Circadian control of global isoprene emissions

To the Editor — Hewitt *et al.*[1] reported the detection of circadian control of isoprene emissions from two tropical rainforests in Malaysia, based on their finding that a model without a circadian control cannot reproduce the observations. By including circadian-controlled isoprene emissions into models of atmospheric chemistry and transport, they suggested that plant circadian rhythms indirectly affect the global concentration of surface-level ozone. Here, we argue that the circadian rhythm postulated by Hewitt *et al.*[1] is not robust, and depends on untested assumptions regarding both the temperature and light response of isoprene emissions, and the unaccounted-for effects of canopy structure. The apparent circadian control disappears if different, biologically realistic, model parameters are used.

Hewitt *et al.* used the Guenther *et al.* algorithms of the MEGAN model[2] to detect the circadian control. We base our hypothesis on the notion that non-random deviations of the model parameters from their unknown true value can lead to an apparent circadian rhythm. We tested our hypothesis using the same algorithms[2] used by Hewitt *et al.*, applying a Bayesian model inversion to synthetic data (Fig. 1).

The optimized MEGAN model proved flexible enough to reproduce the synthetic circadian emissions with parameter changes within parameter uncertainty, and no circadian control (Fig. 1). The net effect of the parameter changes was a shift in the relative importance of radiation in comparison to temperature in the control of isoprene emissions. So why would the Malaysian forests have a different light and temperature response curve to that included in MEGAN?

There are various isoprene emissions models available, and the shape of the light and temperature response curves of each is decidedly different[3]. This reflects significant variations in light and temperature responses of isoprene emissions in and across species, due to inter-specific variations in isoprene synthase expression and differences in dynamic substrate pools[4]. It may, therefore, not be reasonable to expect the dependencies applied in MEGAN, estimated from leaves of temperate forests[2], to apply to Malaysian rainforest canopies.

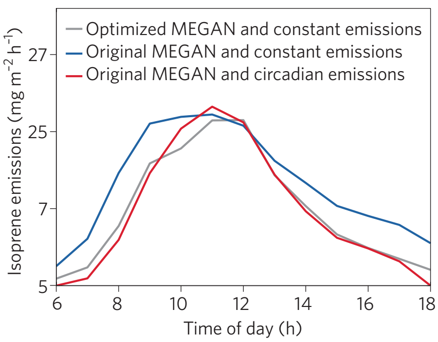

Figure 1 | The three lines represent the three steps in the test of our hypothesis. First, we generated a synthetic emissions time series using the standard MEGAN model with a constant basal emission rate (blue). We then generated a 'circadian' time series using MEGAN, by assuming a circadian basal emission rate (red; see Supplementary Eq. S7 of Hewitt *et. al.*[1]). Finally, we optimized the parameters of the MEGAN model using Markov-chain Monte Carlo with simulated annealing, and tested whether the 'circadian' time series can be modelled without circadian control (grey; a fixed basal emission rate, but with slightly different model parameters). Parameter values were allowed to vary by 30%, which is well within observed and biologically realistic variability[11]. See Supplementary Fig. S1b of Hewitt *et al.*[1] for comparison.

Furthermore, all isoprene models are leaf-level models that are later scaled to the canopy, thereby being highly sensitive to assumptions regarding canopy structure[5,6]. The extraction of basal emissions at a canopy scale is complicated both by strong diurnal gradients in canopy micrometeorology and the high variability of basal emissions rates in the canopy itself[7]. To adhere to the Hewitt *et al.* study, we have used their isoprene model without detailing canopy structure, albeit being another potential factor that could change the expected diurnal pattern of whole-canopy emissions, for example, by altering the contributions of different foliage layers to total canopy emissions.

We agree with Hewitt *et al.* that isoprene emission models should be improved, but we show here that the diurnal response of isoprene emissions in their study cannot be conclusively attributed to a circadian control. Although leaf-level circadian and ultradian controls have been previously reported[8,9], we argue that the extent to which this affects canopy-scale emissions has yet to be rigorously assessed. Clearly, more work is needed to gain insight into variations of light and temperature responses of isoprene emissions across the globe. Model optimization techniques[10], such as those used here, could aid in quantifying the extent of natural variability, and the associated implications for modelling global isoprene emissions. ❐

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Hewitt *et al.* reply — Isoprene emissions from trees are, largely, controlled by light and temperature, due to underlying physiological plant processes. These environmental controls are captured by process-based mathematical functions in the MEGAN modelling framework. Although the parameter values for the process descriptions are not known with certainty[1–3], sensitivity studies that vary parameter values should preserve physiologically realistic light and temperature responses in the model. If such sensitivity studies leave a gap between model and observations that can be filled by improving the process description in the model, then it is methodologically defensible to posit such improvements.

The measurements reported in our study[4] were made above two different tropical biomes: an oil palm plantation and a rainforest. The plantation has homogeneous vegetation with a simple canopy structure, and can therefore be modelled using a 'big leaf' approach. We observed an extremely steep morning increase in isoprene emission fluxes at this site[5], which we cannot biologically explain on the basis of the plants' response to temperature and light. The residual, strongly varying, basal emission rate is consistent with, and explained by, the circadian control we have previously shown for this species in the laboratory[6]. It is therefore entirely appropriate to include this process in the emissions model.

Over the rainforest, we observed a similar, albeit weaker, response to light and temperature, which is again entirely consistent with our attribution of circadian control. Although we cannot rule out other causes, we believe the inference of a circadian influence at this site is fully justified.

In our paper[4], we chose to include a circadian function in the MEGAN algorithms, rather than resort to *ad hoc* global searches of the parameter space as examined in our earlier analyses[5,7] and as suggested by Keenan and Niinemets[8]. This approach is consistent with MEGAN being a process-based (although not physiologically explicit) model. MEGAN is not intended to be a purely empirical model in which parameters can take any value to improve the overall fit to data. The fitting or tuning approach may alias the effects of processes, such as circadian rhythm, into the parameter values, reducing the explanatory power of the model. The power of the process description within a model like MEGAN is then considerably reduced, as each application of the model depends on 'tuning' by (global) parameter estimation, which becomes, methodologically, an endless and uninformative (re)definition of the *ceteris paribus* conditions ascribed to the use of MEGAN. We also note that Keenan and Niinemets used synthetic data that might lead to a 'false' solution to the optimization; that is, one that would not be reached using the real data.

We agree with Keenan and Niinemets that our canopy-scale measurements cannot definitively establish a causal link between circadian control and canopy-scale isoprene emissions, and that the extent to which leaf-level circadian and ultradian controls affect canopy-scale emissions has yet to be rigorously assessed. However, our interpretation is consistent with controlled laboratory observations[6]. Furthermore, our development and use of MEGAN is consistent both with the process-based design of the model and with a realistic view of how to make scientific progress[9]. ❐

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