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Regulation of the Plant Immune Response by the Circadian System

(*Kishor Sharma, Adikshita Sharma, Monica Sharma and Vijay Rana)
College of Horticulture and Forestry, Thunag,
Dr Y S Parmar University of Horticulture and Forestry, Nauni, Solan (HP), India
*Corresponding Author's email: ks4141173@gmail.com

The primary agricultural plant diseases causing pathogens are viruses, fungus, nematodes, parasitic plants, and bacteria. These pathogens account for 40% of crop losses globally. Plants have complex defense mechanisms, and pathogens' constant evolution guarantees a never-ending "arms race" to safeguard disease resistance. Along with many other metabolic functions, the plant circadian framework regulates pathogen defense. Diseases and plants that infect them both have an internal biological clock called the circadian clock. It is noteworthy that there is evidence linking the host circadian clock to control the defensive mechanisms in plants, and vice versa. It is widely understood that a number of abiotic elements, including light and temperature, supply signals to the clock, which in turn develops a variety of output signals that influence the processes that follow.

Growing body of research indicates that the pathogen and plant's circadian rhythms control their mutual interactions. Numerous genes, including FLS2, linked to PTI or PAMP-triggered immunity, exhibit rhythmic expression in Arabidopsis, according to a microarray data analysis. Circadian regulation is demonstrated by pathogen-responsive genes, such as glycine-rich RNA binding protein (GRP), which is present in barley and many other crops. The plant can identify the pathogen and start PTI because GRP binds with PAMPs that are produced by the pathogen directly. Two of the barley's GRPs, HvGRP2 and HvGRP3, were expressed more frequently when the grain was subjected to a 16/8-hour light/dark cycle. Photosynthesis is a day-only process that bears accountability for the diurnal creation of energy in plants. It is predictable that the circadian clock controls the opening of the tiny epidermal pores, or stomata, which are participate in the gas exchange for photosynthesis. In addition, one of the first plant defense responses to pathogens is stomatal closure. In a process known as pattern-triggered immunity (PTI), plants quickly shut their stomata in reaction to the detection of pathogen-associated molecular patterns (PAMPs), that is flagellin. It has been demonstrated that the key morning clock genes CIRCADIAN CLOCK ASSOCIATED 1 (CCA1) and LATE ELONGATED HYPOCOTYL (LHY) target GLYCINE-RICH RNA BINDING PROTEIN 7 (GRP7), often referred to as COLD and CIRCADIAN REGULATED 2 (CCR2). These genes have the ability to influence stomatal immunity.GRP7 is a part of a peripheral loop of the circadian clock that functions in stomatal defense as well. It binds to specific PAMP receptor transcripts and has the capacity to increase the translation of at least one of them during an infection. The night-expressed clock gene TIME FOR COFFEE (TIC) is also required for efficient stomatal defense and the circadian oscillation of stomatal aperture.

It's interesting to note that a darkness intervention alone causes stomatal closure that is larger than a disease when light is present indicating that additional defense mechanisms may be needed to make up for the reduced stomatal defense in the light. For the purpose to evade plant cells or PTI and increase pathogenicity, several diseases have evolved specialized

proteins known as effectors. Plants contain leucine-rich repeat (NB-LRR) and nucleotide-binding receptors (NB-binding) within their cells as a counter measure to identify and neutralize pathogen effectors, as well as the activities that activate effector-triggered immunity (ETI). The diseased tissue's programmed cell death (PCD) is typically involved in ETI, a more severe defensive reaction than PTI. Recognization of *Peronospora parasitica* 4 (RPP4) is an immune receptor gene that recognizes an effector in the oomycete pathogen *Hyaloperonospora arabidopsidis* (Hpa) Emwa1 and targets the core clock component CCA1. The morning is the peak time for Hpa infection risk. Thus, there is a clear genetic relationship between defense and the circadian clock. Another direct clock target is the ISOCHORISMATE SYNTHASE 1 (ICS1) gene, whose expression is controlled by the transcription factor CCA1 HIKING EXPEDITION (CHE), which is involved in the evening-phased clock. It encodes a key enzyme involved in the synthesis of the defense hormone SA. Because of this regulation, the ICS1 gene expresses itself more and the concentration of SA peaks in the middle of the night, perhaps anticipating infection in the morning. Apart from its critical function in initiating broad-spectrum systemic acquired resistance (SAR) in the distal tissue, SA is also vital for local defense against biotrophs.

Interestingly, the che mutant exhibits impaired SAR but robust local defense, indicating that SA oscillation could be involved in gating SAR. This makes sense because "immunizing" the entire plant against future infection requires additional energy, which is best reserved for times when plants have surplus energy to spend. All things considered, the circadian clock primes expensive defense responses (such as immune gene expression) towards morning, when stomata must be opened to enable photosynthesis, which also happens in accordance with the window of infection for several biotrophic diseases. In contrast to SA, the hormone JA, which defends against necrotrophs and herbivores, rises during the midday period. Furthermore, there is disagreement about whether the JA peak, which happens when the pathogen, which is injected at dawn, correlates with *Botrytis cinerea's* resistance. This discrepancy was explained by the estimated 12-hour lag required for *B. cinerea* conidiospore germination and the growth of infectious hyphae. These observations suggest that because the circadian clock may temporally segregate the oscillations of SA and JA, plants may prepare for defense against a specific kind of invader while avoiding any antagonistic interactions between SA and JA.

The model plant *Arabidopsis thaliana's* circadian clock structure is made up of a variety of transcriptional-translational feedback loops, or TTFLs. Transcription factors that attach to DNA are the components of the circadian clock. The two MYB domain-containing transcription factors, Circadian Clock Associated 1 (CCA1) and Late Elongated Hypocotyl (LHY), as well as one pseudo-response regulator (PRR), Timing Of CAB2 expression 1 (TOC1), were initially identified as the key clock components. This was due to the fact that these genes' mutations significantly altered the phase, amplitude and period of the circadian clock.

The transcriptional–translational feedback loops (TTFLs) that comprise the circadian clock structure of the prototype plant *Arabidopsis thaliana* are diverse. The components of the circadian clock are transcription factors that bind DNA. The core clock components were first identified as two MYB domain-containing transcription factors, Circadian Clock Associated 1 (CCA1) and Late elongated Hypocotyl (LHY), and one pseudo-response regulator (PRR), Timing of CAB2 expression 1 (TOC1). This was because mutations in these genes caused significant changes in the circadian clock's phase, amplitude, and period.

Together, these three elements create a negative feedback loop that permits the expression of their particular phase of the day. Most core clock proteins produce negative feedback loops in which they repress their own transcriptional or translational expression. Morning expressed genes include LHY, a close homologue of CCA1, and others. Evening

element (EE) in TOC1's promoter region (an evening-expressed gene) is bound by CCA1/LHY, which suppresses the expression of the gene. Closing the loop, TOC1 in turn directly suppresses CCA1 expression. Nine nucleotides long, the conserved motif EE serves as the binding site for many clock proteins, such as CCA1, LHY, and REVEILLE (RVE). Over the past ten years, advances in the biology of the circadian clock have identified a number of additional essential elements, including PRRs, LUX Arrhythmo (LUX), Early Flowering 3 and 4 (ELF3, 4), and the RVE family of transcription factors. These elements combine to create several feedback loops that are tied to the CCA1–LHY–TOC1 network. Approximately one-third of all transcripts in A. thaliana were shown to be circadian controlled, according to a genome-scale, time-course expression profiling study. Positive regulation of plant resistance to oomycetes and bacterial diseases such as *P. syringae* is regulated by the morning phased CCA1 and LHY genes. CCA1 contributes to resistance responses, which in turn controls the plant-pathogen relationship. In the morning, CCA1-deficient plants exhibit strong resistance, but in the evening, they become more susceptible. CCA1-ox mutants did not exhibit these rhythmic susceptibilities over the course of a day, suggesting a connection between CCA1 and plant immunity. Similar to this, downy mildew resistance is compromised in cca1 seedlings, while resistance is enhanced when CCA1 is overexpressed.

Fungal circadian rhythms have been extensively researched. In fact, the majority of its life processes are dictated by the fungal clock. Spore dispersion and sporulation are the two most significant factors in plant pathogenicity. Certain fungus release their spores during the night. while some at sunrise or sunset. Asexual reproduction has also been shown to exhibit daily cycles. For instance, in *Pilobolus* species, the circadian rhythm controls both spore production and dissemination. *Pellicularia filamentosa* and *Aspergillus nidulans* have both been observed to have the same behavior. At every stage of infection, the plant-pathogen connection is impacted by the circadian rhythms shown by these plant pathogens. In order to comprehend the fungal circadian clock, the fungus Neurospora has been extensively investigated and is used as an example of fungal circadian system.

The late blight disease *Phytophthora infestans* induces the expression of the tomato gene DEA1, which was found to be influenced by both light and the circadian rhythm. According to certain research on plant defense mechanisms through stomata, clock genes regulate the timing of stomatal openings, which in turn controls resistance to bacterial infections. For instance, during night, Arabidopsis displayed resistance to *P. syringae*. When bacteria invade, plants can actively seal their stomata to prevent access after recognizing a PAMP. Importantly, the gating response of stomatal opening and shutting is controlled by both CCA1 and LHY.

Our understanding of the circadian clock controlling the plant defense in responses using targeted interventions will provides a foundation for future work. As earlier, only abiotic factors, mainly light and temperature, were attributed as input signals to the clock. For the purpose of maintaining plant health and managing disease, it is crucial to understand the mechanisms behind the connection between the circadian system and plant immunity. Efficient disease control and reduced crop yield losses could arise from synchronizing disease treatment with plants' internal clock. With this, we will be able to provide knowledge and predictions in the development of plant-pathogen interactions as well as the evolution of plant adaptation in changing environments. Moreover, deeper knowledge of how specific environmental factors affecting the interaction between plants and pathogens and uncovering of genes acting at the converging point of regulating the circadian clock and defense could further novel strategies for the development of highly resistant crops under increasingly unpredictable climatic conditions. This is also valuable for the advancement of transgenic

crop production that can survive in various related stresses which is one of the solutions to global food security problems in the future.

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