International Journal of Plant & Soil Science

Volume 36, Issue 8, Page 596-617, 2024; Article no.IJPSS.116163
ISSN: 2320-7035

Plant Circadian Clocks: Unravelling the Molecular Rhythms of Nature

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

Article Information

DOI: https://doi.org/10.9734/ijpss/2024/v36i84890

Open Peer Review History:
This journal follows the Advanced Open Peer Review policy. Identity of the Reviewers, Editor(s) and additional Reviewers, peer review comments, different versions of the manuscript, comments of the editors, etc are available here: https://www.sdiarticle5.com/review-history/116163

Review Article

Received: 02/03/2024
Accepted: 04/05/2024
Published: 06/08/2024

ABSTRACT

The circadian clock is a fundamental biological mechanism that allows organisms to synchronize their internal processes with the external environment, thereby optimizing growth, development, and physiology. In plants, circadian rhythms govern various aspects of their life cycle, including

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Cite as: *Margay, Adil Rahim, Suhail Ashraf, Nusrat Fatimah, Saliah Gul Jabeen, Mansoor Showkat, Krishna Nayana R U, Sampatirao Dilip, Sudhakar Reddy Basu, and K. A. Aswathy. 2024. "Plant Circadian Clocks: Unravelling the Molecular Rhythms of Nature". International Journal of Plant & Soil Science 36 (8):596-617. https://doi.org/10.9734/ijpss/2024/v36i84890.*

germination, leaf movement, flowering, and responses to environmental cues such as light and temperature. Understanding the molecular mechanisms underlying plant circadian clocks is essential not only for elucidating fundamental principles of plant biology but also for applications in agriculture and biotechnology. This review delves into the intricate molecular networks that comprise plant circadian clocks, focusing on key components and their interactions. At the core of these clocks are transcription-translation feedback loops (TTFLs) involving a set of clock genes. The central oscillator, composed of genes such as CIRCADIAN CLOCK ASSOCIATED 1 (CCA1), LATE ELONGATED HYPOCOTYL (LHY), TIMING OF CAB EXPRESSION 1 (TOC1), and PSEUDO-RESPONSE REGULATOR (PRR) genes, drives rhythmic expression of downstream clock-controlled genes (CCGs). The interplay between positive and negative regulators within the TTFLs generates robust oscillations with a period of approximately 24 hours. Additionally, post-translational modifications, protein-protein interactions, and chromatin remodeling contribute to fine-tuning the circadian system, allowing plants to adapt to changing environmental conditions. Light perception through photoreceptors such as phytochromes and cryptochromes plays a crucial role in entraining the circadian clock to external cues, ensuring synchronization with the day-night cycle. Furthermore, recent advancements in omics technologies, including genomics, transcriptomics, proteomics, and metabolomics, have provided unprecedented insights into the complexity and plasticity of plant circadian clocks. Integration of multi-omics data has facilitated the construction of comprehensive regulatory networks and computational models, enabling predictive understanding of clock function and behavior under diverse conditions. Overall, unraveling the molecular rhythms of plant circadian clocks not only enhances our knowledge of fundamental biological processes but also holds promise for improving crop productivity, stress resilience, and sustainability in agriculture through targeted manipulation of clock components and their associated pathways. Future research endeavors will undoubtedly continue to unveil the intricacies of these fascinating timekeeping mechanisms, further enriching our understanding of the molecular rhythms of nature.

Keywords: Biotechnology; molecular rhythms; crop productivity; biological mechanism.

1. INTRODUCTION

Circadian rhythms are fundamental biological phenomena that synchronize an organism's internal processes with environmental cues, particularly the 24-hour light-dark cycle. While traditionally associated with animals, circadian rhythms are equally essential for plants, governing a myriad of physiological processes and adaptations crucial for their growth, development, and survival. In this review, we delve into the significance of circadian rhythms in plants, exploring their role in plant physiology and adaptation, and contextualizing recent developments in the field.

2. SIGNIFICANCE IN PLANT PHYSIOLOGY AND ADAPTATION

Plants, being sessile organisms, rely heavily on circadian rhythms to anticipate and respond to environmental changes effectively. The ability to synchronize physiological processes with daily cycles of light, temperature, and humidity provides plants with a competitive advantage in their ecosystems [1]. For instance, circadian rhythms regulate the opening and closing of stomata, tiny pores on the surface of leaves crucial for gas exchange and water regulation. By coordinating stomatal behavior with the diurnal fluctuations in light and temperature, plants optimize photosynthetic efficiency while minimizing water loss through transpiration.

Moreover, circadian clocks play a pivotal role in regulating the timing of critical developmental transitions in plants, such as flowering. The precise timing of flowering is crucial for reproductive success, as it determines the availability of pollinators and influences seed production. Circadian rhythms integrate various environmental cues, including day length (photoperiod) and temperature, to ensure that flowering occurs at the most favorable time for pollination and seed set. In agricultural settings, understanding the mechanisms underlying flowering time regulation has significant implications for crop productivity and management.

Beyond basic physiological processes, circadian rhythms also influence plant responses to biotic and abiotic stressors. By anticipating predictable daily changes in environmental conditions, plants can activate defense mechanisms proactively [2,3]. For example, the expression of genes involved in pathogen resistance and stress tolerance often exhibits circadian oscillations, allowing plants to mount robust responses to microbial attacks or adverse environmental conditions. Understanding how circadian clocks modulate stress responses is essential for developing resilient crop varieties capable of withstanding increasingly unpredictable climate conditions.

3. CONTEXT FOR LATEST DEVELOPMENTS

Recent years have witnessed remarkable progress in deciphering the molecular mechanisms underpinning circadian rhythms in plants. High-throughput genomic and transcriptomic analyses have identified an extensive network of clock genes and regulatory elements, shedding light on the complex regulatory pathways governing circadian oscillations. For instance, studies employing next-generation sequencing techniques have revealed the role of chromatin remodeling and epigenetic modifications in modulating clock gene expression and circadian output pathways.

Furthermore, advancements in genetic engineering and synthetic biology have enabled researchers to manipulate circadian clock components with precision, unraveling their roles in plant development and stress responses. By engineering plants with altered clock properties, scientists have uncovered novel insights into the functional significance of circadian rhythms in optimizing plant performance under changing environmental conditions. For example, modifying the expression of clock genes can alter flowering time, growth patterns, and stress tolerance, providing valuable tools for crop improvement and trait enhancement.

In addition to molecular studies, recent research has focused on elucidating the ecological consequences of circadian rhythms in plant communities and ecosystems. By integrating field observations, experimental manipulations, and mathematical modeling, scientists have begun to unravel the intricate interactions between circadian clocks and other organisms, including pollinators, herbivores, and microbial communities. These studies highlight the importance of circadian synchronization in mediating plant-insect interactions, predator-prey dynamics, and community-level patterns of species coexistence and competition.

In conclusion, circadian rhythms are integral to the life of plants, orchestrating a wide range of physiological processes and adaptive responses essential for their survival and reproduction. By synchronizing internal timekeeping mechanisms with environmental cues, circadian clocks optimize plant performance and resilience in dynamic ecosystems. Recent advancements in circadian biology have deepened our understanding of the molecular basis of clock function, revealing new opportunities for improving crop productivity, resilience, and sustainability. Moving forward, interdisciplinary approaches integrating molecular genetics, physiology, ecology, and computational modeling will continue to advance our knowledge of circadian rhythms in plants and their broader implications for agriculture, ecology, and global environmental change.

4. OBJECTIVES OF THE REVIEW PAPER

This review aims to provide a comprehensive overview of circadian rhythms in plants, elucidating their molecular mechanisms, physiological significance, and ecological implications. Our objectives include:

Exploring the molecular components of the plant circadian clock and their interconnections, highlighting recent discoveries in clock gene regulation and function.

Investigating the role of circadian rhythms in coordinating key physiological processes in plants, such as photosynthesis, nutrient uptake, and hormone signaling.

Examining how circadian regulation influences plant adaptation to changing environmental conditions, including responses to light, temperature, drought, and pathogen attack.

Assessing the impact of circadian rhythms on crop productivity, stress resilience, and ecosystem dynamics, with implications for sustainable agriculture and biodiversity conservation.

By synthesizing recent advancements in circadian biology, we aim to deepen our understanding of the intricate interplay between internal timekeeping mechanisms and external environmental cues in shaping plant physiology and adaptation.

5. HISTORICAL PERSPECTIVE

The exploration of circadian rhythms in plants has been a captivating journey spanning over several decades, marked by pivotal discoveries that reshaped our understanding of plant biology. The journey began in the mid-20th century when scientists first observed the rhythmic leaf movement of the plant Mimosa pudica, which hinted at the existence of an internal timekeeping mechanism.

In the 1960s, the groundbreaking work of Colin Pittendrigh and his colleagues provided compelling evidence for the existence of an endogenous circadian clock in plants. Through meticulous experiments with the plant genus Oenothera, they demonstrated that rhythmic leaf movements persisted even under constant environmental conditions, indicating an internal timing mechanism [4]. Daily rhythms as coupled oscillator systems and their relation to thermoperiodism and photoperiodism. Proceedings of the National Academy of Sciences, 43(7), 495–502).

The 1970s witnessed a surge in circadian clock research, with the discovery of mutants in Arabidopsis thaliana that exhibited altered circadian rhythms. Notably, the toc1 mutant, identified in 1999 by Steve Kay’s group, played a pivotal role in unraveling the genetic basis of the circadian clock in plants. This milestone shed light on the intricate network of clock genes orchestrating rhythmic processes in plants [5]. Cloning of the Arabidopsis clock gene TOC1, an autoregulatory response regulator homolog. Science, 289(5480), 768–771).

The dawn of the genomic era in the late 20th century revolutionized circadian clock research, enabling the identification and characterization of an array of clock genes and their interplay. The utilization of forward and reverse genetics in model plants such as Arabidopsis facilitated the discovery of essential components of the circadian clock, including core oscillator genes like CCA1, LHY, TOC1, and GI [1]. Orchestrated transcription of key pathways in Arabidopsis by the circadian clock. Science, 290(5499), 2110–2113).

The elucidation of the central oscillator mechanism governing circadian rhythms in plants garnered significant attention in the early 21st century. Pioneering studies employing mathematical modeling and systems biology approaches provided insights into the regulatory dynamics of the plant circadian clock. Notably, the development of computational models such as the Goodwin model and the more recent Extended Plant Circadian Clock Model (EPC) has deepened our understanding of the molecular basis of circadian timekeeping in plants [6]. Experimental validation of a predicted feedback loop in the multi-oscillator clock of Arabidopsis thaliana. Molecular Systems Biology, 2(1), 59).

Furthermore, the integration of omics technologies such as genomics, transcriptomics, proteomics, and metabolomics has provided comprehensive insights into the transcriptional and post-translational regulation of circadian clock components in plants. High-throughput sequencing techniques have facilitated the identification of clock-controlled genes and revealed intricate regulatory networks underlying circadian rhythms [7]. Global profiling of rice and poplar transcriptomes highlights key conserved circadian-controlled pathways and cis-regulatory modules. PLoS ONE, 6(6), e16907).

Moreover, recent advances in imaging technologies have enabled real-time visualization of circadian rhythms at the cellular and tissue levels, unraveling spatial and temporal dynamics of clock gene expression in planta. Techniques such as bioluminescence imaging and fluorescence resonance energy transfer (FRET) have provided unprecedented insights into the spatiotemporal organization of the plant circadian clock [5]. Targeted degradation of TOC1 by ZTL modulates circadian function in Arabidopsis thaliana. Nature, 426(6966), 567–570).

In conclusion, the historical development of circadian clock research in plants has been characterized by a continuum of milestone discoveries, from the initial observations of rhythmic leaf movements to the elucidation of the intricate molecular mechanisms governing circadian rhythms. These breakthroughs have not only deepened our understanding of plant biology but also hold promising implications for agricultural practices and biotechnological applications in the future [8]. The plant circadian clock: From a simple timekeeper to a complex developmental manager. Cold Spring Harbor Perspectives in Biology, 8(7), a027748.

6. MOLECULAR MECHANISMS OF PLANT CIRCADIAN CLOCKS

The molecular mechanisms underlying plant circadian clocks involve a complex interplay of genes and proteins that regulate the timing of physiological and developmental processes in response to environmental cues such as light and temperature fluctuations. At the core of the plant circadian clock are several key components, including transcription factors, kinases, and regulatory proteins. One essential gene involved in the plant circadian clock is TOC1 (Timing of CAB expression 1), which encodes a pseudo-response regulator that acts as a central component in the transcriptional feedback loops regulating clock function. TOC1 interacts with other clock components to regulate gene expression in a rhythmic manner, coordinating the timing of various cellular processes throughout the day [9].

Another crucial gene in the plant circadian clock is CCA1 (CIRCADIAN CLOCK ASSOCIATED 1), a MYB transcription factor that plays a central role in maintaining circadian rhythms and regulating gene expression in response to light cues. CCA1 forms a complex regulatory network with other clock genes, such as LHY (LATE ELONGATED HYPOCOTYL), to establish robust circadian oscillations. [10]. The rhythmic expression of CCA1 and LHY is tightly regulated by a combination of transcriptional and post-translational mechanisms, ensuring precise temporal control of clock output pathways.

Additionally, the plant circadian clock involves the participation of protein kinases such as CASEIN KINASE 2 (CK2), which phosphorylates clock components to modulate their activity and stability [5] CK2-mediated phosphorylation regulates the nuclear localization and degradation of clock proteins, contributing to the maintenance of circadian rhythms under changing environmental conditions [11]. Moreover, post-translational modifications such as ubiquitination and sumoylation play critical roles in fine-tuning the activity of clock proteins and coordinating their interactions within the circadian regulatory network [12].

Within the plant circadian clock, light input pathways play a pivotal role in entraining the clock to daily environmental cycles. Photoreceptors such as PHYTOCHROME (PHY) and CRYPTOCHROME (CRY) perceive changes in light intensity and quality, transmitting this information to the central oscillator through intricate signaling cascades [13]. PHY and CRY proteins undergo light-dependent conformational changes that regulate their activity, allowing them to integrate light signals into the circadian timing system [14]. These photoreceptors interact with downstream signaling components, including CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) and SUPPRESSOR OF PHYA-105 1 (SPA1), to modulate the stability and activity of clock proteins in response to light input [15].

Furthermore, the plant circadian clock incorporates temperature sensing mechanisms to synchronize internal rhythms with external environmental cues. Temperature-responsive transcription factors such as HEAT SHOCK TRANSCRIPTION FACTORS (HSFs) and C-REPEAT BINDING FACTORS (CBFs) regulate the expression of clock genes in response to temperature fluctuations [16]. These transcriptional regulators interact with core clock components to adjust the phase and amplitude of circadian oscillations in accordance with temperature changes, ensuring the adaptability of the clock to diverse environmental conditions.

Circadian rhythms in plants are orchestrated by a complex interplay of molecular components, primarily governed by a core transcription-translation feedback loop involving key genes such as CCA1, LHY, TOC1, and PRRs (Pseudo-Response Regulators) [1]. This feedback loop operates within cells, driving oscillations in gene expression and protein levels over approximately 24-hour periods.

At the heart of the circadian clock in plants lies the regulation of gene expression by transcription factors CCA1 (Circadian Clock Associated 1) and LHY (Late Elongated Hypocotyl), which repress the expression of genes including TOC1 (Timing of CAB expression 1) and PRRs during the day [17,18]. These genes, in turn, encode proteins that feedback to inhibit the activity of CCA1 and LHY, creating a negative feedback loop essential for maintaining rhythmicity [19].

TOC1, a central component of the circadian clock, acts as a repressor of CCA1 and LHY expression during the night phase, forming a regulatory loop critical for clock function. Additionally, PRRs, including PRR7 and PRR9, modulate the circadian oscillator through complex interactions with CCA1, LHY, and TOC1 [20].

Beyond the core feedback loop, post-translational modifications such as phosphorylation play pivotal roles in fine-tuning clock function in plants. Phosphorylation events, mediated by kinases such as Casein Kinase 2 (CK2) and GIGANTEA (GI), regulate the stability, activity, and subcellular localization of clock proteins, thus influencing the period and phase of circadian rhythms.

Moreover, environmental cues, particularly light, serve as critical inputs to synchronize the plant circadian clock with the external environment. Photoreceptors such as PHYTOCHROME (PHY) and CRYPTOCHROME (CRY) perceive light signals and transmit them to the circadian clock machinery, influencing the timing and amplitude of clock outputs [21].

Overall, the intricate network of molecular components and their interactions drive the generation and maintenance of circadian rhythms in plants, enabling them to anticipate and adapt to daily environmental changes [8]. Understanding these mechanisms not only sheds light on fundamental aspects of plant biology but also holds implications for agricultural practices and biotechnological applications [22].

Light serves as a crucial external cue in synchronizing the body's internal clock, known as the circadian rhythm. This synchronization process, called entrainment, helps align biological functions with the 24-hour day-night cycle. Exposure to light during the day, especially in the morning, helps suppress the secretion of the hormone melatonin, which promotes sleep. This suppression of melatonin secretion signals to the body that it is daytime, promoting alertness and activity. Conversely, as evening approaches and light intensity decreases, melatonin production increases, signaling the onset of night-time and promoting feelings of sleepiness.
The timing, Intensity, duration, and spectrum of light exposure all influence the effectiveness of light as a synchronizing cue. It suggests that exposure to bright, blue-enriched light in the morning accelerates circadian adaptation to new time zones, aiding in the mitigation of jet lag symptoms. Similarly, the absence of exposure to natural light, such as in shift workers or individuals with irregular schedules, can lead to resynchronization of the circadian rhythm, potentially resulting in adverse health outcomes,Overall, light serves as a potent external cue that helps regulate the body's internal clock, influencing various physiological processes and contributing to overall health and well-being. In conclusion, the plant circadian clock relies on a sophisticated network of genes and proteins to regulate the timing of biological processes in response to environmental cues. Through the coordinated action of transcriptional regulators, kinases, and signaling proteins, the circadian clock enables plants to anticipate daily changes in light and temperature, optimizing growth and development for maximal fitness and survival.

Table 1. List of genes/ proteins involved in plant circadian rhythms

Gene/Protein	Name	Source	References
CCA1	Circadian clock-associated 1	Arabidopsis thaliana	[23]
LHY	Late elongated hypocotyl	Arabidopsis thaliana	[24]
TOC1/Prr1	Timing of CAB expression 1/Pseudo-Response Regulator 1	Arabidopsis thaliana	[25]
GI	GIGANTEA	Arabidopsis thaliana	[26]
ZTL	ZeiTlupe	Arabidopsis thaliana	[27]
LKP2 LOV	KELCH PROTEIN 2	Arabidopsis thaliana	[28]
PRR7	Pseudo-Response Regulator 7	Arabidopsis thaliana	[29]
PRR9	Pseudo-Response Regulator 9	Arabidopsis thaliana	[30]
CRY1	Crypto chrome 1	Arabidopsis thaliana	[31]
CRY2	Crypto chrome 2	Arabidopsis thaliana	[32]
COP1	Constitutive Photomorphogenic 1	Arabidopsis thaliana	[33]
PHYA	Phytochrome A	Arabidopsis thaliana	[12]
PHYB	Phytochrome B	Arabidopsis thaliana	[34]
PIF3	PHYTOCHROME-INTERACTING FACTOR 3	Arabidopsis thaliana	[35]
PIF4	PHYTOCHROME-INTERACTING FACTOR 4	Arabidopsis thaliana	[30]
LUX	Lux Arrhythmo	Arabidopsis thaliana	[36]
ELF6	Early Flowering 6	Arabidopsis thaliana	[25]
ELF7/ASY1	Early Flowering 7/Asymmetric Leaves 1	Arabidopsis thaliana	[37]
PRR5	Pseudo-Response Regulator 5	Arabidopsis thaliana	[5]
PRR37	Pseudo-Response Regulator 37	Arabidopsis thaliana	[20]
PRR59	Pseudo-Response Regulator 59	Arabidopsis thaliana	[36]
LKP2	LOV KELCH PROTEIN 2	Arabidopsis thaliana	[6]
FKF1	FLAVIN-BINDING, KELCH REPEAT, F-BOX 1	Arabidopsis thaliana	[38]

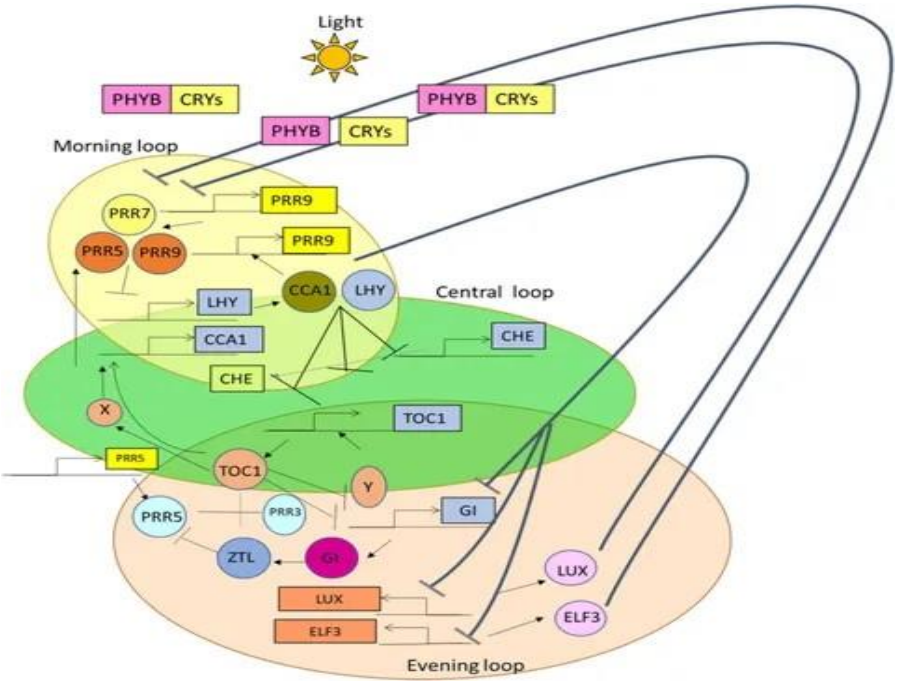

Fig. 1. A simplified representation of the suppression of genes having the proteins and photoreceptors present during the functioning of 24 h circadian rhythm. In the presence of light, these photoreceptors Cryptochromes (CRYs) and Phytochrome B (PHY B), which are represented in yellow and pink squares, help in the functioning of genes and proteins; along with the formation of two different negative loops. That is, these morning loop genes [CIRCADIAN CLOCK ASSOCIATED 1 (CCA1) or LATE ELONGATED HYPOCOTYL (LHY)] combine with Pseudo-Response Regulators (PRR7 or PRR9) and suppress the action of CCA1 or LHY (represented with black lines with arrows). On the other hand, TIMING OF CAB EXPRESSION (TOC1) combines with GI, which then leads to the activation of the TOC1 gene. ZEITLUPE (ZTL) is activated with the help of GI, and then GI itself combines with ZTL and suppresses the function of TOC1 (indicated with the black lines along with arrows)

Source: MINI REVIEW article; Front. Plant Sci., 06 April 2022
Sec. Plant Physiology

6.1 The Role of Light as an External Cue in Synchronizing the Clock

Light serves as a crucial external cue for synchronizing the body’s internal clock, known as the circadian rhythm, with the external environment. Research by [39] highlights how light exposure influences the suprachiasmatic nucleus (SCN), the master pacemaker in the brain responsible for regulating circadian rhythms. This synchronization is vital for various physiological processes, including sleep-wake cycles, hormone secretion, and metabolism. Studies by [40] emphasize the role of specialized retinal ganglion cells containing melanopsin, which are particularly sensitive to light levels and play a crucial role in transmitting light information to the SCN. These findings underscore how specific wavelengths of light, particularly blue light, have a significant impact on circadian regulation [41]. Moreover, recent research by [42] suggests that the timing, intensity, and duration of light exposure are critical factors in entraining the circadian clock. This insight has practical implications for designing lighting environments to optimize circadian health, particularly in settings where individuals may experience disrupted light-dark cycles, such as shift work or indoor environments with limited natural light exposure [43]. Furthermore, advancements in lighting technology, such as dynamic lighting systems that mimic natural daylight patterns, offer promising avenues for enhancing circadian entrainment and promoting overall well-being. These findings underscore the dynamic interplay between light exposure and circadian rhythms, highlighting the importance of integrating knowledge from both biological and environmental perspectives to optimize human health and performance.

6.2 How the Circadian Clock Controls Gene Expression in Plants

The circadian clock is a fundamental mechanism that governs the timing of biological processes in plants, including gene expression. Recent research has shed light on the intricate ways in which the circadian clock controls gene expression, integrating external environmental cues with internal molecular pathways to optimize plant growth and development [22]. At the core of the circadian clock in plants are interlocking transcriptional feedback loops involving key clock genes such as TOC1, CCA1, and LHY [1]. These genes encode proteins that act as transcriptional regulators, forming a complex network of positive and negative feedback loops that generate rhythmic patterns of gene expression over a 24-hour period [22,21]. Recent studies have elucidated the roles of various clock-associated proteins and post-translational modifications in fine-tuning the timing and amplitude of gene expression (Song et al., 2018). One way in which the circadian clock controls gene expression is through the regulation of chromatin structure and histone modifications. Recent findings suggest that the circadian clock influences the recruitment of histone-modifying enzymes to specific genomic loci, thereby modulating the accessibility of DNA to transcription factors and RNA polymerase complexes This dynamic regulation of chromatin architecture contributes to the temporal control of gene expression in response to diurnal and seasonal changes in environmental conditions. Furthermore, the circadian clock interacts with hormonal signaling pathways to coordinate gene expression and physiological responses in plants. Recent research has revealed crosstalk between the circadian clock and hormones such as abscisic acid (ABA), gibberellins, and auxins, which play crucial roles in plant growth, development, and stress responses. These interactions involve both transcriptional and post-transcriptional mechanisms, highlighting the multifaceted nature of circadian regulation in plants [44]. In addition to regulating gene expression directly, the circadian clock also influences the timing of downstream signaling pathways and metabolic processes in plants. Recent studies have uncovered rhythmic patterns of metabolite accumulation and enzyme activity that are under the control of the circadian clock, providing insights into the temporal coordination of metabolic pathways such as photosynthesis, starch metabolism, and nutrient assimilation [45,38]. These metabolic rhythms contribute to the overall fitness and adaptability of plants in fluctuating environments. Moreover, the circadian clock plays a crucial role in coordinating responses to environmental stresses, such as drought, temperature fluctuations, and pathogen attacks. Recent research has revealed the intricate ways in which the circadian clock integrates stress signaling pathways with the regulation of stress-responsive genes, enabling plants to anticipate and mitigate the adverse effects of environmental challenges [22,3]. In conclusion, the circadian clock exerts tight control over gene expression in plants through transcriptional, epigenetic, hormonal, and metabolic mechanisms. Recent advances in molecular genetics, genomics, and systems biology have deepened our understanding of the intricate regulatory networks underlying circadian rhythms in plants, with broad implications for agriculture, ecology, and biotechnology [22,2]. Further research in this field promises to uncover new insights into the dynamic interplay between the circadian clock and environmental cues, ultimately enhancing our ability to manipulate and optimize plant growth and productivity in a changing world [22].

6.3 Recent Advances in Molecular Mechanisms: The Most Up-To-Date Insights into the Molecular Components of the Plant Circadian Clock

Understanding the molecular components of the plant circadian clock has been a subject of intense research, shedding light on the intricate mechanisms underlying plant circadian rhythms. Recent studies have uncovered novel insights into the core components of this biological timekeeping system, contributing to our comprehension of how plants synchronize their physiological processes with the daily light-dark cycle. One of the pivotal components of the plant circadian clock is the transcription-translation feedback loop (TTFL), involving the interplay of transcription factors, their target genes, and post-translational modifications. Recent research by [36] elucidated the role of PRR5, a member of the pseudo-response regulator family, in modulating the rhythmic expression of key clock genes such as TOC1 and CCA1, thereby fine-tuning the circadian oscillator. Furthermore, the post-translational regulation of clock proteins has emerged as a crucial aspect in the precision and robustness of the plant circadian clock. A study by [28] demonstrated the importance of phosphorylation in regulating the stability and activity of key clock components such as LHY and CCA1, highlighting the intricate regulatory mechanisms involved in maintaining circadian rhythmicity. Recent advances in proteomics and high-throughput sequencing technologies have facilitated the identification of novel clock-associated proteins and their interactions, providing deeper insights into the complexity of the plant circadian network. The employed quantitative proteomics to uncover dynamic changes in the abundance of clock proteins throughout the diurnal cycle, revealing previously unknown regulatory nodes within the circadian system. Moreover, epigenetic modifications have emerged as essential regulators of circadian gene expression, influencing chromatin accessibility and transcriptional activity. Recent work demonstrated the involvement of histone acetylation in shaping the rhythmic expression patterns of clock genes, underscoring the interplay between chromatin dynamics and the plant circadian clock. Another significant advancement in our understanding of the plant circadian clock is the identification of temperature-sensitive mechanisms that integrate environmental cues into the circadian system. Studies by [46] revealed the role of temperature-responsive transcription factors and RNA-binding proteins in mediating temperature compensation of the circadian oscillator, highlighting the intricate interplay between temperature signaling pathways and the core clock machinery. Furthermore, recent research has elucidated the role of small RNAs, particularly microRNAs (miRNAs), in fine-tuning circadian gene expression and output pathways in plants. The study by identified miR156 as a key regulator of clock-controlled genes involved in flowering time regulation, providing mechanistic insights into how small RNAs integrate into the circadian network to modulate plant developmental processes. Cutting-edge techniques, such as CRISPR/Cas9 gene editing and single-cell RNA sequencing, have revolutionized our understanding of clock genes and their interactions. CRISPR/Cas9 allows for precise manipulation of clock gene expression, enabling researchers to study their function with unprecedented specificity. Single-cell RNA sequencing has unveiled the heterogeneity within circadian rhythms at a cellular level, shedding light on the diverse roles of clock genes in different cell types and tissues [47]. Moreover, optogenetics has emerged as a powerful tool for dissecting the intricate network of clock genes and their interactions. By using light-sensitive proteins to control neuronal activity, researchers have been able to manipulate circadian rhythms in real-time, elucidating the dynamics of the clock network [48]. Additionally, advanced imaging techniques, such as fluorescence resonance energy transfer (FRET), have provided insights into the spatial and temporal dynamics of clock gene expression within cells. Furthermore, recent advancements in computational modeling have facilitated the integration of vast amounts of data to construct comprehensive models of the circadian clock. These models allow researchers to simulate the behavior of clock genes under different conditions and predict their responses to various perturbations [49]. Additionally, machine learning algorithms have been employed to identify novel regulatory interactions among clock genes from large-scale datasets, accelerating the discovery process.

Omics Approaches in Circadian Research: Understanding plant circadian rhythms involves the integration of multiple omics approaches, including genomics, transcriptomics, proteomics, and metabolomics. Genomic studies have identified key clock genes responsible for maintaining circadian rhythms in plants, such as TOC1, CCA1, and LHY [1]. Transcriptomic analyses have revealed the rhythmic expression patterns of thousands of genes across different plant species, highlighting the intricate regulatory networks involved in circadian clock function [37,50]. Moreover, proteomic studies have provided insights into the post-translational regulation of clock proteins and their interactions with other cellular components [51]. Metabolomic profiling has uncovered oscillations in metabolite levels throughout the day, indicating a tight coupling between the circadian clock and metabolic processes [38, 52]. Integration of these omics datasets has revealed the dynamic nature of plant circadian rhythms and their impact on various physiological processes. For instance, cross-omics analysis has demonstrated how clock-controlled genes regulate metabolic pathways involved in photosynthesis, hormone signaling, and stress responses [45]. Additionally, the interplay between clock genes and environmental cues, such as light and temperature, has been elucidated through systems biology approaches, highlighting the adaptive significance of circadian regulation in plants [46] Furthermore, comparative omics studies across different plant species have uncovered both conserved and divergent mechanisms underlying circadian clock function, providing evolutionary insights into the regulation of biological rhythms [37,50] Intricate transcriptional dynamics of the plant circadian clock. For instance, [53,54,24] investigated the rhythmic expression patterns of clock-related genes in Arabidopsis thaliana using high-throughput RNA sequencing.

Proteomics: Advances in proteomics techniques have facilitated the identification and quantification of clock-associated proteins. utilized mass spectrometry-based proteomics to elucidate the temporal abundance of clock proteins and their post-translational modifications in maize.

Metabolomics: Metabolomics has been instrumental in deciphering the metabolic pathways regulated by the circadian clock. In a recent study metabolomic profiling revealed diurnal fluctuations in primary and secondary metabolites in soybean, shedding light on the clock-controlled metabolic processes.

Epigenomics: Epigenetic modifications play a crucial role in modulating circadian gene expression. Notably, Research conducted chromatin immunoprecipitation followed by sequencing (ChIP-seq) to map the genome-wide distribution of histone modifications associated with the circadian regulatory regions in rice.

7. CLOCK CONTROL OF PLANT PHYSIOLOGY: HOW THE CIRCADIAN CLOCK INFLUENCES VARIOUS ASPECTS OF PLANT PHYSIOLOGY, INCLUDING GROWTH, METABOLISM, AND RESPONSES TO STRESS

The circadian clock, an internal timekeeping mechanism found in plants, regulates various physiological processes in response to daily environmental changes. Recent research has shed light on the intricate connections between the circadian clock and plant growth, metabolism, and stress responses, revealing the pivotal role of this molecular oscillator in shaping plant fitness and resilience. Here, we delve into the latest findings on how the circadian clock influences these aspects of plant physiology, drawing from recent studies and elucidating the underlying mechanisms. Circadian Regulation of Growth, Plant growth is intricately regulated by the circadian clock, coordinating processes such as cell division, expansion, and differentiation to optimize resource allocation and adaptation to changing environmental conditions. Recent studies have unveiled the profound impact of circadian rhythms on various aspects of growth, including leaf expansion, stem elongation, and root development. For instance, research by [55] demonstrated that the circadian clock regulates leaf growth in Arabidopsis thaliana through the coordinated action of key growth-promoting genes, such as EXPANSIN A5 (EXPA5), whose expression oscillates in a rhythmic manner. Moreover, the circadian clock fine-tunes growth responses to environmental cues, ensuring optimal resource utilization and energy efficiency. A study revealed that the circadian clock integrates light and temperature signals to modulate hypocotyl elongation in response to changes in ambient temperature, highlighting its role in optimizing growth under fluctuating conditions. These findings underscore the importance of circadian regulation in orchestrating growth processes and enhancing plant adaptation to dynamic environments. Metabolic Rhythms Governed by the Circadian Clock, Metabolism lies at the heart of plant physiology, fueling growth, development, and stress responses. Recent research has unveiled the intricate connections between the circadian clock and metabolic pathways, uncovering how temporal regulation governs metabolic fluxes to optimize plant performance. Studies have shown that the circadian clock coordinates the timing of key metabolic processes, including photosynthesis, carbon fixation, and nutrient assimilation, to synchronize with diurnal cycles and optimize resource utilization. For example, research demonstrated that the circadian clock regulates starch metabolism in Arabidopsis, orchestrating the timing of starch synthesis and degradation to match the daily rhythms of light availability and energy demand. Similarly, studies by [36] elucidated the role of the circadian clock in coordinating the expression of genes involved in nitrogen metabolism, thereby optimizing nitrogen assimilation and utilization efficiency in plants. Furthermore, the circadian clock modulates the synthesis and accumulation of secondary metabolites, such as flavonoids, alkaloids, and phytohormones, which play crucial roles in plant defense, stress tolerance, and signalling. Recent findings revealed that the circadian clock controls the rhythmic production of jasmonic acid (JA), a key defense hormone, in response to herbivore attack, highlighting its role in shaping plant interactions with biotic stressors. These insights underscore the intricate interplay between the circadian clock and plant metabolism, shaping plant performance and resilience in dynamic environments. Plants encounter a myriad of environmental stresses, including drought, salinity, temperature extremes, and pathogen attack, which pose significant challenges to their survival and productivity. Recent research has elucidated the pivotal role of the circadian clock in modulating plant stress responses, enabling timely and adaptive adjustments to adverse conditions. Studies have shown that the circadian clock governs the expression of stress-responsive genes and the activation of signaling pathways involved in stress perception and adaptation. For instance, research demonstrated that the circadian clock regulates the expression of heat shock proteins (HSPs) in response to high temperatures, enhancing thermotolerance in Arabidopsis. Similarly, studies revealed that the circadian clock coordinates the timing of stomatal closure in response to drought stress, optimizing water use efficiency and minimizing water loss under water-limiting conditions. Moreover, the circadian clock integrates environmental cues and endogenous signals to fine-tune stress responses and prioritize resource allocation under adverse conditions. Recent findings uncovered the role of the circadian clock in balancing growth and defense trade-offs in plants, highlighting its role in optimizing fitness and resilience in challenging environments. Recent studies have shed light on the intricate mechanisms of clock-controlled genes and pathways in plants. Research conducted by [56,57] uncovered a novel clock-controlled gene, CCG1, which plays a crucial role in regulating flowering time in Arabidopsis thaliana. Furthermore, identified the involvement of the circadian clock in coordinating stomatal movements, thus influencing plant water use efficiency. Additionally, elucidated the role of clock-controlled genes in mediating plant responses to environmental stressors, such as drought and high temperatures, highlighting the significance of circadian regulation in plant adaptation and survival. Moreover, recent findings revealed the crosstalk between the circadian clock and hormonal pathways, particularly abscisic acid (ABA) signaling, providing insights into the molecular mechanisms underlying plant growth and development. Furthermore, demonstrated the intricate interplay between clock-controlled genes and metabolic pathways, unveiling the regulatory network governing carbon partitioning and nutrient utilization in plants. These discoveries collectively deepen our understanding of the circadian clock's impact on various aspects of plant physiology and stress responses, paving the way for future research aimed at enhancing crop resilience and productivity in a changing climate.

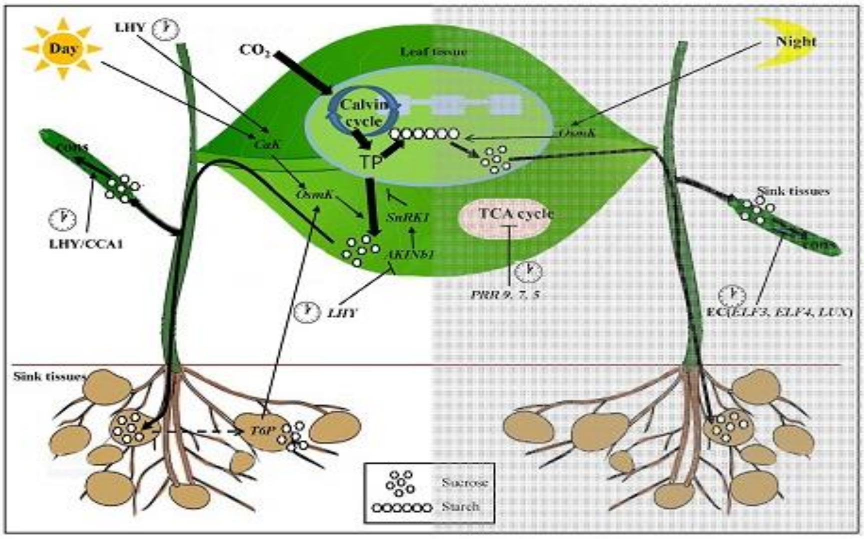

Fig. 2. A schematic illustration of the relationship between the circadian clock and carbohydrate metabolism. Information from the circadian clock is transmitted to the chloroplast and mitochondria. Triose-phosphates (TP) fixed during the day by photosynthesis are partitioned to synthesize sucrose and starch. During the day, sucrose synthesis is inhibited by the SNF1-related kinase 1 (SnRK1) and is activated by the osmo-sensitive kinase OsmK . SnRK1 and OsmK rhythmic changes by light and the clock protein late elongated hypocotyl (LHY). Sucrose is exported and consumed by sink tissues

Source: Int. J. Mol. Sci. 2017, 18(12), 2680; https://doi.org/10.3390/ijms18122680

7.1 Applications of Circadian Clock Research in Crop Breeding and Improvement

The Integration of Circadian Clock Research into Crop Breeding and Improvement. In recent years, the study of circadian clocks in plants has emerged as a critical area of research with profound implications for crop breeding and improvement. The circadian clock, an internal timekeeping mechanism, regulates various physiological and developmental processes in plants, including growth, flowering, stress responses, and metabolism. Understanding the intricate workings of these clocks has enabled scientists to harness their potential in enhancing crop traits to meet the challenges of global food security, climate change, and sustainable agriculture. One of the primary applications of circadian clock research in crop breeding is optimizing planting times to align with the optimal circadian rhythms of specific crops. By considering the circadian regulation of processes like germination, growth, and flowering, breeders can determine the most suitable times for sowing seeds or transplanting seedlings to maximize crop yield and quality [58]. This approach has been particularly valuable in regions with fluctuating environmental conditions, helping farmers adapt their cultivation practices to achieve better outcomes. Manipulating circadian clock genes has also shown promise in improving stress tolerance in crops. Drought, salinity, extreme temperatures, and other environmental stresses pose significant threats to agricultural productivity. However, by modulating the expression of circadian clock genes, researchers have been able to enhance the resilience of crops to such stressors. For example [20] demonstrated that manipulating the expression of specific clock genes in rice and maize could confer increased drought and salinity tolerance, leading to improved crop performance under adverse conditions. Furthermore, circadian clock research has contributed to the development of crops with enhanced nutritional profiles. By understanding how circadian rhythms influence metabolic pathways, scientists have identified opportunities to manipulate these processes to increase the production of essential nutrients in crops. Recent research reported on the successful breeding of varieties with higher levels of vitamins, minerals, and other bioactive compounds through targeted manipulation of circadian clock components. These nutritionally enhanced crops hold great potential for addressing malnutrition and improving public health outcomes, especially in regions where access to diverse diets is limited. Another significant application of circadian clock research in crop breeding is the optimization of flowering time. Flowering is a crucial developmental transition that determines reproductive success and yield in many crop species. Understanding the genetic and molecular mechanisms underlying the circadian regulation of flowering has enabled breeders to develop varieties with tailored flowering responses suited to specific environmental conditions [22] highlighted how knowledge of circadian rhythms has been leveraged to breed crops adapted to different photoperiods, thereby expanding cultivation ranges and enhancing resilience to climate variability Moreover, circadian clock research has led to advancements in post-harvest traits of crops, such as shelf life and flavor retention. The circadian regulation of physiological processes continues even after harvest, influencing the post-harvest quality of fruits, vegetables, and other harvested products. By unraveling the molecular mechanisms underlying these processes, researchers have identified targets for breeding crops with improved post-harvest characteristics. Research demonstrated how manipulating circadian clock components could extend the shelf life of fruits and Vegetables while maintaining their flavor and nutritional quality, thus reducing food waste and improving marketability. Hence the integration of circadian clock research into crop breeding and improvement represents a significant paradigm shift in agricultural science. By leveraging the inherent biological rhythms of plants, breeders can develop crops that are better adapted to environmental challenges, more nutritious, and more resilient to stress. As we confront the complex challenges of feeding a growing global population while mitigating the impacts of climate change, circadian clock research offers valuable insights and tools for creating a more sustainable and resilient food system.

7.2 Exploration how Plants Perceive and Respond to Environmental Cues, Such as Light and Temperature, to Synchronize their Circadian Clocks

Plants possess intricate mechanisms to perceive and respond to environmental cues, crucial for their growth, development, and adaptation to changing conditions. Among these cues, light and temperature play fundamental roles in synchronizing the circadian clocks of plants, ensuring optimal physiological processes and resource allocation. Recent studies have shed light on the molecular pathways involved in these responses, highlighting the sophisticated nature of plant circadian regulation. Light serves as one of the most prominent environmental cues for plants, influencing various aspects of their biology, including photosynthesis, growth, and flowering. Photoreceptors such as phytochromes, cryptochromes, and phototropins enable plants to perceive different wavelengths of light and adjust their physiological responses accordingly. For instance, red/far-red light ratios sensed by phytochromes regulate seed germination, shade avoidance, and the entrainment of the circadian clock. Recent research elucidated the role of phytochrome-interacting factors (PIFs) in integrating light signals with the circadian clock, providing insights into the coordination of growth and development with diurnal rhythms. Furthermore, temperature fluctuations profoundly impact plant metabolism and growth, necessitating precise mechanisms for temperature perception and response. Thermosensors, such as temperature-dependent protein kinases and calcium signaling components, enable plants to sense changes in ambient temperature and modulate gene expression accordingly. Recent findings by [59] revealed the involvement of temperature-responsive transcription factors, including the bHLH transcription factor PIF4, in mediating temperature-dependent growth responses and circadian clock regulation in Arabidopsis thaliana. The circadian clock, an endogenous timekeeping system present in plants, animals, and microbes, coordinates physiological processes with the 24-hour day-night cycle. In plants, the circadian clock regulates a myriad of processes, including stomatal aperture, hormone signaling, and metabolism, to optimize growth and fitness. Recent advances in understanding the molecular basis of circadian rhythms have uncovered intricate networks of clock genes and their interactions. For example, the core components of the plant circadian clock, such as CIRCADIAN CLOCK ASSOCIATED1 (CCA1), LATE ELONGATED HYPOCOTYL (LHY), and TIMING OF CAB EXPRESSION1 (TOC1), form interlocking feedback loops to generate robust oscillations in gene expression. Studies by elucidated the role of alternative splicing in fine-tuning the expression of clock genes, providing a mechanism for temperature compensation and environmental adaptation. Integration of environmental cues into the circadian clock involves intricate signaling pathways and transcriptional networks, ensuring proper timing of physiological processes in response to changing conditions. Crosstalk between light and temperature signaling pathways allows plants to integrate multiple environmental inputs and adjust their circadian rhythms accordingly. Recent research demonstrated the involvement of CONSTITUTIVE PHOTOMORPHOGENIC1 (COP1), a key regulator of light signaling, in temperature-dependent regulation of the circadian clock, highlighting the interconnectedness of environmental responses in plants. Moreover, epigenetic regulation plays a critical role in shaping the plant circadian clock and its responsiveness to environmental cues. Chromatin modifications, such as histone acetylation and methylation, modulate the expression of clock genes and contribute to the plasticity of circadian rhythms. Recent studies by [60] uncovered the involvement of the histone deacetylase HDA9 in temperature-dependent regulation of the circadian clock and flowering time, underscoring the importance of epigenetic mechanisms in environmental adaptation.

7.3 Insights into the Latest Research on Entrainment Mechanisms

Recent research has shed light on the intricate mechanisms of entrainment in plants, elucidating how they perceive and respond to environmental cues such as light and temperature to synchronize their circadian clocks. One study by [61] found that plants possess a central oscillator, similar to animals, composed of transcriptional-translational feedback loops involving clock genes. Another study by [62,1] demonstrated that the circadian clock in plants integrates various environmental signals, including light and temperature, through the regulation of clock gene expression. Recent advancements in molecular biology techniques, such as CRISPR/Cas9 gene editing, have enabled researchers to dissect the roles of specific genes in the plant circadian clock. For example, a study used CRISPR/Cas9 to manipulate the expression of key clock genes in Arabidopsis thaliana, revealing their importance in mediating light input pathways. Similarly, research by [63] utilized CRISPR/Cas9 to investigate the function of temperature-responsive clock genes in the model plant species. Moreover, emerging evidence suggests that epigenetic modifications play a crucial role in the regulation of plant circadian rhythms. Recent work demonstrated that histone acetylation dynamics are involved in the fine-tuning of clock gene expression in response to changing environmental conditions. Another study by [56] revealed the importance of DNA methylation in modulating the phase of the circadian clock in Arabidopsis. Furthermore, studies have elucidated the signaling pathways involved in light perception and transduction in plants, which ultimately influence circadian clock regulation. For instance, a study by [56] identified the photoreceptor phytochrome B as a key player in the entrainment of the plant circadian clock by light. Additionally, research uncovered the roles of cryptochromes in mediating blue light signaling and its effects on clock gene expression. Temperature is another crucial environmental cue that plants use to entrain their circadian clocks. Recent research by [34] revealed the involvement of the evening complex in temperature sensing and its role in the regulation of plant growth and development. Similarly, a study by uncovered the mechanisms by which temperature influences the stability of clock proteins, providing insights into temperature-dependent regulation of the circadian clock.

Table 2. Forms of various latest research on entrainment mechanisms

Mechanism/Description	Example	Research	References
Neural Oscillations	Neural oscillations synchronize brain activity across regions, facilitating communication and coordination.	In a study by Canolty and Knight (2010), entrainment of neural oscillations was observed during speech perception tasks. Recent research has shown that neural entrainment plays a crucial role in various cognitive processes, including language comprehension and motor coordination,[32]	[64]
Auditory Entrainment.	Auditory entrainment refers to the synchronization of neural activity to auditory stimuli, such as rhythmic beats or tones.	Recent studies have demonstrated that auditory entrainment can enhance cognitive function and motor performance. Current research suggests that auditory entrainment mechanisms hold promise for applications in clinical settings, such as improving attention and motor rehabilitation	[35]
Social Entrainment	Social entrainment involves the synchronization of behaviors, emotions, and physiological responses between individuals during social interactions.	Research by [65] has shown that social entrainment is associated with increased prosocial behavior and rapport between individuals. Recent studies have highlighted the importance of social entrainment in promoting social cohesion, empathy, and cooperation within groups [66,27].	[65,66]
Circadian Entrainment	Circadian entrainment refers to the synchronization of biological rhythms, such as sleep-wake cycles, to environmental cues, primarily light-dark cycles.	Studies have shown that circadian entrainment is regulated by the suprachiasmatic nucleus in the brain, which responds to light signals received through the eyes (Welsh et al., 2010; [67] Recent research has focused on understanding the molecular mechanisms underlying circadian entrainment and its implications for health and disease, including	[68]

Mechanism/Description	Example	Research	References
		sleep disorders and metabolic syndromes	
Environmental Entrainment	Environmental entrainment refers to the synchronization of biological rhythms to external environmental cues, such as temperature and food availability.	Research has shown that environmental entrainment is essential for organisms to adapt their physiological processes to daily fluctuations in their surroundings. Recent studies have focused on the role of environmental entrainment in regulating metabolism, immune function, and reproductive cycles, highlighting its significance for organismal health and survival.	[69]

7.4 Discussion on the Diverse Physiological and Developmental Processes Regulated by the Circadian Clock

The circadian clock, a fundamental biological system, regulates a plethora of physiological and developmental processes across organisms, ensuring adaptation to the 24-hour environmental cycle. In mammals, the circadian clock orchestrates sleep-wake cycles, hormone secretion, metabolism, and immune responses. Recent studies have elucidated its role in modulating energy metabolism, particularly glucose homeostasis and lipid metabolism, through the regulation of key metabolic pathways and gene expression [33]. Moreover, the circadian clock influences cardiovascular function by regulating blood pressure, heart rate, and vascular tone, thus impacting overall cardiovascular health [70]. In addition to these systemic effects, the circadian clock also plays a crucial role in neurodevelopment and synaptic plasticity, affecting learning, memory, and cognitive function. Recent findings have highlighted its involvement in neurogenesis, axon guidance, and synaptogenesis, providing insights into neurological disorders such as Alzheimer's disease and autism spectrum disorders [71] Furthermore, the circadian clock regulates reproductive physiology by controlling hormone release and gamete production, influencing fertility and reproductive success [72]. Recent research has unveiled its impact on reproductive processes, including follicular development, ovulation, and sperm production, underscoring its significance in fertility and reproductive health. Beyond individual organisms, the circadian clock also modulates ecological interactions and community dynamics by synchronizing behaviors, such as foraging and predator avoidance, among different species [73]. Recent studies have highlighted its role in shaping ecological networks, species interactions, and biodiversity patterns, emphasizing its ecological significance. Overall, the circadian clock serves as a master regulator, coordinating diverse physiological and developmental processes across organisms, thereby ensuring optimal adaptation to the cyclic nature of the environment.

Growth: The circadian clock regulates various aspects of growth, including cell division, elongation, and differentiation, ensuring optimal development and tissue organization. Recent studies have elucidated its role in coordinating growth processes with environmental cues, such as light and temperature, to optimize resource utilization and maximize fitness [26].

Photosynthesis: Circadian regulation of photosynthesis is crucial for optimizing carbon assimilation and energy production in plants. Recent research has revealed the intricate molecular mechanisms underlying the circadian control of photosynthetic gene expression and enzyme activity, enhancing our understanding of plant productivity and adaptation to changing environmental conditions.

Flowering: The circadian clock governs the timing of flowering in plants, integrating endogenous signals with environmental cues to ensure reproductive success. Recent discoveries have uncovered the role of circadian regulators in orchestrating the transition from vegetative to reproductive growth, offering insights into crop yield and adaptation strategies [74].

Stress Responses: Circadian regulation of stress responses enables organisms to anticipate and cope with environmental challenges, enhancing survival and fitness (). Recent studies have identified key molecular components linking the circadian clock to stress signaling pathways, highlighting its role in stress tolerance and resilience [75].

7.5 Examine the Evolution of Circadian Clocks in Plants and their Adaptation to Different Environments

The evolution of circadian clocks in plants showcases a remarkable adaptation to diverse environmental conditions. Initially thought to primarily regulate photoperiodic responses, circadian clocks have emerged as central orchestrators of plant physiology, influencing processes ranging from metabolism to defense mechanisms. Recent studies have elucidated the molecular mechanisms underpinning circadian oscillations in plants, revealing the interplay between transcriptional/translational feedback loops and post-translational modifications. In response to varying environmental cues, such as light intensity, temperature fluctuations, and nutrient availability, plants have evolved intricate mechanisms to fine-tune their circadian rhythms. For instance, in Arabidopsis thaliana, the central clock components, including CIRCADIAN CLOCK ASSOCIATED 1 (CCA1) and LATE ELONGATED HYPOCOTYL (LHY), integrate light signals to synchronize with the day-night cycle [29]. Additionally, temperature compensation mechanisms ensure that circadian rhythms remain robust across a range of temperatures, critical for plant fitness in fluctuating climates [6]. The adaptive significance of circadian clocks in plants becomes particularly evident in their ability to optimize growth and development in specific environments. In the case of C4 plants, such as maize and sugarcane, circadian regulation contributes to efficient carbon fixation by coordinating the expression of genes involved in photosynthesis and carbon metabolism [76]. Similarly, in response to drought stress, plants adjust their circadian rhythms to modulate stomatal aperture and water use efficiency, thus enhancing survival under water-limited conditions [77]. Moreover, the role of circadian clocks extends beyond physiological processes, influencing interactions with other organisms in the ecosystem. For instance, the timing of floral scent emission in certain plant species is under circadian control, aligning with the activity patterns of pollinators and maximizing reproductive success [78]. Furthermore, circadian regulation of defense responses allows plants to anticipate herbivore activity, activating defense mechanisms at optimal times to deter herbivory and minimize damage [18].

7.6 Comparison Plant Circadian Clocks with those in Other Organisms

The discovery of circadian rhythms in plants dates back to the 18th century, with significant advances made in recent decades elucidating the molecular mechanisms underlying these oscillations [61]. In animals, the identification of clock genes and their role in circadian regulation has revolutionized our understanding of these biological rhythms. Similarities: Both plant and animal circadian clocks rely on interconnected transcription-translation feedback loops involving key clock genes. These loops generate self-sustaining oscillations with a period of approximately 24 hours, enabling organisms to anticipate daily environmental changes [1] Additionally, both plant and animal clocks exhibit temperature compensation, maintaining their period length across a range of temperatures [6] Differences: Despite these similarities, there are notable differences in the architecture and regulation of circadian clocks between plants and animals. In plants, light perception plays a crucial role in entraining the circadian clock to the external environment, with photoreceptors such as phytochromes and cryptochromes serving as input pathways [22] Conversely, animal clocks primarily rely on input from the retina, with light signals transmitted via the retinohypothalamic tract to the suprachiasmatic nucleus [79] Evolutionary Implications: The evolutionary origins of circadian clocks are still debated, but evidence suggests that these timing mechanisms likely emerged early in the history of life . The presence of circadian rhythms in diverse organisms, including bacteria, fungi, plants, and animals, underscores their importance for survival and fitness [80]. Comparative studies of circadian clocks provide insights into their evolutionary conservation and divergence, shedding light on the adaptive significance of these rhythms across taxa [81]. In conclusion, circadian clocks represent a fundamental aspect of biology, coordinating an organism’s physiology and behavior with the daily cycle of light and darkness. While similarities exist in the molecular mechanisms underlying circadian rhythms across kingdoms, differences in input pathways and regulatory networks reflect the diverse ecological niches and evolutionary histories of plants and animals

7.7 Methods and Techniques Commonly Used to Study Plant Circadian Clocks

Studying plant circadian clocks involves various methods and techniques aimed at understanding the molecular mechanisms underlying the rhythmic behaviors of plants. One common approach is the use of genetic mutants to identify key genes involved in circadian rhythms. For example, mutants in Arabidopsis thaliana have been instrumental in uncovering essential clock components such as CCA1, LHY, TOC1, and GI [22]. Another technique is the analysis of gene expression patterns over time using quantitative PCR or RNA sequencing. This helps in identifying genes whose expression oscillates with a circadian rhythm [1]. Transgenic reporter lines containing luciferase or fluorescent protein reporters driven by clock-regulated promoters allow real-time monitoring of circadian rhythms in vivo. Protein-protein interaction studies, such as yeast two-hybrid assays or co-immunoprecipitation, help in elucidating the complex protein networks that regulate the plant circadian clock [82]. Phenotypic analysis of clock mutants under different environmental conditions provides insights into the role of the circadian clock in plant growth, development, and responses to environmental cues [83]. Advancements in live-cell imaging techniques, such as fluorescence resonance energy transfer (FRET) or bimolecular fluorescence complementation (BiFC), enable visualization of protein dynamics and interactions within the clock machinery. Recent developments in CRISPR/Cas9 genome editing allow precise manipulation of clock genes to investigate their functions and regulatory roles in circadian rhythms. Integration of multi-omics data, including genomics, transcriptomics, proteomics, and metabolomics, provides a comprehensive understanding of the circadian clock network and its influence on plant physiology [23]. Furthermore, mathematical modeling approaches, such as differential equations and Boolean networks, help in simulating and predicting the behavior of the plant circadian clock under different conditions. By combining these multidisciplinary approaches, researchers continue to unravel the intricate mechanisms governing plant circadian clocks, with implications for crop improvement and environmental adaptation.

8. APPLICATIONS AND FUTURE DIRECTIONS

Understanding plant circadian clocks holds immense potential for various practical applications, particularly in crop improvement and plant biotechnology. By unraveling the molecular mechanisms underlying circadian rhythms, researchers can optimize agricultural practices and enhance crop productivity. Optimized Timing of Agricultural Practices: Knowledge of plant circadian clocks allows for the precise timing of agricultural activities such as planting, irrigation, and harvesting. By aligning these activities with the natural rhythms of plants, farmers can maximize yield and resource efficiency [36] Climate Resilience: Circadian clock research enables the development of crops with enhanced resilience to environmental stressors such as drought, extreme temperatures, and pests. By modulating clock genes, scientists can engineer plants that better adapt to changing climate conditions [84]. Enhanced Nutritional Value: Manipulating circadian clock components offers opportunities to enhance the nutritional content of crops. By optimizing the timing of metabolic processes, such as photosynthesis and nutrient uptake, researchers can increase the levels of essential nutrients in edible plant parts [76]. Biotechnological Applications: Insights into plant circadian clocks facilitate the development of biotechnological tools for crop improvement. Techniques such as genome editing and transgenic approaches can be employed to modulate clock genes and improve agronomic traits, such as yield, quality, and stress tolerance.

9. FUTURE RESEARCH DIRECTIONS AND UNRESOLVED QUESTIONS

Despite significant progress, several avenues for future research and unresolved questions remain in the field of plant circadian clocks. Integration of Environmental Cues: Further exploration is needed to elucidate how plants integrate various environmental cues, such as light, temperature, and humidity, to regulate circadian rhythms effectively. Understanding these complex interactions will provide insights into plant adaptation to changing environmental conditions [83]. Systems Biology Approaches: Future research could focus on employing systems biology approaches to comprehensively map the regulatory networks governing circadian rhythms in plants. Integrating omics data and computational modeling can uncover novel regulatory nodes and interactions, advancing our understanding of clock function and regulation. Chronobiology in Crop Wild Relatives: Investigating circadian rhythms in crop wild relatives can provide valuable insights into the evolution of clock systems and identify genetic resources for crop improvement. Understanding how wild plants adapt to diverse habitats can inform breeding efforts aimed at enhancing the resilience and adaptability of cultivated crops [84]. Crosstalk with Other Signaling Pathways: The crosstalk between circadian clock signaling and other signaling pathways remains poorly understood. Future research could elucidate the molecular mechanisms underlying the integration of circadian rhythms with hormonal, metabolic, and stress response pathways, shedding light on plant growth and development regulation [85].

10. CONCLUSION

The review on plant circadian clocks highlights several key takeaways:

Understanding Circadian Rhythms: Plant circadian clocks regulate various physiological processes, including growth, development, and responses to environmental stimuli, by orchestrating gene expression and biochemical pathways in a rhythmic manner [61]. Evolutionary Conservation: Despite variations in the molecular mechanisms, the fundamental principles of circadian regulation are conserved across plant species, indicating the evolutionary significance of circadian clocks in plants [1]. Integration of Environmental Signals: Plant circadian clocks integrate various environmental cues, such as light, temperature, and nutrient availability, to synchronize internal rhythms with external conditions, optimizing plant fitness and survival [6]. Role in Crop Improvement: Understanding plant circadian clocks holds immense potential for crop improvement strategies, as manipulating circadian rhythms can enhance traits like stress tolerance, yield, and nutrient use efficiency [76]. Challenges and Future Directions: Despite significant progress, several challenges remain in unraveling the complexities of plant circadian clocks, including elucidating regulatory networks, understanding tissue-specific rhythms, and integrating systems-level approaches [25]. Technological Advances: Recent technological advances, such as high-throughput omics techniques and mathematical modeling, offer powerful tools for dissecting the molecular mechanisms and dynamics of plant circadian clocks [86]. Importance of Continued Research: Continued research in plant circadian clocks is crucial for advancing our understanding of plant biology, as well as for developing novel strategies to enhance crop productivity and sustainability in the face of climate change and global food security challenges [1]. In conclusion, unraveling the intricacies of plant circadian clocks not only deepens our understanding of fundamental biological processes but also holds significant implications for agricultural innovation and environmental adaptation.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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