

The capacity to emit isoprene differentiates the photosynthetic temperature responses of tropical plant species

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Abstract

Experimental research shows that isoprene emission by plants can improve photosynthetic performance at high temperatures. But whether species that emit isoprene have higher thermal limits than non-emitting species remains largely untested. Tropical plants are adapted to narrow temperature ranges and global warming could result in significant ecosystem restructuring due to small variations in species' thermal tolerances. We compared photosynthetic temperature responses of 26 co-occurring tropical tree and liana species to test whether isoprene-emitting species are more tolerant to high temperatures. We classified species as isoprene emitters versus non-emitters based on published datasets. Maximum temperatures for net photosynthesis were ~1.8°C higher for isoprene-emitting species than for non-emitters, and thermal response curves were 24% wider; differences in optimum temperatures (T_{opt}) or photosynthetic rates at T_{opt} were not significant. Modelling the carbon cost of isoprene emission, we show that even strong emission rates cause little reduction in the net carbon assimilation advantage over non-emitters at supraoptimal temperatures. Isoprene emissions may alleviate biochemical limitations, which together with stomatal conductance, co-limit photosynthesis above T_{opt} . Our findings provide evidence that isoprene emission may be an adaptation to warmer thermal niches, and that emitting species may fare better under global warming than co-occurring non-emitting species.

KEYWORDS

climate change, global warming, isoprene emission, leaf biochemistry, photosynthetic temperature response, plant functional traits, thermal tolerance, tropical forest

1 | INTRODUCTION

A key axis differentiating the niches of plant species is the range of temperatures over which performance is optimized. It is hypothesized that low temporal variation in temperatures allows many tropical species to specialize on narrow temperature ranges (Chan et al., 2016; Ghalambor, Huey, Martin, Tewksbury, & Wang, 2006; Janzen, 1967; Sunday, Bates, & Dulvy, 2011). The thermal specialization of tropical species may render them particularly susceptible to global warming (Araújo et al., 2013; Deutsch et al., 2008; Feeley, 2012; Perez, Stroud, & Feeley, 2016; Wright, Muller-Landau, & Schipper, 2009), as

evidenced by the current loss of species with cooler thermal ranges on warming Andean mountainsides (Duque, Stevenson, & Feeley, 2015; Fadrique et al., 2018). However, even among tropical plants, species exhibit large variation in their thermal ranges and tolerances (Fadrique et al., 2018; O'Sullivan et al., 2017; Slot & Winter, 2017a), and thus different species can be predicted to fare better or worse under anthropogenic climate change. To predict the effects of climate change on individual species as well as patterns of composition and biodiversity change, we need a better understanding of the traits that differentiate the fine-scale thermal niches of tropical plant species.

The response of photosynthesis to temperature is a fundamental component of the plant thermal niche (Berry & Björkman, 1980). From low to high temperatures, net photosynthesis tends to increase toward an optimum temperature (T_{opt}) and then decline toward a thermal maximum where net carbon gain reaches zero (T_{max}) (Lin, Medlyn, & Ellsworth, 2012; Slot & Winter, 2017a). The first-order causes of declining net photosynthesis at high temperature are increased respiration (Way & Yamori, 2014) and stomatal closure in response to increased atmospheric water demand (Lloyd & Farquhar, 2008; Slot & Winter, 2017b). At the ecosystem level, these factors can adequately explain the responses of photosynthesis to changes in temperature over short timescales in tropical forests (Tan et al., 2017; Wu et al., 2017). However, these factors are insufficient to explain more subtle variations in temperature responses of co-occurring species.

A study of 42 canopy species at two low-elevation tropical forests in Panama found that species' T_{opt} and T_{max} varied by up to 4.1°C and 9.9°C respectively (Slot & Winter, 2017a). This magnitude of interspecific variation among co-occurring plants is likely sufficient to cause differential growth rates in response to the subtle diurnal-to-interannual temperature variability experienced in the tropics. Mechanisms of photosynthetic temperature responses appear to vary among species without a clear predictor. Slot and Winter (2017b) found that stomatal limitation adequately explained photosynthetic declines in some species, whereas responses of other species were more consistent with constraints on photosynthetic biochemistry. T_{opt} and T_{max} did not correlate with the temperature sensitivity of leaf respiration measured at the same sites (Slot, Rey-Sánchez, Winter, & Kitajima, 2014; M. Slot, unpublished results). Four species in the same region all showed increasing photosynthetic limitation by electron transport capacity as temperatures approached T_{max} (Slot & Winter, 2017b). Even when reduced stomatal conductance is the primary limitation on photosynthesis, the degree to which biochemistry is co-limited or damaged by direct effects of temperature depends on diverse mitigation strategies employed by plant species, from electron-flow management (Niyogi, 2000) to oxidant regulation (Suzuki & Mittler, 2006). Therefore, understanding thermal niche differentiation among tropical plant species requires a more complete knowledge of the mechanisms behind variation in biochemical constraints on photosynthesis at supraoptimal temperatures.

Approximately one third of woody plant species emit isoprene gas from their leaves. The production and emission of isoprene has been shown to enhance leaf thermal tolerances by moderating the direct inhibitory effects of high temperatures on photosynthesis (Behnke et al., 2007; Hanson & Sharkey, 2001; Sharkey, 2005; Sharkey, Chen, & Yeh, 2001; Sharkey & Yeh, 2001; Singsaas, Lerdau, Winter, & Sharkey, 1997). High temperatures disrupt the coordination of diverse enzymes and chemical reactions associated with photosynthesis, each of which has a unique temperature optimum (Suzuki & Mittler, 2006). The resulting biochemical disequilibrium increases the formation rate of harmful oxidants, which can go on to damage components of the photosynthetic machinery (Ahmad, Sarwat, & Sharma, 2008; Apel & Hirt, 2004; Suzuki & Mittler, 2006). Isoprene emission is associated with reduced oxidant accumulation (Ryan et al., 2014; Sharkey,

2005; Sharkey, Wiberley, & Donohue, 2008; Tattini et al., 2015; Velikova, 2008; Vickers et al., 2009), either by acting as a direct anti-oxidant (Jardine et al., 2013; Vickers, Gershenzon, Lerdau, & Loreto, 2009) or as a signalling mechanism that upregulates other secondary metabolic defenses (Fini et al., 2017).

Given the link between isoprene and plant thermal tolerances, simply knowing whether a species emits isoprene or not could increase our ability to predict its response to high-temperature anomalies. Yet since the discovery of plant isoprene emissions in the 1950s, research into its adaptive value has taken an almost exclusively intraspecific approach (Sharkey & Monson, 2017). The stress response of a single species is observed whereas isoprene is either added to, or removed from, the leaves by fumigation (Singsaas et al., 1997), metabolic manipulation (Sharkey et al., 2001), or genetic alteration (Vanzo et al., 2015). The rare attempts to compare isoprene-emitting and non-emitting species (Velikova et al., 2016), or variably-emitting ecotypes (Ahrar et al., 2017), find results akin to those of intraspecific studies. Specifically, the presence or higher rate of isoprene emissions are associated with reduced oxidant accumulation, prolonged photosynthesis during stress, and faster recovery following stress (Ahrar et al., 2017; Velikova et al., 2016). However, these studies only compared two species or ecotypes at a time, limiting their power for generalization. At much larger scales, a biogeographic analysis found an increasing relative abundance of isoprene-emitting tree species with increasing mean air temperatures across low-elevation tropical forest sites (Taylor et al., 2018), consistent with a putative but unmeasured physiological advantage of emitters at hotter sites. To test for a common mechanism that distinguishes the thermal niches of isoprene-emitting from non-emitting plant species, a more systematic comparison of physiology is required from a sufficient number of species to allow for statistical generalization.

In this study, we test the hypothesis that isoprene-emitting tropical woody plant species can photosynthesize at higher temperatures than non-emitting species co-occurring at the same sites. Enhanced tolerance to high temperatures conferred by isoprene emission could influence the shape of the photosynthetic temperature response curve in several ways (Figure 1). Conclusions from intraspecific experiments emphasize a reduction in the rate at which photosynthesis declines above optimum temperatures. This implies that isoprene increases T_{max} but does not change T_{opt} (H1: High-temperature advantage, Figure 1). However, the adaptation of temperature response curves tends to be constrained by resource allocation trade-offs such that unless additional resources are supplied, an increase in performance at one part of the curve tends to be offset by a commensurate decrease in performance at another (Angilletta, Wilson, Navas, & James, 2003). Accordingly, a more realistic expectation may be that an increase in the thermal breadth (T_{br}) of photosynthesis, via increased T_{max} with no change in T_{opt} is offset by a decrease in photosynthetic rate at T_{opt} (P_{opt}), preserving the area under the curve (H2: Thermal generalist trade-off, Figure 1). Alternatively, peak performance rates may be maintained with a shift of the entire response curve toward higher temperatures, increasing both T_{opt} and T_{max} without changing T_{br} or P_{opt} (H3: Thermal specialist trade-off, Figure 1).

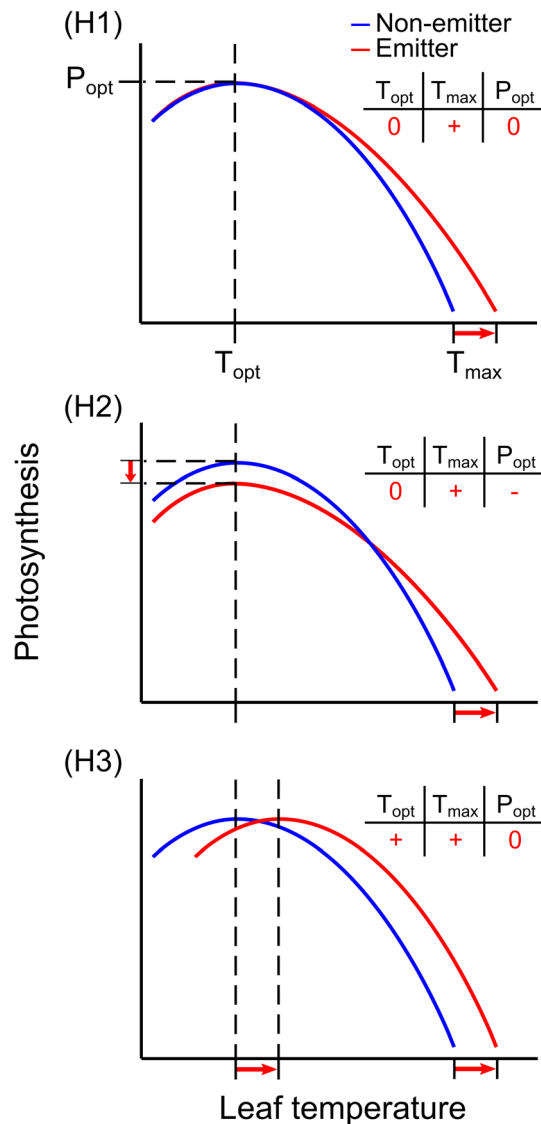


FIGURE 1 Three alternative hypotheses describing how the shape of the photosynthetic temperature response curve might be altered if isoprene enhances tolerance to high temperatures. (H1: High-temperature advantage) Isoprene increases the thermal maximum of photosynthesis ($T_{\max}$) with no apparent compensation at other parts of the curve. (H2: Thermal generalist trade-off) An increase in $T_{\max}$ is offset by a decrease in the photosynthetic rate (P_{opt}) at the thermal optimum (T_{opt}). (H3: Thermal specialist trade-off) Both T_{opt} and $T_{\max}$ increase proportionally, thereby maintaining photosynthetic rates but sacrificing performance at lower temperatures. In H2 and H3, the area under the curve is preserved, reflecting the resource-investment trade-offs that typically shape adaptation in temperature responses. In contrast, in H1, isoprene-emitting species photosynthesize more at all temperatures exceeding T_{opt} , with no apparent consequence to photosynthesis at other temperatures [Colour figure can be viewed at wileyonlinelibrary.com]

Determining if and how isoprene emissions influence the shape and thermal position of the photosynthetic temperature response curves of tropical plants will improve our understanding of species' sensitivities to climate warming and the potential trade-offs associated with thermal resilience.

2 | MATERIALS AND METHODS

To compare the photosynthetic thermal niches of isoprene-emitting and non-emitting plant species, we combined published datasets of species' photosynthetic temperature response curves and isoprene emission surveys. We obtained species' temperature response curves of net photosynthesis (P_{net}) and their summary parameters, along with site-level environmental data, from a published study of two lowland tropical forest sites on either side of the Isthmus of Panama (Slot & Winter, 2017a). The photosynthetic temperature response curves were obtained from upper-canopy leaves of 42 species of adult trees and lianas *in situ* by conducting a diurnal series of gas exchange measurements at standardized light levels. Four parameters were calculated from the curves: (a) the temperature at peak photosynthesis (T_{opt} , °C), (b) the upper temperature at which net photosynthesis reached (or was projected to reach) zero ($T_{\max}$, °C), (c) the “thermal breadth” of the curve (T_{br} , °C) calculated as the difference between T_{opt} and the temperature at which photosynthesis dropped to e^{-1} (37%) of its maximum value (June, Evans, & Farquhar, 2004), (d) and net photosynthesis at T_{opt} (P_{opt} , $\mu\text{mol m}^{-2} \text{s}^{-1}$; Slot & Winter, 2017a).

The two study sites where trees and lianas were sampled for the photosynthetic temperature response curves differed in annual precipitation and air temperature (Slot & Winter, 2017a). The wetter site is a ~300-year old, lowland moist tropical forest that receives an average of 3,200 mm precipitation annually with a short dry season; the drier site is a 100–120 year old seasonally dry forest receiving 1,830 mm precipitation per year, with a pronounced 4-month dry season. Mean annual air temperature at canopy height (25 m above the forest floor) is 25.3°C and 25.9°C at the wet and dry sites, respectively, and mean maximum daily air temperature is 29.9°C and 30.8°C at the wet and dry sites, respectively.

Isoprene emission data was obtained from the literature for the same species or congeners of species used in the study of photosynthetic temperature response curves. The application of isoprene emission data from the literature to the study species followed the methods of Taylor et al. (2018) and is justified by the fact that although emission rates vary among populations (Funk, Giardina, Knohl, & Lerdau, 2006; Niinemets, Copolovici, & Hüve, 2010), the capacity to emit isoprene is genetically determined and rarely varies within species (Monson, Jones, Rosenstiel, & Schnitzler, 2013). Literature sources were drawn from survey-type studies in tropical forests where species were sampled in an unbiased manner to determine which species produce isoprene and which do not. Nine such studies containing isoprene emission data at the genus or species level for our study species were identified (Bracho-Nunez et al., 2013; Geron et al., 2002; Harley et al., 2004; Keller & Lerdau, 1999; Klinger et al., 1998; Lerdau & Keller, 1997; Padhy & Varshney, 2005; Taylor et al., 2018; Varshney & Singh, 2003). One isoprene emission survey (Keller & Lerdau, 1999) was conducted at the drier of the two Panama sites from which the photosynthetic data were obtained (Slot & Winter, 2017a) and likely included some of the same individual plants.

Wherever direct matches occurred between species in the isoprene datasets and the photosynthesis dataset, the binary isoprene emission status was applied accordingly (0 = non-emitter, 1 = emitter; $n = 8$ and 6 species, respectively). Although variability in emission-rate capacities between species may also differentiate responses to temperature, we use only the binary emission status because standardized, high-precision measurements of emission rates are rare for tropical plants, and so we do not include them in this analysis.

Where only genus matches occurred, the genus average of the binary emission status was used to impute the emission status to unmeasured species. Where the genus average was >0.5 , unmeasured species within the same genus were labelled as emitters ($n = 3$), and where the genus average was <0.5 , unmeasured species were labelled as non-emitters ($n = 9$). Genera with averages equal to 0.5 were considered ambiguous and were excluded from subsequent analyses. Genus averaging is justified by the observation that tropical genera tend to predominantly comprise either isoprene-emitting or non-emitting species (Taylor et al., 2018). A genus average therefore serves as a probability of species emission status that propagates on average to accurate community-level results. For the results presented in the main text, all genus averages are included as per Taylor et al. (2018) in order to maximize sample size and statistical power (total $n = 9$ emitting and 17 non-emitting species; Figures 2 and 3). However, confidence in the genus average depends on the number of congeneric species sampled. As such, we also report more conservative analyses using genus averaging for only those genera with at least three species of known isoprene-emission status ("conservative genus averaging approach"; total $n = 7$ emitting and 12 non-emitting species; Figure S1), and using only species-level emissions data ($n = 6$ emitting and 8 non-emitting species; Figure S2). All analyses were also repeated while excluding species with genus averages between 0.3 and 0.7 ($n = 3$). Of the 26 species with inferred or measured isoprene emission statuses, five were liana species (three emitting and two non-emitting).

Slot and Winter (2017a) showed that site-specific mean T_{opt} values closely matched site mean maximum air temperatures. This acclimation of temperature response curves to the local conditions could confound comparisons of species groups when both sites are combined because an unequal representation of emitters and non-emitters across sites would result in unequal site-effects on temperature response curves. To account for this, and remove the effect of site acclimation, we compared functional groups in terms of the deviation of T_{opt} and T_{max} from the site mean maximum air temperature. We convert the T_{opt} and T_{max} of each species to site-relative temperature values (SRT_{opt} and SRT_{max} , respectively) by subtracting the site mean maximum air temperature. We compare each curve component (SRT_{opt} , SRT_{max} , T_{br} , P_{opt}) between species groups by ANOVA. Non-relativized results are also reported (Figures S3 and S5).

For visualizing average photosynthetic temperature response curves of emitters and non-emitters, we produced group-wise average curves by averaging the polynomial parameters defining each species' curve (Figure 3). The photosynthetically fixed carbon that is lost to isoprene emission is not measured by the carbon dioxide analyzers used to produce the photosynthetic response curves, but may still

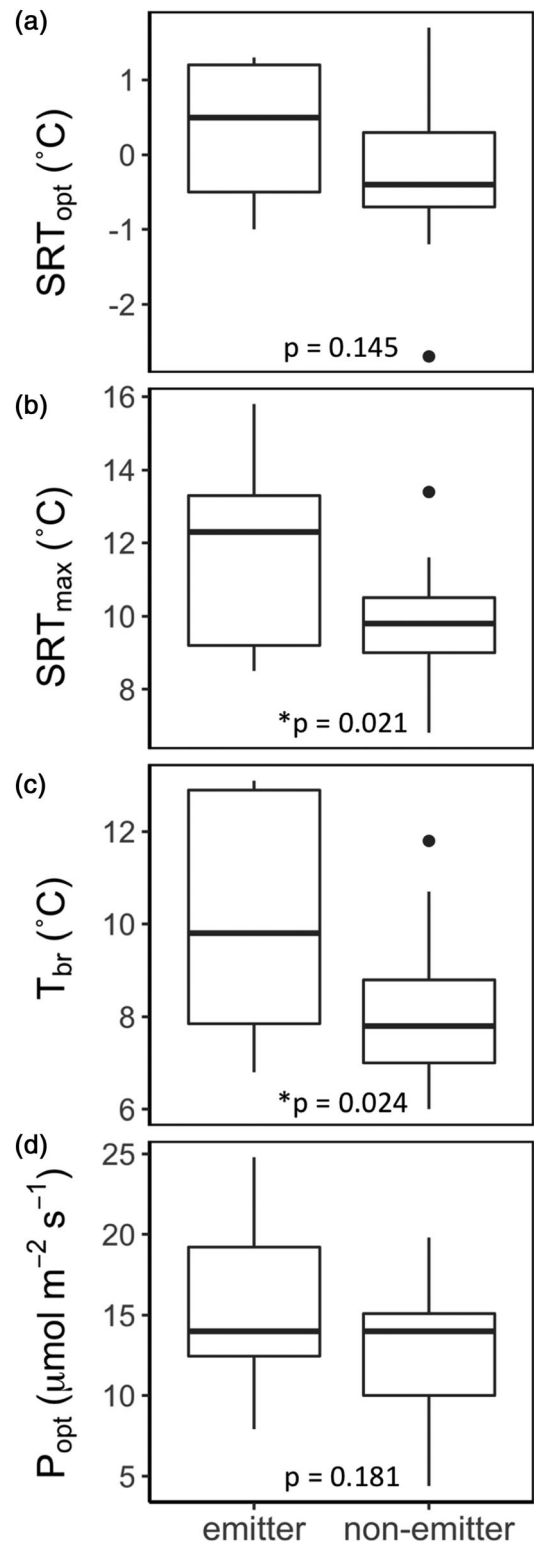


FIGURE 2 Comparisons between isoprene-emitting ($n = 9$) and non-emitting ($n = 17$) species with respect to each species' (a) site-relative temperature optimum (SRT_{opt} ; temperatures relative to site mean maximum air temperature) and (b) site-relative maximum temperature (SRT_{max}) of net photosynthesis, (c) the thermal breadth of the temperature response curve (T_{br}), and (d) net photosynthesis at T_{opt} (P_{opt}). The bold bars indicate median values. Mean SRT_{max} and mean T_{br} were significantly higher in emitting compared to non-emitting species (ANOVA, $p < 0.05$)

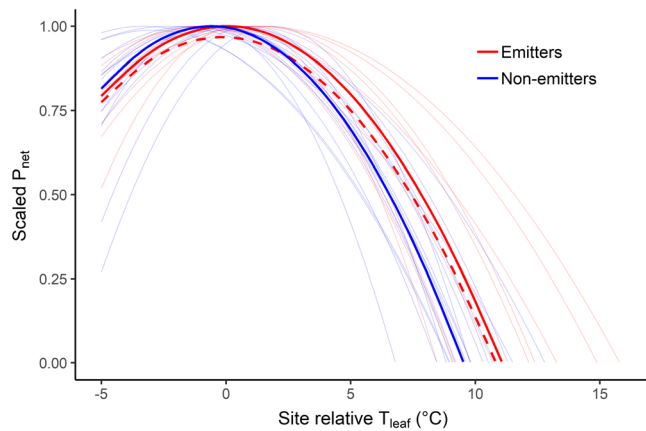


FIGURE 3 Temperature response curves of scaled net photosynthesis (P_{net}) for isoprene-emitting (red, $n = 9$) and non-emitting (blue, $n = 17$) species. Bold lines are averaged curves determined by group-wise averaging of the parameters defining each polynomial. The dashed red line shows P_{net} adjusted for carbon lost to isoprene emission, estimated by modelling a hypothetical strong emission rate ($100 \text{ nmol m}^{-2} \text{ s}^{-1}$ at 30°C) and its temperature dependency across the thermal range (see Materials and Methods). Each species curve is a polynomial fit to leaf-level spot measurements under current ambient $[\text{CO}_2]$ and saturating light. Leaf temperatures are relative to site mean maximum air temperature (site-relative T_{leaf}). P_{net} is scaled in order to emphasize temperature responses, given that P_{opt} did not significantly differ between groups. The functions describing the averaged polynomial curves are provided in Figure S4, with curve heights here scaled to 1. [Colour figure can be viewed at wileyonlinelibrary.com]

represent a significant allocation trade-off such as that described by H2 (Figure 1). We therefore produced an adjusted average-emitter curve accounting for the cost of isoprene emissions (P_{net} minus carbon emitted as isoprene) using the temperature dependence (T) of isoprene described by Guenther, Monson, and Fall (1991) as follows:

$$T = \frac{\exp[T_1(T_{\text{leaf}} - T_s)/RT_{\text{leaf}}T_s]}{1 + \exp[T_2(T_{\text{leaf}} - T_3)/RT_{\text{leaf}}T_s]}$$

where T_{leaf} is leaf temperature (Kelvin); T_s is a normalizing temperature which we set to 30°C (303 K); R is a gas constant ($8.314 \text{ J K}^{-1} \text{ mol}^{-1}$); and T_1 ($95,100 \text{ J mol}^{-1}$), T_2 ($231,000 \text{ J mol}^{-1}$), and T_3 (311.83 K) are empirical coefficients. The emission rate (E) was calculated by multiplying T by a standardized emission capacity ($EC = E$ at T_s). Leaf EC can vary from near 1 to greater than $100 \text{ nmol m}^{-2} \text{ leaf s}^{-1}$ (Harrison et al., 2013). We calculated hypothetical isoprene emission rates (E ; $\text{nmol m}^{-2} \text{ s}^{-1}$) across temperatures based on T and a strong standardized emission rate ($EC = 100$, $T_s = 30^\circ\text{C}$), and calculated the carbon cost ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) as $E \times 5C$ isoprene $^{-1} \times 1,000 \text{ nmol } \mu\text{mol}^{-1}$. Curve positions were adjusted to site-relative temperatures to match the statistical analyses described above, and P_{opt} was scaled to 1 to visually isolate the temperature responses given that P_{opt} did not significantly differ between groups (see Results; Figure 3), but unscaled (Figure S4) and non-temperature-relativized (Figure S5) versions are provided in Supporting Information.

3 | RESULTS

We did not find support for H3, because the mean temperature optimum for photosynthesis relative to site mean maximum air temperature (SRT_{opt}) was not significantly higher for isoprene-emitting ($+0.20^\circ\text{C}$) than for non-emitting tropical woody plant species (-0.39°C ; ANOVA, $p > .05$; Figure 2a). SRT_{max} was significantly higher for emitters ($+11.71^\circ\text{C}$) compared with non-emitters ($+9.87^\circ\text{C}$; ANOVA, $p < .05$; Figure 2b). As implied by the higher SRT_{max} but not SRT_{opt} , T_{br} was significantly wider for emitters (10.0°C) compared with non-emitters (8.1°C ; ANOVA, $p < .05$; Figure 2c). Consistent with both H1 and H2, emitters showed a wider response curve with no shift in T_{opt} . But contrary to H2, the mean of species' photosynthetic rates at T_{opt} (P_{opt}) was not lower and was in fact somewhat higher for emitters ($15.28 \mu\text{mol m}^{-2} \text{ s}^{-1}$) than non-emitters ($12.68 \mu\text{mol m}^{-2} \text{ s}^{-1}$), though differences were not significant (ANOVA, $p > .05$; Figure 2d). Overall, these results support H1: isoprene emission is associated with a photosynthetic advantage at high temperatures with no investment trade-offs manifested in net carbon exchange.

Modelling the carbon emitted as isoprene, net carbon uptake at P_{opt} decreased by 3.3%, but there was little effect on the relative carbon assimilation advantage of emitters compared to non-emitters at temperatures approaching T_{max} (Figure 3). The adjusted emitter curve (dashed line, Figure 3) approximates the "thermal generalist" carbon investment trade-off depicted by H2 (Figure 1). However, although the difference in P_{opt} between species groups was not statistically significant, the average for non-emitters was 17% lower than that for emitters, a difference much larger than the 3.3% reduction due to direct carbon costs of isoprene (Figure S4).

Results from the conservative genus averaging approach (higher confidence in emission status but lower sample size of species) were statistically similar to results from the full dataset, showing no significant differences in SRT_{opt} or P_{opt} , but significantly higher SRT_{max} and T_{br} for emitting compared to non-emitting species (ANOVA, $p < .05$; Figure S1). When using species-level isoprene emission data (highest confidence in emission status, smallest sample size), results were qualitatively similar, but no differences were statistically significant, potentially due to low statistical power (ANOVA, $p > .05$; Figure S2). Results from all genus averages are presented in the main text because they are congruent with results from the more conservative approaches, and the larger sample sizes may better convey the variation in temperature response traits within groups. Mean T_{opt} and T_{max} values (not relative to site temperatures) were both significantly higher for emitters (ANOVA, $p < .05$; Figure S3), but as explained above this result may be attributable to the higher proportion of non-emitters at the cooler (wetter) site. Removing the three species whose genus averages fell between 0.3 and 0.7 did not change the sign or statistical significance (at $\alpha = 0.05$) of any of the results.

4 | DISCUSSION

Our results are consistent with the long-held hypothesis that isoprene enhances the thermal tolerance of plant leaves (Behnke et al., 2007;

Hanson & Sharkey, 2001; Sharkey, 2005; Sharkey et al., 2001; Singaas et al., 1997). Our study is unique in that it demonstrates differences in the photosynthetic temperature responses of co-occurring isoprene-emitting versus non-emitting tropical plant species (Figures 2 and 3). In our dataset, the upper thermal limit of net photosynthesis was on average 1.84°C higher for isoprene-emitting species compared with co-occurring non-emitting species. This difference is similar in magnitude to the isoprene effect estimated from experimental manipulations within species (e.g., 2.5°C increase in $T_{\max}$ observed by Singaas et al., 1997). The results imply not only a mechanism for species variation in thermal tolerance, but also carbon assimilation at high temperatures. For example, the average photosynthetic rate for isoprene-emitters was double the rate for non-emitters at leaf temperatures 8.4°C above mean maximum air temperatures (0.43 vs. 0.21, respectively, in terms of P_{net} scaled relative to P_{opt} , Figure 3). Rising leaf temperatures with global warming may increasingly differentiate the carbon assimilation rates of isoprene-emitting from non-emitting species.

Consistent with H1 (Figure 1), we found that isoprene-emitting species sustained positive net photosynthesis to higher temperatures ($\text{SRT}_{\max}$) than non-emitters, but that species did not differ significantly in their optimum temperatures (SRT_{opt}) or photosynthetic rates at T_{opt} (P_{opt} , Figure 2). Why might the benefits of isoprene be expressed only at leaf temperatures above T_{opt} ? One hypothesis is that the relative importance of different mechanisms that contribute to declining photosynthesis may shift as temperatures increase from T_{opt} to $T_{\max}$. There is mounting evidence that T_{opt} is determined more by stomatal regulation than biochemical limitation or respiration in tropical trees (Lloyd & Farquhar, 2008; Slot & Winter, 2017b; Tan et al., 2017; Wu et al., 2017). Indeed, observations of stomatal conductance and internal CO_2 concentrations recorded during the response curves that we present here were consistent with stomatal limitation beginning at T_{opt} in most of the species (Slot & Winter, 2017a).

However, there is evidence that stomatal conductance and biochemistry (e.g., electron transport rate) can become co-limiting at supraoptimal temperatures (Slot & Winter, 2017b; Vårhammar et al., 2015). A prominent mechanism of biochemical disruption is the accumulation of harmful oxidants. As leaf temperatures increase toward $T_{\max}$, the diverging temperature responses of different electron-transport components leads to increasing oxidant formation (Suzuki & Mittler, 2006). These oxidants damage lipids, proteins, and other components (Ahmad et al., 2008) and thereby reduce electron transport efficiency. Isoprene emission rates increase exponentially with temperature and tend to peak at temperatures (38°C–40°C) slightly below the photosynthetic $T_{\max}$ values of our study species (approximately 41°C–45°C, Figure S5) (Guenther et al., 1991; Harley, Guenther, & Zimmerman, 1997; Sharkey & Monson, 2014). This emission pattern may reflect the increasing need to mitigate oxidative stress as temperatures approach $T_{\max}$. By alleviating electron-transport limitation, isoprene emission would have a greater influence on $T_{\max}$ than on T_{opt} . One approach to test this hypothesis would be to compare the temperature responses of electron transport, specifically, between isoprene-emitting and non-emitting species.

Although the carbon emitted as isoprene represents a trade-off between maximum net carbon assimilation rates and thermal tolerance (Figure 3), the modelled carbon loss was small relative to the (non-significant) difference in P_{opt} between emitters and non-emitters (see Results; Figure S4). If isoprene is responsible for enhanced thermal tolerance, then a lack of a significant trade-off would be surprising because all photosynthetic plants make the substrate for isoprene (the same substrate is used in carotenoids and chlorophyll; Vickers, Gershenzon, et al., 2009), and the emission of isoprene requires just a single enzyme that evolved at the inception of land plants (Hanson, Swanson, Graham, & Sharkey, 1999; Harley, Monson, & Lerdau, 1999). Yet, relatively few plants emit isoprene (Loreto & Fineschi, 2015; Monson et al., 2013). Greater trade-offs may emerge from more comprehensive plant carbon budgets. For example, emissions during drought can drain carbon reserves (Brilli et al., 2007; Funk, Mak, & Lerdau, 2004) and potentially reduce growth rates relative to non-emitters (Ryan et al., 2014). Trade-offs in thermal adaptations can also be indirect, manifesting through related functional axes (Angilletta et al., 2003). For example, there is evidence that the capacity to emit isoprene is associated with a host of protein compositional changes in the chloroplast (Velikova et al., 2014). Its association with more costly compounds might constitute an indirect cost that would be difficult to quantify. Understanding the partitioning of direct costs (gas exchange) and indirect costs (carbon allocation) is relevant to predicting the consequences of isoprene emission for plant and ecosystem gas exchange as well as the fraction of carbon allocated to biomass growth.

Given the limited isoprene data available for tropical plant species, more targeted sampling will be required to test the generality of these results across more species and sites. Implications of variation in the leaf photosynthetic thermal niche to plant growth will also depend on factors that affect leaf temperatures other than ambient air temperature. Species' microhabitat preferences as well as leaf traits, morphology, angle, and transpiration rates, all modulate the effects of air temperature and irradiance on leaf temperatures (Fauset et al., 2018; Michaletz et al., 2016; Wright et al., 2017) and, along with isoprene, are likely to play an important role in the thermal evolution and ecology of plants.

The adaptation of tropical species to narrow temperature ranges (Janzen, 1967; Sunday et al., 2011) raises concern over their susceptibility to even small amounts of climate warming (Duque et al., 2015; Feeley, Malhi, Zelazowski, & Silman, 2012). Species with adaptations for expanded thermal niches may have a competitive advantage in the future. We provide evidence that isoprene emission is associated with the expansion of the thermal niche of plant species and allows for improved photosynthetic performance at higher leaf temperatures compared with co-occurring non-emitters. How that thermal niche expansion translates to differences in tree performance and total forest productivity depends on the frequency distribution of air temperatures as well as other factors that control leaf temperature such as leaf structure and canopy position. This differentiation in thermal niche between isoprene-emitting and non-emitting species could have implications for community assembly shifts (Taylor et al., 2018) and future biodiversity in a warming world.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1: Comparisons of photosynthetic temperature response parameters between isoprene emitting ($n = 7$) and non-emitting ($n = 12$) species. Here, isoprene emission statuses estimated by genus averaging are limited to genera informed by at least three measured species ("conservative genus averaging approach"; see Materials and Methods section). Parameters compared are (a) each species' site-relative temperature optimum (SRT_{opt}) and (b) maximum (SRT_{max}) of net photosynthesis (temperatures relative to site mean maximum air temperature), (c) the thermal breadth of the temperature response curve (T_{br}), and (d) net photosynthesis at T_{opt} (P_{opt}). The bold bars indicate median values. Mean SRT_{max} and mean T_{br} were significantly higher in emitting compared to non-emitting species (ANOVA, $p < 0.05$).

Figure S2: Comparisons of photosynthetic temperature response parameters between isoprene emitting ($n = 6$) and non-emitting ($n = 8$) species. Here, all isoprene emission statuses are inferred from directly measured species and not from genus averages. Parameters compared are (a) each species' site-relative temperature optimum (SRT_{opt}) and (b) maximum (SRT_{max}) of net photosynthesis (temperatures relative to site mean maximum air temperature), (c) the thermal breadth of the temperature response curve (T_{br}), and (d) net photosynthesis at T_{opt} (P_{opt}). The bold bars indicate median values. In this data subset, no photosynthetic parameters significantly differed between species groups.

Figure S3: Comparisons between isoprene emitting ($n = 9$) and non-emitting ($n = 17$) species with respect to (a) each species' temperature optimum (T_{opt}) and (b) maximum (T_{max}) of net photosynthesis. Here, T_{opt} and T_{max} are not relativized to site mean maximum air temperature as in Figure 1 (Main Text). The bold bars indicate median values. Mean T_{opt} and mean T_{max} were significantly higher in emitting compared to non-emitting species (ANOVA, $p < 0.05$).

Figure S4: Temperature response curves of net photosynthesis (P_{net}) for isoprene emitting (red, $n = 9$) and non-emitting (blue, $n = 17$) species. Curves are polynomial fits to leaf-level spot measurements under standardized $[CO_2]$ and saturating light. Leaf temperatures are relative to site mean maximum air temperature (site-relative T_{leaf}). Bold lines are averaged curves determined by group-wise averaging of the parameters defining each polynomial. The dashed red line shows P_{net} adjusted for carbon lost to isoprene emission, estimated by modelling a hypothetical strong emission rate ($100 \text{ nmol m}^{-2} \text{ s}^{-1}$ at 30°C) and its temperature dependency across the thermal range (see Materials and Methods section). The averaged polynomial curves are described by the function $y = a \times x^2 + b \times x + c$, where for isoprene emitters $a = -0.1218$, $b = 0.01074$, $c = 14.80$, and for non-emitters $a = -0.1178$, $b = -0.1431$, $c = 12.04$.

Figure S5: Temperature response curves of net photosynthesis (P_{net}) for isoprene emitting (red, $n = 9$) and non-emitting (blue, $n = 17$) species. Species are from two different sites with different air-temperature distributions, therefore curve positions may partly reflect local acclimation to site temperatures (see Materials and Methods). Curves are polynomial fits to leaf-level spot measurements under standardized $[\text{CO}_2]$ and saturating light. Bold lines are averaged curves determined by group-wise averaging of the parameters defining each polynomial. The dashed red line shows P_{net} adjusted for carbon lost to isoprene emission, estimated by modelling a hypothetical strong emission rate ($100 \text{ nmol m}^{-2} \text{ s}^{-1}$ at 30° C) and its temperature

dependency across the thermal range (see Materials and Methods). The averaged polynomial curves are described by the function $y = a \times x^2 + b \times x + c$, where for isoprene emitters $a = -0.1218$, $b = 7.482$, $c = -100.1$, and for non-emitters $a = -0.1178$, $b = 6.975$, $c = -91.24$.

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