction exhibited minimal gene activity. This implies that BRs, particularly at low doses, may play a role in strawberry fruit ripening. Furthermore, Roghabadi and Pakkish (38) proposed that BRs could mitigate oxidative damage induced by cold stress, enhancing the cold survival capability of sweet cherries stored at 1°C. Exogenous application of Homobrassinolide (HBR), a type of BRs, prompted early maturation in "Tulare" and "Bing" sweet cherry cultivars. This led to improved peel color, fruit firmness, and stem detachment force (39).

BL treatment resulted in increased water-soluble pectin and protopectin levels, along with heightened activity of key fruit-softening enzymes such as polygalacturonase (PG) and pectin methylesterase (PME). Application of BR significantly augmented the weight of orange fruits, exhibiting notable improvements compared to untreated counterparts (40). The utilization of BR analog (BR-3) led to a remarkable 65 percent rise in the predicted yield of yellow passion fruit (41). BR spray application on pear fruits demonstrated enhancements in Total Soluble Solids (TSS), ascorbic acid content, and non-reducing sugar levels (42). Pre-harvest BR application positively influenced apple fruit characteristics, including diameter, weight, firmness, total sugar content, and color (43). EBL treatment significantly elevated the overall antioxidant activity, phenolic content, and anthocyanin levels in fruits, as observed in the study by Sun et al. (44). BR-treated papaya fruits exhibited improved Total Soluble Solids (TSS), titratable acidity, β-carotene content, and reduced respiration rate (45). Specific examples can be found in Table 1.

Future Prospects

Research findings suggest that the application of brassinosteroids (BRs) in tissue culture offers promising benefits for the growth and development of fruit crops. External administration of BRs influences various aspects of plant development, including vegetative growth, flowering, and fruit quality (52, 53). Here are specific potential applications of brassinosteroids in fruit crop tissue culture: (a) Enhanced shoot regeneration: Incorporating BRs into the tissue culture process of fruit crops such as grape, tomato, and strawberry has demonstrated a significant enhancement in shoot regeneration (52). This application results in a higher rate of shoot proliferation, yielding superior quality shoots within the culture medium. (b) Improved rooting: Studies have indicated that the introduction of BRs during the tissue culture of fruit crops contributes to improved root development, thereby facilitating better establishment of plants in the field. This effect may lead to increased rates of plant survival and an overall enhancement in plant performance (52, 53). (c) Enhanced callus formation: Research indicates that the incorporation of BRs into

Table 1: List of Utilization of Brassinosteroids in different fruit crops all over the world.

S. No.	Crop	Parts of crop	Types of Treatment	Effect on any attributes	Region of the experiment conducted	Reference
1.	Grape	Berries	Spray	Enhanced ripening significantly	California, USA	(46)
		Berries	Spray	Increased berry peel colour and anthocyanin content	Jingyang, China	(32)
		Berries	Dipping application	Increased fruit firmness and maintenance of elevated TSS and Titratable Acidity (TA)	Shanxi, China	(33)
2.	Mango	Fruits	Spray	Hastened fruit ripening	Gingin and Dongara, Australia	(34)
3.	Strawberry	Leaves and fruits	Spray	Helped in ripening	Huelva, Spain	(47)
		Fruits	Injection	Fruit ripening	Ponta Grossa, Brazil	(48)
4.	Papaya	Leaves	Spray	Hastened the rate of senescence	Portugues, Brazil	(49)
5.	Sweet Cherry	Vegetative parts and fruits	Spray	Maintained higher TA and TSS; increased fruit firmness; improved anthocyanins, peel colour, ascorbic acid, and organic acids; increased postharvest life	Kerman, Iran	(38)
6.	Litchi	Leaves and fruits	Spray	Increased fruit firmness and decreased fruit drop	Shenzhen, China	(50)
7.	Orange	Fruits	Spray	Increased sugar content and fruit weight	Fujian, China	(40)
		Leaves, flowers and fruits	Spray	Increased fruit set	Shizuoka, Japan	(51)
8.	Pear	Fruit	Spray	Improved TSS, ascorbic acid content, and non-reducing sugar	Uttarakhand, India	(42)
9.	Passion Fruit	Vegetative parts	Spray	Increase in yield	Rio de Janerio, Brazil	(41)

tissue culture techniques has been proven to augment callus formation in specific fruit crops such as apple and pear (54). Callus denotes an aggregate of undifferentiated plant cells that hold potential for applications in genetic transformation and tissue engineering (55). Notably, Azpeitia et al. found that the application of BRs to coconut explants resulted in a favorable response, leading to improved callus proliferation, embryogenic callus generation, and somatic embryo development (56). (d) Improved stress tolerance: Scientific investigations have illustrated that BR utilization can heighten the stress resilience of tissue cultures of fruit crops, bolstering their ability to withstand environmental challenges like salinity, drought, and heat (5, 23). This enhancement subsequently contributes to the viability and overall effectiveness of plants produced through tissue culture methods. In conclusion, the prospective integration of brassinosteroids into tissue culture methodologies for fruit crops holds significant promise due to the manifold advantages they confer on plant growth and maturation. However, comprehensive comprehension of the potential of BRs in diverse tissue culture contexts and for various fruit crops necessitates further extensive research.

Conclusion

Numerous research findings support the notion that modern fruit production benefits not only from traditional growth hormones but also from the inclusion of BRs and their derivatives as a valuable sixth category of phytohormones. The external application of BRs has been demonstrated to exert distinct physiological effects on various aspects of fruit crop characteristics, including plant growth, micropropagation, as well as the overall quality and yield of the harvested produce.

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Authors' contributions

AK and RR conceived the concept and RR, GK, TS, KC, GBGR, and TV supported the idea. AK, GK, TS, KC, GBGR, and TV collected all the literature and composed all the information and wrote the article. RR extensively edited the article and gave valuable suggestions.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

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