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REVIEW

The CCT domain-containing gene family has large impacts on heading date, regional adaptation, and grain yield in rice



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Abstract

There are 41 members of the CCT (CO, CO-like, and TOC1) domain-containing gene family in rice, which are divided into three subfamilies: COL (CONSTANS-like), CMF (CCT motif family), and PRR (pseudoresponse regulator). The first flowering gene to be isolated by map-based cloning, *Heading date 1 (Hd1)*, which is the orthologue of *CO* in rice, belongs to COL. The central regulator of plant development, *Ghd7*, belongs to CMF. The major role in controlling rice distribution to high latitudes, *Ghd7.1/PRR37*, belongs to PRR. Both of *Hd1*, *Ghd7* and *Ghd7.1* simultaneously control grain number, plant height, and the heading date. To date, 13 CCT family genes from these three subfamilies have been shown to regulate flowering. Some of them have pleiotropic effects on grain yield, plant height, and abiotic stresses, and others function as circadian oscillators. There are two independent photoperiod flowering pathways that are mediated by *GI-Hd1-Hd3a/RFT* and *GI-Ehd1-Hd3a/RFT* in rice. CCT family genes are involved in both pathways. The latest study reveals that protein interaction between *Hd1* and *Ghd7* integrates the two pathways. CCT family genes are rich in natural variation because rice cultivars have been subjected to natural and artificial selection for different day lengths in the process of domestication and improvement. Alleles of several crucial CCT family genes such as *Hd1*, *Ghd7*, and *Ghd7.1* exhibit geographic distribution patterns and are highly associated with yield potentials. In addition, CCT family genes are probably involved in the responses to abiotic stress, which should be emphasized in future work. In general, CCT family genes play important roles in regulating flowering, plant growth, and grain yield. The functional identification and elucidation of the molecular mechanisms of CCT family genes would help construct a flowering regulatory network and maximize their contribution to rice production.

Keywords: photoperiod sensitivity, protein interaction, yield potential, geographic distribution, abiotic stress

1. Introduction

Flowering time in rice, often defined by heading date, is one of the most important agronomic traits. Grain yield is positively correlated with heading date that is controlled by a very complex regulatory network involved many CCT-domain (CO, CO-LIKE, and TOC1) containing genes. The CO (*CONSTANS*) gene plays an important role in the regulation of flowering by photoperiod in *Arabidopsis* (Putterill *et al.* 1995). Mutations in *CO* repress *FT* expression and cause

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late flowering under long-day conditions (LD), whereas overexpression of *CO* promotes *FT* expression and leads to early flowering (Samach *et al.* 2000). In *Arabidopsis*, *CO* belongs to a larger family of 17 COL (CONSTANS-like) genes, which is subdivided into three groups. All members in Group I have two zinc finger B-boxes near the amino terminus. Group II genes have one B-box, and Group III genes have one B-box and a second, diverged zinc finger motif. The COL genes in *Arabidopsis* have been studied extensively since 2000. They have been reported to affect on the flowering and involved in many molecular or genetic processes, including the regulation of circadian rhythms and control of the photoperiod response. COL genes also have diverse functions in plant development regulation and abiotic stress responses (Ledger *et al.* 2001; Cheng and Wang 2005; Datta *et al.* 2006; Hassidim *et al.* 2009; Wang *et al.* 2013; Min *et al.* 2015). The *TOC1* (*TIMING OF CAB EXPRESSION 1*) gene is believed to encode a component of the central oscillator in circadian clock, and it controls photoperiodic flowering response through circadian clock (Strayer *et al.* 2000).

Members of the CCT family are classified into three subfamilies, CMF (CCT motif family), COL, and PRR (pseudoresponse regulator), according to their motif composition (Cockram *et al.* 2012). CMF proteins contain a single CCT domain in their predicted protein sequence; COL proteins possess either one or two B-boxes in addition to a CCT domain. B-box is a class of zinc finger motif that is involved in protein-protein interactions (Valverde 2011). PRR proteins contain a response regulator domain towards the amino-terminus, the receiver-like domain (RLD). The RLD is similar to the receiver domain of the response regulators in the histidine to aspartic acid (His-Asp) phosphorelay, a versatile signal transduction system (Sathbai *et al.* 2011). There are five PRR genes in *Arabidopsis*, *PRR1/TOC1*, *PRR3*, *PRR5*, *PRR7*, and *PRR9*. All of PRRs have been reported to be important circadian-clock components in *Arabidopsis* (Yamamoto *et al.* 2003; Farre and Kay 2007; Ito *et al.* 2009).

Because CCT genes play important roles in plant growth and development, more attention has been paid to them in cereals such as in rice, barley and maize. Forty-one CCT family genes have been identified in the rice genome and were named *OsCCT01* to *OsCCT41*. Nineteen genes are included in the CMF sub-class, 17 are included in COL, and the PRR subfamily contains 5 genes (Zhang J *et al.* 2015). The protein sequences deduced from Nipponbare were used to construct a neighbor-joining phylogenetic tree based on the three sub-classes (Fig. 1). In rice, *Hd1* (*Heading date 1*) is a key floral regulator orthologous to *Arabidopsis CO* (Yano *et al.* 2000). Besides *Hd1*, 12 CCT domain family genes have been cloned in rice (Table 1). In addition to being flowering regulators, CCT family genes have been

associated with traits such as plant height, root development, and stress tolerance. Here, we make a comprehensive review on research progress on the CCT family genes in rice.

2. *Hd1*, a key photoperiod flowering gene

Hd1 is the first heading date QTL cloned from the cross between Nipponbare and Kasalath. *Hd1* is homologous to *CO* from *Arabidopsis*, its function is similar to *CO*. Both of them promote flowering under their favorite conditions LD in *Arabidopsis* and short-day conditions (SD) in rice (Yano *et al.* 2000). The *Hd1* allele of Zhenshan 97 also shows photoperiod-sensitive expression, promotes heading in SD, and delays heading in LD in a mixed genetic background of Zhenshan 97 and Miyang 46. In contrast, in the Zhenshan 97 background, the *Hd1* allele of Miyang 46 exhibits photoperiod insensitivity, consistently promoting heading in both SD and LD conditions. This finding suggests that the effect of *Hd1* depends on the genetic background (Zhang Z H *et al.* 2012). In the latest recent report, the near isogenic line *Hd1* (NIL-*Hd1*), with a functional *Ghd7*, heads later under LD and earlier under SD compared with the line NIL-*hd1*. However, with non-functional *ghd7*, NIL-*Hd1* consistently heads earlier than NIL-*hd1* under both LD and SD (Nemoto *et al.* 2016). *Ghd7* has also been identified as the coordinator of photoperiod sensitivity of *Hd1* using two sets of NILs. NIL-*Hd1* of the Minghui 63 background, with functional *Ghd7*, heads later under LD and heads earlier under SD than the line NIL-*hd1*, but in the Zhenshan 97 background, with a complete loss of *Ghd7*, NIL-*Hd1* always heads earlier than NIL-*hd1* (Zhang *et al.* 2017). These results all indicate that an alternative function of *Hd1* in promoting or suppressing heading under LD is dependent on *Ghd7*.

Loss-of-function alleles of *Hd1* associated with rice adaption to abroad latitudinal range. *Hd1^{EH}*, a functional allele of *Hd1*, is never expressed when a 166-bp fragment in its promoter is deleted. A heterotrimeric NF-Y transcription complex can accommodate functional *Hd1^{NB}* to bind the promoter of *Hd3a*, but not accommodate the non-functional *Hd1^{VOI}* without the binding ability to *Hd3a*. Therefore transcriptional and post-transcriptional regulation limits *Hd1* function (Goretti *et al.* 2017).

3. *Ghd7/Hd4*, a central regulator of rice development

Ghd7 (grain number, plant height and heading date 7), is an LD-specific repressor identified through a map-based cloning approach from a cross between Minghui 63 and Zhenshan 97. Under LD, *Ghd7* delays flowering by 23 days, enlarges the stem diameter, and increases both the plant height by 30 cm and the grain yield by 50% in the

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