



Research paper

Circadian rhythms regulate the environmental responses of net CO₂ exchange in bean and cotton canopies

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ABSTRACT

Studies on the dependence of the rates of ecosystem gas exchange on environmental parameters often rely on the up-scaling of leaf-level response curves ('bottom-up' approach), and/or the down-scaling of ecosystem fluxes ('top-down' approach), where one takes advantage of the natural diurnal covariation between the parameter of interest and photosynthesis rates. Partly independent from environmental variation, molecular circadian clocks drive ~24 h oscillations in leaf-level photosynthesis, stomatal conductance and other physiological processes in plants under controlled laboratory conditions. If present and of sufficient magnitude at ecosystem scales, circadian regulation could lead to different results when using the bottom-up approach (where circadian regulation exerts a negligible influence over fluxes because the environment is modified rapidly) relative to the top-down approach (where circadian regulation could affect fluxes as it requires the passage of a few hours). Here we dissected the drivers of diurnal net CO₂ exchange in canopies of an annual herb (bean) and of a perennial shrub (cotton) through a set of experimental manipulations to test for the importance of circadian regulation of net canopy CO₂ exchange, relative to that of temperature and vapor pressure deficit, and to understand whether circadian regulation could affect the derivation of environmental flux dependencies. Contrary to conventional wisdom, we observed how circadian regulation exerted controls over net CO₂ exchange that were of similar magnitude to the controls exerted by direct physiological responses to temperature and vapor pressure deficit. Diurnal patterns of net CO₂ exchange could only be explained by considering effects of environmental responses combined with circadian effects. Consequently, we observed significantly different results when inferring the dependence of photosynthesis over temperature and vapor pressure deficit when using the top-down and the bottom up approaches.

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1. Introduction

Models of land-atmosphere interactions and projections of carbon cycling under climate change rely on accurate representations of the underlying biophysical processes. Diurnal patterns are a key feature of observed ecosystem fluxes and arise largely from plant ecophysiological responses to external drivers of solar irradiance,

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temperature and relative humidity, amongst others (Hollinger et al., 1994; Jones, 2014; Richardson et al., 2007; Schwalm et al., 2010; Sellers et al., 1997). Consequently, models estimating day-time variation in ecosystem fluxes often rely upon the temporal extrapolation of short-term response functions of the flux to a given driver (“bottom-up” hereafter), or upon the temporal co-variation between fluxes and drivers (“top-down” hereafter). Concomitantly, we have known for long that the circadian clock is an important regulator of plant metabolism, including photosynthetic gas exchange in leaves (Edwards et al., 2011; Harmer et al., 2000; Lüttge, 2003). However, the role of circadian regulation of canopy-scale CO₂ exchange remains largely untested. Circadian regulation of canopy photosynthesis, if present and of sufficient magnitude, could have implications for measurement and modeling of ecosystem fluxes.

Circadian regulation leads to daily rhythms of metabolism with a period of ~24 h that persist even in the absence of variation in environmental parameters. Circadian rhythms provide an evolutionary advantage by allowing the plant to anticipate predictable environmental patterns, such as the dawn/dusk transitions (Resco de Dios et al., 2016b), by temporally synchronizing, sequencing or separating processes that are biologically-associated or incompatible (Harmer et al., 2000) and by mediating in the response to the change in seasons thorough photoperiodic responses (Ibanez et al., 2010).

Circadian rhythms in vascular plants arise from the “circadian oscillator”, a complex gene autoregulatory network that comprises interlocked transcription-translation feedback loops. The phase of the oscillator is adjusted based upon the light and temperature regimes of the previous days, a process termed “entrainment”, and that allows correct tracking of dawn and dusk (Takahashi et al., 2015).

The circadian oscillator exerts a prevalent influence upon plant cells. About one-third of all transcripts in the model species *Arabidopsis thaliana* are regulated by the circadian clock (Covington et al., 2008). Among other processes, leaf CO₂ exchange is regulated by the circadian oscillator in a wide variety of species (Dodd et al., 2014; Edwards et al., 2011; Hennessey et al., 1993; Yakir et al., 2007). Moreover, recent studies show that photosynthesis is a key component of the circadian oscillator itself, and sugar signals mediate the output of the circadian oscillator (Haydon et al., 2013). Consequently, a diurnal pattern in leaf level assimilation can be observed even when radiation, vapor pressure deficit, temperature and other environmental drivers are held constant over a few days (Resco et al., 2009).

Although the relevance of circadian controls over cell- and leaf-level processes is well documented (Hsu and Harmer, 2014; Mas and Yanovsky, 2009; Smith and Stitt, 2007), studies on its effects at the scale of ecosystem-level gas exchange are still scarce. Some studies, which apply statistical filtering to the physical drivers to emulate constant conditions, provide circumstantial support for the importance of circadian entrainment in net ecosystem CO₂ exchange (Doughty et al., 2006; Resco de Dios et al., 2012). Moreover, circadian regulation of nocturnal stomatal conductance has been linked to whole-tree sap-flux (Resco de Dios et al., 2013) and canopy-level transpiration (Resco de Dios et al., 2015). Direct evidence for a circadian effect on photosynthesis at high organizational scales (i.e. canopy and ecosystem) has only been recently observed (Resco de Dios et al., 2016a), where 20–28% of the variation in net canopy CO₂ assimilation (A_c) was due to circadian regulation under experimental conditions where there was no temporal variation in radiation, temperature, humidity and other environmental cues during 48 h.

However, although circadian regulation is expressed at canopy scales, its potential implications for inference and interpretation of ecosystem flux dynamics are still poorly understood (Dietze, 2014;

Dodd et al., 2014; Resco et al., 2009). Here we test whether circadian regulation affects current methods of deriving environmental flux dependencies. That is, we test whether similar associations between A_c and air temperature (T_{air}), and between A_c and vapor pressure deficit (VPD), are obtained by either using the natural diurnal co-variation between A_c and drivers (where circadian action could interfere as the method requires environmental variation during a few hours), or using a short-term ramped response function (where circadian action has a negligible effect, as response curves are often conducted within minutes). We propose that there will be differences between both methods due to circadian regulation. That is, we hypothesize that canopy-level carbon assimilation is jointly regulated by endogenous circadian processes and the direct impacts of the physical environment on plant physiology (Resco de Dios et al., 2012). We address this hypothesis by examining canopy assimilation patterns in large macrocosms within an Ecotron (Milcu et al., 2014; Roy et al., 2016) planted with monocultures of *Phaseolus vulgaris* (bean, an herb) and *Gossypium hirsutum* (cotton, a shrub). These two species were chosen as they belong to contrasting functional types (annual herb vs perennial shrub) and show high agronomic and economic value.

2. Material and methods

2.1. Ecotron and general experimental set-up

The experiment was performed at the Macrocosms platform of the Montpellier European Ecotron, Centre National de la Recherche Scientifique (CNRS, France). Full details of experimental set-up have been provided elsewhere (Resco de Dios et al., 2016a; Resco de Dios et al., 2015). In short, we used 6 outdoor macrocosms (3 planted with bean and 3 with cotton) where the main abiotic (radiation, air temperature, humidity and CO₂ concentration) drivers were automatically controlled. In each macrocosm, plants were grown on a soil (area of 2 m², depth of 2 m) collected from the flood plain of the Saale River near Jena, Germany, and used in a previous Ecotron experiment on biodiversity (Milcu et al., 2014). After that experiment, the soil was ploughed down to 40 cm and fertilized with 25/25/35 NPK (MgO, SO₃ and other oligoelements were associated in this fertilizer: Engrais bleu universel, BINOR, Fleury-les-Aubrais, FR).

The soil was regularly watered to ca. field capacity by drip irrigation, although irrigation was stopped during each measurement campaign (few days) to avoid interference with water flux measurements. However, no significant differences (at $P < 0.05$, paired t -test, $n = 3$) in leaf water potential occurred between the beginning and end of these measurement campaigns, indicating no effect of a potentially declining soil moisture on leaf hydration.

Environmental conditions within the macrocosms (excluding the experimental periods) were set to mimic outdoor conditions, but did include a 10% light reduction by the macrocosm dome cover. During experimental periods, light was controlled by placing a completely opaque fitted cover on each dome to block external light inputs (PVC coated polyester sheet Ferrari 502, assembled by IASO, Lleida, Spain), and by using a set of 5 dimmable plasma lamps (GAN 300 LEP with the Luxim STA 41.02 bulb, with a sun-like light spectrum); these lamps were hung 30 cm above the plant canopy and provided a PAR of 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (the maximum possible by those lamps). We ensured target radiation was achieved by measuring PAR at canopy level with a quantum sensor (Li-190, LI-COR Biosciences, Lincoln, NE, USA) in each macrocosm (Fig. 1). CO₂ concentrations were held constant at 400 ppm.

Bean and cotton were planted in 5 different rows within the domes on 10th July 2013, one month before the start of the measurements, and thinned to densities of 10.5 and 9 individuals

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