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Tuning the output of the higher plants Circadian Clock

Aditi Chaudhary, Manikantan Pappuswamy*, Amie Chakma, Ramyashree C S, Kruthika P, Kruttika Subash Jan, Medini K Deshpande, Carol C Morris & Joseph Kadanthottu Sebastian

Department of Life Sciences, Christ (Deemed to be University), Bangalore-560029, India

***Email:** manikantan.p@christuniversity.in

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Abstract

The circadian clock is an ascribed regulator found in the cells of creatures, that keeps biological and behavioral processes in sync with daily environmental changes throughout the 24-hour cycles. When the circadian clock in humans malfunctions or is misaligned with environmental signals, the timing of the sleep-wake cycle is altered and several circadian rhythm sleep disorders result. Due to the Earth's rotation on its axis, predictable environmental changes are anticipated by complex processes. The combined term for these systems is the circadian clock. The circadian rhythm regulates photosynthesis and photoperiodism, making it the "primary controller of plant life." The circadian clock is made up of post-translational alterations to core oscillators, epigenetic tweaks to DNA and histones, and auto regulatory feedback loops in transcription. In addition, the circadian clock is cell-autonomous and regulates the circadian rhythms of distinct organs. Biochemical elements such as photosynthetic products, mineral nutrients, calcium ions, and hormones are used by the core oscillators to communicate with one another. *Arabidopsis* is utilized to identify clock-related genes that govern plant growth, germination, pollination, flowering, abiotic and biotic stress responses, and more. The biological cycles of all species, notably humans, are undoubtedly impacted by other elements, including high altitude and changing ecosystems, in addition to the ones already stated. Although it hasn't yet published any experimental or scientific evidence to support them, the implication that living things have lives does appear inescapable. Hence, the present study elaborates on the higher plants related to the circadian clock.

Keywords

Arabidopsis, circadian clock, molecular mechanism, plant rhythm

Introduction

The control of the circadian rhythm is essential for maintaining people's health in a world where lifestyle choices, environmental influences (such as light, night and day lengths, and seasons), and cosmic events relating to the cosmos and earth all play a part (1). Changes in these elements cause the circadian rhythm to be disrupted, which increases the prevalence of physical conditions like cancer, cardiovascular disease, and diabetes as well as mental illnesses like depression. Temperature, light, humidity, nutrition, tides, gravity, and the Earth's magnetism cycle along with the rotation of the Earth around the Sun and the orbit of the Moon around the Earth. The circadian clock is one example of an adaptation that has helped species thrive: the development of an internal clock (2). According to the work of geneticists Erwin Bünning and Kurt Stern, the 24-hour leaf movement of bean plants is regulated by a hereditary circadian clock (3). Ronald

Konopka and Seymour Benzer uncovered the first mutant period in Drosophila fifty years ago, connecting the circadian clock to the regulation of genes (4). Since then, researchers have comprehended the circadian clock's molecular regulatory mechanism (5).

Chronobiology, the study of time in living beings, focuses on circadian rhythms, that are endogenous and adapted to the local environment through signals known as Zeitgebers ZT (German for "time giver") (6). The circadian clock facets represent the underpinning loop of this biological clock, which governs the bulk of metabolic and physiological processes in all 24-hour creatures, including humans (7). Sleep-wake cycles in mammals and plant development and photosynthesis are only two examples of the numerous behavioral, physiological, and metabolic activities that are orchestrated by circadian rhythms (8). Based on the cyclical expression of 'clock' gene products, it is contended that transcriptional-translational feedback loops are responsible for daily timekeeping by controlling the expression of related genes in about 24-hour cycles (9). There is variation in the transcriptional components of various phyla (10).

The capacity of a plant's circadian clock to maintain time for roughly 24 hours is one of its distinguishing characteristics, known as the "circadian period" (11). This means that plants can anticipate and respond to daily changes in their environment, such as the rising and setting of the sun (12). Understanding the molecular and biochemical mechanisms that regulate the circadian clock in plants has important implications for plant biology and agriculture, as it could help us to understand better and manipulate the growth and development of crops (12). The circadian rhythm is sometimes alluded to as the "chief regulator of plant life" because it governs essential activities like photosynthesis and photoperiodism (2). *Arabidopsis* is a model plant that has been used to uncover clock-related genes that govern plant growth regulation, germination, pollination, flowering, responses to both abiotic and biotic stress, and more (13). This review will look at current advancements in the field of clock study as well as our predictions for the future, starting with the basics and briefings on the plant's rhythmic biology.

Circuitry of the Circadian Clock in *Arabidopsis*

Plants, like animals, have a natural internal biological clock that regulates their development and growth, as well as their responses to the environment. This internal clock, also known as a "circadian clock," helps plants envision and organize for daily and seasonal changes in their environment (3). Plants have a multitude of molecular and biochemical pathways that regulate their circadian clock, including the expression of certain genes and the production of specific proteins (14). These pathways are impressed by a variety of environmental cues, such as light (15), temperature (16), and humidity (17), which help to keep the plant's internal clock in sync with the external environment (18). The molecular pathways that regulate circadian rhythms in *Arabidopsis thaliana* (a model plant often used in genetic and molecular biology research) are similar to those in humans (19). At the core of the molecular machinery that drives circadian rhythms in *Arabidopsis* is a group of proteins known as "clock genes," which include CCA1, LHY, and TOC1 among others. These proteins work together to form a negative feedback loop that drives the expression of clock genes in a rhythmic manner (20).

The CCA1 and LHY proteins activate the transcription of clock genes, including the TOC1 gene, which encodes for the TOC1 protein (15). The cell's TOC1 protein swells up and hampers the function of LHY and CCA1, leading to a decrease in the interpretation of clock genes. As the amount of TOC1 protein goes down, the activity of LHY and CCA1 goes back up, and the cycle starts all over again (21) (Fig. 1).

Other signaling pathways, such as those involving hormones and external indicators like luminance and temperature, which can affect the expression and stability of clock genes and proteins, further regulate this negative feedback loop (20). Abnormalities in the molecular pathways that regulate circadian rhythms in plants can influence a broad spectrum of physiologic processes, such as development, growth, and reaction times to the environment.

Circadian Rhythms in Plants

A plant's circadian clock is an imperative biological timepiece that helps the plant uphold regular growth, fitness, and healthy development. The three main modules that make up the endogenous oscillator (22) are the "canonical clock gene" and other parts that make up the central oscillator, the "input pathway," which gives information about the environment, and the "output pathway," which is made up of clock-driven processes that happen after the clock (22). Complex Transcription-Translation Feedback Loops (TTFLs) are incorporated into the central oscillator when they are combined with post-transcriptional alterations and post-translational modifications (23). The circadian rhythm has been extensively studied in the exemplary plant *Arabidopsis*, notably in rice and potato crops, and may be used to regulate their metabolic processes (19). The circadian clock has a mechanism that is independent of

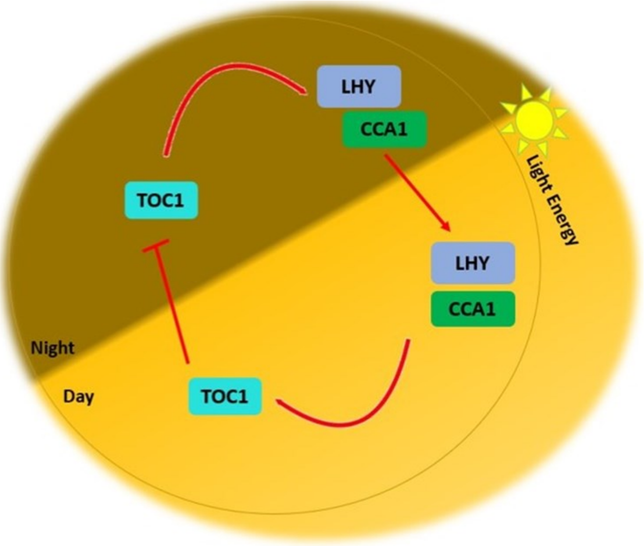

Fig. 1. Basic circuitry of -the circadian clock in plants.

itself, and this has also been researched in the past.

The circadian rhythm is an approximately 24-hour oscillation that is induced by both biotic (24) and abiotic factors such as light, temperature and humidity (15-17). It follows a cycle of light and darkness (6). One study showed that the exemplar organism *Arabidopsis thaliana* comprises three feedback loops that emanate from the central oscillator. These loops are referred to as the morning loop, the center loop, and the evening loop, respectively. The central loop contains the MYB-related transcription factors that are encoded by the genes Circadian Clock Associated 1 (CCA1) and Late Elongated Hypocotyl (LHY). These genes are regarded as manifesting themselves in the morning (20). CCA1 is involved in adjusting clock-dependent and clock-independent responses (25). TOC1, also known as Timing of Cab Expression, is a gene that is expressed in the evening and comes from the central loop. It belongs to the family of Pseudo-Response Regulators (PRR) (26). As a result, the morning and evening loops, as well as these core loops, contribute to the fundamental formation of circadian rhythms in plants (Fig. 2).

Studies have shown that the LHY or CCA1 gene starts a cycle of negative feedback in the morning by working with PRR9 or PRR7 to stop the production of CCA1 and LHY (27). In the same way, the TOC1 gene and Gigantea (GI) create a negative feedback loop in the evening loop. In this loop, TOC1 stops an unknown Y factor from working, which makes more TOC1 molecules. Gigantea causes the Zeitlupe (ZLT) protein to be made, which then works with GI to break down the TOC1 protein (Fig. 3). LUX Arrhythmo (LUX) is another gene implicated in negative feedback loops; it interacts with Early Flowering (ELF) proteins such as ELF4 and ELF3 (29). These proteins constitute the evening complex (EC). The Reveille (RVE) genes, the Light-Regulated WD (LWD) 1 and 2 and the Night Light-Inducible and Clock-Regulated (LNK) genes (transcriptional coactivators) genes have been discovered as positive regulators in the circadian oscillator's feedback loops (30).

The overexpression of the transcription factors BBX19, 18, and 32 (B-Box) in the model plant *A. thaliana* significantly lengthens the circadian cycle (31); BBX18 increases the pace of the biological cycle and overexpression of BBX32 results in delayed flower induction (31). Due to circadian gating, a plant's response is time-dependent on the day of the week rather than the hour of the day (22). The management of the circadian clock is intricately tied to temperature responses. Cold adaptation is regulated by proteins such as C-Repeat/DRE Binding Factor (CBF) (32). Entraining signals, detected by photoreceptors such as Cryptochromes and Phytochrome B (PHY B), reveal to increase the input route's temperature and negative loop components to synchronize the circadian oscillator's phase and waveform (33). The output pathway regulates several tasks, including reproduction (22), hormone synthesis (34), immunological responses (35), and genome expression level (35). Many physiological processes, including stress acclimatization (36), hormone signaling (34), morphogenesis (37), carbon metabolism, and defensive reactions (38), as well as phenotypic, genomic, and metabolic studies (39), include interaction with this circadian clock. A biological clock that is determined by the rhythms of the day and night. Plant circadian direction is a critical system for environmental adaptability (32). A major understanding of the molecular processes governing circadian rhythm in plants comes from experiments conducted in laboratories. Nonetheless, it has now become obvious that in both wild and farmed plant populations, the circadian clock coordinates transcriptomes in complex ways under natural conditions.

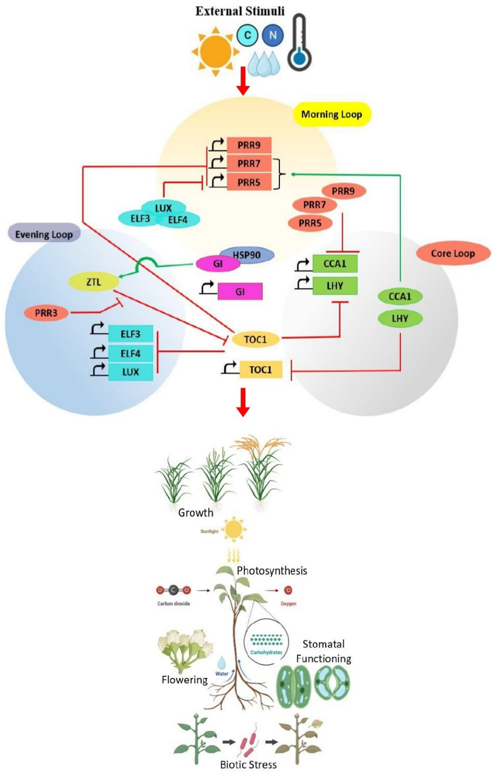

Fig. 2. Diagrammatic representation of looped molecular circadian clock in plants

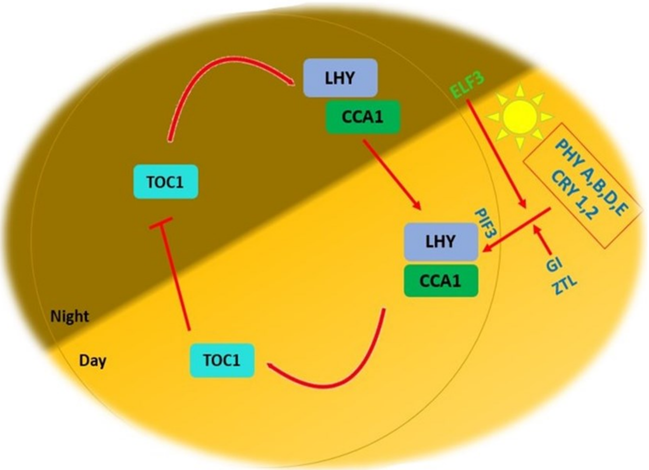

Fig. 3. Modified circuitry of the circadian clock in plants.

Importance of Circadian Rhythms in Plants

Systems plant physiology has a profound impact on the circadian clock and provides an important screening advantage (29). A non-rhythmic circadian clock (CCA1-ox) in *Arabidopsis* results in plants with 53% less biomass than their wild-type counterparts. When compared to 24-hour days, wild-type plants produce considerably less biomass when cultivated under 20- or 28-hour days, suggesting that the internal oscillator's frequency ought to be similar to that of its natural setting for optimum development (40). As a result, the success of a plant depends on the accuracy of its circadian clock.

The circadian schedule influences a variety of aspects of plant existence. According to transcriptome analysis, the 24-hour cycle is responsible for controlling a sizable portion of the genetic makeup of Arabidopsis (41). In steady-state conditions, cyclical expression has been seen in anywhere from one-tenth to one-third of the transcriptome, depending on the approach employed. Many species, including rice (*Oryza sativa*) (42), soybean (*Glycine max*) (43), sugarcane (*Saccharum officinarum*) (44), tomato (*Solanum lycopersicum*) (45) and popular (*Populus trichocarpa*) (46), exhibit circadian patterns in transcript abundance. As it controls multiple genes involved in metabolism, the clock plays a pivotal role in plant biochemistry regulation (20). In plants cultivated under sustained light, the circadian clock modulates leaf gas exchange (47) by causing stomata to open more during the instinctive day than the instinctive night (29). The circadian oscillator regulates not just metabolism but also growth and development (19). The hypocotyls of *Arabidopsis* seedlings grow and the cotyledons move in predictable patterns, as shown in time-lapse videos taken of seedlings growing under constant light (48). Although it is unclear whether or not the clock regulates cell division in higher plants, circadian regulation of water and carbon availability does participate in the periodicity of growth (18).

The oscillator uses several processes to control growth in response to gibberellin and auxin (49). Circadian clock mutants typically blossom later or earlier than wild-type plants when cultivated under extended daylight, suggesting that the circadian clock regulates more than just the timing of daily light and dark cycles (50). The circadian cycle influences many biological processes in plants and is essential for plants to function properly (51) (Fig. 4.). As a result of the evolutionary advantage afforded by the circadian clock, circadian oscillators have independently evolved several times in various kingdoms of life (52). It is feasible to demonstrate this advantage in plants by utilizing the model plant *Arabidopsis* in competitive experiments. When grown under 20-hour-long days, plants with a brief circadian period (toc1) (53) accumulate more biomass than plants with a long circadian period (ztl-1), 10-hour evenings and days. Under 28-hour days, mutant plants with a protracted circadian period (14 h LD) flourish (54). This comparison of mortality rates supports the idea that the circadian oscillator whose dynamics are in tune with those of the external environment confers a substantial fitness advantage (55). An in-depth molecular examination of the connection between photoperiodic rhythms and abiotic stress situations is practicable both in vitro and in vivo (Table 1).

Conclusion

In response to seasonal and daily environmental cues, the plant's cell-independent circadian rhythm supports the stimulant-traverse response. The components of the endogenous clock will be synchronized during transcription or after. It is possible to demonstrate that LHY and CCA1, the two crucial clock components in light signaling, regulate flowering plant circadian timing and control by extracting and displaying clock genes in a specific way. Genes control chlorophyll after sunrise, and clock elements maintain biodiversity and resistance for optimum performance. To assist scientists in more effectively comprehending how the genes of the circadian clock are expressed and work, we explain plant biological processes using the circadian clock in this paper. However, a variety of growing and food crops are abundantly available. Additionally, it offers a comprehensive picture of circadian biology. Chronoculture employs the circadian clock as well as time-associated cultivation and management. The timing of your body's biological clock (amplitude, phase, and period length), and circadian variables, particularly their vulnerability to stress, will be purposefully altered in the future via gene editing technology. Improved circadian clocks in novel germplasm resources will aid agricultural adaptability.

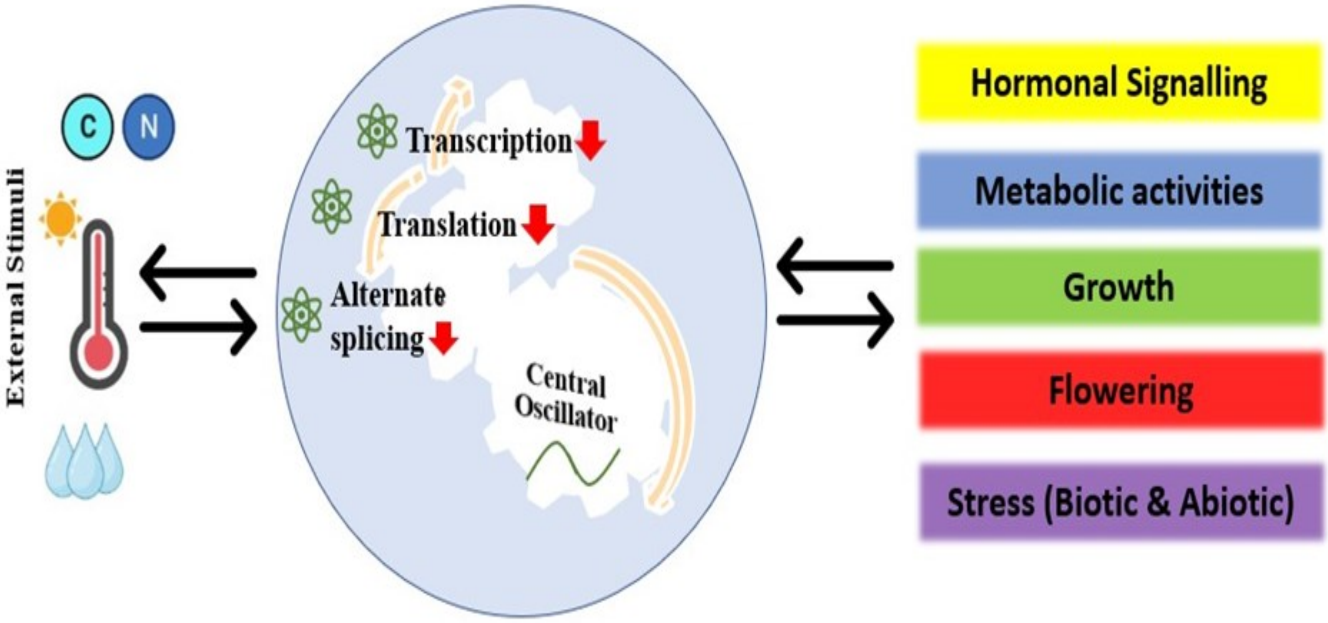

Fig. 4. A diagrammatic representation of the molecular mechanism of the external zeitgebers on the growth and development of plants.

Table 1. Comprehensive table of the novel research in circadian regulation of plants

SL. No.	Experiment Aim	Plant system	Major findings	Conclusion	Year	Reference
1.	To ascertain the effects of circadian regulation on photosynthetic facets of *Marchantia polymorpha*	*Marchantia polymorpha*	the circadian regulation of photosynthetic biochemistry Light-dark cycles synchronize the phase of photosynthesis's 24-hour cycles. For light harvesting to be controlled by a clock, chloroplast translation is required.	Terrestrial plants have well -preserved circadian control of photosynthesis.	2022	(56)
2.	To fixate into the way *Arabidopsis* plant rhizosphere bacterial and fungal rhythms are affected by plant circadian rhythms	Rhizosphere of *Arabidopsis thaliana*	An erratic function of the plant circadian clock corresponds with - altered rhythmicity of rhizosphere fungus and bacteria changes in rhizosphere microbial diversity	The aberrant function of the plant circadian clock is associated with altered rhythmicity of rhizosphere bacteria and fungi.	2022	(57)
3.	To determine how the molecular regulatory system of SEPALLATA3's (SEP3) functions in flowering time.	*Arabidopsis thaliana*	the trait of early blossoming LATE ELONGATED HYPOCOTYL (AtLHY) expression was dramatically reduced. ZjSEP3 suppressed AtLHY transcription	A brand-new regulatory mechanism for managing blooming time is the ZjSEP3-AtLHY pathway.	2021	(58)
4.	To investigate the role of stomatal conductance and photosynthetic efficiency in lycophytes and ferns' circadian regulation of gas exchange.	*Marsilea azorica* and *Regnellidium diphyllum*	Stomatal regulation by light in ferns and lycophytes	Lycophytes and ferns have fundamentally different control of gas exchange than angiosperms.	2023	(59)
5.	To delve into the promoter: luciferase system's ability to detect the addition of metal salts to the root-interaction environment.	*Arabidopsis thaliana*	Metal salts in the root-interaction environment may exert an effect on rhythms.	Classified broad sets of responses to the metal salts	2022	(60)
6.	To examine the intra -day dynamics of plant-pollinator networks	*Crepis capillaris* and *Leontodon hispidus*	At the aggregated (full-day) network level, minimizing modularity and enhancing plant generality.	The diel dynamics of plant-pollinator interactions are profoundly impacted by the transient shortage of floral resources.	2021	(61)
7.	Do the circadian clock and the herbicide response in rice interact cross -talk?	*Oryza sativa*	Glyphosate, s-Metolachlor, fenclorim, metcamifen, and GA3 response genes have consistent circadian cycles. OsCCA1 binding peaks were found in the promoter regions of OsCYP81A12, OsCYP81E22, OsCYP76C2, and OsCYP76C4 genes	The expression of several of the rice circadian clock's key oscillator genes may be impacted by herbicide use.	2023	(62)
8.	To ascertain if magnesium limits the *Arabidopsis* circadian period's periodic movement	*Arabidopsis thaliana*	The increase in CCA1 promoter (pCCA1:LUC) activity caused by Mg dearth was light-dependent.	Mg affects transcription and translation levels rather than just one component of the circadian oscillator.	2021	(63)
9.	To ascertain that plants have evolved the SALT OVERLY SENSITIVE (SOS) pathway for halotolerant.	*Arabidopsis thaliana*	SOS1, the plasma membrane Na+/ H+ antiporter, acts as a salt-specific circadian clock regulator via GIGANTEA (GI). SOS1 interacts with GI in a salt-dependent manner, stabilizing it to maintain a healthy clock period under salinity conditions.	Under high or daily variable salt levels, SOS1 maintains salt response homeostasis.	2022	(64)
10.	To indicate that K+ transfer from roots reduces variation in period duration in shoots.	*Arabidopsis thaliana*	Root clock gene expression is regulated by shoot-derived sucrose.	Time-series observations with prr7 mutants revealed that root PRR7 controls K+ transport and decreases variation in shoot period duration.	2023	(65)

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Authors' contributions

AC devised the article, searched the literature, wrote the manuscript, and plotted figures. MP and JKS revised the work. AmC, RCS, KP, KJ, MD, and CCM, searched and supplemented the literature. MP conceived of the study and participated in its design and coordination. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: The authors confirm that they have no personal or fiscal relationships that might be seen as jeopardizing the results of the submitted study.

Ethical issues: None.

References

1. Ghanei M, Ahmady K, Babaei M, Tavana AM, Bahadori M, Ebadi A, Poursaid SM. Knowledge of healthy lifestyle in Iran: a systematic review. Electron Physician. 2016;8(3):2199-207. https://doi.org/10.19082/2199
2. Krahmer J, Hindle M, Perby LK, Mogensen HK, Nielsen TH, Halliday KJ, van Ooijen G, Le Bihan T, Millar AJ. The Circadian Clock Gene Circuit Controls Protein and Phosphoprotein Rhythms in *Arabidopsis* thaliana. Mol Cell Proteomics. 2022;21(1):100172. https://doi.org/10.1016/j.mcpro.2021.100172
3. Xu, Xiaodong & Yuan, Li & Yang, Xin & Zhang, Xiao & Wang, Lei & Xie, Qiguang. (2022). Circadian clock in plants: Linking timing to fitness. Journal of Integrative Plant Biology. 64:792–811. https://doi.org/10.1111/jipb.13230
4. Takahashi JS. The 50th anniversary of the Konopka and Benzer 1971 paper in PNAS: Clock Mutants of Drosophila melanogaster. Proc Natl Acad Sci U S A. 2021 Sep 28;118 (39):e2110171118. https://doi.org/10.1073/pnas.2110171118
5. Kim JH, Bell LJ, Wang X, Wimalasekera R, Bastos HP, Kelly KA, Hannah MA, Webb AAR. *Arabidopsis* sirtuins and poly (ADP-ribose) polymerases regulate gene expression in the day but do not affect circadian rhythms. Plant Cell Environ. 2021 ;44 (5):1451-1467. https://doi.org/10.1111/pce.13996
6. Sanchez SE, Rugnone ML, Kay SA. Light Perception: A Matter of Time. Mol Plant. 2020;13(3):363-385. https://doi.org/10.1016/j.molp.2020.02.006
7. Papazyan R, Zhang Y, Lazar MA. Genetic and epigenomic mechanisms of mammalian circadian transcription. Nature structural & molecular biology. 2016;23(12):1045-52. https://doi.org/10.1038/nsmb.3324
8. O'Neill JS, van Ooijen G, Dixon LE, Troein C, Corellou F, Bouget FY, Reddy AB, Millar AJ. Circadian rhythms persist without transcription in a eukaryote. Nature. 2011;469:554-8. https://doi.org/10.1038/nature09654
9. Montaruli A, Castelli L, Mulè A, Scurati R, Esposito F, Galasso L, Roveda E. Biological Rhythm and Chronotype: New Perspectives in Health. Biomolecules. 2021;11(4):487. https://doi.org/10.3390/biom11040487
10. Yan J, Kim YJ, Somers DE. Post-Translational Mechanisms of Plant Circadian Regulation. Genes (Basel). 2021;12(3):325. https://doi.org/10.3390/genes12030325.
11. Román Á, Li X, Deng D, Davey JW, James S, Graham IA, Haydon MJ. Superoxide is promoted by sucrose and affects amplitude of circadian rhythms in the evening. Proc Natl Acad Sci U S A. 2021;118(10):e2020646118. https://doi.org/10.1073/pnas.2020646118
12. Fitzpatrick TB, Noordally Z. Of clocks and coenzymes in plants: intimately connected cycles guiding central metabolism? New Phytol. 2021;230(2):416-432. https://doi.org/10.1111/nph.17127
13. Paul E Verslues and others, Burning questions for a warming and changing world: 15 unknowns in plant abiotic stress, The Plant Cell. 2023;35(1): 67–108 https://doi.org/10.1093/plcell/koac263
14. Davis W, Endo M, Locke JCW. Spatially specific mechanisms and functions of the plant circadian clock. Plant Physiol. 2022;190(2):938-951. https://doi.org/10.1093/plphys/kiac236
15. Su C, Wang Y, Yu Y, He Y, Wang L. Coordinative regulation of plants growth and development by light and circadian clock. aBIOTECH. 2021;2(2):176-189. Published 2021. https://doi.org/10.1007/s42994-021-00041-6
16. Yamashino T. From a repressilator-based circadian clock mechanism to an external coincidence model responsible for photoperiod and temperature control of plant architecture in *Arabidopsis thaliana*. Biosci Biotechnol Biochem. 2013;77 (1):10-16. https://doi.org/10.1271/bbb.120765
17. Xu X, Yuan L, Yang X, Zhang X, Wang L, Xie Q. Circadian clock in plants: Linking timing to fitness. J Integr Plant Biol. 2022;64(4):792-811. https://doi.org/10.1111/jipb.13230
18. Nakamichi N. The Transcriptional Network in the *Arabidopsis* Circadian Clock System. Genes (Basel). 2020;11(11):1284. https://doi.org/10.3390/genes11111284
19. Más P. Circadian clock signaling in Arabidopsis thaliana: from gene expression to physiology and development. Int J Dev Biol. 2005;49(5-6):491-500. https://doi.org/10.1387/ijdb.041968pm
20. Sanchez SE, Kay SA. The Plant Circadian Clock: From a Simple Timekeeper to a Complex Developmental Manager. Cold Spring Harb Perspect Biol. 2016;8(12):a027748. https://doi.org/10.1101/cshperspect.a027748
21. Hemmes H, Henriques R, Jang IC, Kim S, Chua NH. Circadian clock regulates dynamic chromatin modifications associated with Arabidopsis CCA1/LHY and TOC1 transcriptional rhythms. Plant Cell Physiol. 2012;53(12):2016-29. https://doi.org/10.1093/pcp/pcs148
22. Venkat A and Muneer S (2022) Role of Circadian Rhythms in Major Plant Metabolic and Signaling Pathways. Front. Plant Sci. 13:836244. https://doi.org/10.3389/fpls.2022.836244
23. Yan J, Kim YJ, Somers DE. Post-Translational Mechanisms of Plant Circadian Regulation. Genes (Basel). 2021;12(3):325. https://doi.org/10.3390/genes12030325
24. de Los Reyes P, Romero-Campero FJ, Ruiz MT, Romero JM, Valverde F. Evolution of Daily Gene Co-expression Patterns from Algae to Plants. Front Plant Sci. 2017;8:1217. https://doi.org/10.3389/fpls.2017.01217
25. Chen ZJ, Mas P. Interactive roles of chromatin regulation and circadian clock function in plants. Genome Biol. 2019;20 (1):62. https://doi.org/10.1186/s13059-019-1672-9
26. Hotta CT. The evolution and function of the Pseudo Response Regulator gene family in the plant circadian clock. Genet Mol Biol. 2022;45(3):e20220137. https://doi.org/10.1590/1678-4685-GMB-2022-0137

27. Lopez L, Fasano C, Perrella G, Facella P. Cryptochromes and the Circadian Clock: The Story of a Very Complex Relationship in a Spinning World. Genes. 2021;12(5):672. https://doi.org/10.3390/genes12050672

28. Staiger D, Shin J, Johansson M, Davis SJ. The circadian clock goes genomic. Genome Biol. 2013;14(6):208. https://doi.org/10.1186/gb-2013-14-6-208

29. de Leone MJ, Hernando CE, Mora-García S, Yanovsky MJ. It's a matter of time: the role of transcriptional regulation in the circadian clock-pathogen crosstalk in plants. Transcription. 2020;11(3-4):100-16. https://doi.org/10.1080/21541264.2020.1820300

30. Sorkin ML, Tzeng SC, King S, Romanowski A, Kahle N, Bindbeutel R, Hiltbrunner A, Yanovsky MJ, Evans BS, Nusinow DA. Cold Regulated Gene 27 and 28 antagonize the transcriptional activity of the RVE8/LNK1/LNK2 circadian complex. Plant Physiol. 2023;192(3):2436-2456. https://doi.org/10.1093/plphys/kiad210

31. Li Yuan and others, BBX19 fine-tunes the circadian rhythm by interacting with Pseudo-Response Regulator proteins to facilitate their repressive effect on morning-phased clock genes, The Plant Cell, 2021; 33(8):2602–17, https://doi.org/10.1093/plcell/koab133

32. Zhang Y, Ma Y, Zhang H, Xu J, Gao X, Zhang T, Liu X, Guo L, Zhao D. Environmental F actors coordinate circadian clock function and rhythm to regulate plant development. Plant Signal Behav. 2023;18(1):2231202. https://doi.org/10.1080/15592324.2023.2231202

33. Ponnu J, Hoecker U. Signaling Mechanisms by Arabidopsis Cryptochromes. Front Plant Sci. 2022;13:844714. https://doi.org/10.3389/fpls.2022.844714.

34. Soy J, Leivar P, González-Schain N, Martín G, Diaz C, Sentandreu M, Al-Sady B, Quail PH, Monte E. Molecular convergence of clock and photosensory pathways through PIF3-TOC1 interaction and co-occupancy of target promoters. Proc Natl Acad Sci U S A. 2016;113(17):4870-5. https://doi.org/10.1073/pnas.1603745113

35. Maric A, Mas P. Chromatin Dynamics and Transcriptional Control of Circadian Rhythms in Arabidopsis. Genes. 2020;11 (10):1170. https://doi.org/10.3390/genes11101170

36. Nakamichi N, Takao S, Kudo T, Kiba T, Wang Y, Kinoshita T, Sakakibara H. Improvement of Arabidopsis Biomass and Cold, Drought and Salinity Stress Tolerance by Modified Circadian Clock-Associated Pseudo-Response Regulators. Plant Cell Physiol. 2016;57(5):1085-97. https://doi.org/10.1093/pcp/pcw057

37. Fitzpatrick TB, Noordally Z. Of clocks and coenzymes in plants: intimately connected cycles guiding central metabolism? New Phytol. 2021;230(2):416-432. https://doi.org/10.1111/nph.17127

38. Swift J, Greenham K, Ecker JR, Coruzzi GM, Robertson McClung C. The biology of time: dynamic responses of cell types to developmental, circadian and environmental cues. Plant J. 2022;109(4):764-778. https://doi.org/10.1111/tpj.15589

39. Bassi R, Dall'Osto L. Dissipation of Light Energy Absorbed in Excess: The Molecular Mechanisms. Annu Rev Plant Biol. 2021;72:47-76. https://doi.org/10.1146/annurev-arplant-071720-015522

40. Lei J, Jayaprakasha GK, Singh J, Uckoo R, Borrego EJ, Finlayson S, Kolomiets M, Patil BS, Braam J, Zhu-Salzman K. Circadian Clock-Associated1 Controls Resistance to Aphids by Altering Indole Glucosinolate Production. Plant Physiol. 2019;181(3):1344-59. https://doi.org/10.1104/pp.19.00676

41. Yang Y, Li Y, Sancar A, Oztas O. The circadian clock shapes the Arabidopsis transcriptome by regulating alternative splicing and alternative polyadenylation. J Biol Chem. 2020;295 (22):7608-19. https://doi.org/10.1074/jbc.RA120.013513

42. Ji X, Van den Ende W, Van Laere A, Cheng S, Bennett J. Structure, evolution, and expression of the two invertase gene families of rice. J Mol Evol. 2005;60(5):615-34. https://doi.org/10.1007/s00239-004-0242-1

43. Xie Q, Wang Y, Yuan L, Xu X. Measurement of Luciferase Rhythms in Soybean Hairy Roots. Methods Mol Biol. 2022;2398:65-73. https://doi.org/10.1007/978-1-0716-1912-4_6

44. Alves LC, Llerena JPP, Mazzafera P, Vicentini R. Diel oscillations in cell wall components and soluble sugars as a response to short-day in sugarcane (*Saccharum sp.*). BMC Plant Biol. 2019;19(1):215. https://doi.org/10.1186/s12870-019-1837-4.

45. Facella P, Lopez L, Carbone F, Galbraith DW, Giuliano G, Perrotta G. Diurnal and circadian rhythms in the tomato transcriptome and their modulation by cryptochrome photoreceptors. PLoS One. 2008;3(7):e2798. https://doi.org/10.1371/journal.pone.0002798

46. Chen Z, Gao K, Su X, Rao P, An X. Genome-Wide Identification of the Invertase Gene Family in Populus. PLoS One. 2015;10 (9):e0138540. https://doi.org/10.1371/journal.pone.0138540

47. Hassidim M, Dakhiya Y, Turjeman A, Hussien D, Shor E, Anidjar A, Goldberg K, Green RM. Circadian Clock Associated1 (CCA1) and the Circadian Control of Stomatal Aperture. Plant Physiol. 2017;175(4):1864-1877. https://doi.org/10.1104/pp.17.01214

48. Mark Greenwood and Mirela Domijan and Peter D. Gould and Anthony J.W. Hall and James C.W. Locke.Coordinated circadian timing through the integration of local inputs in Arabidopsis thaliana. Cold Spring Harbor Laboratory. 2019. https://doi.org/10.1101/617803

49. Lymperopoulos P, Msanne J and Rabara R (2018) Phytochrome and Phytohormones: Working in Tandem for Plant Growth and Development. Front. Plant Sci. 9:1037. https://doi.org/10.3389/fpls.2018.01037

50. Creux N, Harmer S. Circadian Rhythms in Plants. Cold Spring Harb Perspect Biol. 2019 Sep 3;11(9):a034611. https://doi.org/10.1101/cshperspect.a034611

51. Xiong L, Zhou W, Mas P. Illuminating the *Arabidopsis* circadian epigenome: Dynamics of histone acetylation and deacetylation. Curr Opin Plant Biol. 2022 Oct;69:102268. https://doi.org/10.1016/j.pbi.2022.102268

52. Patnaik A, Alavilli H, Rath J, Panigrahi KCS, Panigrahy M. Variations in Circadian Clock Organization & Function: A Journey from Ancient to Recent. Planta. 2022;256(5):91. https://doi.org/10.1007/s00425-022-04002-1

53. Ito S, Kawamura H, Niwa Y, Nakamichi N, Yamashino T, Mizuno T. A genetic study of the Arabidopsis circadian clock with reference to the Timing of Cab Expression 1 (TOC1) gene. Plant Cell Physiol. 2009;50(2):290-03. https://doi.org/10.1093/pcp/pcn198

54. Yamamoto Y, Tabata K. Enhancement of Arabidopsis growth by non-24 hour day-night cycles. Plant Direct. 2022;6(3):e391. https://doi.org/10.1002/pld3.391

55. Huang H, Nusinow DA. Into the Evening: Complex Interactions in the Arabidopsis Circadian Clock. Trends Genet. 2016;32(10):674-86. https://doi.org/10.1016/j.tig.2016.08.002

56. Cuitun-Coronado D, Rees H, Colmer J, Hall A, de Barros Dantas LL, Dodd AN. Circadian and diel regulation of photosynthesis in the bryophyte Marchantia polymorpha. Plant Cell Environ. 2022;45(8):2381-94. https://doi.org/10.1111/pce.14364

57. Newman A, Picot E, Davies S, Hilton S, Carré IA, Bending GD. Circadian rhythms in the plant host influence rhythmicity of rhizosphere microbiota. BMC Biol. 2022;20(1):235. https://doi.org/10.1186/s12915-022-01430-z

58. Gao W, Zhang L, Wang J, Liu Z, Zhang Y, Xue C, Liu M, Zhao J. ZjSEP3 modulates flowering time by regulating the LHY promoter. BMC Plant Biol. 2021;11;21(1):527. https://doi.org/10.1186/s12870-021-03305-x

59. Aros-Mualin D, Guadagno CR, Silvestro D, Kessler M. Light, rather than circadian rhythm, regulates gas exchange in ferns and lycophytes. Plant Physiol. 2023; 17;191(3):1634-47. https://doi.org/10.1093/plphys/kiad036

60. Hargreaves JK, Oakenfull RJ, Davis AM, Pullen F, Knight MI, Pitchford JW, Davis SJ. Multiple metals influence distinct properties of the Arabidopsis circadian clock. PLoS One. 2022;17(4):e0258374. https://doi.org/10.1371/journal.pone.0258374

61. Schwarz B, Dormann CF, Vázquez DP, Fründ J. Within-day dynamics of plant-pollinator networks are dominated by early flower closure: an experimental test of network plasticity. Oecologia. 2021;196(3):781-94. https://doi.org/10.1007/s00442-021-04952-5

62. Chen K, Su X, Yang H, Peng Y, Wu L, Zhao Z, Lin T, Bai L, Wang L. Multi-omics analyses reveal the crosstalk between the circadian clock and the response to herbicide application in Oryza sativa. Front Plant Sci. 2023;14:1155258. https://doi.org/10.3389/fpls.2023.1155258

63. de Melo JRF, Gutsch A, Caluwé T, Leloup JC, Gonze D, Hermans C, Webb AAR, Verbruggen N. Magnesium maintains the length of the circadian period in Arabidopsis. Plant Physiol. 2021 Mar 15;185(2):519-532. https://doi.org/10.1093/plphys/kiaa042

64. Cha JY, Kim J, Jeong SY, Shin GI, Ji MG, Hwang JW, Khaleda L, Liao X, Ahn G, Park HJ, Kim DY, Pardo JM, Lee SY, Yun DJ, Somers DE, Kim WY. The Na+/H+ antiporter Salt Overly Sensitive 1 regulates salt compensation of circadian rhythms by stabilizing GIGANTEA in Arabidopsis. Proc Natl Acad Sci U S A. 2022; 16;119(33):e2207275119. https://doi.org/10.1073/pnas.2207275119

65. Uemoto K, Mori F, Yamauchi S, Kubota A, Takahashi N, Egashira H, Kunimoto Y, Araki T, Takemiya A, Ito H, Endo M. Root PRR7 Improves the Accuracy of the Shoot Circadian Clock through Nutrient Transport. Plant Cell Physiol. 2023 Mar 15;64(3):352-62. https://doi.org/10.1093/pcp/pcad003