

# Mechanisms of brassinosteroids interacting with multiple hormones

Shanshan Zhang,<sup>†</sup> Ying Wei,<sup>†</sup> Yangning Lu and Xuelu Wang\*

State Key Laboratory of Genetic Engineering; Institute of Plant Biology; School of Life Sciences; Fudan University; Shanghai, China

<sup>†</sup>These authors contributed equally to this work.

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**Abbreviations:** BR, brassinosteroid; ABA, abscisic acid; GA, gibberellin; JA, jasmonate

Various environmental and internal cues play essential roles in regulating diverse aspects of plant growth and development. Phytohormones usually coordinate multiple stimuli to directly regulate multiple developmental programs. Recent studies have provided progresses into the complexity of their cross talk. Particularly, the signaling pathways of various phytohormones have been revealed, leading to the discovery of the mechanisms of the interplay among different hormone signaling pathways. This review focuses on the recent advances of the signaling cross-talk between brassinosteroids and other hormones, including abscisic acid, auxin, gibberellins, ethylene and jasmonate.

## Introduction

Different from animals, plants need to constantly regulate their developmental and physiological processes to respond to various external and internal stimuli in their sessile lifestyle. Studies have revealed that multiple networks among different hormones and their signaling pathways exist, and play key roles in establishing the developmental program in plants.<sup>1,2</sup> In addition, a large set of microarray data demonstrated that many genes are co-regulated by different sets of hormones, suggesting the importance of hormone signaling in coordinately regulating the same biological process in plants.<sup>3,4</sup> With the hormonal biosynthesis and signaling pathways established, recent studies have discovered many physiological and molecular mechanisms of hormonal cross-talk.

Brassinosteroids (BRs) distribute in almost all tissues of plants as a unique class of plant polyhydroxysteroids that are structurally analogous to the well-studied animal and insect steroids. Physiological studies, as well as the characterization of BR biosynthetic and signaling mutants, have demonstrated that BRs inhibit root elongation, and promote stem elongation, pollen tube growth, leaf bending, epinasty, early flowering and xylem differentiation, through regulating cell expansion, cell division, and cell differentiation.<sup>5,6</sup>

In the last decade, many key components of the BR signaling pathway have been isolated and characterized, although there is still a significant gap present in the pathway. The BR's receptor BRI1 was discovered as a plasma membrane-localized leucine-rich-repeat receptor kinase.<sup>7</sup> Direct binding of BRs to the island domain of BRI1,<sup>7-10</sup> triggers the phosphorylation of BRI1 on multiple sites, which leads to the conformational change of the preformed homodimer of BRI1, dissociation of a negative regulator of BRI1 from plasma membrane, and association of BAK1 with BRI1,<sup>11,12</sup> and further promote the activity of receptor complex.<sup>13,14</sup> Two downstream components, a GSK3-like protein kinase BIN2<sup>15,16</sup> and a protein phosphatase BSU1,<sup>17</sup> control the phosphorylation states of a family of plant-specific transcription factors, including BES1 and BZR1.<sup>18,19</sup> Phosphorylated BES1 and BZR1 are less stable,<sup>18,20</sup> are more likely to be retained to the cytoplasm by 14-3-3 proteins,<sup>21</sup> and have less DNA binding affinity,<sup>22</sup> than the dephosphorylated forms, which can directly bind to the promoter regions of BR-responsive genes and regulate BR-related biological processes. Recently, proteomic study identified other substrates of BRI1 kinase, three homologous BR-signaling kinases BSKs, that may activate downstream BR signal transduction.<sup>23</sup> However, the links between the BRI1 receptor and BIN2 are still missing.

Recently, it is found that BRs can cross talk with numerous other hormones in regulating many developmental processes in plants. With many components of signaling pathways of BRs and other hormones found and characterized, it becomes possible to explore the mechanisms underlying the cross talk between BRs and other hormones. In this review, we will describe the recent advances in addressing how BRs interact with other plant hormones, including abscisic acid (ABA), auxin, gibberellins (GAs), ethylene, cytokinin and jasmonate (JA).

## Brassinosteroids and Abscisic Acid

To date, many physiological and genetic studies have demonstrated that BRs and ABA can co-regulate many developmental processes.<sup>24-27</sup> It is well known that ABA is required to establish seed dormancy during embryo maturation and to inhibit seed germination,<sup>24</sup> whereas BRs promote seed germination, possibly through enhancing the embryo growth potential to antagonize

\*Correspondence to: Xuelu Wang; Email: xueluw@gmail.com

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ABA's effect.<sup>24,27,28</sup> It is reported that the BR related mutants also have altered response to ABA. In Arabidopsis, the BR biosynthetic mutant *det2-1*, the BR responsive mutant *bri1*, and the BKI1 overexpression line (*BKII-OX*) are more sensitive to ABA on seed germination than wild types, although these mutants germinate well under normal growth condition;<sup>27,29</sup> by contrast, overexpression of *BRI1* leads to an enhanced resistance to ABA on seed germination.<sup>29</sup> Moreover, studies also have revealed that mutants of possible components of ABA signaling pathway, *gpa1*, *agb1* and *gcr1* are more sensitive to ABA on seed germination, and also show altered sensitivities to BRs.<sup>30-32</sup>

Microarray data showed that BRs and ABA can co-regulate the expression of hundreds of genes.<sup>4</sup> Specifically, more than thirty-five percent of BR-regulated genes are also regulated by ABA, indicating that ABA may regulate BR signaling.<sup>3,4</sup> Early responsive genes of ABA, *RD29A* and *RD22* are also regulated by BRs in Arabidopsis,<sup>33</sup> further indicating the possible cross-talk between BR and ABA. However, whether the interaction between of BR and ABA is through their primary signaling cascades, parallel pathways, or secondary effect, is largely unknown.

Using genetic and biochemical approaches, Zhang et al.<sup>29</sup> proposed a model to describe the interplay between BR and ABA primary signaling pathways in Arabidopsis. The authors found that exogenously-applied ABA rapidly inhibits BRs' signaling outputs in wild-type and an ABA biosynthetic mutant *aba1* background, and ABA has a similar effect in the BR receptor mutant *bri1* background. However, when the downstream component *BIN2* was inhibited by LiCl, or in the ABA insensitive mutants *abi2* and *abi1*, the inhibitory effect of ABA on BR signaling outputs is annihilated. They further defined the facet of their cross talk, which is after BR perception, and at or before the negative regulator, *BIN2*. This work provides a reasonable explanation for why a large proportion of BR-responsive genes are also regulated by ABA, and gives significant insight into the molecular mechanisms by which BRs could interact with ABA.

It is likely that one or a few components in the ABA signaling pathway directly interact or regulate some specific components in the BR signaling pathway. With more components of both pathways identified or clarified, the complicated molecular nature of the cross-talk between BRs and ABA will be disclosed.

### Brassinosteroids and Auxin

Physiological interaction between BRs and auxin has been observed with either hypocotyl elongation or root development.<sup>1,34</sup> Previous studies suggest that BRs act synergistically with auxin to promote cell elongation, and mutants of either pathway show similar developmental defects, including dramatic dwarf phenotype.<sup>1,35</sup> Utilizing hypocotyl elongation as an assay, researchers have found that the auxin-responsive mutants *axr1*, *axr2*, *axr3*, *tir1* and *arf2* have reduced sensitivity to BRs to a considerable degree,<sup>36,37</sup> implying that BR's function on hypocotyl elongation relies partially on a functional auxin signal transduction pathway. Similarly, BR treatment significantly enhances auxin response in hypocotyl elongation,<sup>37</sup> and BR signaling mutant *bri1* is insensitive to temperature-induced hypocotyl elongation, which is likely

mediated by auxin.<sup>36</sup> Taken together, the above evidence suggests that auxin response is also dependent on a functional BR signal transduction pathway. The fact that BRs and auxin cross-talk was further consolidated by root-development assay: the expression of several genes, such as *AXR3/IAA17* in root, is altered by BR treatment or in BR-deficient mutants;<sup>38</sup> the transcription levels of *PIN4* and *PIN7*, which encode auxin transporters, are also repressed in BR deficient mutant *det2*, and BRs stimulate plant tropisms through regulating localization of *PIN2* in root and modulating the auxin polar transport.<sup>36,39,40</sup>

Several studies have been conducted to illustrate the potential molecular mechanisms of the cross-talk between BRs and auxin. Numerous microarray data show that BRs and auxin share a number of early responsive genes, and many of them are involved in plant growth.<sup>3,4,41</sup> A potential molecular link between BRs and auxin pathways was identified by a recent research, in which authors proposed that the regulatory regions of BR-responsive genes are enriched with predicted ARF-binding sites.<sup>36,41</sup> Nemhauser et al.<sup>36</sup> used Arabidopsis mutants with perturbed BRs or auxin signaling and demonstrated the interplay of these two hormones in the control of hypocotyl elongation. More recently, it was demonstrated that the BR signaling component *BIN2* can directly interact with an auxin signaling component *ARF2*, a member of the Auxin Response Factor family of transcriptional regulators.<sup>37</sup> Phosphorylation of *ARF2* by *BIN2* results in a loss of *ARF2* DNA binding and repression activities. With all of the above evidences considered, the authors propose that *BIN2* increases the expression of auxin-induced genes by directly inactivating the repressor *ARF2* and leads to the synergistic enhancement of transcription.

Most likely, this mode of cross-talk is only part, if not all, of the mechanism of the interplay between BRs and auxin.<sup>37</sup> Apparently, other potential pathways are present to illustrate the complexity of their interaction.

### Brassinosteroids and Gibberellins

GAs are a class of phytohormones that mainly promote plant growth, including promoting stem elongation, seed germination, and flowering, and inhibiting leaf and fruit senescence.<sup>42,43</sup> However, it is poorly understood whether BRs cross-talk with GAs. Previous physiological studies have pointed out that BRs and GAs enhance plant growth in an additive manner,<sup>44</sup> indicating that the two hormones may act independently at the cellular level.

However, there is accumulating evidence to support that cross-talk between BRs and GAs signaling pathways may also occur either synergistically or antagonistically. First, physiological study suggests that BRs could partially rescue the germination of GA biosynthetic and GA insensitive mutants, possibly via embryo expansion.<sup>27</sup> Second, G-proteins (*GCR1*, *GPA1* and *AGB1*) deficient mutants have reduced sensitivities to both BRs and GAs in seed germination.<sup>31</sup> Finally, microarray data both in Arabidopsis and rice shows that the expression of a large number of genes is coordinately regulated by BRs and GAs.<sup>3,4,45</sup> Studies in rice also show that *OsGSR1* promotes BR biosynthesis by directly

regulating a BR biosynthetic enzyme, and when *OsGSR1* was knocked-down, an elevated level of endogenous GAs was observed, suggesting that *OsGSR1* may mediate the two pathways.

Studies also showed that BRs and GAs antagonistically regulate the accumulation of mRNAs of a GA-responsive gene *GASA1* and GA-suppressed gene *GA5*.<sup>46</sup> Additionally, BRs and GAs regulate the expression of GA-responsive gene  $\gamma$ -*TIP* in an antagonistic manner, and the mRNA level of  $\gamma$ -*TIP* accumulates ectopically in BR biosynthetic and responsive mutants.<sup>47</sup> Given that  $\gamma$ -*TIP* encodes a tonoplast-intrinsic aquaporin, it is reasonable to suspect that BRs and GAs regulate turgor pressure or solute flow antagonistically.

Unlike the cross talk between BRs and ABA or BRs and auxin, our understanding on the mode of the cross-talk between BRs and GAs stays at the physiological level. Whether their interaction is through the modification or interaction of their primary signaling cascades, or parallel pathways, remains unclear.

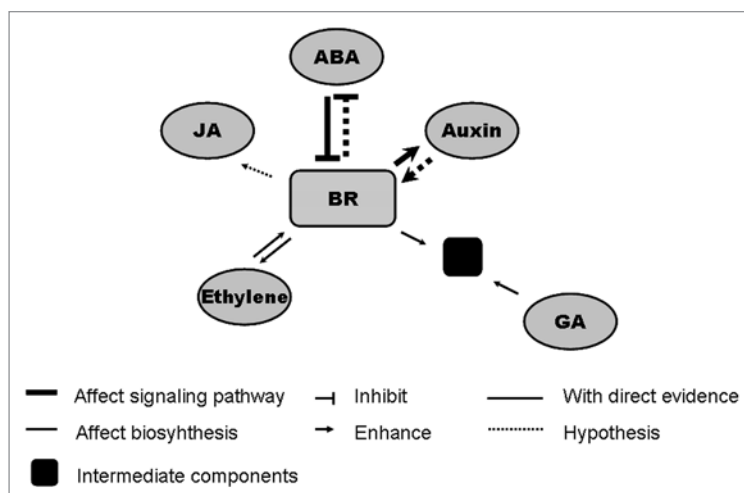
## BR and Other Hormones

Ethylene is a gaseous hormone that regulates various plant developmental processes, such as seed germination, abscission, senescence, plant defense and fruit ripening.<sup>48,49</sup> It was found that the expression of *BRP*, a BR-repressed reporter gene, can be activated by ethylene.<sup>50</sup> BRs regulate the biosynthesis of ethylene via stabilizing the ACC synthase that catalyzes a rate-limiting step in ethylene biosynthesis.<sup>51</sup> Other research implies that ethylene and BR may promote the biosynthesis of each other.<sup>52</sup> Furthermore, both ethylene and BRs can promote the growth of cotton fiber. However, ethylene could overcome the inhibitory effect of BRZ on fiber cells, while BRs counteract the effect of AVG, which is the ethylene biosynthesis inhibitor, on fiber elongation to a much lesser degree, suggesting BRs act on the upstream of ethylene in cotton fiber elongation.<sup>52</sup>

There are a few studies indicating that BRs may also interact with other hormones. A previous study implies that BRs may influence stress responses of plants by stimulating synthesis of JA. The expression of the *OPR3*, encoding a 12-oxo-phytodienoic acid reductase, is induced by BRs and JA, depending on environmental and developmental conditions, which drops a hint on the possible relationship between BRs action and JA synthesis.<sup>53</sup>

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**Figure 1.** A proposed network of brassinosteroids interacting with multiple plant hormones. BR signaling pathway is primarily inhibited by ABA signaling through certain unknown components, and BR may also regulate the ABA signaling outputs. BRs regulate auxin signaling via BIN2, while, reciprocally, BR signaling may also be regulated by auxin. BR affects the biosynthesis of ethylene and, in all probability, that of JA. Also, BR co-regulates physiological processes (black boxes), such as solute flow, with GA through primary signaling pathway or the level of phytohormones.

## Perspectives

In summary, a proposed network of BRs interacting with multiple hormones is summarized in Figure 1. Many great progresses have been made in hormonal interaction, but most of these studies remain at the physiological level. For this reason, a shift of priority in researches from physiological to molecular evidences, is bound to be intensified. Within the foreseeable future, studies on the relationship between BRs and other hormones at molecular and biochemical level will draw us a systematic and clarified picture depicting the sophisticated interactive network of BRs and multiple hormones.

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