LETTER TO THE EDITOR

Reply: Brassinosteroid Regulates Gibberellin Synthesis to Promote Cell Elongation in Rice: Critical Comments on Ross and Quittenden’s Letter

Brassinosteroid (BR) and gibberellin (GA) are two important hormones regulating plant cell elongation. A defect in either of these hormone pathways leads to reduced plant growth and dwarfism. Because an early attempt in pea (Pisum sativum) failed to correlate BR level with active GA level (Jager et al., 2005), it was presumed that BR does not regulate GA synthesis in plants, despite the fact that BR promotes expression of GA biosynthetic genes in Arabidopsis thaliana (Bouquin et al., 2001; Sun et al., 2010; Stewart Lilley et al., 2013). In 2012, three studies in Arabidopsis reported the physical interaction between GA repressors DELLAs and BZR1 in mediating BR-GA crosstalk (Bai et al., 2012; Gallego-Bartolomé et al., 2012; Li et al., 2012). In Tong et al. (2014), we published results showing that BR modulates GA levels to regulate cell elongation in rice (Oryza sativa). In our article, we suggest that rice may have a different mechanism from Arabidopsis, as we found that rice BR-deficient mutants (d11-2) showed a normal response to GA, in contrast to Arabidopsis BR-deficient or -insensitive mutants (det2-1, bri1-5, and bri1-119) that were reported to be insensitive to GA application at early seedling stages (Bai et al., 2012). Unterholzner et al. (2015) subsequently reported similar results in Arabidopsis, confirming our finding in rice that BR promotes GA biosynthesis to regulate plant growth. They also showed that BR-deficient mutants (cpd, bri1-1, and bri1-301) have normal responses to GA at different growth stages. Integrating all of these results, Unterholzner et al. (2015) proposed an updated model for BR-GA crosstalk: BR promotes BZR1/BES1 to induce GA biosynthesis and the increased GA level promotes DELLAs degradation to further release BZR1/BES1 activity.

Ross and Quittenden (2016) attempt to split this integrated model into two separate ones: a “synthesis” model and “signaling” model. They dispute our evidence showing that BR regulates GA biosynthesis and argue that the signaling model is more dominant than the synthesis model. However, Unterholzner et al. (2015) proposed an updated model for BR-GA crosstalk: BR promotes BZR1/BES1 to induce GA biosynthesis and the increased GA level promotes DELLAs degradation to further release BZR1/BES1 activity.

Ross and Quittenden argued that brd1, the severe rice BR-deficient mutant, has “no response to GA” because GA application does not restore the phenotype to wild type. However, GA application is not necessarily expected to restore the elongation to wild-type levels; it is only expected that the ratio of the response will be the same or similar. We note that even BR application cannot rescue the brd1 mutant to wild type as shown in two original articles (Hong et al., 2002; Mori et al., 2002). In our article and the one by Mori et al. (2002), the leaf blade of brd1 elongated normally in response to GA. We believe that exogenous GA, however, both Unterholzner et al. and Tong et al. showed that moderate to strong BR mutants can have largely normal GA growth responses. Ross and Quittenden claim that the severe BR-deficient mutants are insensitive to GA in both Arabidopsis and rice; however, we think that this is a misinterpretation of our data and others showing that GA can rescue many of the BR response phenotypes of strong BR mutants (Tong et al., 2014; Unterholzner et al., 2015, 2016).

Ross and Quittenden argued that brd1, the severe rice BR-deficient mutant, has “no response to GA” because GA application does not restore the phenotype to wild type. However, GA application is not necessarily expected to restore the elongation to wild-type levels; it is only expected that the ratio of the response will be the same or similar. We note that even BR application cannot rescue the brd1 mutant to wild type as shown in two original articles (Hong et al., 2002; Mori et al., 2002). In our article and the one by Mori et al. (2002), the leaf blade of brd1 elongated normally in response to GA. We believe that
et al. (2012) showed that there is dramatic stream of BR-regulated growth? Although Bai levels? What about the other branches downstream? happens at both biosynthesis and signaling under the synthesis model. We believe that this is an oversimplification of the situation and falsely sets up one model against the other. What is expected if BR-GA crosstalk happens at both biosynthesis and signaling levels? What about the other branches downstream of BR-regulated growth? Although Bai et al. (2012) showed that there is dramatic increase of BR response in a DELLA-deficient mutant in Arabidopsis, our data showed that there is no such increase in BR sensitivity in a DELLA-deficient rice mutant. In the rice DELLA-deficient mutant slr7, BR sensitivity is increased (from 1.7- to 1.9-fold) at lower BR concentration and decreased (from 3.0- to 2.7-fold) at higher BR concentration (Tong et al., 2014, Figure 3C). These data argue for the existence of the integrated model of BR-GA crosstalk in that a decreased BR response from the biosynthesis model is likely offset by an increased BR response from the signaling model.

It is important to emphasize that the difference between BR and GA functions depends on environmental conditions and tissue specificities in rice, and likely in other species as well. For example, only BR, but not GA, is essential for rice skotomorphogenesis in the dark (Yamamura et al., 2000). In addition, BR controls lamina bending and grain size, whereas GA has very subtle effects on these processes: BR is not believed to influence these processes by regulating either GA synthesis or GA signaling (Tong et al., 2014; Che et al., 2015; Sun et al., 2015). Ross and Quittenden listed several results from other species to suggest that BR and GA levels show no consistent changes across different species. However, early studies clearly showed that different species have different BR responses (Bishop, 2003). For example, BR-deficient mutants of both Arabidopsis and rice show a deetiolated phenotype in the dark (defective skotomorphogenesis), whereas BR-deficient mutants of both pea and tomato (Solanum lycopersicum) appear to have a relatively normal etiolated phenotype in the dark (Bishop, 2003). We note that, coincidentally, all the examples cited by Ross and Quittenden to show the inconsistency between BR and GA levels come from pea and tomato. Ross and Quittenden fail to consider many other factors, including tissue specificity, hormone concentration, developmental stage, environmental condition, cell type, and species, when discussing these complex results. Differential contexts are well known to be critical factors for understanding BR functions, as highlighted in a recent review (Singh and Savaldi-Goldstein, 2015).

Our understanding of BR functions is moving forward, accompanied by debates and many unanswered questions. The present integrated model regarding BR-GA crosstalk is applicable to certain processes (cell elongation) in certain tissues under certain conditions in certain species. Although the biological significance of the SLR1-BZR1 interaction needs to be further verified in rice, GA synthesis and signaling must be coordinated or form a positive loop for full BR function, at least in Arabidopsis (Unterholzner et al., 2015).

Hongning Tong
State Key Laboratory of Plant Genomics and National Center for Plant Gene Research (Beijing)
Institute of Genetics and Developmental Biology
Chinese Academy of Sciences
Beijing 100101, China

Chengcai Chu
State Key Laboratory of Plant Genomics and National Center for Plant Gene Research (Beijing)
Institute of Genetics and Developmental Biology
Chinese Academy of Sciences
Beijing 100101, China
cccchu@genetics.ac.cn

ACKNOWLEDGMENTS
This work was supported by grants from National Natural Science Foundation of China (91335203, 91436106, and 31170715) and the Youth Innovation Promotion Association CAS (20150706 to H.T.).

AUTHOR CONTRIBUTIONS
Both authors contributed to writing the article.

Received February 12, 2016; revised March 10, 2016; accepted March 10 2016; published March 22, 2016.

REFERENCES
Bouquin, T., Meier, C., Foster, R., Nielsen, M.E., and Mundy, J. (2001). Control of specific gene


Hong, Z., et al. (2002). Loss-of-function of a rice brassinosteroid biosynthetic enzyme, C-6 oxidase, prevents the organized arrangement and polar elongation of cells in the leaves and stem. Plant J. 32: 495–508.


Reply: Brassinosteroid Regulates Gibberellin Synthesis to Promote Cell Elongation in Rice: Critical Comments on Ross and Quittenden's Letter
Hongning Tong and Chengcai Chu
Plant Cell 2016;28;833-835; originally published online March 22, 2016; DOI 10.1105/tpc.16.00123
This information is current as of September 20, 2017

| References | This article cites 17 articles, 8 of which can be accessed free at: /content/28/4/833.full.html#ref-list-1 |
| eTOCs | Sign up for eTOCs at: http://www.plantcell.org/cgi/alerts/ctmain |
| CiteTrack Alerts | Sign up for CiteTrack Alerts at: http://www.plantcell.org/cgi/alerts/ctmain |
| Subscription Information | Subscription Information for The Plant Cell and Plant Physiology is available at: http://www.aspb.org/publications/subscriptions.cfm |