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# Circadian regulation of photosynthesis and transpiration from genes to ecosystems

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## ABSTRACT

Circadian regulation is an endogenous self-sustaining mechanism that drives temporal gene expression and, amongst others, affects the diurnal patterns of photosynthesis ( $A$ ) and stomatal conductance ( $g_s$ ). Here we review current knowledge on how circadian regulation drives diurnal gas exchange from genes to ecosystems in the field. Molecular mechanisms underlying the structure of circadian clocks and how they regulate  $A$  and  $g_s$  in a few model species are starting to be elucidated but additional data are required to understand regulation across phylogenies, especially within the gymnosperms, and across environments and scales. Circadian rhythms were responsible for 15–25% and for 30–35% of the daytime oscillations in  $A$  and  $g_s$ , respectively, across the C3 and C4 species for which data are available. Consequently, circadian effects over diurnal gas exchange are of similar magnitude to the effects of temperature or vapor pressure deficit. Moreover, recent findings indicate how circadian rhythms could exert significant impacts on ecosystem patterns of gas exchange, which would challenge conventional approaches to derive the environmental flux dependences. Progress in transferring laboratory findings to the field is being hampered by lack of suitable experimental and modeling facilities that can disentangle circadian effects from environmental responses in the field and in ecosystems, and methodological recommendations are offered. The effects of environmental stressors on circadian regulation of gas exchange are also poorly understood. We document how circadian control of gas exchange may be adaptive by allowing plants to anticipate highly predictable environmental cues, but also by increasing the diversity of potential gas exchange responses to environmental variation in plant populations.

## 1. Introduction

The Earth rotates on its axis every day and around the sun every year. Day and night transitions and photoperiodic oscillations vary deterministically as a function of time and location and, consequently, constitute the most predictable environmental cue. These cyclic oscillations, repeated for a few billion years, have influenced life through the evolution of circadian clocks, amongst others (Pittendrigh, 1981). The circadian clock is an endogenous subcellular mechanism that allows organisms to tell the time and to consequently adjust their metabolism in advance of predictable environmental cues, such as dawn and dusk transitions.

The discovery of circadian rhythms predates that of photosynthesis and is often attributed to de Mairan (1729), who observed continuous nyctinastic movements under protracted darkness. Circadian regulation in photosynthesis in C3 “higher” plants was first described by Hillman (1971) (although it had been previously described in algae), and first measurements of circadian regulation in stomatal aperture were

provided by Mansfield and Heath (1963) in the dark and by Martin and Meidner (1971) in the light. A large body of literature documenting circadian regulation in gas exchange has developed over the last five decades, but most of this work has concentrated in a few model species and within lab settings, where environmental conditions can be controlled straightforwardly.

Understanding diurnal variations in photosynthesis and transpiration in the field has also been the subject of considerable research in the last few decades, but this work has mostly focused on understanding direct physiological responses to temperature, radiation and other changes in the physical environment over the day and the night. The effect of circadian regulation over diurnal patterns of field gas exchange has traditionally been considered negligible. However, recent studies on the ecological relevance of circadian rhythms indicate how circadian regulation could explain up to 30% of the diurnal variation in net CO<sub>2</sub> exchange ( $A$ ) and 70% in stomatal conductance ( $g_s$ ) at leaf and at whole canopy scales during a 24-h cycle (Resco de Dios et al., 2016a), and how the effects of circadian regulation over the temporal pattern of

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nighttime  $g_s$  could be equal or more important than the effects of vapour pressure deficit (Resco de Dios et al., 2013a,b).

In this manuscript, we will review our current knowledge on circadian regulation of photosynthesis and transpiration in C3 and C4 plants, taking trees and other woody species into particular account. More specifically, we seek to synthesize our current knowledge on how circadian regulation affects diurnal gas exchange in the field at leaf, canopy and ecosystem scales. We will first explain what the circadian clock is and what are its mechanistic underpinnings. Next, we will describe the mechanisms by which circadian regulation affects transpiration and then the mechanisms underlying circadian regulation of photosynthesis. Within these sections we provide an account of the species where circadian transpiration and photosynthesis have been examined and discuss how the mechanisms may vary across phylogenies. We will furthermore discuss different methods to measure circadian regulation in the field and we will explain why current methods used by molecular biology cannot be readily applied. We will then focus on how to model circadian regulation and on why it is necessary to study the role of circadian clocks as drivers of gas exchange under field conditions. Finally, we will show the adaptive potential for circadian regulation of gas exchange. The review is based upon the articles that have been published on “circadian AND stomata\*” and “circadian AND photosynthesis”, according to Web of Science (search strings entered on 5th July 2017). Ultimately, we hope that our review will help in bridging the gap between molecular studies on clock action, mainly performed under lab conditions, and ecological studies on diurnal gas exchange including old-grown trees and forest ecosystems.

## 2. What is the plant circadian clock

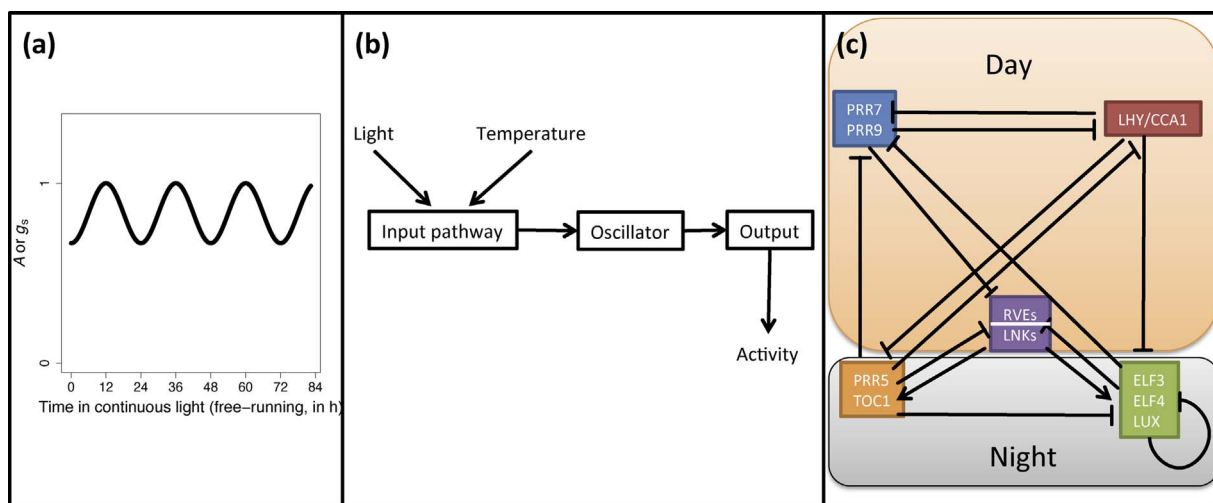
The circadian clock regulates the temporal pattern of expression in ~30% of the genome in the model plant *Arabidopsis thaliana* in a manner that is independent, to some extent, of environmental fluctuations (Michael et al., 2008). The end-result is a rhythmic oscillation in various aspects of metabolism. For instance, upon exposure to constant environmental conditions of light, temperature, etc. for a few days, an oscillation in gas exchange, amongst other processes, with a 24-h period becomes apparent (Fig. 1a). Moreover, circadian oscillations are temperature-compensated, meaning that the period is preserved across different temperatures and can be phase-shifted by light. Circadian rhythms are sometimes mistaken for diurnal variations (King et al., 2013), but the word *circadian* implies the presence of a self-sustaining oscillator with a period of approximately (*circa*) 24-h (*dies*).

Detailed reviews on the structure of circadian clocks have been recently published (Greenham and McClung, 2015; Hernando et al., 2017; Millar, 2016). Here we seek to provide an introductory view on circadian clocks that provides a basic understanding for field plant or ecosystem scientists.

The circadian clock was initially viewed as having three different components: an input system, providing environmental information; a central oscillator, composed of the “canonical clock genes” and that constitutes the core structure of the clock; and the outputs, comprising the clock-driven downstream processes (Lakin-Thomas, 2001) (Fig. 1b). The central oscillator is composed by different transcription–translation feedback loops, whereby the canonical clock genes are rhythmically transcribed and translated into proteins that feedback to inhibit their own transcription. In its current model, the transcription–translation feedback loops conforming the central oscillator consist of a ring of four repressors (quadrirepressilator) with some transcriptional activators (Fig. 1c) (Hernando et al., 2017; Millar, 2016).

The expression of CIRCADIAN CLOCK ASSOCIATED 1 (CCA1), LATE ELONGATED HYPOCOTYL (LHY) increases from midnight until reaching a peak at dawn, and inhibit the transcriptional induction of PSEUDORESPONSE REGULATOR 5 (PRR5) and TIMING OF CAB EXPRESSION 1 (TOC1). The expression of PRR7 and PRR9 increase during the morning and inhibit expression of LHY and CCA1, ending the morning phase. In turn, falling levels of CCA1 and LHY allow for expression of EARLY FLOWERING 3 (ELF3), ELF4 and LUX ARRHYTHMO (LUX), the so-called evening complex, with expression peaks before dusk. The evening complex then inhibits expression of the PRRs and ends the day phase. Additionally, the transcriptional regulators associated to the photoreceptors NIGHT LIGHT INDUCIBLE AND LOCK REGULATED 1 and 2 (LNK1 and LNK2) promote the expression of PRR5, TOC1 and ELF4 and, in turn, PRRs and TOC1 bind to LNK promoters and inhibit their expression (Hernando et al., 2017; Millar, 2016). Such a complex molecular structure is thought to be a requirement for allowing accurate response under varied, real-life photo-periodic oscillations (Troein et al., 2009). Additionally, inputs (light and temperature signaling) and outputs (metabolism) interact with the central oscillator such that different metabolic reactions (such as photosynthesis) are both, masters and slaves to the clock (Shin et al., 2017).

Circadian clocks occur in every cell individually. In fact, coordination across circadian clocks within an organ is more driven by external cues than by internal communication signals (Wenden et al., 2012). Consequently, circadian clocks within an organism or organ may show contrasting phases and, for instance, guard cell clocks show different



**Fig. 1.** Structure of the circadian clock. (a) 24-h oscillations in C assimilation (A) or stomatal conductance ( $g_s$ ) are often observed in the free-run (continuous illumination). (b) the classical view of the circadian clock includes inputs, the central oscillator, and outputs. (c) simplified view of the structure of the transcriptional-translational feedbacks that form the central oscillator (modified from (Hernando et al., 2017) and Millar (2016)). Arrows indicate activation, lines with a flat head indicate inhibition.

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