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Interactions between Photosynthesis and the Circadian System

Abstract

The rising and setting of the sun provides a regular transition between two starkly different environmental conditions for photosynthetic organisms such as plants. Since photosynthetic organisms rely on light as both an environmental signal and an energy source it is beneficial for plants to respond to and utilize light in a time-dependent manner. This timing information is provided by the circadian system, a complex biological oscillator that provides an internal reference that can be used to modify plants' responses to light signals. In this review, we will discuss how the circadian system regulates photosynthetic processes, while also exploring how photosynthetic products can themselves feed into the circadian system to optimise interactions between plants and their environment.

Introduction

Evolution has driven plants to optimise their metabolism so that they can adapt to environmental challenges. This is crucial as day length and light intensity vary during the year, as do maximum/minimum temperatures and the availability of water. Each of these abiotic factors influences photosynthetic efficiency, since plants must balance photosynthetic potential against water retention and the damage induced by completing photosynthesis in sub-optimal conditions. Plants have developed several biochemical and physiological strategies to mitigate these challenges including stomatal closure, chloroplast and leaf movements, changes in respiration rate, and photoinhibition (Schulze et al., 2019). However, when should plants utilise these strategies? How can plants distinguish transient changes in illumination (e.g. from sunflecks or cloud cover) from longer-term changes induced by the daily rising and setting of the sun? One solution is provided by the circadian system, a molecular mechanism that provides an endogenous timing reference. This biological clock enables anticipation of environmental signals such as dawn and daily temperature fluctuations, as well as providing a yardstick to determine daylength. These features enable plants to respond more appropriately to environmental change as well as modulating biochemical and physiological behaviours to optimise growth in varied conditions. In this review, we will discuss how the circadian system regulates photosynthetic metabolism, and how these metabolic signals can feedback into the circadian clock itself.

The Circadian System is a Global Regulator of Metabolism

Daily rhythms of light and temperature have driven the evolution of the circadian system. Each individual cell is capable of entraining its own circadian system, with additional linking between neighbouring cells and tissues to enable organismal responses (Sorkin & Nusinow, 2021). These Transcriptional and Translation Feedback Loops (TTFL) are promoted by external signals that coordinate endogenous gene expression and metabolism, and maintain their rhythmicity under light and temperature changes, although the circadian system will persist under constant conditions. The core of the molecular circadian clock consists of interlocking positive and negative feedback loops that control gene expression combined with a smaller number of transcriptional activators (Figure 1; Sorkin & Nusinow, 2021). Morning-phased clock components including *CIRCADIAN CLOCK ASSOCIATED1* (*CCA1*), *LATE ELONGATED HYPOCOTYL* (*LHY*), and *PSEUDO RESPONSE REGULATOR9* (*PRR9*) are activated by light (Ito et al., 2003; Rugnone et al., 2013; Z. Y. Wang & Tobin, 1998), while PRR9 and PRR7 are important for entrainment to temperature (Mizuno et al., 2014; Salomé & McClung, 2005). GIGANTEA (GI) regulates ZEITLUPE (ZTL) protein stability and its subsequent regulation of TOC1 (Kim et al., 2013; Kim et al., 2007). CCA1 and LHY repress the expression of *PRR9*, *PRR7*, *PRR5* and *PRR1* (or *TIMING OF CAB EXPRESSION1 - TOC1*), with TOC1 having the peak expression close to dusk. In turn, the PRRs repress CCA1/LHY expression (Figure 1; Hsu & Harmer, 2014). Myb-like REVEILLE8 (RVE8) is a transcriptional activator and dynamically interacts with NIGHT LIGHT–INDUCIBLE AND CLOCK-REGULATED1 (LNK1) and LNK2 to activate transcription of evening-phased genes (EARLY FLOWERING3 [ELF3], ELF4 and LUX ARRHYTHMO [LUX]) (Xie et al., 2014). Beyond these transcriptional controls, additional layers of regulation, including post-transcriptional and post-translational modification, also contribute to circadian timing (Harms et al., 2004). For example, reversible phosphorylation can regulate the pace of circadian rhythms by activating, inactivating or providing a targeting signal that contributes to post-translational degradation (Brenna & Albrecht, 2020).
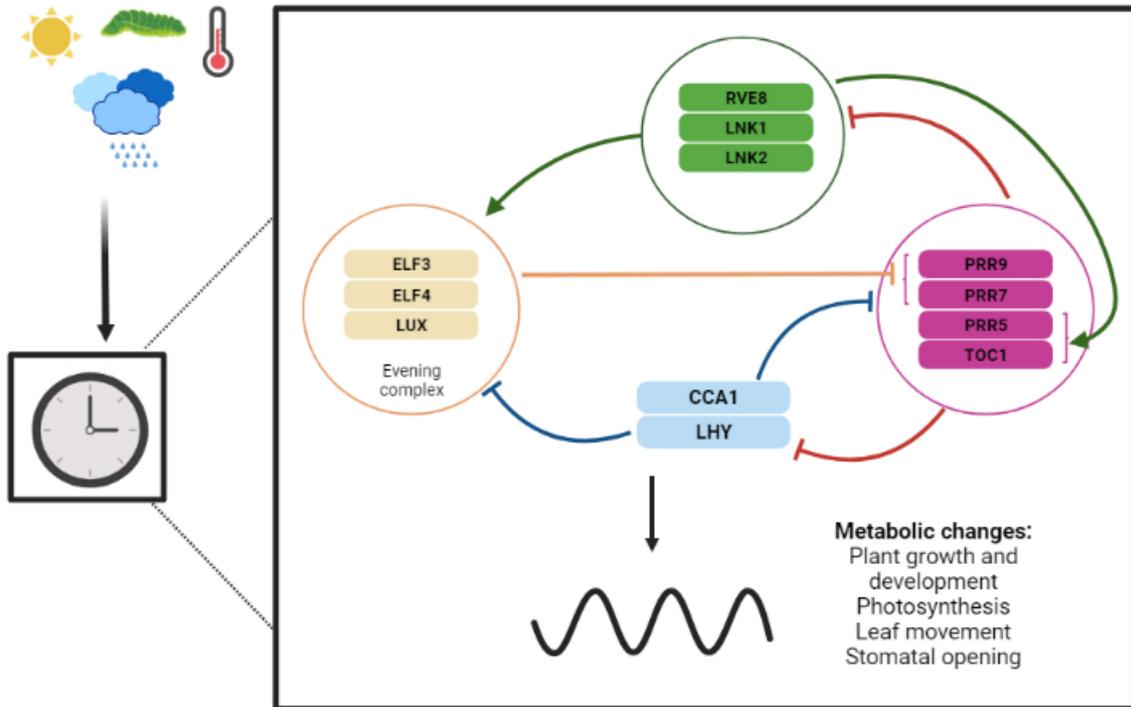
Figure 1 – The circadian clock is regulated by several genes acting within transcription-translation feedback loops to generate rhythms that subsequently guide physiological and metabolic processes. REVEILLE8 (RVE8), NIGHT LIGHT–INDUCIBLE AND CLOCK-REGULATED1 (LNK1), and LNK2 are positive regulators of gene expression, whereas PSEUDORESPONSE REGULATORS (PRRs), CIRCADIAN CLOCK ASSOCIATED1 (CCA1), LATE ELONGATED HYPOCOTYL (LHY), and components of the Evening Complex (EARLY FLOWERING3 [ELF3], ELF4, and LUX ARRHYTHMO) are transcriptional repressors. This biological oscillator is sensitive to light and temperature to enable synchronisation between environmental and endogenous signals. Created with Biorender.com.

The circadian system contributes to the regulation of photosynthesis

Although photosynthesis is ultimately dependent upon light, the complex interplay between photosynthesis and other aspects of plant physiology requires coordination of many different aspects of metabolism. One such coordinator is the circadian system that enables timing information to be integrated into biological processes. It has been apparent for many years that photosynthesis is regulated by the circadian system since carbon assimilation follows a rhythmic pattern in plants transferred to constant light (Dodd et al., 2004; Hennessey & Field, 1991; Salomé et al., 2002). Both wild type plants and plants with a slower circadian clock (such as *ztl-1* seedlings) display circadian rhythms of CO_2 assimilation that correspond to the timing of the molecular timekeeper (Dodd et al., 2004).

One physiological component that likely contributes to these circadian phenotypes is the regulation of guard cells. Guard cells play a major role in regulating stomatal opening by increasing and decreasing their volume via osmotic changes to regulate stomatal pore size (Misra et al., 2015). More importantly, guard cells are responsive to external stimuli like light, heat, water availability, and internal signals such as ROS, hormones, lipids and sugar (Misra et al., 2015). Circadian regulation of guard cell movement and stomatal opening (Hassidim et al., 2017) provides a physiological mechanism by which the clock has a fundamental role in carbon assimilation, contributing to photosynthesis by varying intercellular CO_2 availability and consequently regulating the operating efficiency of PSII ($\frac{F_q'}{F_m'}$, or ϕPSII; Murchie and Lawson 2013). Several photosynthetic parameters oscillate over circadian time in C3 and CAM species, most likely as a consequence of differential gas exchange (Litthauer et al., 2015; Malpas & Jones, 2016; Rascher et al., 2001). Circadian patterns of gas exchange are also observed at the leaf-to-canopy scale, with a significant portion of daytime gas exchange regulated by the clock (Resco de Dios et al. 2016b).

Another benefit of circadian regulation of guard cell function is enhanced Water Use Efficiency (WUE) (Hassidim et al., 2017; Lawson & Blatt, 2014; Simon et al., 2020). A primary role for the circadian system appears to be the pre-emptive opening of stomata prior to dawn, which promotes growth at the expense of WUE (Resco de Dios et al. 2016b, Hassidim et al. 2017). *Arabidopsis cca1, elf3, gi, prr9, toc1* and *ztl* circadian knockout mutant seedlings all have lower WUE than wild-type plants, demonstrating a crucial role for the circadian clock in this activity (Simon et al., 2020). Such WUE phenotypes are likely conferred by altered guard cell function since disruption of the circadian clock through guard cell-specific over-expression of morning-phased *CCA1* inhibits stomatal opening before dawn and promotes WUE in well-watered conditions (Hassidim et al., 2017; Simon et al., 2020). However disruption of circadian function in these transgenic lines reduced drought tolerance, emphasising the contribution of the circadian system to the optimisation of plant growth in sub-optimal environments (Hassidim et al., 2017).

The circadian system contributes to the regulation of photosynthesis in C4 and CAM species

Evolutionary pressures to adapt to high temperatures and low water availability have driven the development of C4 and Crassulacean acid metabolism (CAM) photosynthesis. These photosynthetic derivations aim to reduce the negative effects of photorespiration by increasing the ribulose-1,5-bisphosphate carboxylase activity through the concentration of CO_2, thereby improving WUE, and photosynthetic efficiency. Ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco) is the main enzyme that drives the balance between photorespiration and CO_2 fixation (Voet et al., 2016). The affinity of Rubisco to CO_2 or O_2 is affected by temperature, with Rubisco oxygenase activity increasing at elevated temperatures, leading to increased photorespiration (Dusenge et al., 2019). The occurrence of photorespiration is significantly higher in C3 plants, compared to C4 and CAM metabolism, which leads to a decrease in the photosynthetic efficiency of these plants and consequently reduced growth and development in high temperatures (Schulze et al., 2019).

Although both C4 and CAM mechanisms limit photorespiration, C4 photosynthesis benefits from the anatomical separation in the leaves, while in CAM plants photosynthetic processes are divided by time (Black & Osmond, 2003; Hatch et al., 1988). C4 metabolism occurs in parallel in mesophyll and bundle sheath cells. In mesophyll cells, C4 plants have a circular arrangement called the Kranz anatomy where CO_2 is fixed by phosphoenolpyruvate (PEP) carboxylase giving oxaloacetate which will convert into malate or aspartate (Hatch et al., 1988). The malate is transported to the bundle sheath cells where it is converted to pyruvate, releasing CO_2 the input to the Calvin-Benson Cycle in which Rubisco is responsible for the carbon fixation (Hatch et al., 1988).

CAM plants also have a specific leaf structure with thick cuticles, large vacuoles, and small stomata. Besides that, the striking feature of CAM metabolism is the temporal separation between carbon fixation and stomatal opening (Gilman & Edwards, 2020). The assimilation of CO_2 from the atmosphere occurs at night via the enzyme PEP carboxylase, as the production of malic acid and its accumulation in the vacuole (Nimmo, 2000; Winter & Smith, 2022). In addition, PEP is regenerated via glycolysis. During the daytime, malic acid is released into the cytosol, with the decarboxylation of malate releasing CO_2 that will be assimilated via Rubisco into the Calvin-Benson Cycle (Schiller & Bräutigam, 2021). Storage carbohydrates are also regenerated through gluconeogenesis of pyruvate or PEP (Winter, 2019). To control the flux of PEP carboxylase during day/night shifts,

plants have developed a mechanism that was first identified in *Kalanchoë fedtschenkoi*. PEP carboxylase is phosphorylated at night, being inhibited by an increase in malate levels, and dephosphorylated during the day when the levels of malate decrease (Nimmo, 2000). This phosphorylation/dephosphorylation is controlled largely by the activity of PEP carboxylase kinase (PEPCK), an enzyme that is under circadian regulation (Carter et al., 1991; Nimmo, 2000; Nimmo et al., 2001).

In spite of these pronounced changes in metabolism, the circadian system in CAM species is broadly conserved compared to Arabidopsis. However, some changes in the timing of peak transcript abundance have been observed. For example, some orthologous genes peak at midday in *Kalanchoë fedtschenkoi* but are morning phased in Arabidopsis. Conversely, another group of *Kalanchoë fedtschenkoi* genes peaking at midday had Arabidopsis orthologues that peaked just after dusk, suggesting differential regulation of rhythmic orthologous gene pairs (Moseley et al., 2018). In addition, the evening complex genes *ELF4, ELF3*, and *LUX* have a shift of expression mostly to midday in *Kalanchoë fedtschenkoi* whereas *ELF4* was altered in gene copy number (Moseley et al., 2018).

Although not as pronounced, C4 plants also utilise circadian timing to coordinate metabolism during the day. As in CAM plants, clock genes are functionally retained between C4 and C3 species since studies in maize (*Zea mays*) found several orthologs of Arabidopsis circadian clock such as *PRR7* and *LUX* (Khan et al., 2010). Besides that, the genes encoding PEP carboxylase, an enzyme that fixes CO_2, are rhythmically expressed (Khan et al., 2010). Moreover, the expression of maize enzymes related to Calvin-Benson cycle and the other components of photosynthesis, like light-harvesting complex B and rubisco activase proteins, follows a coordinated expression phased preceding dawn or at dawn (Khan et al., 2010). In commercial sugar cane (*Saccharum* hybrids), the expression of transcripts regulating photosynthesis and carbohydrate metabolism are mainly expressed during the day, meanwhile, at night the genetic machinery has a fundamental role with DNA replication, histone regulation and RNA polymerase, ribosomes and proteins synthesis (Hotta et al., 2013). Despite these differences, clock components are highly conserved in sugarcane and about 32% of sugarcane transcripts exhibit a rhythmic expression (Hotta et al., 2013). Comparing two C4 species, sugarcane and maize, is possible to affirm that sugarcane has a higher number of ortholog clusters controlled by the clock (114 against 29 from maize) (Hotta et al., 2013). This is likely due to an increase

in the ploidy and aneuploidy levels that come from agronomic crossings and selections to improve yield (Hotta et al., 2013).

Despite the similarity between the clock of C4 and CAM species to that found in Arabidopsis, in CAM plants the circadian downregulation of photosynthesis is made through regulation of PEP carboxykinase (PEPCK) expression. This enzyme phosphorylates PEP carboxylase reducing the feedback inhibition of PEP by malate and enhancing nocturnal CO_2 fixation to stored malate, the first product from the CO_2 fixation in CAM plants. In addition, PEPCK presents a peak transcript accumulation and enzyme activity in the mid-to-late night (Carter et al., 1991; Nimmo, 2000; Nimmo et al., 2001). In *K. daigremontiana* it has been shown that *PPC1*, a gene that is responsible for control the expression of the enzyme PEPCK, is connected to the regulation of guard cell genes (Boxall et al., 2020).

Interactions between photosynthates and the circadian system

In order to synchronise with prevailing environmental conditions, the circadian system is highly responsive to environmental factors such as light and temperature. The majority of circadian rhythms comprise sinusoidal waves that vary by phase, period and amplitude. These factors can be modified in response to different environmental conditions to maximise growth and synchronize physiological responses, improving fitness and conferring competitive advantage (Dodd et al., 2005; Harmer, 2009). Indeed, circadian period is not fixed and circadian phase can be advanced or delayed throughout the day in response to environmental factors (Webb et al., 2019). Although the role of photoreceptors has been well explored (Oakenfull & Davis, 2017), the contribution of metabolic signals such as sugars, Reactive Oxygen Species (ROS) and signalling ions have only recently emerged (Webb et al., 2019). In this section we will discuss how the circadian system regulates the metabolism of photosynthates, and also highlight how these metabolites can feedback into the circadian system.

Starch metabolism ensures a consistent energy supply during the night

Photosynthesis allows plants to accumulate photosynthates during the day, but how best to utilise this harvested energy? Given the metabolic expense of gluconeogenesis, it is beneficial for plants to accumulate sufficient starch to allow respiration to continue during the night (Smith & Stitt, 2007). Conversely, unutilised starch remaining at dawn

represents an inefficient use of resources. For example, plants unable to accumulate starch (or those with impaired starch catabolism) have reduced growth rates except in continuous light or very long days (Smith & Stitt, 2007). The production of starch is regulated by ADP glucose pyrophosphorylase (AGPase), due to an increasing ratio of glycerate-3-phosphate to inorganic phosphate (Stitt et al., 2010; Zeeman et al., 2010). Considering all carbon fixed, only 15% is turned into starch, with the remaining amount is distributed to compose cell structures and metabolites such as proteins, cell walls, lipids, pigments, and waxes. This carbon exportation from source leaves to sink organs begins immediately after dawn (Kölling et al., 2015). At dusk, there is a decrease in carbon exportation from source organs coordinate with a raising in starch production (Kölling et al., 2015), which contributes to the accumulation of starch in the leaves that can be used during the night (Sulpice et al., 2014). Nevertheless, the ratio of fixed carbon/starch synthesis is pliable and will be modified in response to the photoperiod. For example, to prevent starvation Arabidopsis plants increase the proportion of fixed carbon into starch at the beginning of the diel period when grown under only 3 h of light per day (Gibon et al., 2004; Sulpice et al., 2014). This change in allocation is complemented by a reduced rate of starch degradation that prioritizes plant preservation over growth enabling plants to survive under shading or changing seasons (Jones, 2017).

In order to optimise the utilisation of starch reserves during the night, plants utilise the circadian system to anticipate the timing of dawn (Graf et al., 2010). This mechanism ensures carbohydrate availability is stable until dawn by managing the resources between catabolism and metabolism. Importantly, plants with an accelerated circadian system (for example *cca1-11 lhy-21* seedlings) utilise starch at night much faster than in wildtype plants, resulting in the consumption of starch and the presentation of starvation responses in these plants (Graf et al., 2010). The most presumable connection between starch accumulation and the circadian clock is PHOSPHOGLUCAN WATER DIKINASE (PWD), which is fundamental for normal starch degradation through a cycle of phosphorylation reactions, retaining starch at dawn (Smith, 2012). The degradation of starch was not observed in plants lacking PWD following an unpredicted early dusk, moreover, the levels of phosphate bound to the granules are connected to cellular starch content during the day, suggesting that a phosphate-derived signal is sufficient to control cellular starch content (Scialdone et al., 2013). Alternately, plants could regulate starch degradation depending on the accumulation of Tre6P in source leaves, connecting starch

metabolism to the demand for sucrose (Figueroa & Lunn, 2016). This metabolic approach is favorable to balance source/sink relationships, thereby improving plant growth.

Indicators of cellular energy status are integrated into the circadian system

Carbohydrate (triose phosphate) synthesis occurs in the chloroplast stroma during the second stage of photosynthesis via the Calvin-Benson cycle (Sharkey, 2019). The reduction of CO_2, and consequently carbon fixation, requires energy in the form of ATP and NADPH, which has been provided by the light reaction of photosynthesis. The amount of NADPH and ATP produced is regulated by photosynthetic parameters such as the efficiency of carboxylation and the regeneration rate of Rubisco, as well as by photorespiration and the rate of transport of carbohydrates out of the cell (Baker, 2008). These endogenous sugars provided by photosynthesis serve as a metabolic signal that can be integrated into the circadian system [Figure 2, (Dodd et al., 2005; Haydon et al., 2013)]. But how do plants monitor the accumulation of photosynthates and adjust circadian timing as required?

Trehalose 6-phosphate (Tre6P) acts as a global regulator of metabolism and transcription promoting plant growth and triggering developmental phase transitions in response to sugar availability (Tsai & Gazzarrini, 2014). Tre6P enables plants to control their intracellular sucrose levels, forming a negative feedback looping where sucrose induces Tre6P production and Tre6P limits sucrose accumulation (Dos Anjos et al., 2018; Figueroa & Lunn, 2016). Sucrose and Tre6P concentrations consequently follow the same pattern, increasing during the day and decreasing at night. One of the targets of Tre6P is the SUCROSE-NON-FERMENTING1-RELATED KINASE1 (SnRK1) family, which allows cells to maintain energetic balance and homeostasis during harmful conditions (Tsai & Gazzarrini, 2014). SnRK1 is induced during starvation conditions, resulting in reduced anabolism and upregulated catabolism to limit energy expenditure (Wurzinger et al., 2018). Processes such as storage compound mobilization and autophagy are also promoted to recover an energy deficit, while energetically demanding processes such as protein translation and cell proliferation are inhibited (Tsai & Gazzarrini, 2014). SnRK1 has consequently been a prime candidate to integrate metabolic signals into the circadian system.

Photosynthates can entrain the circadian system through two pathways: a feedback loop involving regulation of *PRR7* expression in the morning and a GI/ZTL dependent post-translational regulation in the evening [Figure 2, (Dalchau et al., 2011; Haydon et al., 2017; Haydon et al., 2013)]. *prr7* seedlings are unable to adjust circadian timing in response to light or sugar, suggesting that this gene has an essential role in integrating photosynthate-mediated signals (Haydon et al., 2013). Indeed, SnRK1 promotes the activity of bZIP63 (a transcriptional activator that induces *PRR7* expression) thereby connecting SnRK1 and Tre6P to circadian timing (Frank et al., 2018; Mair et al., 2015). During the day, photosynthesis leads to the accumulation of sugar, inactivating SnRK1 and repressing *PRR7*, contributing to the coordination of circadian and metabolic signals (Haydon et al., 2013; Frank et al., 2018).

Separately, the addition of sucrose to growth media is sufficient to maintain circadian rhythms during extended dark periods, with GIGANTEA having an important role (Dalchau et al., 2011). GIGANTEA is necessary to maintain this sucrose-dependent rhythmicity under dark through the stabilization of GIGANTEA and ZTL aggregations (Dalchau et al., 2011; Haydon et al., 2017). In the absence of sucrose, GIGANTEA (along with other circadian components) are degraded, therefore reducing circadian amplitude (Haydon et al., 2017). This latter pathway may serve to limit circadian rhythms under low light (or starvation) conditions, although additional experimentation will be needed to test this hypothesis.
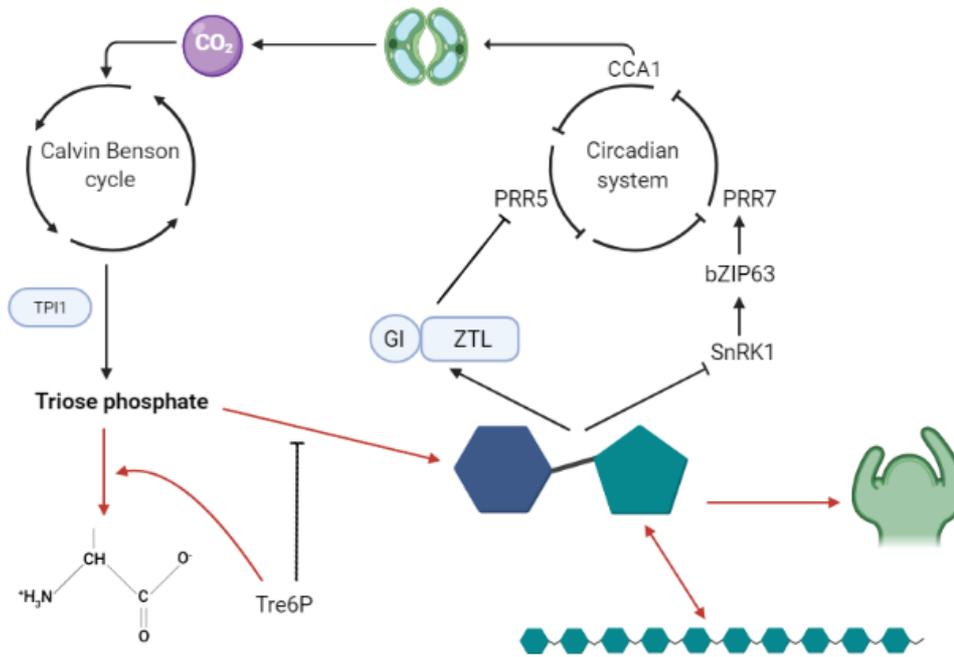
Figure 2 – The circadian regulation of the products of photosynthesis. Triose phosphates generated from photosynthesis can to utilised to produce organic acids, amino acids and sugar. Sugars are utilised immediately for plant metabolism and development, or can be diverted for starch synthesis- this partitioning is controlled in part by Trehalose 6-phosphate (Tre6P). Sugars feed into the circadian system via two identified pathways. SnRK1 activity is inhibited by sugar, leading to the repression of *PRR7* within the circadian system. Separately, sucrose enhances the accumulation of GIGANTEA (GI) and ZTL, leading to the repression of other circadian factors including *PRR5*. Circadian rhythms can induce stomatal opening, allowing CO_2 entry into the leaf for carbon fixation. Red lines indicate sugar partitioning pathways. Created with Biorender.com.

Generation of Reactive Oxygen Species during photosynthesis

The generation of Reactive Oxygen Species (ROS) is a natural process that occurs as a consequence of metabolic processes such as photosynthesis and respiration, as well as being utilised as a mechanism to dissipate excess absorbed light energy (Khorobrykh et al., 2020). Absorbed energy harvested by the photosynthetic antennae oxidizes a water molecule and initiates the electron transfer pathway. The electron can follow 3 paths enabling cyclic, pseudocyclic, and noncyclic phosphorylation. Noncyclic phosphorylation generates an electrical gradient with the production of the NADPH from $NADP^+$ as the electron acceptor, ATP, and molecular oxygen ending the photochemistry stage of photosynthesis, whereas cyclic and pseudocyclic pathways are non-productive (Allen, 2003). Cyclic phosphorylation only occurs at PSI without the production and

consumption of oxygen. The pseudocyclic path (water-water cycle) requires both PSII and PSI, with the production and consumption of oxygen as oxygen serves as an electron acceptor (Allen, 2003).

Due to an imbalance on O_2 reduction in the PSI the pseudocyclic path can produce superoxide anions radical ($O_2^{\bullet-}$) through two main mechanisms: reduced plastoquinone donates electrons to O_2 via the plastid terminal oxidase (PTOX; Heyno et al., 2009) and unbalance of PSI due to disparity between demand and supply of electron acceptors such as $NADP^+$, nitrite or sulfite, which transfers electrons from ferredoxin or the Fe-S-center Fx to O_2 (Dietz, 2016). The superoxide anion radical is converted into H_2O_2 by the action of thylakoids superoxide dismutase (SODs). Produced H_2O_2 is reduced to water by chloroplast ascorbate peroxidases (APXs) and the 2-cysteine peroxiredoxins (PRXs), creating the water-water cycle to preserve the photosynthetic apparatus (Awad et al., 2015).

Plants have complex regulatory pathways to balance the accumulation of ROS as signaling and its degradation to limit potential damage (Foyer, 2018). When these compounds reach a high enough level, apoptosis is activated to regulate growth, development and eliminate damaged or infected cells (Wang et al., 2013). The imbalance between ROS production and ROS scavenging (which happens under stress conditions) causes fluctuations in the redox state of the cell, modifying the levels of reduced and oxidized forms of antioxidants like ascorbate (AscH2), glutathione (GSH) and thiol-containing compounds (Foyer, 2018; Khorobrykh et al., 2020). Superoxide anion and H_2O_2 are largely generated at PSI on the stromal side of non-appressed thylakoid membranes (Wang et al., 2016), although it has been reported that H_2O_2 could be directly transferred to the nucleus from attached chloroplasts or via stromules (Caplan et al., 2015; Exposito-Rodriguez et al., 2017). In addition, several retrograde signalling pathways have been identified that report oxidative damage in the chloroplast and mitochondria via secondary messengers that accumulate in response to impaired organelle performance (Jones 2019).

Integration of ROS into circadian timing
The change in light availability during the day leads to changes in the rate of photosynthesis and therefore affects the generation of ROS and the redox status of the

cell (del Río, 2015). Interestingly, PRX hyper-oxidation varies with a circadian rhythm in many species, leading to speculation that redox rhythms may have contributed to the ancestral circadian system (Edgar et al. 2012). Despite this possibility, it remains to be determined if rhythms in PRX oxidation contribute to the maintenance of nuclear circadian oscillations, or whether PRX rhythms simply contribute towards observed rhythms of photosynthetic capacity (Litthauer et al. 2015; Simon et al., 2019).

In addition to these chloroplastic PRX rhythms, the nuclear circadian system has been shown to contribute to cellular ROS homeostasis (Lai et al., 2012). Mutations in *CCA1* and *LHY* increased the sensitivity of these plants to ROS, emphasising the importance of a functional clock for ROS homeostasis (Lai et al., 2012). It has also been reported that sucrose initiates the accumulation of O_2^-, suggesting that sugar and ROS signals could be linked within the circadian system (Román et al. 2021). Despite these advances, it still remains unclear how ROS contribute to circadian timing, and the link between photosynthesis and these pathways remains a promising avenue for future investigation. Such work will allow us to understand how photosynthetic performance can be integrated with daily and seasonal changes.

Perspectives

Recent advances have enabled the integration of photosynthetic metabolism with the circadian system. These efforts reveal how photosynthetic products feed into the circadian system as an indicator of metabolic health and/or productivity. In turn, the role of circadian biology in regulating photosynthesis and gas exchange is becoming apparent. Future advances will provide better comprehension of the association between the circadian system and photosynthesis and will enable advances in crop growth under stressful conditions. This will allow better management of natural resources and more effective exploitation of marginal land.

References

Allen, J. F. (2003). Cyclic, pseudocyclic and noncyclic photophosphorylation: New links in the chain. *Trends in Plant Science*, *8*(1), 15–19. https://doi.org/10.1016/S1360-1385(02)00006-7

Awad, J., Stotz, H. U., Fekete, A., Krischke, M., Engert, C., Havaux, M., Berger, S., & Mueller, M. J. (2015). 2-Cysteine Peroxiredoxins and Thylakoid Ascorbate Peroxidase Create a Water-Water Cycle That Is Essential to Protect the Photosynthetic Apparatus under High Light Stress Conditions. *Plant Physiology*, *167*(4), 1592–1603. https://doi.org/10.1104/pp.114.255356

Baker, N. R. (2008). Chlorophyll fluorescence: A probe of photosynthesis in vivo. *Annual Review of Plant Biology*, *59*, 89–113. https://doi.org/10.1146/annurev.arplant.59.032607.092759

Black, C. C., & Osmond, C. B. (2003). Crassulacean acid metabolism photosynthesis: "Working the night shift." *Photosynthesis Research*, *76*(1–3), 329–341. https://doi.org/10.1023/A:1024978220193

Boxall, S. F., Kadu, N., Dever, L. V, Kneřová, J., Waller, J. L., Gould, P. J. D., & Hartwell, J. (2020). Kalanchoë PPC1 Is Essential for Crassulacean Acid Metabolism and the Regulation of Core Circadian Clock and Guard Cell Signaling Genes[CC-BY]. *The Plant Cell*, *32*(4), 1136–1160. https://doi.org/10.1105/tpc.19.00481

Brenna, A., & Albrecht, U. (2020). Phosphorylation and Circadian Molecular Timing. *Frontiers in Physiology*, *11*(November), 1–19. https://doi.org/10.3389/fphys.2020.612510

Caplan, J. L., Kumar, A. S., Park, E., Padmanabhan, M. S., Hoban, K., Modla, S., Czymmek, K., & Dinesh-Kumar, S. P. (2015). Chloroplast Stromules Function during Innate Immunity. *Developmental Cell*, *34*(1), 45–57. https://doi.org/10.1016/j.devcel.2015.05.011

Carter, P. J., Nimmo, H. G., Fewson, C. A., & Wilkins, M. B. (1991). Circadian rhythms in the activity of a plant protein kinase. *The EMBO Journal*, *10*(8), 2063–2068.

Dalchau, N., Baek, S. J., Briggs, H. M., Robertson, F. C., Dodd, A. N., Gardner, M. J., Stancombe, M. A., Haydon, M. J., Stan, G.-B. B., Gonçalves, J. M., & Webb, A. A. R. R. (2011). The circadian oscillator gene GIGANTEA mediates a long-term response of the Arabidopsis thaliana circadian clock to sucrose. *Proceedings of the National Academy of Sciences*, *108*(12), 5104–5109. https://doi.org/10.1073/pnas.1015452108

del Río, L. A. (2015). ROS and RNS in plant physiology: an overview. *Journal of Experimental Botany*, *66*(10), 2827–2837. https://doi.org/10.1093/jxb/erv099

Dietz, K. J. (2016). Thiol-based peroxidases and ascorbate peroxidases: Why plants rely on multiple peroxidase systems in the photosynthesizing chloroplast? *Molecules and Cells*, *39*(1), 20–25. https://doi.org/10.14348/molcells.2016.2324

Dodd, A. N., Belbin, F. E., Frank, A., & Webb, A. A. R. (2015). Interactions between circadian clocks and photosynthesis for the temporal and spatial coordination of metabolism. *Frontiers in Plant Science*, *6*, 1–7. https://doi.org/10.3389/fpls.2015.00245

Dodd, A. N., Parkinson, K., & Webb, A. A. R. (2004). Independent circadian regulation of assimilation and stomatal conductance in the ztl-1 mutant of Arabidopsis. *New Phytologist*, *162*(1), 63–70.

Dodd, A. N., Salathia, N., Hall, A., Kévei, E., Tóth, R., Nagy, F., Hibberd, J. M., Millar,

A. J., & Webb, A. A. R. (2005). Plant Circadian Clocks increase Photosynthesis, Growth, Survival and Competitive Advantage. *Science*, *309*(57), 630–633. https://doi.org/10.1126/science.os-2.57.341-a

Dos Anjos, L., Pandey, P. K., Moraes, T. A., Feil, R., Lunn, J. E., & Stitt, M. (2018). Feedback regulation by trehalose 6-phosphate slows down starch mobilization below the rate that would exhaust starch reserves at dawn in Arabidopsis leaves. *Plant Direct*, *2*(8), e00078–e00078. https://doi.org/10.1002/pld3.78

Dusenge, M. E., Duarte, A. G., & Way, D. A. (2019). Plant carbon metabolism and climate change: elevated CO2 and temperature impacts on photosynthesis, photorespiration and respiration. *New Phytologist*, *221*(1), 32–49. https://doi.org/10.1111/nph.15283

Exposito-Rodriguez, M., Laissue, P. P., Yvon-Durocher, G., Smirnoff, N., & Mullineaux, P. M. (2017). Photosynthesis-dependent H2O2 transfer from chloroplasts to nuclei provides a high-light signalling mechanism. *Nature Communications*, *8*(1), 49. https://doi.org/10.1038/s41467-017-00074-w

Figueroa, C. M., & Lunn, J. E. (2016). A tale of two sugars: Trehalose 6-phosphate and sucrose. *Plant Physiology*, *172*(1), 7–27. https://doi.org/10.1104/pp.16.00417

Foyer, C. H. (2018). Reactive oxygen species, oxidative signaling and the regulation of photosynthesis. *Environmental and Experimental Botany*, *154*(April), 134–142. https://doi.org/10.1016/j.envexpbot.2018.05.003

Frank, A., Matiolli, C. C., Viana, A. J. C., Hearn, T. J., Kusakina, J., Belbin, F. E., Wells Newman, D., Yochikawa, A., Cano-Ramirez, D. L., Chembath, A., Cragg-Barber, K., Haydon, M. J., Hotta, C. T., Vincentz, M., Webb, A. A. R., & Dodd, A. N. (2018). Circadian Entrainment in Arabidopsis by the Sugar-Responsive Transcription Factor bZIP63. *Current Biology : CB*, *28*(16), 2597-2606.e6. https://doi.org/10.1016/j.cub.2018.05.092

Gibon, Y., Bläsing, O. E., Palacios-Rojas, N., Pankovic, D., Hendriks, J. H. M., Fisahn, J., Höhne, M., Günther, M., & Stitt, M. (2004). Adjustment of diurnal starch turnover to short days: depletion of sugar during the night leads to a temporary inhibition of carbohydrate utilization, accumulation of sugars and post-translational activation of ADP-glucose pyrophosphorylase in the followin. *The Plant Journal*, *39*(6), 847–862. https://doi.org/https://doi.org/10.1111/j.1365-313X.2004.02173.x

Gilman, I. S., & Edwards, E. J. (2020). Crassulacean acid metabolism. *Current Biology*, *30*(2), R57–R62. https://doi.org/10.1016/j.cub.2019.11.073

Graf, A., Schlereth, A., Stitt, M., & Smith, A. M. (2010). Circadian control of carbohydrate availability for growth in Arabidopsis plants at night. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(20), 9458–9463. https://doi.org/10.1073/pnas.0914299107

Harmer, S. L. (2009). The circadian system in higher plants. *Annual Review of Plant Biology*, *60*, 357–377. https://doi.org/10.1146/annurev.arplant.043008.092054

Harms, E., Kivimäe, S., Young, M. W., & Saez, L. (2004). Posttranscriptional and Posttranslational Regulation of Clock Genes. *Journal of Biological Rhythms*, *19*(5), 361–373. https://doi.org/10.1177/0748730404268111

Hassidim, M., Dakhiya, Y., Turjeman, A., Hussien, D., Shor, E., Anidjar, A., Goldberg, K., & Green, R. M. (2017). CIRCADIAN CLOCK ASSOCIATED1 (CCA1) and the Circadian Control of Stomatal Aperture . *Plant Physiology*, *175*(4), 1864–1877. https://doi.org/10.1104/pp.17.01214

Hatch, M. D., Agostino, A., & Burnell, J. N. (1988). Photosynthesis in phosphoenolpyruvate carboxykinase-type C4 plants: Activity and role of mitochondria in bundle sheath cells. *Archives of Biochemistry and Biophysics*,

261(2), 357–367. https://doi.org/10.1016/0003-9861(88)90351-7

Haydon, M. J., Hearn, T. J., Bell, L. J., Hannah, M. A., & Webb, A. A. R. (2013). Metabolic regulation of circadian clocks. *Seminars in Cell and Developmental Biology*, *24*(5), 414–421. https://doi.org/10.1016/j.semcdb.2013.03.007

Haydon, M. J., Mielczarek, O., Frank, A., Román, Á., & Webb, A. A. R. (2017). Sucrose and ethylene signaling interact to modulate the circadian clock. *Plant Physiology*, *175*(2), 947–958. https://doi.org/10.1104/pp.17.00592

Haydon, M. J., Mielczarek, O., Robertson, F. C., Hubbard, K. E., & Webb, A. A. R. (2013). Photosynthetic entrainment of the Arabidopsis thaliana circadian clock. *Nature*, *502*(7473), 689–692. https://doi.org/10.1038/nature12603

Hennessey, T. L., & Field, C. B. (1991). Circadian rhythms in photosynthesis: Oscillations in carbon assimilation and stomatal conductance under constant conditions. *Plant Physiology*, *96*(3), 831–836. https://doi.org/10.1104/pp.96.3.831

Heyno, E., Gross, C. M., Laureau, C., Culcasi, M., Pietri, S., & Krieger-Liszkay, A. (2009). Plastid Alternative Oxidase (PTOX) Promotes Oxidative Stress When Overexpressed in Tobacco. *Journal of Biological Chemistry*, *284*(45), 31174–31180. https://doi.org/10.1074/jbc.M109.021667

Hotta, C. T., Nishiyama Jr, M. Y., & Souza, G. M. (2013). Circadian Rhythms of Sense and Antisense Transcription in Sugarcane, a Highly Polyploid Crop. *PLoS ONE*, *8*(8). https://doi.org/10.1371/journal.pone.0071847

Hsu, P. Y., & Harmer, S. L. (2014). Wheels within wheels: The plant circadian system. *Trends in Plant Science*, *19*(4), 240–249. https://doi.org/10.1016/j.tplants.2013.11.007

Ito, S., Matsushika, A., Yamada, H., Sato, S., Kato, T., Tabata, S., Yamashino, T., & Mizuno, T. (2003). Characterization of the APRR9 Pseudo-Response Regulator Belonging to the APRR1/TOC1 Quintet in Arabidopsis thaliana. *Plant and Cell Physiology*, *44*(11), 1237–1245. https://doi.org/10.1093/pcp/pcg136

Jones, M. A. (2017). Interplay of Circadian Rhythms and Light in the Regulation of Photosynthesis-Derived Metabolism. In *Progress in Botany* (pp. 147–171). https://doi.org/10.1007/124_2017_12

Khan, S., Rowe, S. C., & Harmon, F. G. (2010). Coordination of the maize transcriptome by a conserved circadian clock. *BMC Plant Biology*, *10*(1), 126. https://doi.org/10.1186/1471-2229-10-126

Khorobrykh, S., Havurinne, V., Mattila, H., & Tyystjärvi, E. (2020). Oxygen and ROS in Photosynthesis. In *Plants* (Vol. 9, Issue 1). https://doi.org/10.3390/plants9010091

Kim, J., Geng, R., Gallenstein, R. A., & Somers, D. E. (2013). The F-box protein ZEITLUPE controls stability and nucleocytoplasmic partitioning of GIGANTEA. *Development*, *140*(19), 4060–4069. https://doi.org/10.1242/dev.096651

Kim, W. Y., Fujiwara, S., Suh, S. S., Kim, J., Kim, Y., Han, L., David, K., Putterill, J., Nam, H. G., & Somers, D. E. (2007). ZEITLUPE is a circadian photoreceptor stabilized by GIGANTEA in blue light. *Nature*, *449*(7160), 356–360. https://doi.org/10.1038/nature06132

Kölling, K., Thalmann, M., Müller, A., Jenny, C., & Zeeman, S. C. (2015). Carbon partitioning in Arabidopsis thaliana is a dynamic process controlled by the plants metabolic status and its circadian clock. *Plant, Cell & Environment*, *38*(10), 1965–1979. https://doi.org/https://doi.org/10.1111/pce.12512

Lai, A. G., Doherty, C. J., Mueller-Roeber, B., Kay, S. A., Schippers, J. H. M., & Dijkwel, P. P. (2012). Circadian Clock-Associated 1 regulates ROS homeostasis and oxidative stress responses. *Proceedings of the National Academy of Sciences*

of the United States of America, *109*(42), 17129–17134. https://doi.org/10.1073/pnas.1209148109

Lawson, T., & Blatt, M. R. (2014). Stomatal size, speed, and responsiveness impact on photosynthesis and water use efficiency. *Plant Physiology*, *164*(4), 1556–1570. https://doi.org/10.1104/pp.114.237107

Litthauer, S., Battle, M. W., Lawson, T., & Jones, M. A. (2015). Phototropins maintain robust circadian oscillation of PSII operating efficiency under blue light. *Plant Journal*, *83*(6), 1034–1045. https://doi.org/10.1111/tpj.12947

Mair, A., Pedrotti, L., Wurzinger, B., Anrather, D., Simeunovic, A., Weiste, C., Valerio, C., Dietrich, K., Kirchler, T., Nägele, T., Vicente Carbajosa, J., Hanson, J., Baena-González, E., Chaban, C., Weckwerth, W., Dröge-Laser, W., & Teige, M. (2015). SnRK1-triggered switch of bZIP63 dimerization mediates the low-energy response in plants. *ELife*, *4*, e05828. https://doi.org/10.7554/eLife.05828

Malpas, K. R., & Jones, M. A. (2016). Natural Variation of Circadian Rhythms in Kalanchoe Species. *Haseltonia*, *2016*(22), 35–42. https://doi.org/10.2985/026.022.0107

Misra, B. B., Acharya, B. R., Granot, D., Assmann, S. M., & Chen, S. (2015). The guard cell metabolome: functions in stomatal movement and global food security. *Frontiers in Plant Science*, *6*, 334. https://doi.org/10.3389/fpls.2015.00334

Mizuno, T., Nomoto, Y., Oka, H., Kitayama, M., Takeuchi, A., Tsubouchi, M., & Yamashino, T. (2014). Ambient temperature signal feeds into the circadian clock transcriptional circuitry through the EC night-time repressor in arabidopsis thaliana. *Plant and Cell Physiology*, *55*(5), 958–976. https://doi.org/10.1093/pcp/pcu030

Moseley, R. C., Mewalal, R., Motta, F., Tuskan, G. A., Haase, S., & Yang, X. (2018). Conservation and Diversification of Circadian Rhythmicity Between a Model Crassulacean Acid Metabolism Plant Kalanchoë fedtschenkoi and a Model C3 Photosynthesis Plant Arabidopsis thaliana. *Frontiers in Plant Science*, *9*(November), 1757. https://doi.org/10.3389/fpls.2018.01757

Murchie, E. H., & Lawson, T. (2013). Chlorophyll fluorescence analysis: A guide to good practice and understanding some new applications. *Journal of Experimental Botany*, *64*(13), 3983–3998. https://doi.org/10.1093/jxb/ert208

Nimmo, H. G. (2000). The regulation of phosphoenolpyruvate carboxylase in CAM plants. *Trends in Plant Science*, *5*(2), 75–80. https://doi.org/10.1016/S1360-1385(99)01543-5

Nimmo, H. G., Fontaine, V., Hartwell, J., Jenkins, G. I., Nimmo, G. A., & Wilkins, M. B. (2001). PEP carboxylase kinase is a novel protein kinase controlled at the level of expression. *New Phytologist*, *151*(1), 91–97. https://doi.org/https://doi.org/10.1046/j.1469-8137.2001.00155.x

Oakenfull, R. J., & Davis, S. J. (2017). Shining a light on the Arabidopsis circadian clock. *Plant, Cell & Environment*, *40*(11), 2571–2585. https://doi.org/10.1111/pce.13033

Rascher, U., Hütt, M. T., Siebke, K., Osmond, B., Beck, F., & Lüttge, U. (2001). Spatiotemporal variation of metabolism in a plant circadian rhythm: The biological clock as an assembly of coupled individual oscillators. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(20), 11801–11805. https://doi.org/10.1073/pnas.191169598

Resco de Dios, V., Anderegg, W. R. L., Li, X., Tissue, D. T., Bahn, M., Landais, D., Milcu, A., Yao, Y., Nolan, R. H., Roy, J., & Gessler, A. (2020). Circadian regulation does not optimize stomatal behaviour. *Plants*, *9*(1091), 1–10.

https://doi.org/10.3390/plants9091091

Resco de Dios, V., Díaz-Sierra, R., Goulden, M. L., Barton, C. V. M., Boer, M. M., Gessler, A., Ferrio, J. P., Pfautsch, S., & Tissue, D. T. (2013). Woody clockworks: circadian regulation of night-time water use in Eucalyptus globulus. *New Phytologist*, *200*, 743–752. https://doi.org/10.1111/nph.12382

Resco de Dios, V., Gessler, A., Ferrio, J. P., Alday, J. G., Bahn, M., Del Castillo, J., Devidal, S., García-Muñoz, S., Kayler, Z., Landais, D., Martín-Gómez, P., Milcu, A., Piel, C., Pirhofer-Walzl, K., Ravel, O., Salekin, S., Tissue, D. T., Tjoelker, M. G., Voltas, J., & Roy, J. (2016a). Circadian rhythms have significant effects on leaf-to-canopy scale gas exchange under field conditions. *GigaScience*, *5*(1), 43. https://doi.org/10.1186/s13742-016-0149-y

Resco de Dios, V., Loik, M. E., Smith, R., Aspinwall, M. J., & Tissue, D. T. (2016b). Genetic variation in circadian regulation of nocturnal stomatal conductance enhances carbon assimilation and growth. *Plant Cell and Environment*, *39*(1), 3–11. https://doi.org/10.1111/pce.12598

Rugnone, M. L., Soverna, A. F., Sanchez, S. E., Schlaen, R. G., Hernando, C. E., Seymour, D. K., Mancini, E., Chernomoretz, A., Weigel, D., Mas, P., & Yanovsky, M. J. (2013). LNK genes integrate light and clock signaling networks at the core of the Arabidopsis oscillator. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(29), 12120–12125. https://doi.org/10.1073/pnas.1302170110

Salomé, P. A., & McClung, C. R. (2005). Pseudo-response Regulator 7 and 9 are partially redundant genes essential for the temperature responsiveness of the Arabidopsis circadian clock. *Plant Cell*, *17*(3), 791–803. https://doi.org/10.1105/tpc.104.029504

Salomé, P. A., Michael, T. P., Kearns, E. V., Fett-Neto, A. G., Sharrock, R. A., & McClung, C. R. (2002). The out of phase 1 mutant defines a role for PHYB in circadian phase control in arabidopsis. *Plant Physiology*, *129*(4), 1674–1685. https://doi.org/10.1104/pp.003418

Schiller, K., & Bräutigam, A. (2021). Engineering of Crassulacean Acid Metabolism. *Annual Review of Plant Biology*, *72*, 77–103. https://doi.org/10.1146/annurev-arplant-071720-104814

Schulze, E.-D., Beck, E., Buchmann, N., Clemens, S., Müller-Hohenstein, K., & Scherer-Lorenzen, M. (2019). *Plant Ecology* (2nd ed.). Springer. https://doi.org/10.1007/978-3-662-56233-8

Scialdone, A., Mugford, S. T., Feike, D., Skeffington, A., Borrill, P., Graf, A., Smith, A. M., & Howard, M. (2013). Arabidopsis plants perform arithmetic division to prevent starvation at night. *ELife*, *2*, e00669. https://doi.org/10.7554/eLife.00669

Sharkey, T. D. (2019). Discovery of the canonical Calvin–Benson cycle. *Photosynthesis Research*, *140*(2), 235–252. https://doi.org/10.1007/s11120-018-0600-2

Simon, N. M. L., Graham, C. A., Comben, N. E., Hetherington, A. M., & Dodd, A. N. (2020). The circadian clock influences the long-term water use efficiency of Arabidopsis1[open]. *Plant Physiology*, *183*(5), 317–330. https://doi.org/10.1104/pp.20.00030

Simon, N. M. L., Litthauer, S., Jones, M. A., & Dodd, A. N. (2019). *Interactions Between Circadian Rhythms, ROS and Redox BT - Redox Homeostasis in Plants: From Signalling to Stress Tolerance* (S. K. Panda & Y. Y. Yamamoto (eds.); pp. 67–84). Springer International Publishing. https://doi.org/10.1007/978-3-319-95315-1_4

Smith, A. M. (2012). Starch in the Arabidopsis plant. *Starch/Staerke*, *64*(6), 421–434.

https://doi.org/10.1002/star.201100163

Smith, A. M., & Stitt, M. (2007). Coordination of carbon supply and plant growth. *Plant, Cell and Environment*, *30*(9), 1126–1149. https://doi.org/10.1111/j.1365-3040.2007.01708.x

Sorkin, M. L., & Nusinow, D. A. (2021). Time Will Tell: Intercellular Communication in the Plant Clock. *Trends in Plant Science*, *26*(7), 706–719. https://doi.org/10.1016/j.tplants.2020.12.009

Stitt, M., Lunn, J., & Usadel, B. (2010). Arabidopsis and primary photosynthetic metabolism – more than the icing on the cake. *The Plant Journal*, *61*(6), 1067–1091. https://doi.org/https://doi.org/10.1111/j.1365-313X.2010.04142.x

Sulpice, R., Flis, A., Ivakov, A. A., Apelt, F., Krohn, N., Encke, B., Abel, C., Feil, R., Lunn, J. E., & Stitt, M. (2014). Arabidopsis Coordinates the Diurnal Regulation of Carbon Allocation and Growth across a Wide Range of Photoperiods. *Molecular Plant*, *7*(1), 137–155. https://doi.org/10.1093/mp/sst127

Tsai, A. Y. L., & Gazzarrini, S. (2014). Trehalose-6-phosphate and SnRK1 kinases in plant development and signaling: The emerging picture. *Frontiers in Plant Science*, *5*(APR), 1–11. https://doi.org/10.3389/fpls.2014.00119

Voet, D., Voet, J. G., & Pratt, C. W. (2016). *Fundamentals of Biochemistry: Life at the Molecular Level.* (5th ed.). Wiley.

Wang, L., Kim, C., Xu, X., Piskurewicz, U., Dogra, V., Singh, S., Mahler, H., & Apel, K. (2016). Singlet oxygen- and EXECUTER1-mediated signaling is initiated in grana margins and depends on the protease FtsH2. *Proceedings of the National Academy of Sciences*, *113*(26), E3792 LP-E3800. https://doi.org/10.1073/pnas.1603562113

Wang, Y., Loake, G., & Chu, C. (2013). Cross-talk of nitric oxide and reactive oxygen species in plant programed cell death. In *Frontiers in Plant Science* (Vol. 4, p. 314). https://www.frontiersin.org/article/10.3389/fpls.2013.00314

Wang, Z. Y., & Tobin, E. M. (1998). Constitutive expression of the CIRCADIAN CLOCK ASSOCIATED 1 (CCA1) gene disrupts circadian rhythms and suppresses its own expression. *Cell*, *93*(7), 1207–1217. https://doi.org/10.1016/S0092-8674(00)81464-6

Webb, A. A. R., Seki, M., Satake, A., & Caldana, C. (2019). Continuous dynamic adjustment of the plant circadian oscillator. *Nature Communications*, *10*(1), 4–9. https://doi.org/10.1038/s41467-019-08398-5

Winter, K. (2019). Ecophysiology of constitutive and facultative CAM photosynthesis. *Journal of Experimental Botany*, *70*(22), 6495–6508. https://doi.org/10.1093/jxb/erz002

Winter, K., & Smith, J. A. C. (2022). CAM photosynthesis: the acid test. *New Phytologist*, *233*(2), 599–609. https://doi.org/10.1111/nph.17790

Wurzinger, B., Nukarinen, E., Nägele, T., Weckwerth, W., & Teige, M. (2018). The snrk1 kinase as central mediator of energy signaling between different organelles. *Plant Physiology*, *176*(2), 1085–1094. https://doi.org/10.1104/pp.17.01404

Xie, Q., Wang, P., Liu, X., Yuan, L., Wang, L., Zhang, C., Li, Y., Xing, H., Zhi, L., Yue, Z., Zhao, C., McClung, C. R., & Xu, X. (2014). LNK1 and LNK2 Are Transcriptional Coactivators in the Arabidopsis Circadian Oscillator . *The Plant Cell*, *26*(7), 2843–2857. https://doi.org/10.1105/tpc.114.126573

Zeeman, S. C., Kossmann, J., & Smith, A. M. (2010). Starch: Its Metabolism, Evolution, and Biotechnological Modification in Plants. *Annual Review of Plant Biology*, *61*(1), 209–234. https://doi.org/10.1146/annurev-arplant-042809-112301