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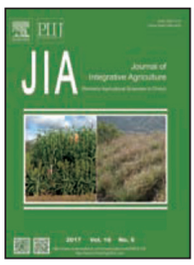

RESEARCH ARTICLE

BRITTLE CULM16 (*BRITTLE NODE*) is required for the formation of secondary cell walls in rice nodes

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Abstract

Plant cell walls constitute the skeletal structures of plant bodies, and thus confer lodging resistance for grain crops. While the basic cell wall synthesis machinery is relatively well established now, our understanding of how the process is regulated remains limited and fragmented. In this study, we report the identification and characterization of the novel rice (*Oryza sativa* L.) *brittle culm16* (*brittle node*; *bc16*) mutant. The brittle node phenotype of the *bc16* mutant appears exclusively at nodes, and resembles the previously reported *bc5* mutant. Combined histochemical staining and electron microscopy assays revealed that in the *bc16* mutant, the secondary cell wall formation and thickening of node sclerenchyma tissues are seriously affected after heading. Furthermore, cell wall composition assays revealed that the *bc16* mutation led to a significant reduction in cellulose and lignin contents. Using a map-based cloning approach, the *bc16* locus is mapped to an approximately 1.7-Mb region of chromosome 4. Together, our findings strengthen evidence for discretely spatial differences in the secondary cell wall formation within plant bodies.

Keywords: rice (*Oryza sativa* L.), brittle node, sclerenchyma tissue, secondary cell wall

1. Introduction

Lodging is a major cause of yield loss in crops and lodging resistance has been a key agronomical trait targeted by breeders. Plant cell wall constitutes the skeletal structures of plant bodies (McNeil *et al*. 1984; York *et al*. 1986; Carpita and Gibeaut 1993; Doblin *et al*. 2010). Cellulose, hemicellulose, and pectin are three major components that constitute plant cell wall polysaccharides. In some specific cell types of higher plants (e.g., sclerenchyma tissues and xylem elements), after a maximum development size has been reached, a secondary cell wall is formed between the cell membrane and primary wall (Reiter *et al*. 2002). The late-developed secondary cell wall in sclerenchyma tissues and xylem can greatly enhance the mechanical strength of plant bodies (Carpita and Gibeaut 1993; Doblin *et al*. 2010;

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Somerville *et al*. 2010).

Previous studies have revealed a transcriptional regulatory network for the secondary cell wall biosynthetic process in plant cells (Zhong and Ye 2007). In this network, a set of secondary cell wall-related NAC (NAM, ATAF1/2, and CUC2) domain-containing transcription factors (including SND1 and its close homologs NST1, NST2, NST3, VND6, and VND7) act as master switches, responsible for activation of the secondary cell wall biosynthesis program (Mitsuda *et al*. 2005, 2007; Zhong *et al*. 2006; Ohashi-Ito *et al*. 2010; Yamaguchi *et al*. 2011). Among them, SND1 functions in activating the expression of genes related to the secondary cell wall biosynthesis, which further induces the deposition of the secondary walls in cells (Zhong *et al*. 2006). NST1, NST2, and NST3 play redundant functions in regulating secondary cell wall thickening (Mitsuda *et al*. 2005; Mitsuda *et al*. 2007). VND6 and VND7 are direct regulators of genes related to the secondary cell wall formation (Ohashi-Ito *et al*. 2010; Yamaguchi *et al*. 2011). In addition, some MYB transcription factors are also implicated in the biosynthesis of the secondary cell wall (McCarthy *et al*. 2009; Zhou *et al*. 2009; Zhong *et al*. 2011). For example, MYB83 and MYB46 that are directly targeted by SND1, act redundantly in the transcriptional regulation of the secondary cell wall biosynthesis (McCarthy *et al*. 2009; Zhong *et al*. 2011). MYB58 and MYB63 are transcriptional activators required specifically for lignin biosynthesis in the SND1-mediated transcriptional network (Zhou *et al*. 2009). These lines of evidence indicate a relatively clear regulatory network for the secondary cell wall biosynthesis in plants.

Rice mutants with defects in stem strength are excellent genetic material for dissecting the molecular mechanisms of biosynthesis and regulation of the plant cell wall. Several genes directly involved in cell wall biosynthesis have already been identified and characterized with mutants of this type. For example, the disruptions of *CesA* (cellulose synthase catalytic subunit) genes, *OsCesA4/BC7/BC11*, *OsCesA7*, and *OsCesA9/bc6*, cause a dramatic reduction in cellulose content and the mechanical strength of plant tissues, suggesting their essential roles in synthesis of the secondary cell wall in rice (Tanaka *et al*. 2003; Yan *et al*. 2007; Zhang *et al*. 2009; Kotake *et al*. 2011; Wang *et al*. 2012; Rao *et al*. 2013). Additionally, regulatory mutations, indirectly involved in cell wall synthesis, also cause fragility in plant tissues. For example, the *BC1* gene, encoding a COBRA-like protein, has been shown to affect the mechanical strength of rice plant bodies through modulation of the expression of the secondary cell wall biosynthetic pathway (Li *et al*. 2003). The *BC3* gene encodes a typical dynamin protein, OsDRP2B, essential for cellulose biosynthesis of the secondary cell wall (Hirano *et al*. 2010). A deficiency of *BC10*, a gene encoding a DUF266-containing and Golgi-located type II membrane protein, causes a reduction in both cellulose and AGPs (arabinogalactan proteins) contents, accompanied by inferior mechanical properties (Zhou *et al*. 2009). BC12, a dual-targeting kinesin protein, has been proved to function in cellulose microfibril deposition and cell wall composition in rice (Zhang *et al*. 2010). BC15/OsCTL1 is a class II chitinase-like protein that functions in cellulose biosynthesis (Wu *et al*. 2012). A conspicuous phenotype for the *bc* mutants listed above is systemic fragility of the plant bodies (e.g., culms and leaves), implying that these regulatory factors are required for the global synthesis of cell walls in plant bodies. These findings raise the question that whether there are any regulators responsible specifically for the synthesis of plant cell walls. The isolation of *bc5* mutant helps us answer the question convincingly (Aohara *et al*. 2009). The *bc5* mutant was ever unique for its node-specific phenotype, accompanied by the disrupted secondary cell wall deposition of node sclerenchyma tissues after heading. Although the gene responsible for *bc5* phenotypic defects remains to be identified, this finding provides new insights into the spatial regulation of cell wall development in rice plant bodies (Aohara *et al*. 2009).

In this study, we identified a novel brittle node mutant, *bc16*. Similar to the *BC5*, *BC16* is also required for node development. Further assays showed that the sclerenchyma tissue of *bc16* nodes have dramatically reduced the secondary cell wall thickness, probably due to the disrupted biosynthesis of cell wall polysaccharides. Our findings support the notion that the secondary cell wall deposition within plant bodies is discretely regulated in rice, and further suggest a complex regulatory network involving at least *BC5* and *BC16* for node development in rice.

2. Materials and methods

2.1. Plant materials and growth conditions

The *bc16* mutant (*Oryza sativa* L.) was isolated from a ^{60}Co-irriated M_2 population of the *indica* rice variety 9311. An F_2 mapping population was generated from a cross between the *bc16* mutant and the *japonica* rice variety Nanjing 35. All plants were grown in paddy fields during the normal rice growing seasons or in a greenhouse at the Institute of Crop Sciences, Chinese Academy of Agricultural Sciences, in Beijing. For analysis of the cell wall properties, we used the uppermost nodes before heading and at 1 and 2 weeks after heading (WAH).

2.2. Measurements of physical properties

The breaking forces of the uppermost nodes were measured with a digital force/length tester (5848 Microtester, Instron, http://www.instron.com).

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