



## Night and day – Circadian regulation of night-time dark respiration and light-enhanced dark respiration in plant leaves and canopies



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### ABSTRACT

The potential of the vegetation to sequester C is determined by the balance between assimilation and respiration. Respiration is under environmental and substrate-driven control, but the circadian clock might also contribute.

To assess circadian control on night-time dark respiration ( $R_D$ ) and on light enhanced dark respiration (LEDR) – the latter providing information on the metabolic reorganization in the leaf during light-dark transitions – we performed experiments in macrosystems hosting canopies of bean and cotton. Under constant darkness (plus constant air temperature and air humidity), we tested whether circadian regulation of  $R_D$  scaled from leaf to canopy respiration. Under constant light (plus constant air temperature and air humidity), we assessed the potential for leaf-level circadian regulation of LEDR.

There was a clear circadian oscillation of leaf-level  $R_D$  in both species and circadian patterns scaled to the canopy. LEDR was under circadian control in cotton, but not in bean indicating species-specific controls.

The circadian rhythm of LEDR in cotton might indicate variable suppression of the normal cyclic function of the tricarboxylic-acid-cycle in the light. Since circadian regulation is assumed to act as an adaptive memory to adjust plant metabolism based on environmental conditions from previous days, circadian control of  $R_D$  may help to explain temporal variability of ecosystem respiration.

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### 1. Introduction

Terrestrial ecosystems provide important stores for carbon (C) vulnerable to global change agents, including altered precipitation and increased temperature and CO<sub>2</sub> concentrations (Ciais et al.,

2005; Reichstein et al., 2013; Schimel et al., 2015). The potential of the vegetation to sequester C from the atmosphere is mainly determined by the balance between C assimilation – well studied and central in many studies (Farquhar et al., 1980; Ainsworth and Long, 2005; Chaves et al., 2009) – and the much less well understood complex set of processes, collectively referred to as ecosystem respiration, that return CO<sub>2</sub> to the atmosphere on a range of timescales (Högberg and Read, 2006; Trumbore, 2006). There are particular conditions and systems where emissions of volatile organic compounds (VOC, e.g. Kesselmeier et al., 2002; Brüggemann and Schnitzler, 2002) or wildfires (Bond Lamberty et al., 2007) might be of importance, but respiration has been postulated to be the main determinant of the C balance in terrestrial ecosystems (Valentini et al., 2000). Various processes are important to this balance and they are interlinked on many different spatial and temporal scales.

Plant respiration is known to be directly controlled by environmental factors among which temperature is the most important one, with plants experiencing long- and short-term acclimation (e.g. Atkin and Tjoelker, 2003). Increasing air temperatures in the future might cause substantial increases in respiratory carbon fluxes at leaf and canopy scales, which would impact the carbon balance of terrestrial vegetation (Slot and Kitajima, 2014). Plant respiration also depends on the amount and availability of respiratory substrate, which is in turn related to light availability and photosynthesis (Högberg and Read, 2006). Moreover, the demand of sink tissues strongly affects respiration (e.g. Hagedorn et al., 2016). Substrate supply depends on plant physiological processes that regulate yield and composition of C assimilates, as well as their distribution among maintenance, defense, growth, storage, and export of organic compounds to the rhizosphere (Trumbore, 2006). These processes act on timescales of hours to months depending on the plant species.

In addition to direct environmental and substrate-driven control, respiration might also be under circadian regulation, but there are conflicting reports in the literature, with circadian rhythms observed in some species (Hillman, 1970; Hansen, 1977) but not in others (e.g. Hennessey et al., 1993). The circadian clock is an endogenous timer that regulates the transcription of up to 90% of the genome in the model species *Arabidopsis thaliana* (Michael et al., 2008). The interactive regulation between different clock genes with transcriptional-translational negative feedback loops is central for the function of the circadian oscillator (Alabadí et al., 2001) and substantial increases in photosynthesis, growth and survival are conferred by correct matching of the circadian clock period with that of the external light-dark cycle (Dodd et al., 2005). The daily protein expression rhythms observed for enzymes central to glycolysis (e.g. pyruvate kinase) or to the tricarboxylic acid (TCA) cycle (e.g. isocitrate dehydrogenase and succinate dehydrogenase) suggest that these respiratory pathways may also be under circadian control (Wijnen and Young, 2006). Even though the molecular mechanisms of the circadian control are well described (Harmer, 2009), the results become more ambiguous at higher organizational scales, such as the organ level, and we still lack information whether circadian rhythms scale to plant canopies or whole ecosystems. Using statistical filtering techniques, there is indirect evidence that net ecosystem CO<sub>2</sub> exchange (NEE) is affected by circadian regulation (Doughty et al., 2006; Resco de Dios et al., 2012). Moreover, Resco de Dios et al. (2015) showed that circadian control of stomatal conductance affected night-time canopy transpiration. However, it is unknown whether these scaling effects from the leaf to the canopy or the whole ecosystem also matter for night-time respiration. If ecosystem respiration were affected by circadian control, this could have impacts on the calculation of ecosystem gross CO<sub>2</sub> assimilation rates. For many of these approaches the temperature dependency of night-time respiration is used to infer day-time ecosystem

respiration assuming that temperature is the main driver for respiration fluxes. From the measured NEE and the calculated day-time respiration, photosynthetic CO<sub>2</sub> fluxes are derived (Reichstein et al., 2005). Not accounting for circadian rhythms of respiration could thus introduce errors to ecosystem flux separation approaches.

Dark respiration of autotrophic tissues is strongly suppressed in the light (Atkin et al., 2000; Tcherkez et al., 2005) with the reorganization of the TCA cycle under illumination considered an important underlying mechanism (Tcherkez et al., 2009). When light exposed leaves are transferred into darkness, an intensification of the respiratory flux is observed in the short-term that is referred to as light enhanced dark respiration (LEDR). LEDR has been defined as the enhancement of the flux of respiratory CO<sub>2</sub> directly after darkening of a light acclimated leaf in a photosynthesis-dependent manner (Azcon-Bieto and Osmond, 1983; Atkin et al., 2000). It has been observed that the CO<sub>2</sub> released directly after darkening is also <sup>13</sup>C enriched (Barbour et al., 2007) and that the extent of <sup>13</sup>C enrichment is related to the cumulative amount of photosynthetically fixed CO<sub>2</sub> during the day (Hymus et al., 2005). LEDR is not simply a measurement artifact that occurs when light-acclimated leaves are darkened under experimental conditions, as it also occurs in the field in day-night transitions (Barbour et al., 2011). These authors observed that an increase in δ<sup>13</sup>C of leaf- and ecosystem-respired CO<sub>2</sub> occurs after sunset and they estimated that significant amounts of carbon could be released by LEDR, depending on the amount of cumulatively fixed carbon in the preceding light period.

Several studies indicated that malate accumulation over the day and decarboxylation after darkening could be a reason for the observed <sup>13</sup>C enrichment (Gessler et al., 2009; Tcherkez, 2010; Werner, 2010). Werner et al. (2011) provided a mechanistic concept for the observed <sup>13</sup>C enrichment pattern and the linked increase of respiration during LEDR. Both can be explained by the closure of the TCA cycle, which is non-cyclic in the light (Tcherkez et al., 2009), occurring immediately after the light-to-dark transition, in connection with the interplay of the malate catabolizing enzymes that facilitate the degradation of the <sup>13</sup>C enriched malate pool accumulated under illumination. The intensity of the respiration pulse and its <sup>13</sup>C isotopic enrichment seem to be directly indicative of the extent of malate accumulation in the light and the ability to degrade this malate upon darkening (Lehmann, 2014). Still, in different species different organic acids besides malate might be involved in fueling LEDR (Lehmann et al., 2016). Assessment of LEDR provides insights into the reorganization of central metabolic pathways in leaves during light-dark transitions (Werner et al., 2011). The two processes (malate accumulation and degradation) seem to be directly related to the cumulative carbon assimilation before darkening, as this parameter is also correlated with LEDR. However, we do not know yet whether the processes involved are also under circadian control. Gessler et al. (2009) did not observe a dependence of LEDR <sup>13</sup>C enrichment on cumulative photosynthesis in *Ricinus communis*, and this observation suggests that other factors might additionally affect the metabolic pathways responsible for malate accumulation and degradation.

In order to assess circadian control on night-time dark respiration (R<sub>D</sub>) and LEDR, we performed two experiments in experimental macrocosms (Milcu et al., 2014) hosting canopies of *Phaseolus vulgaris* (bean, a herb) and *Gossypium hirsutum* (cotton, a shrub) exposed to constant darkness and constant light, respectively, together with constant temperature and air humidity. In the first experiment (constant darkness), we tested whether circadian regulation of night-time leaf R<sub>D</sub> scaled to whole canopy respiration. In this experiment, the plant canopies were exposed, after an entrainment phase with typical diel light-dark rhythms, to

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