

# Unlocking Nature's Rhythm: Harnessing the Circadian Clock in Seed Production

RAJENDRA PRASAD S<sup>1\*</sup>, B ROOPASHREE<sup>2</sup>, SP JEEVAN KUMAR<sup>3</sup>

<sup>1</sup>Former Vice- Chancellor, University of Agricultural Sciences, Bangalore, Karnataka-560065, India

<sup>2</sup> Department of Seed Science & Technology, University of Agricultural Sciences, Bangalore, Karnataka-560065, India

<sup>3</sup>ICAR-Directorate of Floricultural Research, Pune, Maharashtra-411036, India

\*srprasad1989@yahoo.co.in

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**ABSTRACT:** Seeds have an internal clock, known as the circadian clock, that helps them regulate their daily activities and respond to environmental changes. This clock is made up of three main parts: the input pathway, the central oscillator, and the output pathway. It influences important processes such as seed dormancy and germination, ensuring that seeds sprout at the right time and under favorable conditions. The circadian clock also affects how seeds manage energy, through processes like carbon metabolism. Understanding how this clock works can help improve germination, seedling vigour and seed quality during storage as well as develop new ways to protect seeds from pests. This review explains the parts and functions of the seed circadian clock and discusses its potential applications in agriculture to enhance seed quality and productivity.

**Keywords:** Circadian clock, dormancy, seed germination, seed storage

## INTRODUCTION

Within the realm of biology, there is an internal clock that regulates the daily cycles of existence. The endogenous circadian clock is the timekeeper, and it is present in a variety of living things, such as archaea, eubacteria and eukaryotes [1]. The term "circadian" is a combination of two Latin words: "circa" means "around" and "diem or dies" means "day." These species can anticipate and adjust to daily and seasonal changes in their surroundings because of the circadian clock [2].

Three primary parts make up the plant circadian clock: the input pathway, the central oscillator, and the output pathway [3]. While the "canonical clock genes" that make up the primary oscillator of the clock are sensed by the input route in response to external stimuli like light [4]. The clock's signals are translated into different downstream processes via the output pathway. These elements work together to form a self-regulating system that affects the growth, development, and metabolic functions of plants [5].

Through reverse and forward genetics methods, it has been deciphered that the circadian rhythm in plants is firmly controlled by several interlocked transcriptional-translational feedback loops [6]. Three interconnected feedback loops such as morning, central and evening

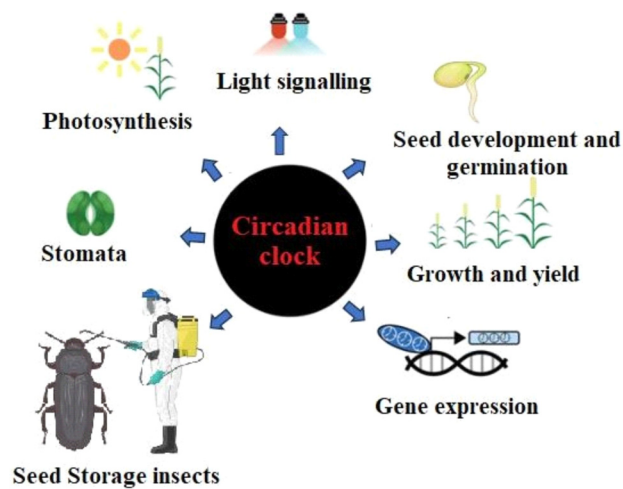
loops have been identified in *Arabidopsis thaliana*, a model plant. Certain genes and proteins that affect the plant circadian rhythm make up these loops. For instance, the morning loop contains genes that are essential to the regulation of the clock, such as *LATE ELONGATED HYPOCOTYL (LHY)* and *CIRCADIAN CLOCK ASSOCIATED 1 (CCA1)*. The evening gene *TIMING OF CAB EXPRESSION (TOC1)*, which works with other proteins to build the plants circadian rhythm is another important component of the circadian clock. Plants develop a strong circadian rhythm because of the complex interactions between these loops and genes [7].

The circadian rhythm regulates several functions, including hormone production, photosynthesis, carbon metabolism, and opening and closing of stomata that control gas exchange. Additionally, the seed development, germination, dormancy, storage, and quality control of seeds are also influenced by the circadian cycle (Fig. 1).

## The Circadian Clock: Nature's Timekeeper

### Controlling Circadian Rhythms for Enhanced Production

Research studies illustrate that disturbing the circadian clock can significantly affect plant physiology and



**Figure 1.** Circadian oscillators regulating various processes of seed development, germination and storage

consequently, crop production. For instance, in *Arabidopsis thaliana*, overexpressing transcription factors, like *BBX18*, *BBX19*, and *BBX32*, can prolong the circadian cycle and affect plant stability. The *C-REPEAT/DRE BINDING FACTOR (CBF)*, which is a key regulator in cold adaptation, is another important regulator of responses to temperature changes that are governed by the circadian clock [3].

Photoreceptors like Phytochrome B (PHY B) and Cryptochromes (CRYs) are part of the circadian clock input pathway, which enables plants to adapt to changes in temperature and light. Processes like reproductive development, hormone production, immune responses, and gene expression levels are subsequently impacted by these photoreceptors [7].

**Circadian Regulation of Carbon Assimilation and Allocation:** Several studies have underscored the significance of the circadian clock in coordinating metabolic pathways associated with carbon fixation, starch synthesis, and sucrose metabolism in leaf tissues. The rhythmic expression of key enzymes involved in sucrose synthesis and starch degradation is tightly regulated by circadian clock components such as *SNF1-related kinase 1 (SnRK1)* kinase and *osmo-sensitive kinase OsmK* [8]. Moreover, phytochrome-interacting transcription factors like PIF4 and PIF5 modulate sugar consumption, further highlighting the intricate regulatory network governing carbon partitioning in plants [9].

Another important process of plant physiology that is affected by the circadian clock is carbon metabolism. The circadian rhythm controls the activity of several carbon

metabolism-related enzymes including Ribulose-1, 5 bisphosphate carboxylase/oxygenase (RuBisCO). The timing of carbon fixation and the synthesis of substances like starch comply with the daily cycle of the plant. Plants produce starch, a carbohydrate that is stored, during the day, and then break it down at night to produce energy for metabolism and growth. The timing and speed of these processes are influenced by the circadian clock, which maintains a balance between carbon storage and utilization [10].

### Photosynthesis: A Key Focus of Circadian Regulation

One of the main functions controlled by the circadian clock is photosynthesis, the process by which plants transform light energy into chemical energy. The circadian rhythm affects the stomata, which are microscopic pores on leaves that facilitate the exchange of carbon dioxide, water, and oxygen.

Stomatal opening and closing play a key role in controlling the uptake of carbon during photosynthesis. The flow of carbon dioxide into leaves is impacted by the circadian clock's effect on stomatal conductance, which in turn affects the rate of photosynthesis. Other aspects of photosynthesis, such as chlorophyll content, chlorophyll fluorescence, and net carbon assimilation rate, are also influenced by the circadian clock [11].

The circadian clock and photosynthesis have a bidirectional relationship, which means that photosynthesis can be influenced by circadian regulation and that the circadian clock can also be influenced by photosynthesis. The overall health and productivity of the plant is influenced by this interaction, which is necessary for coordinating the diurnal variations in stomatal conductance and photosynthesis [12].

The circadian clock exerts intricate control over various aspects of plant metabolism, orchestrating a finely tuned balance between photosynthetic carbon fixation, carbohydrate synthesis, and storage. Transcriptomic and metabolomic studies in *A. thaliana* have unveiled the pervasive influence of the circadian clock on the expression of genes encoding enzymes crucial for primary metabolism. Notably, approximately 30% of primary metabolite accumulation exhibits circadian oscillations under normal growth conditions, underscoring the pervasive impact of circadian regulation on plant physiology. Carbohydrates, serving as vital energy sources for cellular processes, undergo dynamic turnover,

with mature leaves acting as primary sites for sucrose synthesis during the day, which is subsequently transported to sink organs to sustain plant growth.

The diurnal cycle of photosynthetic CO<sub>2</sub> fixation drives the synthesis of sucrose and starch, crucial for sustaining plant metabolism during the night. Disruption of starch turnover rhythms due to premature onset of night time can lead to carbon starvation, triggering rapid metabolic and gene expression changes, ultimately affecting biomass production. The regulation of starch-related genes by circadian clock components further elucidates the intricate control mechanisms underlying carbohydrate metabolism. Additionally, circadian oscillations extend to other metabolic pathways, including lipid biosynthesis and nitrogen assimilation, highlighting the comprehensive influence of the circadian clock on plant metabolism [13].

### Circadian Regulation of Seed Metabolism

The circadian clock exerts significant control over seed metabolism, particularly during energy storage and utilization. During seed development, the clock regulates the timing of starch and lipid biosynthesis to optimize energy storage. In oilseed crops like *Brassica napus*, the expression of key enzymes involved in fatty acid synthesis shows diurnal rhythms, peaking during the day to coincide with maximal photosynthetic output from maternal tissues [14].

There are several other mechanisms which regulate the carbon and lipid metabolism during the seed filling and development. Upon imbibition, the seed circadian clock becomes reactivated and plays a crucial role in coordinating the metabolic transitions required for germination. The clock regulates the expression of enzymes involved in reserve mobilization, such as  $\alpha$ -amylases for starch breakdown, ensuring that energy release is synchronized with the demands of the germinating seedling [15].

Interestingly, the circadian clock also influences seed respiration rates. Studies in various crop species have shown that seed oxygen consumption exhibits diurnal rhythms, with peaks typically occurring during the daytime [16]. This rhythmic respiration may help optimize energy utilization and prevent oxidative stress during early seedling growth.

### Seed Filling

The regular course of daily seed growth and development is aided by the rhythmic expression of genes. The

accumulation of seed storage proteins in legumes undergoes a progressive increase during seed filling until desiccation. Typically, legume seeds contain a substantial amount of protein, ranging from 17% to 30% on a dry weight basis. Cowpea, for instance, exhibits protein content varying between 14.8% and 23.6%, particularly in Spanish landraces. Within cowpea seeds, globulins represent the predominant seed proteins, comprising about 55% to 58% of the total protein content [17].

Among the globulins, legumes primarily accumulate 7S vicilin-type globulins and 11S legumin-type globulins. The proportions of legumin (LEG) and vicilin (VIC) are genetically and environmentally determined in pea seeds, synthesized from multiple genes and genetic loci. Despite their functional divergence, LEG and VIC share significant sequence identity at both the amino acid and nucleotide levels, suggesting a common evolutionary origin. Gene clusters, such as *LEGA*, *LEGB*, *LEGJ*, and *LEGK*, contribute to the synthesis of these storage proteins in legumes [18-19].

Recent work has uncovered a direct molecular link between the circadian clock and fatty acid biosynthesis in *Arabidopsis* seeds. Researchers demonstrated that the core clock proteins *LATE ELONGATED HYPOCOTYL (LHY)* and *CIRCADIAN CLOCK ASSOCIATED 1 (CCA1)* bind to and activate the promoter of  $\beta$ -ketoacyl-ACP synthase III (*KASIII*), which catalyzes the initial condensation reaction in fatty acid synthesis. Overexpression of *LHY* or *CCA1* increased seed oil content, while the *lhycca1* double mutant showed reduced oil accumulation. Metabolic labeling experiments indicated that *LHY/CCA1* promote fatty acid synthesis rather than affecting lipid turnover. In the research study, it was found that phosphatidic acid can inhibit *LHY* binding to the *KASIII* promoter, suggesting a potential feedback mechanism. This study reveals how circadian clock components can directly modulate lipid biosynthesis to regulate seed oil production, providing insights into the integration of circadian and metabolic networks in plants [20].

The core circadian clock component *TIMING OF CAB EXPRESSION 1 (TOC1)* has recently been implicated in regulating fatty acid metabolism in *Arabidopsis* seeds. Researchers found that *toc1* mutant seeds exhibited significant changes in their fatty acid profile, including increased total fatty acid content, higher levels of linolenic acid (18:3), and lower levels of linoleic acid (18:2). Lipidomic analysis of glycerolipids reflected these

changes, with *toc1* seeds showing increases in triacylglycerols containing 18:3, 18:0, 20:0, and 22:1. Furthermore, the expression of key fatty acid biosynthesis genes and transcription factors was upregulated in developing *toc1* seeds. These findings suggest that TOC1 plays a crucial role in modulating seed fatty acid metabolism, likely by regulating the expression of genes involved in fatty acid synthesis and modification. Together with previous research on CCA1/LHY, this study highlights the importance of core circadian clock components in controlling lipid metabolism during Arabidopsis seed development, expanding our understanding of how circadian rhythms impact seed oil production in plants [21].

While the Arabidopsis circadian clock serves as a model, variations exist across species and tissues. The circadian network differs in timing and genetic architecture among plant tissues, with distinct rhythms observed in leaves, roots, and vascular tissues. Despite conservation of core clock genes, expression patterns vary, reflecting adaptations to environmental stimuli and tissue-specific functions.

### Seed Germination and Dormancy Through Timing

Seed dormancy, an important trait among biological organisms, serves as a pivotal mechanism allowing plants to temporally coordinate growth with favorable environmental conditions, thereby optimizing survival and reproductive success. Dormant seeds remain in a quiescent state until conditions become conducive for germination, ensuring that seedling emergence occurs when resources are plentiful and environmental stresses are minimized. The regulation of seed dormancy and germination involves intricate molecular, physiological, and environmental cues, with diverse signaling pathways converging to modulate the timing and extent of seedling emergence [22, 23].

One of the key factors influencing seed dormancy and germination is environmental signaling. Environmental cues such as temperature, light, moisture, and nutrient availability play crucial roles in triggering dormancy release and promoting seed germination. For instance, temperature fluctuations during seed development and maturation can influence dormancy depth and duration, with exposure to chilling or warm temperatures often serving as dormancy-breaking signals. Similarly, light can act as a germination stimulant for certain seeds, while others require darkness for germination initiation.

Additionally, moisture availability and nutrient status in the soil also impact seed dormancy and germination, with fluctuations in nitrate levels known to influence dormancy release in some species [24].

Dry after-ripening, a process occurring over predictable time scales in low-hydrated seeds, represents another important mechanism promoting dormancy loss upon imbibition. Analogous to a drought response, dry after-ripening primes dormant seeds for rapid germination upon rehydration, facilitating the transition from dormancy to germination. Furthermore, dry after-ripening and cold exposure have been shown to substitute for each other, both promoting the germination of dormant seeds in the presence of light. Importantly, the role of after-ripening extends beyond dormancy release, as it also modulates the sensitivity of seeds to further dormancy-breaking treatments over time, suggesting intricate crosstalk between dormancy-related signaling pathways [25].

At the molecular level, the balance between gibberellins (GAs) and abscisic acid (ABA) plays a central role in regulating seed dormancy and germination. Environmental signals are known to modulate the levels of these phytohormones in seeds, primarily through transcriptional regulation of enzymes involved in hormone metabolism. Enzymes responsible for the synthesis, degradation, and conjugation of ABA and GA undergo transcriptional regulation in response to environmental cues, thereby fine-tuning hormone levels to promote or inhibit germination as per prevailing conditions. For instance, the expression of genes encoding GA biosynthetic enzymes is induced by light, cold, and after-ripening, whereas ABA catabolic enzymes are transiently induced post-imbibition in a phytochrome- and after-ripening- dependent manner, facilitating ABA breakdown and promoting germination [26].

Recent work has uncovered a direct molecular link between the circadian clock and abscisic acid (ABA) signaling during Arabidopsis seed germination. Research studies demonstrated that the core clock proteins *PSEUDO-RESPONSE REGULATOR 5 (PRR5)* and *PRR7* physically interact with and stimulate the activity of *ABSCISIC ACID-INSENSITIVE 5 (ABI5)*, a key transcription factor in ABA signaling. The *prr5 prr7* double mutant and *prr5 prr7 prr9* triple mutant exhibited reduced sensitivity to ABA during germination, while overexpression of *PRR5* enhanced ABA responses. Mechanistically, *PRR5* was found to promote the transcriptional activity of *ABI5* on target genes like *LATE*

*EMBRYOGENESIS ABUNDANT 6 (EM6)* and *EM1* without affecting *ABI5* protein stability. This study reveals how circadian clock components can directly modulate ABA signaling to fine-tune seed germination responses, providing insight into the integration of circadian and hormone signaling networks during this critical developmental transition [27].

Intriguingly, components of the circadian clock, known for their role in regulating physiological processes in response to daily light-dark cycles, have recently emerged as potential regulators of seed dormancy and germination. The circadian clock comprises interlocked transcriptional feedback loops involving key clock genes such as *TIMING OF CAB EXPRESSION1 (TOC1)*, *LATE ELONGATED HYPOCOTYL (LHY)/CIRCADIAN CLOCK ASSOCIATED1 (CCA1)*, and *GIGANTEA (GI)*, which modulate the expression of downstream target genes in response to environmental cues. While the precise role of circadian clock genes in seed dormancy remains incompletely understood, recent studies have suggested their involvement in integrating environmental signals to regulate hormone metabolism and seed developmental processes. For instance, the interaction between the central seed dormancy regulator *ABSCISIC ACID INSENSITIVE3 (ABI3)* and the *TOC1* protein highlights a potential link between the circadian clock and seed dormancy regulation [28]. Furthermore, genetic manipulation of circadian clock components has been shown to alter seed dormancy and responsiveness to dormancy-breaking signals, providing further evidence of their regulatory role in seed development.

The transition from seed dormancy to active growth in *Arabidopsis* involves a complex regulatory network controlling plastid-associated protein (PAP) gene expression. Researchers uncovered a multifaceted regulation of PAP genes during seed germination and early seedling development. Their study revealed a rapid and significant upregulation of PAP gene expression within 24 hours of germination onset, occurring in both light and dark conditions. They observed that the expression peaks of certain PAP genes shifted depending on the time of day when germination was initiated, suggesting an early activation of the circadian clock, possibly even during seed imbibition. This circadian influence operates in concert with developmental cues and light-dependent signals. Furthermore, the study demonstrated the swift induction of both plastid-encoded (PEP) and nuclear-encoded (NEP) RNA polymerase

genes upon germination commencement. These findings underscore the intricate temporal coordination of gene expression essential for plastid biogenesis in the earliest stages of plant development, integrating circadian, light, and ontogenetic regulatory mechanisms [29].

### Circadian Influence on Seed Quality and Vigor

The circadian clock has emerged as an important factor influencing overall seed quality and vigor. Research studies shown that disruption of circadian rhythms during seed development can have significant impacts on seed performance. A study on *Arabidopsis thaliana* demonstrated that seeds developed under constant light conditions, which disrupts normal circadian rhythms, showed reduced dormancy and altered germination responses compared to seeds developed under normal light-dark cycles [28]. This suggests that proper circadian entrainment during seed maturation is crucial for establishing appropriate dormancy levels.

The timing of seed harvest has also been shown to affect seed quality in an apparently circadian-dependent manner. In several crop species, seeds harvested at different times of day exhibit variations in germination rates, seedling vigor, and stress tolerance. While the mechanisms are not fully elucidated, it is hypothesized that these time-of-day effects are related to circadian regulation of protective antioxidant systems and stress response pathways in seeds.

Furthermore, the seed circadian clock appears to influence longevity and storage potential. Recently circadian rhythms in postharvest soybean sprouts were investigated using gene expression analysis. They found that core clock genes (*GmLCL1*, *GmTOC1*, and *GmPRR7*) maintained rhythmic expression under constant dark conditions, with periods close to 24 hours. The study employed cosine curve analysis to quantify circadian parameters. Postharvest controlled atmospheric storage treatments (4°C, 1% O<sub>2</sub>, or 20% CO<sub>2</sub>) disrupted these rhythms, altering the amplitude and phase of gene expression. Concurrently, these treatments improved quality retention, reducing respiration rates by 20-40%, weight loss by 50-70%, and browning index by 30-50% compared to controls [30].

The researchers also examined the expression of genes related to quality attributes, such as *GmPAL* (involved in phenylpropanoid metabolism) and *GmLOX* (linked to lipid peroxidation). These genes showed altered expression patterns under the postharvest treatments, correlating

with improved quality metrics. The study highlights the complex relationship between circadian clock function and postharvest physiology, suggesting that clock disruption may contribute to quality preservation in harvested plant products [31]. A study in *Medicago truncatula* found that mutations in core clock genes led to reduced seed longevity and altered expression of genes involved in protection against oxidative stress during storage [31]. This highlights the potential for manipulating circadian rhythms to enhance seed storability in agricultural applications.

### Seed storage insects

The development of resistance in storage insects to standard insecticides is one of the biggest issues in managing seed storage. This resistance can be overcome by playing with an insect chronobiology, the study of how an organism's internal clock influences its physiology and behavior.

**Chronobiological Vulnerable Phases:** Insects also display clock-dependent periods of susceptibility, much like people do during specific times of the day (like feeling sleepy in the afternoon). We can fix the time of use of pesticides for optimum efficiency by recognizing these sensitive stages in pests.

**Distorting the Circadian Clock:** One alternative approach to pest control in storage areas involves interfering with the circadian rhythms of storage pests. By manipulating external stimuli or altering the light-dark patterns within storage facilities, we can potentially alter the pests internal timekeeping mechanisms. This disruption may hinder their ability to anticipate and adjust to their environment, ultimately making pest management more effective [32].

The exploration of circadian rhythms and their implications for agro-chronobiology in managing stored product insects unveils a realm of potential solutions to longstanding agricultural challenges. By unraveling clock-driven behavioral, physiological, and genomic processes, a pathway emerges for innovative approaches to combat storage insects. These pests, often causing food shortages and economic losses, especially in developing countries, present formidable obstacles. However, the proposition of manipulating circadian rhythms offers a promising avenue for pest control.

### CONCLUSION

The circadian clock is a fundamental regulator of plant and seed physiology, influencing a wide array of

processes from photosynthesis and carbon metabolism to seed development and storage. Understanding the molecular mechanisms underlying circadian regulation, particularly the interactions between clock genes, environmental signals, and physiological outputs, provides valuable insights into optimizing plant growth and productivity. Deciphering molecular mechanisms pertinent to circadian rhythms could help to harness functional allelic diversity (stress or trait responsive) in core oscillator networks for the development of diverse germplasm and climate resilient varieties. The manipulation of circadian rhythms offers promising avenues for enhancing seed yields. Furthermore, the potential application of chronobiology in pest management in storage represents an innovative approach to addressing agricultural challenges. Future research should continue to unravel the complexities of the circadian clock, exploring its diverse roles across different plant species and tissues, to harness its full potential in agriculture and beyond.

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