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АГЛЯДЫ
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BRASSINOSTEROIDS AS BORON-BINDING PLANT STEROIDS

Abstract. Brassinosteroids (BRs) constitute a unique class of polyhydroxylated steroidal phytohormones that regulate plant growth, development, and stress responses. A defining and conserved structural feature of all biologically active BRs is in the presence of vicinal 1,2-diol motifs, most prominently at the 2α,3α-positions of the A ring and at the 22,23-positions of the side chain. These *cis*-diol functionalities impart chemical properties that distinguish brassinosteroids from all other major phytohormone classes and enable reversible coordination with boron species. This review summarizes analytical, chemical, and physiological evidence supporting the concept of 1,2-diol brassinosteroids as boron-responsive phytohormones, highlights parallels between boronate derivatization chemistry and *in vivo* boron complexation, and proposes boron coordination as a previously underappreciated regulatory layer in brassinosteroid biology. Integrating inorganic chemistry with plant hormone signaling allows improving our understanding of brassinosteroid evolution, transport, and function, and positions 1,2-diol BRs as a model system for mineral–hormone co-regulation in plants.

Keywords: brassinosteroids, vicinal diols, boron complexes, function

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БРАССИНОСТЕРОИДЫ В КАЧЕСТВЕ БОР-СВЯЗЫВАЮЩИХ СТЕРОИДОВ РАСТЕНИЙ

Аннотация. Брассиностероиды (БС) представляют собой уникальный класс полигидроксилированных стероидных фитогормонов, регулирующих рост, развитие и реакции на стресс у растений. Определяющей и консервативной структурной особенностью всех биологически активных БС является наличие вицинальных 1,2-диольных мотивов, наиболее выраженных в 2α,3α-положениях А-кольца и в 22,23-положениях боковой цепи. Эти *цис*-диольные функциональные группы придают химические свойства, которые отличают брассиностероиды от всех других основных классов фитогормонов и делают возможной обратимую координацию с соединениями бора. Обобщаются аналитические, химические и физиологические данные, подтверждающие концепцию 1,2-диольных БС как фитогормонов, чувствительных к бору, проводятся параллели между химией образования боронатных производных *in vitro* и комплексообразованием с бором *in vivo*, а также предлагается рассматривать координацию с бором в качестве ранее недооцененного регуляторного уровня в биологии брассиностероидов. Интегрируя неорганическую химию с сигнализацией растительных гормонов, данная концепция углубляет наше понимание эволюции, транспорта и функции брассиностероидов и позиционирует 1,2-диольные БС в качестве модельной системы для изучения корегуляции минералов и гормонов у растений.

Ключевые слова: брассиностероиды, вицинальные диолы, боратные комплексы, функция

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Introduction. Brassinosteroids (BRs) constitute a distinct class of polyhydroxylated steroidal phytohormones that play a central role in plant growth and development. Since their discovery, BRs have been recognized as key regulators of fundamental physiological processes, including cell elongation

and division, rhizogenesis, seed germination, vascular differentiation, flowering, senescence, and reproductive development. In addition to their growth-promoting activity, brassinosteroids significantly enhance plant tolerance to abiotic stresses, such as salinity, drought, temperature extremes, and nutrient imbalance, highlighting their importance in plant adaptation and resilience [1, 2].

The structural identity of brassinosteroids was first elucidated through X-ray crystallographic analysis of a biologically active steroid isolated from *Brassica napus* pollen. This compound, later named brassinolide, was shown to be a highly oxygenated steroid closely resembling animal steroid hormones. Its systematic name – (22*R*,23*R*,24*S*)-2α,3α,22,23-tetrahydroxy-24-methyl-B-homo-7-oxa-5α-cholestan-6-one – reflects the defining feature of the BR family: the presence of vicinal hydroxyl groups at positions C-2 and C-3, often accompanied by additional hydroxylation in the side chain [1]. This 1,2-diol motif is of particular chemical significance, as it provides a canonical binding site for boron coordination. To date, approximately 70 naturally occurring brassinosteroids have been isolated from a wide range of plant species and organs, including pollen, anthers, seeds, leaves, stems, and roots (Fig. 1) [3].

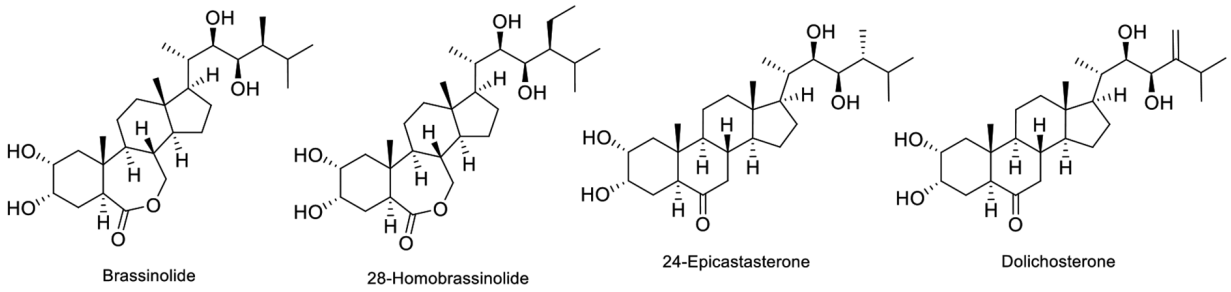


Fig. 1. Structures of some typical natural brassinosteroids. The most representative BRs share conserved oxygenation patterns, notably A-ring hydroxylation (often including a 2,3-diol) and, in many C27–C29 BRs, a side-chain 22,23-diol. These vicinal diol motifs provide potential boron-binding "handles", enabling reversible cyclic boronate formation with boric acid/borate under physiological pH conditions and thereby offering a plausible route for boron-dependent modulation of BR mobility and local bioavailability

Boron is known as one of the essential micronutrients for plant growth and development [4]. The influence of boron on plant development is mediated through its structural function in the cell wall, the regulation of hormonal signaling, and its metabolic integration with other elements. Recently, a number of studies have been published examining the combined effects of brassinosteroids and boron on plant growth and development. It was shown that boron at toxic concentrations stimulates BR biosynthesis in plants while simultaneously suppressing its inactivation, leading to sustained BR activity throughout seedling development [5]. Under boron deficiency conditions, exogenous 24-epibrassinolide reversed the inhibition of root growth [6]. The synergistic effect of foliar application of boron and 24-epibrassinolide on *Camelina sativa* alleviated water deficit stress, increased oil content, and improved oil quality [7]. Foliar treatment of grapevines with epibrassinolide combined with boric acid had a positive effect on chemical and reproductive characteristics, as well as on the percentage of fruit set [8]. Combined treatment with brassinolide and boric acid led to a significant improvement in the growth and flowering characteristics of aster plants [9]. The vegetative growth and flowering characteristics, as well as the quality of corms, were enhanced after gladiolus plants were treated with boron and brassinolide [10].

This review synthesizes analytical, chemical, and physiological data to support the concept that 1,2-diol brassinosteroids function as boron-responsive phytohormones, drawing clear connections between boronate derivatization reactions and biologically relevant boron complexation. Framing brassinosteroid action through the lens of inorganic coordination chemistry deepens insight into BR evolution, transport, and signaling, and identifies 1,2-diol brassinosteroids as a valuable model for studying mineral–hormone integration in plants.

The ability of boron to form complexes with steroids. Structural identification of BRs requires highly sensitive analytical techniques, as these phytohormones occur in plant tissues at extremely low concentrations. Boronic acids have been employed to form boron complexes with brassinosteroids,

creating derivatives suitable for detection in plants and biological samples (Fig. 2). This approach is effective because BRs contain a pair of diol groups – the precise structural motif that organoboronic acids exploit to form stable, cyclic boronate esters. To date, several dozen alkyl/aryl boronic acids have been proposed for the synthesis of such esters (Table 1). These well-defined esters are ideal for analytical quantification. In contrast, the use of boric acid or borax typically fails to yield a single, clean, and instrument-friendly derivative for routine analysis.

Among the most widely applied microanalytical methods are gas chromatography–mass spectrometry (GC–MS) and GC–MS with selected ion monitoring (GC–MS–SIM), which provide both sensitivity and structural specificity. For GC-based analysis, brassinosteroids must first be converted into volatile derivatives [11]. Brassinosteroids containing two sets of vicinal diol functions—such as brassinolide and castasterone – readily form bismethylboronate (BMB) derivatives upon reaction with methylboronic acid in the presence of pyridine. In contrast, 2-deoxybrassinosteroids, including typhasterol and teasterone, are typically derivatized through selective methylboronation of the side chain, followed by trimethylsilylation of the 3-hydroxyl group to yield methylboronate–trimethylsilyl (MB–TMS) derivatives. HPLC of boronate ester derivatives offers a robust alternative to GC-MS for BR analysis.

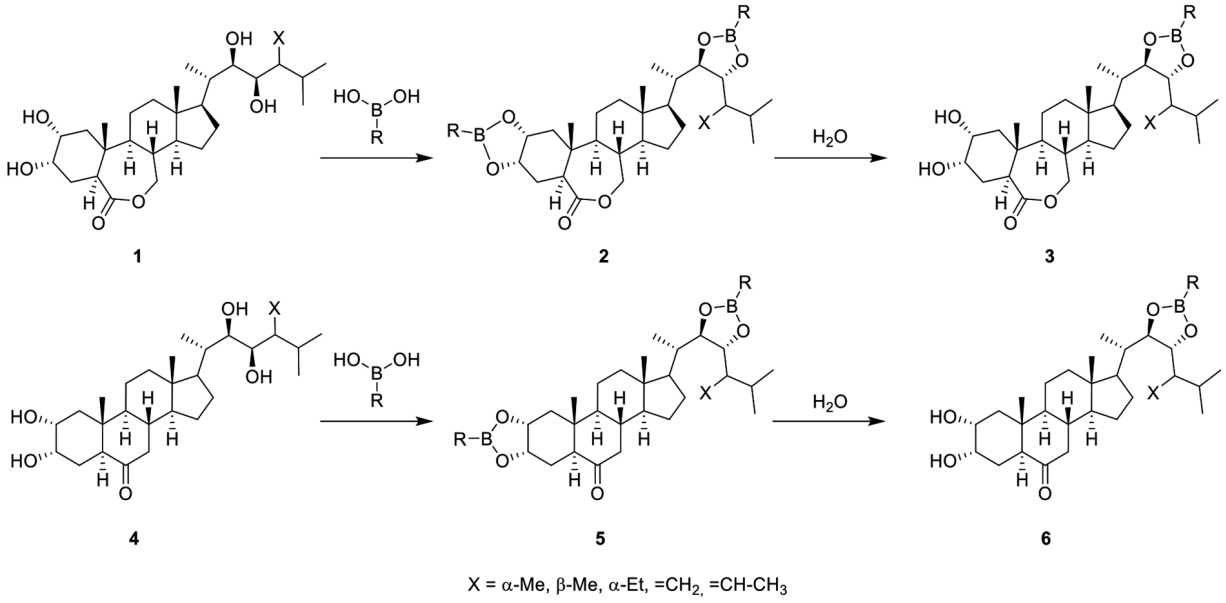
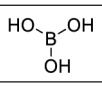
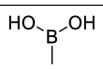
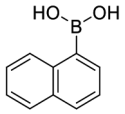
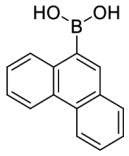
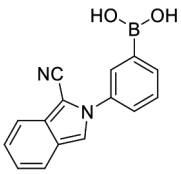
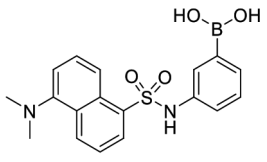
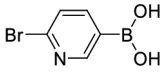
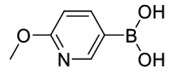
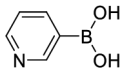
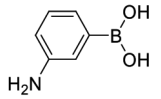
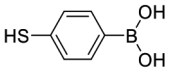
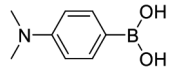
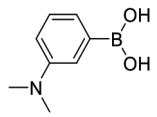
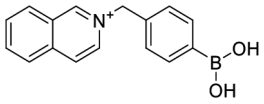
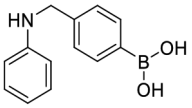
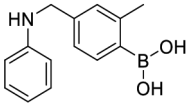
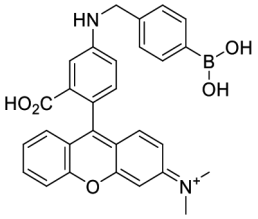
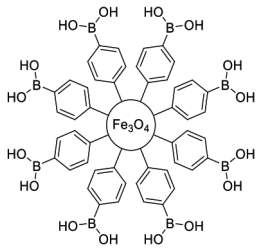
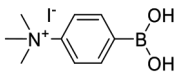
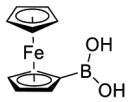


Fig. 2. The reaction of brassinosteroids with boric/boronic acids. In anhydrous media, the reaction can proceed with the formation of bis-boronate derivatives. The boronate fragment in the A ring undergoes hydrolysis even under conditions of silica gel chromatography, whereas the 22,23-boronates **3** and **6** are very stable

Table 1. **Structure of boric (boronic) acids used for the synthesis of complexes with brassinosteroids**

Name	Structure	References	Name	Structure	References
boric acid		[12]	methylboronic acid		[13–15]
naphthalene-boronic acid		[16]	9-phenanthrene-boronic acid		[17]
1-cyanoisoindole-2-*m*-phenylboronic acid		[18]	(dansylamino)-phenylboronic acid		[19, 20]

End of table 1

Name	Structure	References	Name	Structure	References
2-bromopyridine-5-boronic acid		[21, 22]	6-methoxy-3-pyridinylboronic acid		[22]
3-pyridylboronic acid		[22, 23]	*m*-amino phenylboronic acid		[23–25]
4-mercaptophenyl-boronic acid		[26, 27]	4-(*N*,*N*-dimethyamino)-phenylboronic acid		[28–30]
3-(*N*,*N*-dimethyamino)-phenylboronic acid		[23]	2-(4-boronobenzyl) isoquinolin-2-ium		[31]
4-phenylamino-methyl-benzeneboric acid		[32]	2-methyl-4-phenyl-aminomethylphenyl-boronic acid		[33–35]
rhodamine B-boronic acid		[36]	boronate-functionalized magnetic nanoparticles		[22, 37]
4-borono-*N*,*N*,*N*-trimethylbenzen-aminium iodide		[38]	ferroceneboronic acid		[39]

Electron impact (EI) mass spectra of both BMB brassinosteroids and MB–TMS derivatives provide rich structural information. In addition to the presence of a diagnostic molecular ion, these spectra display characteristic fragment ions that enable reliable determination of side-chain composition as well as the core steroidal framework. Fragmentation of brassinosteroids under EI conditions is dominated by side-chain cleavages, producing complementary ions that reflect both the nature of the side chain and the underlying steroid skeleton [11, 40].

Why is boric acid or borax not used to make "BR derivatives" for analysis? Even though boric acid/borate can interact with diols, the obtained derivatives are usually poor choices as analytical derivatization reagents compared with organoboronic acids (methyl-, phenyl-, naphthyl-, dansyl-aminophenyl-boronic acids, etc.).

They do not add a detection "tag." Derivatization in HPLC/LC-MS is often done to add a UV/fluorescence handle or to improve MS response. Boric acid/borax do not introduce a strong chromophore/fluorophore (unlike arylboronic reagents used explicitly for BR derivatization workflows). Product stability/speciation is messy in aqueous samples. Boric acid is a weak Lewis acid and borate–diol complexation is highly pH- and water-activity-dependent, often giving equilibrating mixtures (mono-/diesters, borate complexes) rather than one clean, isolable derivative – exactly what analysts try to avoid for quantitation and reproducibility [41, 42].

Poor compatibility with GC and MS hardware. Boric acid and borax are inorganic, highly polar, and nonvolatile - they are not suitable for GC derivatization (since neutral, volatile derivatives are required). Borax introduces alkali metal salts (e.g., sodium) that can cause ion suppression in ESI-MS and can contaminate sources/columns.

Organoboronic acids give predictable cyclic boronate esters and better chromatography. Aryl/alkyl boronic acids are designed to form neutral cyclic boronate esters with vicinal diols under controlled

conditions, improving extraction into organic solvents, chromatographic retention/separation, and (often) MS response. That is why protocols explicitly choose such reagents for BR derivatization prior to UPLC–MS/MS.

Boron chemistry makes complexation with plant metabolites inevitable. In water, boron is present mainly as boric acid, $B(OH)_3$, which behaves as a Lewis acid and readily forms tetrahedral borate diesters with vicinal (cis) diols and related dianionic O-donor motifs (e.g., sugar diols, polyols, and α-hydroxy-carboxylates). This is the same fundamental chemistry exploited in boronate derivatization for analytical methods [43–45].

A centerpiece of "hard evidence" is the borate–diol ester cross-linking of rhamnogalacturonan II (RG-II) in primary cell walls. RG-II exists predominantly as a borate-crosslinked dimer, where boron forms a 1:2 borate–diol diester bridge between RG-II chains. This has been demonstrated experimentally (and is widely accepted as a key biochemical function of boron in higher plants) [46, 47].

Boron is not just present—it is covalently and reversibly incorporated into wall architecture via borate ester chemistry, and the monomer↔dimer behavior is pH-dependent, consistent with borate ester formation/hydrolysis [43–45].

Boron is famously poorly phloem-mobile in many species, but becomes more mobile in plants that produce polyols (e.g., sorbitol, mannitol), because boron can form stable boron–polyol complexes. This is a well-documented explanation for species differences in boron transport and partitioning [46, 48].

From these points, it is reasonable to hypothesize that any plant metabolite with an appropriate diol geometry could form borate esters under the right pH (microenvironment) and concentration conditions. However, for brassinosteroids specifically, the arguments are currently chemical plausibility by analogy (diol-containing scaffolds can form borate esters), whereas direct in-plant evidence would require targeted experiments (e. g., ^{11}B NMR in extracts, LC–MS detection of boronated adducts under near-physiological conditions, and isotope tracing). The RG-II and polyol cases show that plants do form boron complexes naturally; they do not, however, automatically prove which small-molecule hormones do so [45, 46].

Because boron in plants is present largely as boric acid/borate and is well known to form reversible tetrahedral borate esters with vicinal diols, it is plausible that a subset of brassinosteroids (BRs) could transiently engage boron through their 1,2- and/or 1,3-diol motifs (where present), generating short-lived BR–borate adducts in boron-rich microenvironments. Such complexation, if it occurs, could act as a conditional "masking/solubilizing" handle that modulates local mobility, compartmentalization, or protection from nonspecific interactions, with release favored upon acidification or shifts in local polarity/ionic strength (conditions that generally destabilize borate–diol ester equilibria). Importantly, this should be framed as a working model, because BR action is often described as largely local rather than long-distance in plants, implying that any boron-assisted "carrier" role would most likely operate at the tissue/microdomain scale rather than as a general systemic transport mechanism.

If BR–borate adducts form *in vivo*, they could in principle influence apparent distribution via aqueous phases (including sap), but any such "delivery" function should be considered speculative and likely dependent on local pH and diol availability rather than a universal long-range transport mechanism [45–48].

Vicinal 1,2-diols (*cis*-diols) are known to form reversible covalent boron complexes with boric acid or boronic acids, typically yielding five-membered cyclic boronate esters. This interaction occurs readily under mildly acidic to neutral conditions, where boric acid predominates, and is strongly favored by rigid molecular scaffolds that enforce an optimal diol geometry. The steroidal backbone of brassinosteroids provides such rigidity, locking the diol system into a favorable spatial orientation and promoting selective, transient boron binding [43–45, 49].

Importantly, this chemical feature distinguishes brassinosteroids from other major classes of plant hormones. Auxins (such as indole-3-acetic acid) and gibberellins generally lack stable cis-vicinal diol motifs and therefore do not form comparable boron complexes. While these hormones may interact with boron indirectly through signaling crosstalk or downstream metabolic effects, they do not possess an intrinsic structural capability for direct boron coordination. In contrast, brassinosteroids are uniquely equipped among phytohormones to engage in direct boron–ligand chemistry, placing them at a critical intersection between hormone signaling and boron nutrition.

The reversibility of boron–brassinosteroid complexation suggests a dynamic regulatory mechanism rather than permanent modification. In plant tissues – particularly within the apoplast and phloem sap – boric acid may transiently associate with the 2,3-diol system of brassinosteroids, modulating their solubility, transport, and local availability. Such interactions may help explain observed links between boron status and brassinosteroid-dependent growth responses, including alterations in cell elongation, vascular development, and stress tolerance.

Taken together, the conserved A-ring vicinal diol motif of brassinosteroids provides a clear structural and chemical basis for their classification as potential boron-coordinating phytohormones. This feature links analytical boronate chemistry with in vivo physiological function and supports the emerging concept of bioactive plant boronosteroids, in which boron acts as a reversible, structure-directing modulator of steroid hormone behavior.

When the environment shifts toward alkaline pH, boric acid is converted into its tetrahedral borate anion [$B(OH)_4^-$], which exhibits enhanced affinity for vicinal 1,2-diols. Under these conditions, boron acts as a Lewis acid, coordinating with the lone pairs of the two adjacent hydroxyl oxygen atoms to form a five-membered cyclic boronate ester. This coordination involves reversible covalent B–O bonds and is favored by rigid molecular frameworks that preorganize the diol groups in a cis configuration.

For most simple 1,2-diols – such as those present in sugars, sugar alcohols, and polyhydroxylated steroids – boron complex formation is thermodynamically favored at higher (alkaline) pH (Table 1). Alkalinity increases the nucleophilicity of the hydroxyl groups and promotes the formation of the reactive borate species, a behavior that has been extensively characterized using ^{11}B NMR, ^{1}H NMR, and mass spectrometry. These studies consistently show increased stability and lifetime of boronate esters under mildly to moderately alkaline conditions.

Taken together, these observations emphasize that boron–diol complexation is highly sensitive to pH, molecular architecture, and the local chemical environment. In biological systems, where pH gradients exist between compartments such as the apoplast, cytosol, and phloem sap, this dynamic chemistry provides a plausible mechanism for reversible boron coordination, enabling boron to act as a transient modulator of polyol- and steroid-containing biomolecules rather than a static structural element [45, 50, 51].

Boron–brassinosteroid complexation and transport in alkaline phloem sap. Most naturally occurring brassinosteroids (BRs), including C_{27}, C_{28}, and C_{29} members, share a conserved structural feature: vicinal hydroxyl groups in the side chain at positions C-22 and C-23, in addition to the characteristic 2,3-diol motif in ring A. These *cis*-diol arrangements provide ideal coordination sites for boron and place brassinosteroids among the small subset of phytohormones capable of forming stable yet reversible boron complexes.

In plant physiology, this chemistry becomes particularly relevant in the context of phloem transport. Phloem sap is mildly alkaline (typically pH 7.5–8.5) and enriched in soluble boron species, predominantly as borate [$B(OH)_4^-$] complexed with sugars and polyols. Under these alkaline conditions, borate readily coordinates with 1,2-diols, forming cyclic boronate esters that increase the solubility, stability, and long-distance mobility of organic ligands [52, 53].

For brassinosteroids, boron complexation at the C-22/C-23 side-chain diol provides a plausible chemical mechanism for enhanced phloem mobility. Formation of BR–boron complexes would (i) increase aqueous solubility of otherwise highly lipophilic steroids, (ii) protect labile hydroxyl groups from metabolic modification, and (iii) facilitate reversible binding–release cycles during long-distance transport. This behavior closely parallels the well-established role of boron in mediating the phloem mobility of sugar alcohols such as sorbitol and mannitol [43–45].

Importantly, the same boronate chemistry exploited analytically in GC–MS derivatization (e. g., bismethylboronates of brassinolide and castasterone) mirrors the coordination modes expected *in vivo*. Thus, what is traditionally viewed as an analytical artifact may, in fact, reflect a physiologically relevant coordination motif, linking boron chemistry directly to brassinosteroid distribution and signaling [11, 40].

Upon arrival in target tissues – where local pH, ionic strength, or competing diols differ – these boron complexes would dissociate, releasing free brassinosteroids capable of binding their membrane-localized receptor complexes (BRI1–BAK1) and activating downstream signaling cascades. In this way, boron acts not as a hormone itself, but as a transient molecular chaperone, modulating brassinosteroid transport and bioavailability.

Table 2. **Boron coordination with brassinosteroids under acidic vs alkaline conditions**

Feature	Acidic Conditions (pH < 7)	Alkaline Conditions (pH > 7)
Dominant boron species	Boric acid, $B(OH)_3$	Borate anion, $B(OH)_4^-$
Coordination mode	Neutral cyclic borate ester	Anionic cyclic boronate ester
Preferred diol sites in BRs	C-22/C-23 (side chain), C-2/C-3 (ring A)	Same sites, stronger binding
Ring type formed	Five-membered tetrahedral boron ring	Five-membered boronate ring
Bond character	Reversible covalent (B–O)	Reversible covalent + electrostatic
Stability	Moderate	High
Biological implication	Local stabilization, transient binding	Enhanced solubility and long-distance phloem transport
Relevance	Apoplast, acidic compartments	Phloem sap, long-distance signaling

Boron as a phytohormone modulator. Although boron has traditionally been classified as a structural micronutrient essential for plant cell wall integrity – primarily through its role in cross-linking rhamnogalacturonan II – accumulating evidence indicates that boron also exerts regulatory effects on phytohormone biology. Rather than functioning as a classical signaling molecule, boron acts as a chemical modulator, influencing hormone stability, mobility, and availability through reversible coordination with *cis*-diol–containing metabolites [54, 55].

This mode of action is particularly relevant for brassinosteroids (BRs), which possess conserved vicinal diol motifs in both the A ring (C-2/C-3) and the side chain (C-22/C-23). These structural features distinguish BRs from most other phytohormones and render them uniquely competent to form boron complexes under physiological conditions. In this context, boron may be viewed as a non-covalent regulator that fine-tunes hormone behavior without altering receptor binding or gene expression directly.

Boron-mediated control of hormone mobility. One of the most compelling roles for boron in phytohormone regulation lies in its influence on long-distance transport. Phloem sap is mildly alkaline and enriched in soluble borate species, creating an environment favorable for cyclic boronate ester formation with 1,2-diols [56, 57]. For brassinosteroids, boron coordination at the side-chain diol is expected to: (i) increase aqueous solubility of otherwise highly lipophilic steroid hormones; (ii) protect reactive hydroxyl groups from premature metabolic inactivation; (iii) enable reversible binding that supports transport without permanent sequestration.

This mechanism parallels the well-established role of boron in facilitating the phloem mobility of sugar alcohols such as sorbitol and mannitol. By analogy, boron–brassinosteroid complexes may represent a mobile hormone pool, capable of translocation from biosynthetic sites (e.g., young tissues) to distal targets where BR signaling is required [56–58].

Modulation of hormone availability and signaling competence. Importantly, boron coordination is reversible and environment-sensitive, responding dynamically to local pH, competing diols, and ionic conditions. Upon arrival in target tissues – where apoplastic pH, membrane composition, or boron availability differ – boronate complexes can dissociate, releasing free brassinosteroids capable of engaging the BRI1–BAK1 receptor complex.

In this way, boron does not interfere with receptor recognition or downstream transcriptional responses but instead modulates the spatiotemporal availability of the hormone. Such a mechanism provides a chemical explanation for the well-documented interactions between boron nutrition and brassinosteroid-dependent developmental processes, including cell elongation, vascular differentiation, and stress tolerance.

Specificity among phytohormones. The concept of boron as a phytohormone modulator is inherently structure-dependent. Brassinosteroids are particularly well suited to this interaction due to their stable *cis*-diol motifs. In contrast, major phytohormone classes such as auxins (e. g., indole-3-acetic acid), gibberellins, and abscisic acid lack appropriately positioned vicinal diols and therefore do not form stable boron complexes under physiological conditions. Cytokinins and certain nucleoside-based regulators may exhibit weak boron binding via ribosyl diols, but these interactions are generally less stable and more transient than expected for BRs [59, 60].

This structural selectivity provides a compelling chemical rationale for why boron deficiency disproportionately affects growth processes associated with brassinosteroid signaling, while leaving other hormonal pathways comparatively less disrupted.

Integration with boron stress responses. Boron deficiency and toxicity are known to alter plant growth patterns, vascular development, and stress resilience – phenotypes that overlap significantly with brassinosteroid-regulated processes. The boron–brassinosteroid modulation model offers a unifying explanation: under boron deficiency, reduced formation of BR–boron complexes may impair hormone mobility and availability, leading to attenuated BR signaling even when hormone biosynthesis remains intact [61–63]. Conversely, adequate boron supply may optimize BR distribution and amplify growth-promoting and stress-protective responses.

Conceptual implications. Taken together, these observations support a revised view of boron in plant biology – not merely as a static micronutrient but as a dynamic chemical co-factor that modulates phytohormone behavior through reversible coordination chemistry. In this framework, boron acts as a molecular "facilitator," integrating mineral nutrition with hormone-regulated development and environmental adaptation [64–66].

This concept of boron-mediated hormone modulation bridges analytical chemistry, plant physiology, and signaling biology, and it opens new perspectives on how micronutrients can shape complex regulatory networks without classical receptor-mediated signaling.

Why are brassinosteroids unique among phytohormones? Among the diverse classes of plant hormones, brassinosteroids (BRs) occupy a unique chemical and physiological niche. While auxins, gibberellins, cytokinins, abscisic acid, and jasmonates primarily rely on specialized transport proteins or conjugation–deconjugation cycles for their distribution, brassinosteroids possess intrinsic structural features that directly facilitate their transport, stabilization, and regulation through coordination chemistry. Central to this uniqueness is the presence of vicinal 1,2-diol motifs, a hallmark absent from most other phytohormones.

Structural design for boron-mediated transport. Most biologically active brassinosteroids share a conserved A-ring 2α,3α- and side-chain 22,23-diols. These *cis*-diols are ideally configured to form reversible cyclic boronate esters with boric acid or borate ions. Under the mildly alkaline conditions characteristic of xylem and phloem sap, these interactions are favored, allowing brassinosteroids to exist as transient boron complexes during transport.

As mentioned above, cyclic esters of boric acid with 2α,3α-diols are unstable in an aqueous environment; therefore, in plants, one can expect the formation of only 22,23-derivatives. It is known from the literature that esters of boric acid with vicinal diols in an alkaline medium exist as a rather complex equilibrium mixture [67, 68]. Although such studies have not been conducted for brassinosteroids to date, by analogy with other esters, the transformation scheme shown in Fig. 3 can be proposed for 22,23-diols. The *cis*-diol monoborate ester **8**, which is stable in an acidic medium, will form complexes **9** and **10** in an alkaline medium.

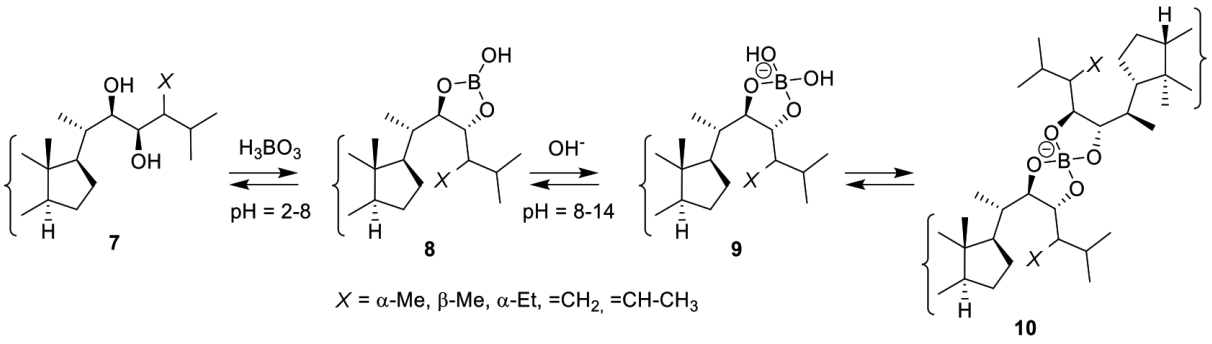


Fig. 3. Plausible scheme of boron complexation with brassinosteroids

This structural feature provides a plausible chemical explanation for why plants synthesize polyhydroxylated steroids rather than simpler hydrophobic analogues: 1,2-diol brassinosteroids are intrinsically adapted for mobility in aqueous sap, where reversible boron coordination enhances solubility, protects hydroxyl groups from premature metabolism, and enables controlled release at target tissues.

In contrast, phytohormones such as auxins (indole-3-acetic acid), gibberellins, and abscisic acid lack stable *cis*-diols and therefore cannot exploit boron-mediated transport mechanisms. Their movement instead depends on active transporters, diffusion gradients, or chemical conjugation, making their distribution fundamentally different from that of BRs [59, 60].

Chemical protection and stability in the vascular system. Beyond transport, boron complexation may also confer chemical protection to brassinosteroids during circulation. The formation of cyclic boronate esters can temporarily mask reactive hydroxyl groups, reducing susceptibility to oxidation, hydrolysis, or enzymatic modification. This reversible "chemical shielding" ensures that BRs can traverse long distances without loss of biological activity.

Such protection is particularly relevant in the vascular system, where hormones encounter fluctuating pH, redox-active metabolites, and microbial challenges. By forming boron complexes, brassinosteroids may persist longer in sap and maintain a bioavailable pool that can be rapidly mobilized when developmental or stress signals arise.

Integration with boron-based plant defense. Plants also employ boron chemistry as part of their innate defense strategies. Boron-containing complexes – particularly those formed with polyols, phenolics, and sugars – exhibit antimicrobial properties and contribute to resistance against bacterial and fungal pathogens. In this broader context, brassinosteroid–boron complexes may serve a dual function: facilitating hormone transport while simultaneously participating in chemical defense.

This duality is noteworthy. Unlike classical phytoalexins, which are synthesized de novo in response to infection, boron–BR complexes could represent constitutive, mobile defense-associated metabolites, linking growth regulation with antimicrobial preparedness. Such integration reflects an efficient evolutionary strategy in which hormonal signaling and defense chemistry share common molecular tools [69, 70].

Evolutionary and functional implications. The biosynthesis of 1,2-diol–containing brassinosteroids is unlikely to be accidental. From an evolutionary perspective, these structures appear optimized for: (i) reversible complexation with boron, a widely available micronutrient; (ii) efficient long-distance transport in aqueous plant sap; (iii) chemical protection during circulation; (iv) compatibility with defense-related boron chemistry.

No other major class of phytohormones combines these features. Brassinosteroids therefore represent a chemically pre-adapted hormone class, whose molecular architecture enables direct interaction with inorganic elements to regulate distribution and function [1, 43–45].

Summary perspective. Brassinosteroids are unique among phytohormones because their 1,2-diol-rich steroidal framework is inherently compatible with boron coordination chemistry. This compatibility provides a chemically elegant solution to two fundamental plant challenges: long-distance hormone transport and chemical defense. By synthesizing 1,2-diol brassinosteroids and exploiting boron-mediated complexation, plants integrate mineral nutrition, hormonal regulation, and antimicrobial protection into a unified physiological strategy.

Conclusion. Brassinosteroids are unique among plant hormones not only for their strong biological activity but also for their conserved 1,2-diol structure, which enables reversible coordination with boron. This chemical feature distinguishes them from all other major phytohormone classes and provides a unifying explanation for aspects of their transport, stability, and distribution in plants.

Although brassinosteroids readily form borate complexes, boric acid itself is not used for their analytical determination because complexation is weak, pH-dependent, reversible, and non-selective under typical analytical conditions. These properties limit its usefulness for quantitative detection or stable derivatization, especially compared with chromatographic or mass-spectrometric methods. Thus, the absence of boric acid in analytical protocols reflects practical limitations, not a lack of underlying chemical affinity.

In vivo, however, the situation is different. In mildly alkaline, boron-containing plant fluids, the formation of cyclic boronate esters is chemically favored and may enhance brassinosteroid solubility, protect vicinal diols from premature metabolism, and facilitate long-distance transport through the xylem and phloem. Boron coordination may therefore act as a physiological modulator of hormone availability and signaling, linking micronutrient status to growth regulation and stress responses.

Overall, these observations support a revised view of brassinosteroids as boron-responsive phytohormones, whose molecular architecture intrinsically couples hormonal function to mineral chemistry. Recognizing boron complexation as a functional, context-dependent interaction opens new perspectives on hormone transport, nutrient–signal integration, and the chemical logic underlying plant hormone evolution

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