Letters to the Editor

Circadian regulation and diurnal variation in gas exchange

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Dear Sir,

The uptake of carbon dioxide through the stomata inexorably leads to transpirational water losses and evolutionary theories hold that plants balance this trade-off by optimizing carbon gain per unit water lost. However, the physiological mechanisms underpinning optimal stomatal regulation remain to be elucidated. In particular, a key assumption is that assimilation and stomatal conductance are tightly coordinated at diurnal time scales, but recent reviews highlight that whether and how such coordination is achieved remains elusive (Matthews et al., 2017). Circadian regulation is emerging as an additional mechanism potentially affecting the synchrony of the photosynthesis \( (A) \) and stomatal conductance \( (g_s) \) responses.

The circadian clock is an endogenous timer of plant metabolism that regulates the diurnal pattern of gene expression. Amongst other processes, \( A \) and \( g_s \) are under circadian control (Fig. 1). However, there is not a single “master rhythm” that leads to a unique temporal pattern of gas exchange in plants. On the contrary, clocks in plants are, to a certain degree, tissue-specific and different clocks are entrained with different phases, amplitudes and periods. For instance, guard cell clocks often show longer periods than mesophyll clocks (Yakir et al, 2011). In turn, circadian regulation in \( A \) is independent from circadian regulation in \( g_s \) (Dodd et al. 2004), and the existence of these different, and to a degree mutually independent, clock types could explain why.

I digitized published records of circadian oscillations in \( A \) and \( g_s \) measured for different C3 crop species under continuous light to informally assess potential in circadian regulation as a driver of diurnal gas exchange (Fig. 1). The overall variation during the “subjective day”, was of 15-25% in \( A \) and of 30-35% in \( g_s \), respectively, across the analyzed species. Importantly, this degree of variation was comparable to that observed in response to diurnal changes in temperature or vapour pressure deficit (Resco de Dios et al. 2017). Furthermore, the temporal pattern in \( A \) and \( g_s \) was decoupled in, for instance, \( A. \ thaliana \), where \( g_s \) increased in the subjective morning and decreased in the subjective afternoon, while \( A \) increased at subjective midday and stayed high through the subjective afternoon. Additionally, peaks in \( A, g_s \) and \( W_i \) (intrinsic water use efficiency) varied in a species-specific manner although the environment did not change. For instance, \( W_i \) peaked in the subjective early morning in \( M. \ indica \) and in the subjective late afternoon for \( P. \ vulgaris \) and \( L. \ esculentum \). Consequently, a significant proportion of the diurnal variation in \( A \) and \( g_s \) may be largely recreated when solely examining circadian regulation, and the amplitude of the circadian control over \( A \) is relatively smaller than over \( g_s \).

Afternoon declines in \( A \) and \( g_s \) have also been investigated for long, and the response has been partly attributed to feedback inhibition from photosynthate accumulation, photorespiration, and hydraulic feedbacks, amongst other process. Data from Fig. 1 was always collected under levels of photosynthetically active radiation that limit \( A \) (between 40 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) in Arabidopsis and 500 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) in cotton and bean) and well-watered conditions, where carbohydrate build-up, photorespiration or hydraulics would have exerted a
limited impact. Alternatively, circadian “gating”, whereby the effect of a stimulus depends on
time of day, presents an alternative, yet much less explored, explanation for understanding
afternoon declines in gas exchange. For instance, Mencuccini et al. (2000) observed how, for
a given level of leaf water potential and of abscisic acid (ABA) concentrations, \( g_s \) was lower in
the afternoon than in the morning. This is because stomatal closure is more sensitive to ABA
in the afternoon than in the morning due to interactions between the clock component
TIMING OF CAB EXPRESSION 1 (TOC1) and ABA-related genes (Seo and Mas, 2015).
There are additional gated responses in stomata and also additional mechanisms that could
explain how circadian regulation would lead to an afternoon decline in gas exchange. A full
review is not intended here, but these examples may suffice to illustrate how circadian
rhythmicity may help to better understand afternoon declines in \( A \) and \( g_s \).

It is also poorly understood how circadian effects over diurnal gas exchange scale up
to affect canopies and ecosystems and whether inclusion in models would provide significant
increases in model performance. Recent studies have quantified that circadian regulation in
gas exchange was responsible for 30% and 70% of the diurnal oscillations in \( A \) and \( g_s \),
respectively, in bean and cotton at canopy scales (Resco de Dios et al., 2016). But the
generality of these results across phylogenies and ecosystem types needs to be more
broadly examined. Similarly, there are conflicting results on the literature on the importance of
including circadian regulation in models of diurnal gas exchange (Resco de Dios et al., 2016).
To date, only empirical models have been derived and, to make predictions under novel
environmental conditions, we will need more mechanistic approximations.

It is well documented that circadian regulation exerts a major influence over the
physiology and behavior of mammals but, unlike plants, where circadian regulation drives
temporal expression in ~30% of the genome, only ~10% of the mammal genome is clock
regulated. Paradoxically, circadian effects in the field have been examined to a much larger
extent in mammals than in plants. The potential role of circadian regulation within ecological
or agricultural settings is often not considered, and this may lead to incomplete descriptions of
the processes regulating diurnal gas exchange. Testing circadian regulation in the field is
challenging because its expression is often masked by direct physiological responses to
environmental changes. However, the use of statistical and modeling techniques, or of
advanced experimental facilities could help overcome this problem (Resco de Dios et al.,
2016). Indeed, evidence is building up that circadian regulation is an important driver of gas
exchange in canopies, with potential effects on current approaches for scaling and modeling
plant-atmosphere interactions (Resco de Dios et al., 2017). It is time to explicitly and broadly
evaluate the role of circadian regulation as a driver of diurnal gas exchange in the field,
across phylogenies and scales.

References
chill induces a delayed inhibition of photosynthesis at midday in mango (Mangifera


