
REVIEW ARTICLE

Circadian Clock *CCA1* Gene and its Correlation with Important Agricultural Traits

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ABSTRACT

Circadian clocks are internal timers that generate 24 h rhythms in plants biological processes in response to external environmental conditions. The circadian clock controls a number of central plant physiological processes, including growth, biomass, photosynthesis, starch biosynthesis, development and reproduction. This review examines the beneficial role of core circadian clock *CCA1* gene in the important agricultural traits.

Key words: Circadian clock, *CCA1* gene, Agricultural traits.

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INTRODUCTION

Circadian rhythm is any biological process that displays an- endogenous clock, entrainable to external environment, and universally present from *Cyanobacteria* to eukaryotes [1] and generate rhythmic behaviour on a number of key plant physiological and behavioural processes [2-5]. Circadian clock-generated rhythms also play key role in anticipation of daily and seasonal environmental changes and help the plant to adapt with respect to external environmental conditions. In this fashion, the circadian clock generates a fitness benefit [6-8]. The majority of research work with respect to plant circadian clock has been done in the model plant *Arabidopsis thaliana*. However, more recent research work has extended our knowledge regarding genetic and molecular components of circadian clock to a number of other plant species, including rice, soybean, *Brassica rapa* and *Maize* [9-12].

Much of the current understanding of the circadian clock in plants is mostly based on transcription factors that mutually repress each other [13-15], which have been characterized in the model plant *Arabidopsis*. Circadian clocks are the master regulator of plant gene expression, and they control more than 30% of transcriptome not only in *Arabidopsis* [16-18] but also in crops, namely, rice, papaya, maize, soybean, and poplar (19-24). Circadian clock control a number of important physiological and signaling pathways, namely, phytohormone synthesis [25-27] biomass synthesis, starch biosynthesis, growth and vigour [28], abiotic stress responses [29], flowering time [30,31], plant-pathogen interactions [32], growth control [33] and metabolic rate [34].

At the molecular level, in *Arabidopsis*- the core circadian clock is made up of number of genes that interact through a series of transcriptional and post-transcriptional levels to generate rhythmic gene expression [35-40]. Although circadian clock genes are expressed throughout the day, but there exist distinctive dawn and dusk transcriptional phases, and in each phase the level of multiple core circadian clock proteins peaks. The two MYB transcription factors, *Circadian Clock Associated1* (*CCA1*) and *Late Elongated Hypocotyl* (*LHY*) (41) together with the *PRR 5, 7, 9* jointly function as a Morning Element Loop, both mRNA and Post Translational level peaking at dawn. It interlocks with an Evening Element Loop comprising of *Timing of Cab Expression 1* (*TOC1*) or *PRR1, GIGANTEA* (*GI*). The Evening Element Loop also contains

EARLY FLOWERING 3 & 4 (EFF3 & ELF4) as well as *Lux Arrhythmo(LUX)*. *TOC1* expression oscillates peaking during early evening, opposite to *CCA1* and *LHY*. In particular, the transcription factors *CCA1* and *LHY*, which are mostly produced in the morning, are thought to repress the expression of the gene that codes for another transcription factor, *TOC1*, which is mostly produced in the evening and, in turn, represses expression of the genes *CCA1* and *LHY*. The cycle starts with light induced *LHY/CCA1* expression at dawn, this results in accumulation of *LHY/CCA1*, which further represses *TOC1* expression which in turn results in reduced activation of *LHY/CCA1*. As the cycle progresses there is a decrease in *LHY/CCA1* expression allowing increase in *TOC1* transcript levels and reach a maximum at dusk, when *LHY/CCA1* are at their lowest. It has been proposed that *TOC1* increases *LHY/CCA1* expression allowing *LHY/CCA1* expression to reach a peak at dawn beginning the cycle again [38,42-44]. *TOC1* exhibit feedback inhibition to repress its own expression [38, 45, 46].

ROLE OF CCA1 GENE IN KEY AGRICULTURAL TRAITS

CCA1 Influences Diverse Plant Physiological Processes-

Mari Kamioka *et al.* (2016) discovered the genes that are directly as well as indirectly targeted by *CCA1* gene. *CCA1* potential target genes showed altered expression *i.e.* either up regulated or down regulated in the *cca1* lhy mutant plants when compared with the wild type plants expressing native *CCA1* and *LHY* proteins. *CCA1* influences diverse physiological processes partly through regulating the set of Transcription Factors-TFs [47]. A number of *CCA1*-potential target has been reported such as Dehydration-Responsive Element Binding 2A [DREB2A], DREB2B, DREB2C, DREB2H, and DECREASE WAX BIOSYNTHESIS [DEWAX]), *TOC1*, *PRR7*, and *PRR5*, *RVE7*, two B-BOX DOMAIN PROTEIN (*BBX8* and *BBX13*), *LUX* and *BROTHER OF LUX ARRHYTHMO* [*BOA*; also known as *NOX*]), *ABSCISIC ACID-RESPONSIVE KINASE SUBSTRATE2* [*AKS2*] and *ACTIVATION-TAGGED BRI1 SUPPRESSOR1-INTERACTING FACTOR1* [*AIF1*]), *ABA INSENSITIVE5* [*ABI5*]), a *TCP* (*CCA1 HIKING EXPEDITION* [*CHE*]), *C2H2* (*BALDIBIS* [*BIB*]), *ARF6* (a DNA binding auxin response factor), a *NAC* (*NAC019*), a *HSF* (*HSFC1*), a *CCAAT* TF (*NF-YB2*), *GAI*, *RGA*, and *SCR* (*GRAS*) (*SCR-LIKE13* [*SCL13*]) [47]. *TOC1*, *PRR7*, and *PRR5*, *LUX*, *BOA*, and *CHE*, all take part in circadian clock control [48, 49]. *DREB2A* and *DREB2B* proteins are involved in drought stress response (Liu *et al.*, 1998), *DREB2C*, *AKS2*, and *ABI5* are ABA signaling proteins (50-52), *DREB2C* is involved in heat stress response [53], *DEWAX* help in regulation of wax biosynthesis (54), *ARF6* is important for flower maturation [55], *AIF1* and *MYBL2* involved in brassinosteroid signaling [56, 57], *MYBL2* is required for anthocyanin biosynthesis [58], *BIB* is help in root development (59), *SNF-YB2* regulate flowering time [60], *RVE7* helps in controlling the cotyledonary opening and flowering time [61], *NAC019* is a protein that regulate water stress [62], and *HSFC1* involved in heat stress [63].

CCA1 Gene Role In The Control of Hypocotyls Length and Flowering Time-

The role of *CCA1* and *ELF3* has been reported in the control of hypocotyl length and flowering time in *Arabidopsis* [64]. Overexpression of *CCA1* results in circadian dysfunction, elongation of hypocotyls, and late flowering. *CCA1* gene binds strongly to the *FT* (*FLOWERING LOCUS T*) gene promoter and regulates the photoperiodic flowering [65]. *LHY* and *CCA1* in addition to floral transition repression under SD and LD conditions, they also accelerate flowering under continuous light [66-69]. *LHY* and *CCA1* hasten the flowering by promoting *FT* expression via a genetic pathway that seems to be independent of the canonical photoperiodic pathway involving *GIGANTEA* (*GI*) and *CONSTANS* (*CO*) proteins [66].

CCA1 Gene Role in Growth Vigor

Heterosis, also called hybrid vigour, the increase or improvement in characteristics such as size, growth rate, fertility, and yield of a hybrid organism over those of its parents. Hybrids are generally larger and more vigorous as compared to their parents. In *Heterosis*, there is increased photosynthetic rates, carbohydrate and starch metabolism. So keeping in view advantages of heterosis, majority of crops are grown as hybrids. The altered circadian clock could affect metabolic and photosynthetic pathways that are altered in F1 hybrids [70,71] as well as overall regulatory networks related to growth and development [72]. The *CCA1* has been shown to directly modulate *TOC1* and other downstream genes in circadian clock, photosynthesis and starch metabolism as well as for increased biomass and growth vigor in *Arabidopsis thaliana* (28). Similar effect has been observed in allopolyploids. In both the hybrids as well as allopolyploids the increased expression of genes involved in photosynthesis, starch, and sugar metabolism has been observed from noon to dusk. This is due to the fact that *CCA1* repress these genes and *CCA1* expression peaks at dawn and then repressed at noon, which result in activation of genes involved in photosynthesis, starch, and sugar metabolism. Similarly, modifying *CCA1* expression in diploids showed some positive effects on growth vigour as in the hybrids and allotetraploids, *cca1* single and *cca1 lhy* double mutants and RNAi constructs used for the study [28].

The increased metabolic vigor in developing embryos reported when the maternal copy of *CCA1* is repressed. When the maternal *CCA1* is repressed, growth vigor is increased and while the maternal *CCA1* expression is up regulated, growth vigor is reduced. These findings are in consistent with parental conflict theories of imprinting [34]. In this way epigenetic modulation of *CCA1* can act as potential tool incrop plants improvement.

CCA1 Gene Role in Abiotic Stress Management-

It has been reported that *CCA1* over-expressing (*CCA1-ox*) plants have improved ability to grow in ROS stress-inducing conditions due to the fact that *CCA1* regulates genes involved in production, response, and transcriptional regulation of ROS in *Arabidopsis* [73]. Reactive oxygen species (ROS) are toxic by-products of plant's metabolic processes such as photosynthesis and respiration that can results into cellular damage at high levels [74]. Production of ROS and transcriptional regulation of ROS responsive genes are centrally controlled by the circadian clock *CCA1* gene. On the other hand, ROS production acts as an input signal that affects the transcriptional regulation of circadian clock genes help the circadian clock to keep an eye on the oxidative state of plant cells. Revealing an important link between ROS signaling and circadian output [73].

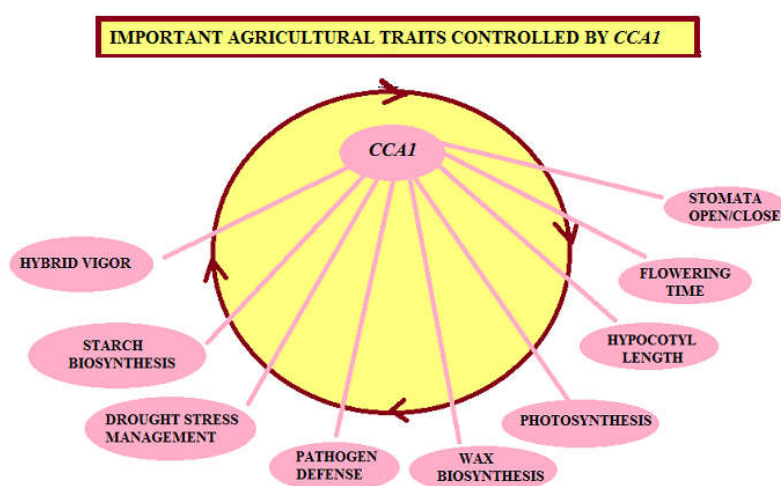


Figure 1: Diverse Plant Physiological Processes Controlled By *CCA1* Gene

CCA1 Gene Role in Biotic Stress Management-

The circadian clock *CCA1* plays a central role in plant defense by activating the plant defense responses to anticipate the attack of likely pathogen. Two broad classes of plant defense responses are there, one is referred as primary or basal resistance and second one is secondary or R-gene mediated resistance. The R-genes mediated resistance is principle immune defense mechanism against biotrophic pathogens and it is under temporal regulation by *CCA1* protein. It is at dawn, the pathogens downy mildew normally disperses the spores and at this time, the immune responses upon anticipation of different pathogenic signals increase expression of R-genes (75). In *cca1-ox* plants improved resistance to downy mildew has been observed while *incca1* mutant plants, reduced R-gene expression and reduced resistance to downy mildew has been observed, thus demonstrating the molecular link between circadian *cca1* gene and plant defense response (75).

The similar mechanism of plant defense in early morning against a virulent strain of the bacterial pathogen *Pseudomonas syringae* (Pst DC3000) has been reported in *Arabidopsis*. In this case, callose deposition around the cell wall is the underline defense mechanism that is activated in the morning. The morning-specific callose deposition was found to be significantly higher in wild-type plants inoculated with Pst DC3000 *hrpA*, while no such response was reported in arrhythmic *CCA1-ox* and *elf3-1* mutants [76].

CONCLUSION

CCA1 gene is the central Circadian clock gene and it regulates a number of important agricultural traits, such as those highlighted above. *CCA1* gene can be a powerful tool to alter single or multiple agricultural

traits simultaneously. Exploiting *CCA1* gene, and existing other circadian clock gene alleles holds the potential for crops improvement with respect to number of agricultural traits such as biotic and abiotic stress resistance, growth, biomass, starch biosynthesis, flowering time.

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