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Commentary

Pushing the thermal limit for cacao—will we have chocolate also in a warmer future?

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This scientific commentary refers to 'Effects of simulated climate change conditions of increased temperature and [CO_2] on the early growth and physiology of the tropical tree crop, *Theobroma cacao* L.' by Mateus-Rodriguez et al. (doi: 10.1093/treephys/tpad116).

Depending on the specific global climate model projection, we can expect a warming within the range of 1–5 °C in the tropical forest regions during the present century. Although the range is smaller compared with higher latitudes forest regions (IPCC 2021), this does not necessarily mean that tropical forests are at lower risk as temperatures continue to increase. It has been suggested through model simulations that especially in the tropics and subtropics regions climate change may produce novel climatic regimes (Williams et al. 2007, and references therein). In contrast to higher latitude forest trees, tropical tree species have experienced thermal stability over a longer period (see the essay by Trewin 2014), thus theoretically many tropical trees may operate in a much smaller thermal window (Janzen 1967, Lloyd and Farquhar 2008, Sentinella et al. 2020, Dusenge et al. 2021). However, to what extent this also affects their thermal acclimation capacity in a warmer future is unclear. High species diversity in tropical forest ecosystems is a natural challenge for the scientific community. To complicate matters we have a strong biome- and taxon-bias in plant science, focusing significantly more on boreal and temperate species, as well as model plants and economically important crops, including cacao (Marks et al. 2023).

Cacao is an economically, ecologically and culturally important crop with significant global importance. As a key crop for chocolate production, it supports the livelihoods of many farmers and workers in related industries (ICCO 2023). Like many crop species (Kaniewski et al. 2023), climate change poses a significant challenge to cacao cultivation and its long-term sustainability (Cilas and Bastide 2020, and references therein). Breeding and sustainable practices are some of the tools we have. However, these tools are only efficient if we have an underlying physiological understanding of the species' physiological acclimation capacity and its response to key environmental factors, such as temperature and atmospheric CO_2 concentration (Lahive et al. 2019, Tezara et al. 2020). The challenge is that several of these factors interact and seem to either ameliorate, as demonstrated by Mateus-Rodriguez et al., or exacerbate the negative effects of climate change.

Here in this issue, Mateus-Rodriguez et al. present results from a classic growth chamber experiment with young cacao plants of two different genotypes. Effects of elevated [CO_2] and temperature were evaluated with a specific focus on physiology, phenology and growth. The study mimics a likely future climate (only 57 years from now) with a [CO_2] of 700 p.p.m. and three different day temperature regimes (31 °C, 34 °C and 36 °C), similar to IPCC's SSP3-7.0 climate scenario (IPCC 2021). Considering that Balasimha et al. (1991) reported that field-grown cacao's photosynthetic optimum is around 31–33 °C when measured at current sub-ambient [CO_2] levels, the warmer temperature treatment stretches the physiological capacity of young cacao plants. However, it is worth noting that cacao is cultivated in a large geographical area, with air temperatures not only varying daily but also between wet and dry seasons. Thus, the thermal growth limitations likely depend on site, season and plant water availability (see review Lahive et al. 2019).

Empirical and modeling studies have suggested that many tropical plants currently grow at temperatures close to their photosynthetic thermal optimum (Slot and Winter 2017, Tan et al. 2017, Doughty et al. 2023), and maybe also close to their upper thermal growth limits (Lloyd and Farquhar 2008, Sentinella et al. 2020). For cacao, this seems not to be the case. In fact, a key finding by Mateus-Rodriguez et al. is that elevated levels of [CO_2] ameliorate some of the negative temperature effects in cacao. This is especially evident in the total biomass accumulation, which is likely driven by greater values of P_n, and faster leaf development (i.e., longer growth season) under elevated temperature and [CO_2]. Amelioration effects have also been described in other crop trees, such as in peach, where higher temperature tolerance was observed under elevated CO_2 conditions (Centritto et al. 2002). Whether this implies that the thermal growth limits will be displaced under field conditions as the atmospheric CO_2 concentration increases remains an open question. However, a direct implication of this amelioration effect by elevated [CO_2] is that we need to be careful when interpreting older empirical data on photosynthetic or growth thermal limits, as many are collected under lower levels of CO_2 compared with the present day, for example in Balasimha et al. (1991).

Maybe more importantly, the observed amelioration temperature effect by elevated [CO_2] may only be valid under stable warm climatic conditions, as simulated in the current study (see Mateus-Rodriguez et al.). In the field, cacao will most likely experience multiple extreme heat waves and periods of drought (IPCC 2021), resulting in high leaf temperatures and a greater need for evaporative leaf cooling to avoid irreversible damage. As also observed by Mateus-Rodriguez et al., stomatal density is often reduced under elevated CO_2 concentration (see for example Woodward and Kelly 1995), thus likely limiting the leaves' evaporative cooling capacity. This may in some cases result in premature senescence and reduced canopy size (Warren et al. 2011), thus potentially counteracting the amelioration effect by elevated [CO_2].

Another key finding by Mateus-Rodriguez et al. is that the physiological and growth response to elevated CO_2 and temperature seems to be strongly linked to the genotype. The two genotypes (PA107 and SCA6) used in the study differed significantly, with the PA107 genotype outperforming SCA6 for most traits reported. A direct implication of this result is that breeding cacao plants with specific genotypes could potentially improve production in a future with elevated [CO_2] and warmer climates, benefitting growers by ensuring a more robust yield. The relevance of observing different performances of two genotypes in a simulated future climate extends beyond breeding purposes. It provides valuable information about the biological capacity of a species, such as cacao, to adapt to a warmer climate. This variation can be utilized to shed light on the window of acclimation, highlighting how species may adapt to changing environmental conditions.

A major question for us chocolate lovers (and the cacao sector) is: will elevated levels of [CO_2] also ameliorate some of the negative temperature effects observed on fruit development, and thus push the thermal limit for cacao fruit (pod) production? Although cacao pod development is faster at higher temperatures, the final pod and bean size are reduced with increasing temperature (Daymond and Hadley 2008, Hendley 2016). Variation in the saturated fatty acid content of the high-energy bean when cacao trees are grown in warmer conditions results in an increased melting point of cacao butter (see Lahive et al. 2019). The high-energy beans in the pods require a high carbohydrate input, and enhanced levels of photosynthesis as the CO_2 concentration raises may theoretically facilitate this. Shading by rapid leaf development, as observed by Mateus-Rodriquez et al., may also affect pod physiology and development (Lahive et al. 2019), potentially leading to significantly greater losses (Daymond and Hadley 2008, Hendley 2016). Thus, for cacao, determining the upper thermal limit for photosynthesis, growth and fruiting is important as atmospheric CO_2 is rising.

Conflict of interest

None declared.

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Data availability statement

No data were used.

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