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Redesigning green revolution trait with increased grain yield and nitrogen utilization efficiency by reducing brassinosteroid signaling in semidwarf wheat

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Securing food and feed for the increasing world population and decreasing arable land is one of the major challenges of our time. Green revolution or agriculture revolution was propelled by the use of semidwarf rice and wheat varieties around the world since the 1960s (Peng et al., 1999; Sasaki et al., 2002). The semi-dwarfness leads to lodging resistance and thus allows planting of crops in high densities, which compensates for the grain yield reduction on a per plant basis. The main green revolution genes are involved in the biosynthesis of plant hormone gibberellin (GA) in rice and GA signaling in wheat. GA is required for plant growth and stem elongation. GAs function through their receptors to degrade a group of repressor proteins (termed DELLA repressors), which subsequently represses GA regulated gene expression. The reduced GA signaling in semidwarf wheat is conferred by gain-of-function *Reduced Height-1* (*Rht-1*) alleles (*Rht-B1b* and *Rht-D1b*) that encode stabilized DELLA repressors, leading to reduced GA signaling and hence reduced plant height (Figure 1, right). While semi-dwarfness of *Rht-1* allows for high planting densities, the same gene also causes reduced grain size and nitrogen utilization efficiency (NUE), as GA signaling promotes GFR4 (GROWTH-REGULATING FACTOR 4) that regulates nitrogen utilization (Duan et al., 2015; Li et al., 2016; Li et al., 2018). A large amount of nitrogen fertilizer is needed to maintain high yield of the current semidwarf varieties, causing issues in environmental sustainability. Overcoming these limitations caused by the traditional green revolution genes is therefore of high importance for agriculture.

Brassinosterods (BRs) are a class of steroid hormones that promote plant growth, like GA, yet with completely different biosynthesis and signaling pathways (Nolan et al., 2020; Tong and Chu, 2018). BRs signal through receptor BRI1 and co-receptor to regulate the activity of transcription factors, which subsequently regulates the expression of thousands of genes to promote plant growth and coordinate stress responses (Li and Chory, 1997). BR signaling is negatively regulated by several negative regulators including BKI1 that binds to BRI1 and inhibits BRI1 function (Wang and Chory, 2006). Manipulating BR levels and signaling has potential in improving crop yield (Nolan et al., 2020; Tong and Chu, 2018).

Recently, Song et al. (2023) discovered an elegant new strategy to overcome the limitation caused by *Rht-1* allele by simultaneously deleting the *Rht-1* gene and a new BR signaling component *ZnF-B* in semidwarf wheat (Song et al., 2023). While deletion of the semidwarf gene *Rht-1* recovered plant height, grain yield, and NUE, deletion of the positive BR signaling component ZnF-B led to a "new" semidwarf trait that had less deleterious effects on grain yield and NUE (Figure 1).

Song et al. made the discovery by analyzing the quantitative trait loci (QTL) with a cross involving semidwarf wheat (named Shi), which harbors *Rht-1* gene that causes

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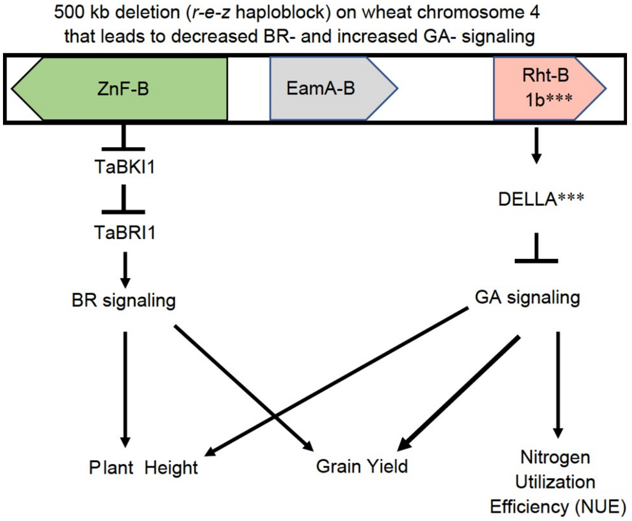

Figure 1 A new strategy to redesign the semidwarf wheat by reducing BR signaling through deletion of BR positive regulator ZnF-B (ZnF-B degrades BKI1, a negative regulator of BR receptor BRI1). The deletion of *r-e-z* haploblock also includes *Rht-B1b*, a classical green revolution gene that encodes a more stabilized (***) DELLA repressor for GA signaling. This leads to a "new" semidwarf phenotype with improved grain yield and NUE than the classical *Rht-1* wheat strain. The regulation of plant height, grain yield, and NUE by BR or GA signaling is shown, which is reduced in loss-of-function *ZnF-B* and gain-of-function *Rht-B1b* mutants.

reduced GA signaling. They identified a new wheat haploblock named *r-e-z* that led to increased grain yield, yet maintained semidwarf stature. Further analysis revealed that the *r-e-z* allele had a 500 kb deletion containing three genes, *ZnF-B*, *EamA-B* and *Rht-B1b* (Figure 1). To identify which genes account for the phenotypes when deleted, the authors deleted these three genes individually in a semidwarf wheat fielder that has the same genes *ZnF-B*, *EamA-B* and *Rht-B1b* but is more amenable for plant transformation. They found that deletion of *Rht-B1b* led to increase in plant height and grain yield, and the deletion of *Znf-B* had the opposite phenotype with reduced plant height and slightly decreased grain yield. However, deletion of *EamA-B* had no effects on these traits. Moreover, deletions of both *Rht-B1b* and *Znf-B* led to a semidwarf trait with increased grain yield when compared to the original *fielder* strain. Therefore, the combination of deletions of *Rht-B1b* and *ZnF-B* contributed to the new semidwarf trait with improved grain yield.

Through a set of elegant genetic and biochemical studies, the authors discovered that *ZnF-B* was involved in BR signaling (Song et al., 2023). The Nil-Heng plants with *r-e-z* haploblock deletion had reduced BR responses compared to Nil-Shi, and deletion of *ZnF-B* gene caused similar reduced BR responses. *ZnF-B* encodes an E3 ubiquitin ligase and is proposed to degrade a negative regulator in the BR pathway. The authors indeed found that ZnF-B interacted with and degraded the BR negative regulator TaBKI1, which renders ZnF-B a positive regulator of the BR pathway. Deletion of *ZnF-B* thus led to reduced BR signaling and semidwarf phenotype, which "restores" the semidwarf trait while *Rht-B1b* is deleted.

The simultaneous deletion of *Rht-B1b* and *ZnF-B* leads to an increased grain yield by more than 10% when planted at high density. Interestingly, the Near Isogenic Line (Nil) "Heng" appears to have a higher NUE compared to "Nil-Shi", likely due to the increased GRF4 protein level with reduced DELLA repressor and increased GA signaling in "Nil-Heng" (Song et al., 2023). The new strategy of reducing BR signaling through deletion of *ZnF-B* thus can lead to a semidwarf wheat with increased grain yield and NUE compared to the semidwarf wheat generated by reduced GA signaling with *Rht-1* mutation.

While Mother Nature created the magical double deletion of *Rht-1* and *ZnF-B* in one block, which leads to the optimized agriculture trait, finding the genes and defining the underlying mechanisms are a great achievement by the authors (Song et al., 2023). Going forward, it would be important to test if a similar strategy can be used in other crops in improving grain yield and NUE by reducing BR signaling. To achieve this, identifying orthologous *ZnF-B* genes in other crops, and studying their expression patterns and genetic functions are essential. Similarly, many other BR signaling and biosynthesis genes have been identified and characterized in crops. It will be equally important to determine if manipulation of other genes in the BR pathway can have similar effects in reducing plant heights but maintaining NUE and grain yield. Finally, further mechanistic understanding of how NUE is regulated will help design new crops that have optimal plant architecture, grain yield, and NUE by manipulating hormonal biosynthesis and signaling pathways.

The work also highlighted the importance of basic research in identifying new strategies to improve crop production and environmental sustainability. While genetic and genomic studies in crop plants are essential, fundamental studies in simpler model plants such as Arabidopsis are equally important, for example, the BR signaling pathway is best established in Arabidopsis, which in this case greatly helped the delineation of the *ZnF-B* functions in BR signaling pathway in wheat.

Compliance and ethics *The author(s) declare that they have no conflict of interest.*

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