

Article Addendum

# Regulatory Networks Involving *YABBY* Genes in Rice Shoot Development

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rice, shoot, meristem, *Wuschel*-like homeobox, *YABBY*, *KNOX1*, gibberellin, feedback regulation and repression

Addendum to:

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## ABSTRACT

Shoot development is regulated by specific gene expression programs depending on the interplay between transcription factors and growth hormones that function in specific domains of the meristem and lateral organs. Functional relationship between different regulators is not clearly established. In the May issue of *Plant Physiology* (2007) we have shown that *Wuschel-like Homeobox3* and *YABBY3* are coexpressed in the leaf primordia and young leaves, and that *WOX3* functions as a transcriptional repressor of *YAB3*. Overexpression of *WOX3* or downregulation of *YAB3* induced ectopic expression of *Knotted 1-like homeobox1* genes in leaves and consequently produced a phenotype similar to plants ectopically expressing *KNOX1* genes. In a parallel work published in the same issue, we have shown that another *YABBY* gene, *YAB1*, which is expressed in the same domains as *YAB3* or *WOX3*, binds to the gibberellic acid responsive element and is involved in the feedback regulation of gibberellin biosynthesis. Our study demonstrates that rice *YABBY* genes are involved in two pathways to control cell division and differentiation during leaf formation and growth and establishes a rice shoot developmental regulatory hierarchy involving *WOX3*, *YAB3*, *KNOX1* and gibberellin.

The development of shoot apical meristem (SAM) is regulated by a complex network involving many transcription factors and hormones that have a function either in the meristem identity and maintenance or in the initiation and formation of lateral organs.<sup>1</sup> The meristem identity of cells in the SAM is correlated with the expression of specific regulatory genes. *Class 1 KNOTTED1-like homeobox (KNOX1)* transcription factors are expressed in overlapping domains within the SAMs of both monocot and dicot plants, but excluded from the leaf founder cells and primordia.<sup>2</sup> *KNOX1* genes promote meristem function partly through the repression of biosynthesis of the growth regulator gibberellin (GA).<sup>3</sup>

The *YABBY* family transcription factors are encoded by a small gene family in Arabidopsis and rice.<sup>4,5</sup> All of the Arabidopsis genes show a polar expression pattern and function to determine the abaxial cell fate of one or more above ground lateral organs.<sup>4</sup> Activity of the *YABBY* family of putative transcription factors also contributes to the exclusion of *KNOX* gene expression from Arabidopsis. Rice *YABBY* genes are also expressed in leaf primordia and young leaves, but do not show any adaxial/abaxial polar distribution.<sup>5,7,8</sup>

The meristem stem cell specification requires the activity of the *WUSCHEL* homeobox gene that is expressed in the meristem organizing center in Arabidopsis.<sup>9</sup> The *WUS*-related homeobox genes (*WOX*) are suggested to play an important role in region-specific transcription programs early during embryogenesis and lateral organ development in Arabidopsis.<sup>10</sup> However, none of the isolated rice or maize *WUS* orthologues displays an organizing center-type expression pattern in the vegetative SAM as in Arabidopsis,<sup>11</sup> while the *WOX* orthologues from Arabidopsis (*PRS*) and maize (*narrow sheath1/narrow sheath2*, *NS1/NS2*) genes have been shown to function in a lateral domain of the SAM for lateral organ formation.<sup>12,13</sup> This suggests that both functional divergence and conservation could be attributed to this class of transcription regulators.

## A *WOX/YABBY/KNOX/GA* CONNECTION

In our recent work, we have established a link between a *WOX* gene (*WOX3*) and a *YABBY* gene (*YAB3*) in rice.<sup>5</sup> Both genes are expressed in the leaf primordia and young

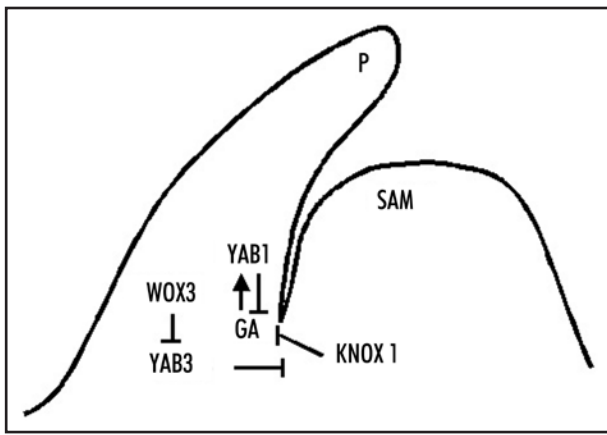


Figure 1. Functional relationship between WOX3, YAB3, KNOX1 and gibberellin in the control of rice shoot development. SAM, shoot apical meristem. P, leaf primordium.

leaves but excluded from the SAM. The expression of the genes in young leaves or leaf primordia did not show any adaxial/abaxial polarity. Over-expression of *WOX3* repressed the endogenous *YAB3* and induced a similar phenotype as *YAB3* RNAi plants, which resembles that induced by *KNOX1* ectopic expression,<sup>14</sup> whereas *WOX3* RNAi or *YAB3* overexpression produced no visible phenotype. Indeed, rice *KNOX1* genes *Osh1* and *Osh3* are ectopically induced in leaves of *WOX3* overexpression or *YAB3* RNAi plants, suggesting that *YAB3* is required to repress *KNOX1* genes in leaves. In addition, *WOX3* binds to a conserved DNA element found in *YAB3* and is shown to directly repress *YAB3*, indicating that *WOX3* is a transcriptional repressor of *YAB3*. Thus, the data establish a transcriptional regulatory hierarchy between *WOX3/YAB3/KNOX*, which is likely required to regulate the balance between cell division and differentiation during leaf initiation and growth in rice (Fig. 1).

In a parallel work,<sup>8</sup> we have shown that another *YABBY* gene, *YAB1*, exhibits a similar expression pattern in the shoot as *YAB3* or *WOX3*. In fact, this expression pattern overlaps with that of key GA biosynthetic genes in rice.<sup>15</sup> GA is required to promote cell growth during lateral organ formation from the SAM. *YAB1* is induced by GA, but in turn represses the GA biosynthetic gene *GA3ox2* by binding to the GA-responsive element (GARE) within the gene, showing that *YAB1* is involved in the feedback regulation of GA biosynthesis in the shoot. Accordingly, overexpression of *YAB1* induced a semi-dwarf phenotype that could be complemented by applied GA. These data establish that *YAB1* is involved in the control of GA homeostasis during leaf cell growth, while previous work has shown that *KNOX1* genes exclude GA biosynthesis from the SAM to maintain the SAM cell identity.<sup>16</sup> Therefore, GA biosynthesis turns out to be a common target of two otherwise antagonistic transcriptional regulators.

## CONCLUSIONS AND PERSPECTIVES

Therefore, there are two parallel pathways involving *YABBY* genes to control cell division and differentiation during rice leaf growth (Fig. 1). Studying the interplay between transcriptional regulators and growth hormones is important to decipher the mechanism controlling meristem activity and organogenesis. Further work is required to show if there is any link between the two pathways in the control of rice leaf development. Importantly, the relationship between GA and the other *YABBY* genes needs to be determined.

In addition, it remains to know whether other *YABBY* members (including *YAB3*) also bind to the GARE, as rice *KNOX1* genes likely contain this DNA-binding motif. The repression of *KNOX1* genes in leaves also involves the myb transcription factor AS1/RS2/PHAN,<sup>17</sup> which likely induces chromatin modification to maintain *KNOX1* gene repression through interaction with histone chaperone proteins.<sup>18</sup> Therefore, experiments will be required to show whether the *YAB3* is directly involved in the *KNOX1* repression and whether the transcriptional repression mediated by *YABBY* proteins and *WOX3* involves also chromatin modification.

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