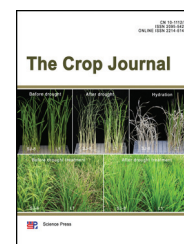
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CCT family genes in cereal crops: A current overview

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ABSTRACT

Control of flowering time is crucial for reproductive success of cereal crops, and has a significant impact on grain yield as well as adaptation to diverse environmental conditions. Plants integrate signals from both environmental cues and endogenous regulatory pathways to fine-tune flowering time. The CCT domain originally described to a 43-amino acid sequence at the C-terminus of three Arabidopsis proteins, namely CONSTANS (CO), CO-LIKE, and TIMING OF CAB1 (TOC1). The CCT domain-containing genes (CCT genes), which encode transcription co-factors, are the major genetic determinants that modulate flowering time, and this in turn enables plants to effectively expand their territory to take advantage of favorable habitats. Moreover, certain CCT genes have pleiotropic effects on morphological traits and confer resistance/tolerance to biotic/abiotic stresses. CCT genes can be classified into three families, namely COL (CONSTANS-like), PRR (Pseudo-response regulator), and CMF (CCT motif family), based on their non-CCT domains. During domestication, natural and artificial selection resulted in reduced nucleotide diversity of CCT genes in modern cultivated cereals than their wild types. Here, we review the features and functions of CCT genes in cereal crops and propose future research to focus on CCT genes and their utilization in crop breeding.

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1. Introduction

Food shortage remains a serious global threat despite the substantial progress in increasing agricultural production since the 1960s [1]. Flowering time is one of the most important agronomic traits in crops because of its impact on plant morphology, grain yield, ease of domestication and adaptation to local environments. Hence, the control of flowering time is a central issue for the reproductive success of plants because precise flowering time enables the completion of pollination, seed development, and plant dispersal to favorable habitats.

Plants are able to integrate environmental signals, such as the day length (photoperiod) and winter temperature (vernalization), their endogenous regulatory pathways to modulate the timing of flowering [2]. While wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) are long-day (LD) crops, rice (*Oryza sativa* L.), maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* L.) are short-day (SD) crops. These cereal crops differ in response to changes in photoperiod, and hence photoperiod can have diverse impacts on flowering time in each species [3]. By virtue of the rapid progress in cereal genomics, researchers have cloned a number of genes involved in flowering time in cereal crops such as rice, wheat, barley, maize and sorghum, and in horticultural crops such as tomato (*Solanum lycopersicum* L.) and sugar beet (*Beta vulgaris* L.). Although having distinct functions most of these flowering time genes have homologs in *Arabidopsis* (*Arabidopsis thaliana*). Thus, information and/or conceptions pertaining to flowering time in *Arabidopsis* are helpful for understanding flowering mechanisms in cereal crops.

The CCT domain originally corresponded to a 43-amino acid sequence at the C-terminus of three *Arabidopsis* proteins, namely CONSTANS (CO), CO-LIKE, and TIMING OF CAB1 (TOC1), that are involved in modulation of photoperiod-induced flowering, light-induced signaling, and circadian rhythms, respectively [4–6]. Thereafter, CCT genes were identified in various plant species ranging from the unicellular green alga *Chlamydomonas reinhardtii* to tree species such as *Populus tremula*. Here we review the CCT genes involved in controlling flowering time in rice, maize, sorghum, barley, and wheat, and discuss their roles in domestication. Moreover, we discuss factors that cause functional differentiation of CCT family members and the potential value of these genes for enhancing cereal plant performance in response to climate change.

2. Divergence of CCT gene families

Numerous CCT genes regulate flowering time in plants. In addition to the CCT domain, these genes may also encode an

N-terminal zinc-finger B-box domain or a response-regulator domain. Furthermore, several CCT domain-containing genes even encode GATA or TIFY domains. However, the most recently identified CCT genes, such as *Ghd7* in rice and *ZmCCT* in maize, have only a single CCT domain and lack any additional domains. These genes have key roles in the modulation of flowering time and adaptation to diverse environments in rice and maize [7,8].

CCT genes can be divided into three families based on their non-CCT domains [9]. These are: 1) the CONSTANS-like (COL) gene family, whose members encode one or two zinc-finger B-box domains, such as CO and *Hd1* (Fig. 1); 2) the Pseudo-response regulator (PRR) family that is characterized by two conserved regions - a pseudo receiver domain and a CCT domain that were initially described as being involved in circadian function to influence photoperiod response in barley (Fig. 1); and 3) the CCT motif family (CMF), in which the encoded proteins contain a single CCT domain and are critical for domestication and adaptation in cereal crops (Fig. 1). Discovery of the CMF family has broadened our understanding of the evolution and function of CCT family members. A combined comparative and phylogenetic analysis of the CMF, COL, and PRR families in Poaceae revealed that the CMF branch evolved from common ancestors of the COL genes after monocot/dicot divergence (Fig. 2). It has been speculated that COL gene evolution continues to lead to B-box degradation in which B-box domains are reduced from two to one, and then to none, as a consequence of double-strand DNA breaks [9].

Taking CO and rice DTH2 (days to heading on chromosome 2) protein as examples CCT genes constitute a family of transcription factors. The middle portion of the amino acid sequence between the B-box and CCT domain was reported to be essential for transactivation activity, as neither the B-box nor CCT domain alone had this activity [10,11]. However, a recent study suggested that *Ghd7* has intrinsic transcription repression activity *in vivo* [12]. Although precise functions of B-boxes and the CCT domain are not well understood, they are assumed to be critical for transcriptional function of CCT-containing proteins.

3. CCT genes in *Arabidopsis*

Studies of flowering time in *Arabidopsis* have contributed substantially to our understanding of how crops respond to day length and hence control flowering time. CO was the first cloned CCT gene regulating flowering time in *Arabidopsis* through the photoperiod pathway. CO is a central player in this photoperiod pathway, in which three other genes, GIGANTEA (*GI*), FLAVIN KELCH F BOX 1 (*FKF1*), and FLOWERING LOCUS T (*FT*), also play major regulatory roles [13]. In LD

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