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## IN BRIEF

### Novel dwarfing alleles for the next green revolution: mutations in *DTL* and *OSH15* alter internode elongation and grain size in rice

The green revolution that transformed agriculture in the 1960s encompassed an array of new technologies that doubled the productivity of cereal crops mainly in Mexico and Asia. Together with innovative agricultural practices (e.g., use of agrochemicals, irrigation, mechanization), the development of semi-dwarf high-yielding varieties greatly reduced harvest loss due to increased resistance to lodging (i.e., stem bending towards the soil) and improved the harvest index (i.e., grain to straw ratio) due to efficient use of nutrients for the development of grains rather than vegetative organs. In contrast to semi-dwarf cultivars, taller plants are more prone to lodging while shorter plants produce less seeds. Thus, the success of modern cultivation methods also relies on genetic improvement of plant architecture through optimization of plant height.

In rice (*Oryza sativa*), dwarfism is caused by mutations in genes involved in the metabolism or signal transduction of the phytohormones gibberellins (GAs) and brassinosteroids (BRs), which regulate the elongation of internodes via complex feedback mechanisms (Tong et al., 2014). In the last decades, GA-related genes have been extensively characterized and shown to control the favorable traits selected during the green revolution, including the shortening of the upper internode (IN1). However, little is known about components of the BR pathway controlling stem elongation. Among few mutations affecting BR-signaling described so far, a deletion in the coding region of a member of the GRAS family of transcription factors underlies the *dwarf and low tillering* (*dlt*, also known as *d62*) phenotype (Tong et al., 2009). Functional *DLT* is involved in feedback inhibition of BR biosynthesis genes and its loss of function causes impaired BR sensitivity, leading to the shortening of internodes.

In this issue, Mei Niu and colleagues (Niu et al., 2022) screened a population obtained by large-scale mutagenesis of the *dlt* genotype and identified enhancers of the semidwarf phenotype. Specifically, two mutants in the *dlt* background (named *d76* and *d140*) displayed shortening of all internodes below IN1. Genetic analysis of backcross generations revealed that the dwarf phenotype of single mutants (named *s76* and *s140*) was caused by novel defective alleles of *Oryza sativa homeobox 15* (*OSH15*, also known as the causal gene of *d6*), a *KNOTTED-like* gene previously described as a key regulator of internode elongation (Sato et al., 1999). Phenotypic analysis of single (*s76* and *s140*) and double (*d76* and *d140*) mutants suggested a complex genetic interaction between *DLT* and *OSH15* that also depends on the tissue including different internodes. The authors proposed that these regulators have synergistic/additive effects on stem elongation and grain width (Figure 1) but an antagonistic effect on tiller formation.

In internodes, *DLT* and *OSH15* showed opposite expression patterns: the promoter activity of *DLT* gradually decreased from IN1 to IN3 whereas that of *OSH15* increased in the division zone of IN2. Interestingly, transcriptome analyses of single and double mutants revealed that more genes are mis-regulated in IN1 of *dlt* and in IN2 of *s140*. Nevertheless, several genes involved in BR metabolism and signaling were differentially expressed in all mutants examined, suggesting that *DLT* and *OSH15* might cooperatively control BR-mediated stem elongation. Additional experiments demonstrated that *OSH15* directly regulated several BR-related genes and interacted with *DLT* to form a complex that targeted *Rice BRASSINOSTEROID INSENSITIVE1* (*OsBRI1*, also known as the causal gene of *d61*), an important gene encoding a BR receptor kinase.

To conclude, this study indicates that BR plays a crucial role in the control of rice architecture, besides the known crosstalk with GA. Novel alleles of regulatory genes involved in the BR pathway might be employed in breeding strategies to optimize not only plant height through modulating elongation of specific internodes but also grain morphology. Since the development of internodes begins during the vegetative

phase but their elongation occurs during the reproductive phase, it will be interesting to further investigate the function of these regulators in coordinating stem growth and panicle development upon the floral transition.

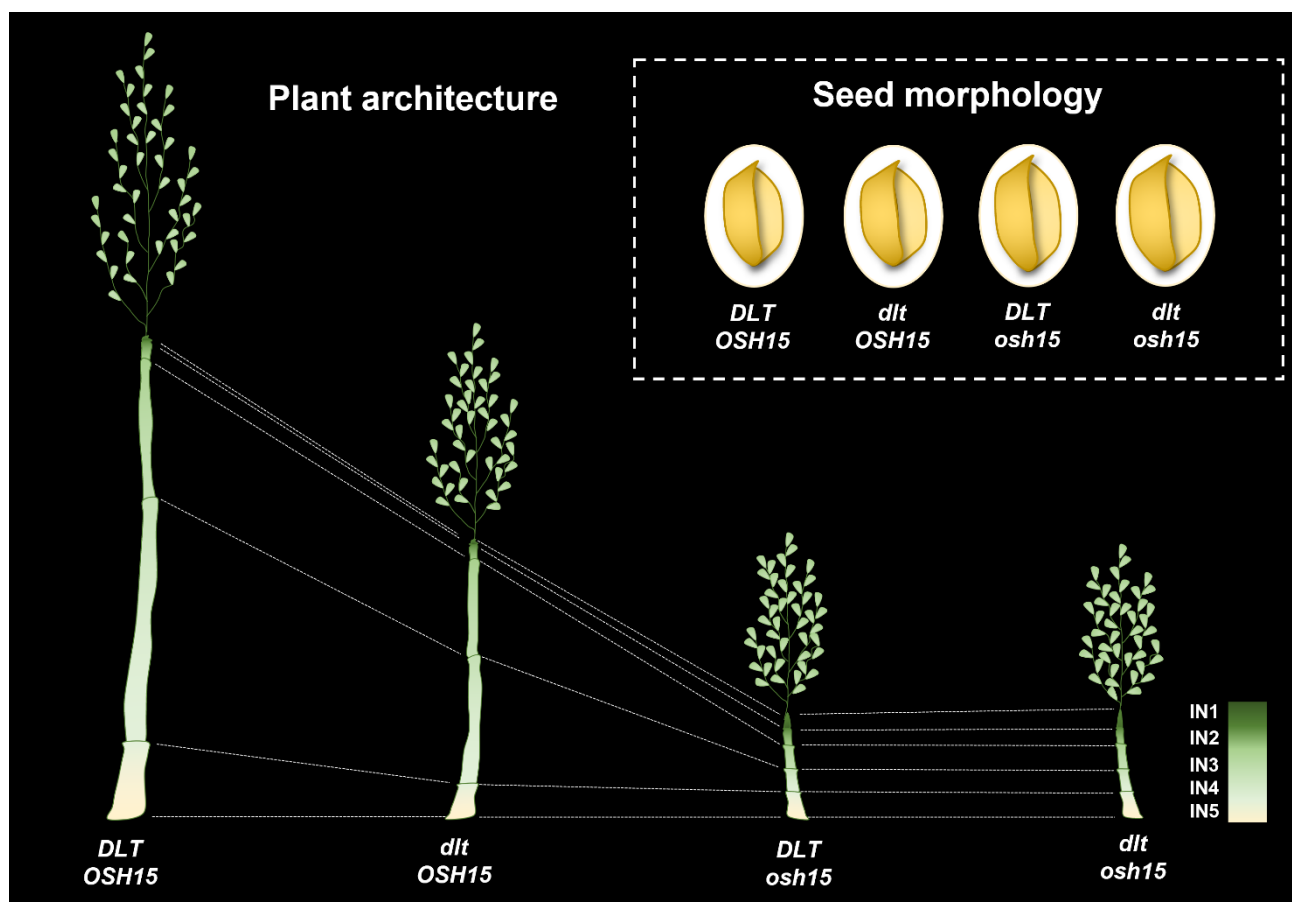
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**Figure 1. Synergistic/additive effect of *DTL* and *OSH15* on plant architecture and seed morphology in rice** Compared to wild-type plants (*DLT OSH15*), single and double mutants show a compact stature due to shortening of internodes (below IN1) and inflorescence branches before heading as well as increased seed width at ripening. Figure credits: M. Osnato (modified schematic model from Niu et al. [2022] Figures 3 and 6).

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