Dear Editor:

We are pleased to submit a revised version of our manuscript, “Thermal sensitivity across forest vertical profiles: patterns, mechanisms, and ecological implications” (NPH-TR-2021-38020), for consideration for publication in *New Phytologist*. We have addressed all points raised by the reviewers, as detailed below. The most significant changes include:

* We have brought in an additional author, Thomas N. Buckley, to round out the expertise of the author team and help address some of the reviewer comments (particularly Reviewer 2).
* We did some modest reorganization, including moving the content on and VOCs to the traits section (the former suggested by Reviewer 2) and reorganizing the traits section around trait groupings, as opposed to intra-specific/ interspecific. This rearrangement of the traits section better parallels Table 1 and the following section on leaf gas exchange.
* We revised three figures (Figs. 1-4) based on reviewer comments, including some standardization of style, but have not perfected the styling because the journal illustrators will fix up all figures.

Regarding production of the figures, below are some specific criteria:

* It will generally be fine to adjust colors, layout, and spacing on the figures.
* We really like Figure 1 and would like to retain the background painting (by the lead author)

Thank you for considering this revised version, and we look forward to your response.

Sincerely,

Nidhi Vinod & Kristina Anderson-Teixeira (on behalf of all coauthors)

# Response to Reviewer(s)’ Comments to Author:

## Referee: 1

### General comment:

The article is easy to read and well structured, I appreciated reading it. It covers a broad area and explains relatively complex ideas in simple terms and efficiently. I also enjoyed the changes in scale (leaf scale to ecosystem scale). I think this paper will be very useful as a reference for the plant physiologist community and for modelers.

**Thank you for the review!**

I have been really interested in the comparison between gradients in canopy of individual trees and canopy made of an assemblage of species (paragraph 3.1 and 3.2. However, the paragraph 3.2 is relatively short, and I am curious if it can be developed a little bit more (maybe not!).

**We ended up removing former section 3.2 because we reorganized the traits section around trait groupings, as opposed to intra-specific/ interspecific. This rearrangement of the traits section better parallels Table 1 and the following section on leaf gas exchange. We integrated the content that was previously in this section throughout the traits section, as appropriate.**

**Unfortunately, we’ve been unable to find many studies examining vertical gradients at the interspecific level, and have included those of which we are aware.**

I find it interesting to try and link the empirical and theoretical knowledge on vertical gradients in forests with what is done in DGCMs and what should be done to improve their accuracy. However, I think there is a big step between the review (part I and II) and the author’s view on the implications for models (Scaling across space and time). I wonder if it would be possible to link a little bit more the different parts, and maybe without going that much in the technical details (cohort, big leaf, multi layers, …) which I think are sometimes imprecise or maybe wrong. Would it be possible to explain more simply what are the vertical gradients presented in the section II, that are misrepresented today in DGCMs? Maybe by explaining which of the ‘biophysical variables’ and ‘leaf traits’ that you listed, are considered constant when they should be variable vertically?

**Thank you for the comment. We included a section that explains how vertical gradients are represented in models:**

* **Models partition radiation above and within the forest vertical profile (i.e., direct vs. diffuse light) using radiative transfer models or a system of two coupled ordinary differential equations, referred to as a two-stream approximation (Sellers, 1985; Fisher *et al.*, 2018). Using the latter method, single canopy layers are divided into sun and shade fractions (e.g., in the Community Land Model, CLM model), while models with multiple vegetative layers can analytically solve the two-stream approximation for each layer. Thus, even in single-layer models, key physiological parameters like and vary, decreasing with increasing cumulative LAI or lower light conditions (Table 2, e.g., Krinner *et al.*, 2005).**

**Given that models vary greatly in how they capture vertical light gradients, what biophysical variables are included and how those variables are parameterized to vary (or not) across vertical gradients, we feel that it is beyond the scope of this paper to comprehensively list or explain which of those variables vary vertically across different models.**

### Minor details that I hope will be of interest for the authors. Consider them as you see fit.

L30 I did not understand ‘Scaling up’ in this sentence.

**We specified “Scaling up” here as “Scaling up from leaves to trees,”.**

Figure 1 is nice. I struggled with ‘Tleaf sensitivity to shortwave radiation’ but I think it is clear after, when reading the text. Consider using the same words in the paragraph where you detail it (line 268?) and adding the reference to the figure in the text. Or maybe change the term (‘thermal capacitance’ ?) if this is the part you are referring to in the text.

**Done**

Figure 2: Homogenize the units (in parenthesis or in bracket) and add the unit for PAR.

**Done.**

I like your figures, but maybe consider homogenizing a little bit the styles for the plots between figures 2 3 and 4.

**This will be done by the New Phytologist illustrators (because it is a Tansley review). We will work with them to ensure that all the figures look good.**

L205-206 Maybe add some references. How many degrees? In your Figure 3 there is not really a difference between Tleaf and Tair when SWR = 0. Given that the transpiration nearly stops at night (high humidity, low conductance) I would expect Tleaf – Tair to be very close to zero.

**We revised and added references to this sentence in question, which now reads:**  **Leaves are often cooler than the air on clear nights due to radiative coupling with the very cold sky, and under some daytime conditions (cloudy skies, high wind speeds, and high , Vogel, 2009; Rey-Sánchez *et al.*, 2016; Cavaleri, 2020).**

**Figure 3 shows the effect of each variable while the others are held constant (as specified in the caption). Thus, it does not represent the full suite of night-time conditions.**

L219, repetition with L 216

**Done**

Figure 3: TLeaf and Tleaf.

**Done**

l258 under soil wet conditions?

**We have reworded this sentence to read, “In contrast, under conditions conducive to stomatal opening, higher wind speeds and enable cooling in the upper canopy, whereas lower wind and in the understory limit evaporative cooling (Fig.3 b,d, Roberts *et al.*, 1990; Martin *et al.*, 1999; Leigh *et al.*, 2017).”**

L298-299 Far red to red light: I think this could be developed here or somewhere else. You covered the vertical variation in light quantity inside the canopy, but you could also report the vertical change in light quality (light spectrum) as the leaves absorb preferentially some wavelengths but reflects or transmit others.

**Thank you for the suggestion, we added the following here:“Canopy foliage absorbs a large portion of PAR (400-700nm), and selectively filters light, thereby altering the spectrum of PAR creceived in the lower canopy and understory layers. The ratio of red (~685-690 nm) to far red (~730-740 nm) light declines along qith total PAR with increasing depth in the canopy, and understories receive diffuse light enriched in near infrared radiation (700-1000 nm) (de Castro, 2000; Poorter *et al.*, 2000).”**

L 322 consider homogenizing the photosynthetic capacity (AA) with the other notations in Table 2.

**Done**

Table 1: Unit for PAR absorptance (should be % I think)

**Done**

Paragraphs 3.1 and 3.2: I thought that the comparison between intra species and interspecies gradients is very interesting. I wondered if there are more studies to expand it. One key article that I know is (Lloyd et al., 2010) which showed that within tree gradients and between tree gradients are similar for a lot of leaf traits in tropical forests. I think this is one of the reasons why DGCMs are relatively accurate even if the canopy description is quite simple. (The vertical gradients in photosynthetic parameters are scaled on Na gradients, which are the same intra and between species in this study).

**We ended up removing former section 3.2 because we reorganized the traits section around trait groupings, as opposed to intra-specific/ interspecific. This rearrangement of the traits section better parallels Table 1 and the following section on leaf gas exchange. We integrated the content that was previously in this section throughout the traits section, as appropriate.**

**Unfortunately, we’ve been unable to find many studies examining vertical gradients at the interspecific level, and have included those of which we are aware.**

**Thanks for pointing out the Lloyd reference, which we had previously missed. We have added citations to this (e.g., *2nd* paragraph of the traits section), and have also added it to our tables).**

L429 I am not fully sure if I understood this sentence, consider maybe developing the idea. Do you mean that the variation is higher in canopy made of multi species than on the canopy of single species? If so, I didn’t understand the comparison with understory species.

**We removed this sentence because we agreed that it was confusing, and the points addressed from comments above provide substantial information for inter- and intra-canopy leaf traits.**

L470 A thought: Stomatal conductance is highly correlated to photosynthetic capacity (Wong et al., 1979) so the gradients in conductance are expected to follow the gradients in photosynthetic capacity. The water use efficiency (gs/A) or the slope parameter of conductance models (Medlyn et al., 2011) could change vertically inside the profiles. I don’t know if there are a lot of studies on the vertical variation of the water use efficiency or the slope parameter, but that could be something interesting to mention. See for example (Buckley, 2021).

**We appreciate this comment, and have added mention of the fact that maximum increases with light in the canopy because it typically tracks photosynthetic capacity, per Wong *et al.* (1979). There is a great deal of literature showing that the relative limitation of photosynthesis by stomata (gs/A, or intrinsic WUE) tends to be greater in the upper canopy, which results in lower intercellular CO2 and C isotope discrimination, as noted in the original manuscript (lines 478).**

I also think you could describe a little bit more the hydraulic constraints that increase with height. See for example (Koch et al., 2004). I think there are also other papers discussing the effect of height on water potential and stomatal conductance. You mention some aspects of it later, around L 636.

**We have added mention of a few papers documenting the hydraulic constraints with height as they affect stomatal conductance (Yoder *et al.*, 1994; Koch *et al.*, 2004; Sillett *et al.*, 2010).**

L471, I think the word conductance is missing.

**Done**

L 513 Vcmax (c in subscript?)

**Done**

L 609 It is a detail, but you sometimes use the word ‘canopy’ to describe the top of the vegetation, and sometimes you precise ‘top of canopy’. You also use canopy to describe all the vegetation from understory to the canopy, and you sometimes change definition from one sentence to another. Usually, it is easy to understand with the context of the sentence, but you might want to be consistent everywhere.

**Thanks for pointing this out. We have revisited the use of the term “canopy” throughout the entire manuscript and employed with consistent terminology, using “canopy” to refer only to the layer formed by dominant trees, and using a term such as to “vertical profile” to refer to the entire gradient from understory to the canopy.**

L 665 though

**Done**

More details on my thoughts for the ‘Scaling across space and time’ paragraph:

Most DGCMs represent a vertical variability in the main physiological parameters (Vcmax, Jmax, Rdark, Na). See for example (Krinner et al., 2005; Clark et al., 2011; Oleson et al., 2013). They all use some form of an exponential decrease in the photosynthetic parameters from the canopy to the ground. Since a lot of parameters and variables depend on Vcmax (for example A and therefore gs), this allows the representation of the vertical variation of a lot of leaf traits and variables. Big leaf models have this capability (see for example Krinner et al. 2005 that you cited, Appendix, or Clark et al. 2011). I think it is not clear in the way you wrote this paragraph, and it looks like ‘big leaf’ models do not represent any vertical variation at all. Note also that it is possible to use multi-layer models with or without considering shaded and sunlit leaves (See for example Clark et al. 2011).

**Thank you for noting the need to clarify this point. We have added a passage at the end of the sentence that mentions big-leaf models to clarify that they do indeed account for assumed vertical profiles: “…to big-leaf models that reduce 3D vegetation structure to a single vegetation layer, *implicitly capturing vertical profiles in light, photosynthetic capacity and other features by assuming those profiles are exponential and thus can be integrated analytically…”*(added text italicized here). We also deleted the clause that occurred two sentences later, that had said about big-leaf models: “…which do not represent any vertical stratification…”**

**In addition, we also added a paragraph that more clearly describes the methods used for light competition that enables the type of variation in physiological traits that you described (e.g., Vcmax):**

* **Owing to differences in the representation of forest vertical strata, DVGMs vary in their capacity to incorporate vertical variation in leaf traits and physiological processes.In general, however, this variation is accounted for via light competition. Models partition radiation above and within the forest vertical profile (i.e., direct vs. diffuse light) using radiative transfer models or a system of two coupled ordinary differential equations, referred to as a two-stream approximation (Sellers, 1985; Fisher *et al.*, 2018).Using the latter method, single canopy layers are divided into sun and shade fractions (e.g., in the Community Land Model, CLM model), while models with multiple vegetative layers can analytically solve the two-stream approximation for each layer.Thus, even in single-layer models, key physiological parameters like and vary, decreasing with increasing cumulative LAI or lower light conditions (Table 2, e.g., Krinner *et al.*, 2005).**

To me, an important remark is that most gradients in DGVMs are prescribed. More data would of course help to better understand and quantify the gradients, and to compare them with model representations (part ‘Scaling in situ data with remote sensing’ of your paper). But in the end, the mechanisms explaining those gradients are still not really known, in the sense that they can’t be efficiently modeled prognostically. This is due to the multiple sources of parameters variation that you highlighted (light environment, temperature, hydraulic, …). A lot of research is done using optimality frameworks to try and predict the photosynthetic and other vegetation traits based on environmental variables. See for example (Ali et al., 2016; Buckley, 2021). A question I have, is if including more precise cohorts as you suggest, would improve the accuracy of models given all the uncertainty in the parametrization of their traits.

**We agree that there is a recognition in the modeling community that we do need improved understanding of the mechanisms to better represent the level of vertical variation desired by some. We added the following sentence to acknowledge that: “Moreover, given the anticipated importance of mid-canopy and understory trees in ecosystem resilience given increasing mortality of canopy trees, it is essential that models separately represent these strata.”. We also removed some of the language that emphasizes cohort based models as the only or best way to do this.**

**We note that addressing the question poosed here is essentially impossible to answer without doing the research. The value of different modeling approaches is difficult to judge a priori.**

Table S3: Including the words vertical or vertical gradient could have been useful.

**Thanks for the suggestion. We agree, but at the same time are confident that the search terms we used covered the majority of the relevant literature. Adding additional search terms could always turn up additional papers, but we feel that we have reached a point of diminishing returns, and unfortunately don’t have time to expand the search (lead author has moved on from the institution where she performed the work to a PhD program).**

I included below some more references, mostly in the tropics.

**Thank you for the references. We have reviewed these and incorporated as appropriate.**

(Kitajima et al., 1997; Valladares et al., 1997, 2000; Thomas & Bazzaz, 1999; Carswell et al., 2000; Koch et al., 2004; Coste et al., 2005; Domingues et al., 2005; Lloyd et al., 2010; Van Goethem et al., 2014; Crous et al., 2020; Béland & Baldocchi, 2021)

Ali AA, Xu C, Rogers A, Fisher RA, Wullschleger SD, Massoud EC, Vrugt JA, Muss JD, McDowell NG, Fisher JB, et al. 2016. A global scale mechanistic model of photosynthetic capacity (LUNA V1.0). Geoscientific Model Development 9: 587–606.

Béland M, Baldocchi DD. 2021. Vertical structure heterogeneity in broadleaf forests: Effects on light interception and canopy photosynthesis. Agricultural and Forest Meteorology 307: 108525.

Buckley TN. 2021. Optimal carbon partitioning helps reconcile the apparent divergence between optimal and observed canopy profiles of photosynthetic capacity. New Phytologist 230: 2246–2260.

Carswell FE, Meir P, Wandelli EV, Bonates LCM, Kruijt B, Barbosa EM, Nobre AD, Grace J, Jarvis PG. 2000. Photosynthetic capacity in a central Amazonian rain forest. Tree Physiology 20: 179–186.

Clark DB, Mercado LM, Sitch S, Jones CD, Gedney N, Best MJ, Pryor M, Rooney GG, Essery RLH, Blyth E, et al. 2011. The Joint UK Land Environment Simulator (JULES), model description – Part 2: Carbon fluxes and vegetation dynamics. Geoscientific Model Development 4: 701–722.

Coste S, Roggy J-C, Imbert P, Born C, Bonal D, Dreyer E. 2005. Leaf photosynthetic traits of 14 tropical rain forest species in relation to leaf nitrogen concentration and shade tolerance. Tree physiology 25: 1127–1137.

Crous KY, Campany CE, Lopez Rodriguez RA, Cano FJ, Ellsworth DS. 2020. [In Press] Canopy position affects photosynthesis and anatomy in mature Eucalyptus trees in elevated CO2. Tree Physiology.

Domingues TF, Berry JA, Martinelli LA, Ometto JP, Ehleringer JR. 2005. Parameterization of canopy structure and leaf-level gas exchange for an eastern Amazonian tropical rain forest (Tapajos National Forest, Para, Brazil). Earth Interactions 9: 1–23.

Kitajima K, Mulkey SS, Wright SJ. 1997. Seasonal leaf phenotypes in the canopy of a tropical dry forest: photosynthetic characteristics and associated traits. Oecologia 109: 490–498.

Koch GW, Sillett SC, Jennings GM, Davis SD. 2004. The limits to tree height. Nature 428: 851–854.

Krinner G, Viovy N, Noblet-Ducoudré N de, Ogée J, Polcher J, Friedlingstein P, Ciais P, Sitch S, Prentice IC. 2005. A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. Global Biogeochemical Cycles 19.

Lloyd J, Patiño S, Paiva RQ, Nardoto GB, Quesada CA, Santos AJB, Baker TR, Brand WA, Hilke I, Gielmann H, et al. 2010. Optimisation of photosynthetic carbon gain and within-canopy gradients of associated foliar traits for Amazon forest trees. Biogeosciences 7: 1833–1859.

Medlyn BE, Duursma RA, Eamus D, Ellsworth DS, Prentice IC, Barton CVM, Crous KY, Angelis PD, Freeman M, Wingate L. 2011. Reconciling the optimal and empirical approaches to modelling stomatal conductance. Global Change Biology 17: 2134–2144.

Oleson K, Lawrence D, Bonan G, Drewniak B, Huang M, Koven C, Levis S, Li F, Riley W, Subin Z, et al. 2013. Technical description of version 4.5 of the Community Land Model (CLM). Boulder, Colorado, US: NCAR TECHNICAL NOTES.

Thomas SC, Bazzaz FA. 1999. Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. Ecology 80: 1607–1622. Valladares F, Allen MT, Pearcy RW. 1997. Photosynthetic responses to dynamic light under field conditions in six tropical rainforest shrubs occuring along a light gradient. Oecologia 111: 505–514.

Valladares F, Wright SJ, Lasso E, Kitajima K, Pearcy RW. 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. Ecology 81: 1925–1936.

Van Goethem D, Potters G, De Smedt S, Gu L, Samson R. 2014. Seasonal, diurnal and vertical variation in photosynthetic parameters in Phyllostachys humilis bamboo plants. Photosynthesis Research 120: 331–346.

Wong SC, Cowan IR, Farquhar GD. 1979. Stomatal conductance correlates with photosynthetic capacity. Nature 282: 424–426.

## Referee: 2

A defining feature of forest canopies is their vertical variation in environment and morphology and physiology, originally described through the sun-shade leaf dichotomy or even earlier through vertical stratification diagrams as in Pearson (1971), dating further back such as the classic work of P. W. Richards (1952). Such observations were carried through to the forest meteorology community by Monteith, Jarvis and others in the 1980s (Monteith & Unsworth 1990), and there are well-known patterns in micrometeorology through canopies and first-principle understanding of their meaning for energy balance within canopies. I read this review keenly interested in what these known aspects would mean for the interactions amongst leaf traits and sensitivity to temperature, tie them back to some empirical findings of more recent vintage, and possibly to gain some insights into canopy dieback phenomena during heat events or with climate warming. In the end, the latter weren’t discussed but the authors are applauded for taking on such a huge topic. Fig. 1 is a useful entrée to the subject area.

**Thank you for the review. We have added citations to the references mentioned here (Matusick *et al.*, 2013; Teskey *et al.*, 2015; Breshears *et al.*, 2021).**

**We have also added the following sentence on canopy dieback to the canopy disturance section:** **“Increasing severity and frequency of heat waves, accompanied with increases in VPD and ET, can exacerbate effects of drought on predominantly canopy trees, potentially causing large scale canopy die-back (Matusick *et al.*, 2013; Teskey *et al.*, 2015; Breshears *et al.*, 2021).”**

Given the depth of what is known about within-canopy micrometeorology, I would have thought taking this on in a review wouldn’t be needed, or would be daunting and require too much detail to cover it all. As it is, I found the article launches into the empirical info too early in such an article. The article could be improved by going through the theory of how momentum and mass-transfers are attenuated through canopies and then show the empirical info from NEON in America. Overall there is too little on the theory end of things and too much ‘case study’ for this kind of article (see Monteith and Unsworth, and Gates to enhance the first-principle theory). As an aside, there need to be a number of improvements in Fig. 2, with lines made bolder and also height should be normalised to height relative to the top of the canopy given that trees were very different heights and meteorological masts went above the canopy to different degrees. Doing so would help make the authors’ point about differences in the Figure as well as convergence in certain properties inside canopies rather than everything being on a different y-scale.

**Regarding incorporation of more theory, please see our response to the comment below.**

**We have made the suggested improvements to figure 2: lines are bolder, and height normalized to height at the top of the canopy.**

Certainly, a discussion with a micrometeorologist or atmospheric scientist, if not already had, could improve the manuscript. Statements like l. 156: ‘Wind speeds are also higher at the top of the canopy, owing to the buffering effect of the canopy’ are an awkward read. Buffering? There could be much improvement by looking at it the other way: wind will blow as it does at the top of the canopy until encountering the plant canopy top as an aerodynamic drag element; then the additional leaf area entrains air movement and sweep-eject motion and eddies are attenuated through the canopy resulting in progressively lower windspeeds deeper into canopies. I don’t know how buffering enters into this, or what the authors mean here.

**We appreciate these comments and have added a discussion of canopy transport from a more theoretical perspective (lines 169-192), immediately after the paragraph about canopy radiation profiles and before those on CO2, H2O and temperature profiles. We have also modified the subsequent paragraph about wind speeds to eliminate the use of the confusing term “buffering”.**

**We had also used the words “buffering”, “buffer”, or “buffered” in a different context, where the intention was to describe how canopy attenuation (of radiation and wind) can reduce daily extremes of temperature in the lower canopy and understory. We have modified the text in those places to clarify, generally reducing use of the terms. However, the term has been widely used in recent publications on this theme, and we therefore did not feel it was necessary to eliminate it’s usage. Examples of modified sentences include the following:**

* **“Canopy foliage is the primary physical barrier between the atmosphere and the forest floor, buffering multiple aspects of the understory conditions** *from large fluctuations in conditions experienced above the canopy.”; (line xxx)***(new text italicized)**
* **“Commonly, attenuation of radiation and vertical transport of sensible heat by the canopy buffers the lower canopy and understory from large diel and seasonal swings in air temperature (Zellweger *et al.*, 2019; De Frenne *et al.*, 2021; Haesen *et al.*, 2021)” (line 229)**
* **“Typically, *diel temperature range is smaller beneath dense canopies than above, resulting from,*~~lower maximum daytime and warmer nighttime minimum than beneath open canopies or in nearby clearings.” (line 232)**

I was eager to see the part of the manuscript about photoprotection and also its relationship to heat damage. The opening sentence (l. 384) was obvious to the point of being painful to read. Of course photoprotection is higher in the upper canopy: radiation levels are higher! Can this first sentence get revised to increase information content? This is one of the more exciting topics of the review, yet is handled only in a cursory fashion. If the authors could manage a bit more discussion of this topic it would be useful – instead they move (in the same paragraph) to VOC emissions, something I view as a separate capability of some plants. This is also confused in Fig. 1 where VAZ and VOC are placed on the same line. I’d like to see a more complete discussion of photoprotection and heat dissipation by NPQ first, and a separate paragraph about VOC. Also, there is nothing about critical temperature until late in the manuscript even though the authors skirt the issue in their text about photoprotection. This kind of thermal sensitivity is different from gas exchange (the section where the text about Tcrit occurs, l. 530-555), and should have been discussed earlier in the manuscript.

**We have revised the first sentence here to read: “Biochemical protection against light and heat damage increases with peak radiation loads, and thus tends to be higher in the upper canopy than in the understory (Table 1).” We note that it is not necessarily obvious that mid- or lower-canopy leaves should have less photoprotection, given that they may experience nearly the same peak radiation loads, during sunflecks, as leaves in the upper canopy, despite generally having less capacity to dissipate light by photochemistry. We also choose to keep this rather obvious sentence because we feel that basic topic sentences are important for helping to guide readers from a diversity of sub-disciplines through the manuscript.**

**We separated VAZ section from VOC, and provided further context to NPQ in the following paragraph:**

* **Further, by reducing photosynthesis, VPD-associated stomatal closure can reduce the capacity to use light energy for photochemistry, thereby increasing the potential for photoinhibition (Niinemets, 2007).Accumulation of excess light energy causes overreduction of the electron transport chain and the formation of harmful reactive oxygen species (Niyogi, 2000; Suzuki & Mittler, 2006).A ubiquitous defense is a rapidly inducible non-photochemical quenching (NPQ) mechanism that responds to the increased thylakoid pH gradient caused by excess light (Niyogi, 2000; Goss & Lepetit, 2015).This form of NPQ entails interconversion of xanthophyll cycle pigments—violaxanthin, antheraxanthin, and zeaxanthin (VAZ)—which regulates the capacity for de-excitation of chlorophyll through thermal dissipation instead of photochemistry.Due to higher leaf temperatures and hydraulic limitations, upper canopy leaves spend more time with stomata closed (Table 2), and therefore require a high capacity to dissipate excess light energy (Niinemets, 2007). Correspondingly, leaves in higher light environments show a greater capacity for NPQ and higher concentrations of VAZ as well as other carotenoids (e.g., beta carotene and lutein) employed as antioxidant defenses (Table 1, Niinemets *et al.*, 1998; García-Plazaola *et al.*, 2004; Scartazza *et al.*, 2016).In contrast, to maximize photosynthesis and minimize damage during surges caused by sunflecks (see section 2.2), shade-acclimated leaves tend to induce photochemical processes more quickly (Urban *et al.*, 2007), and also show a steeper response of NPQ to light than sun-acclimated upper canopy leaves (Scartazza *et al.*, 2016).**

**We also moved thermal sensitivity content to the traits section (now with its own sub-heading).**

In the first part of Section 5.1, the authors conclude this paragraph stating the ‘dominant role of vertical profiles in microclimate in shaping tree growth rates’. However, I believe the text has confused the very large effect of light with other aspects of forest microclimate, and they very much need to clarify this. If they believe other aspects of microclimate apart from light are drivers, then I believe this would be a minority opinion in the forest biology community. If they wish to speculate about other microclimate factors that cannot be disentangled from light, I suggest that they clearly indicate their opinion and speculation. It is perhaps an area for future research to disentangle light microclimate from aspects of vertical microclimate.

**We did not intend to argue that light was not the dominant factor, but the wording was misleading. This sentence has been revised to read, “This points to a dominant role of vertical profiles in the biophysical environment, particularly light (Fig. 2) in shaping tree growth rates within forests.”**

I am uncomfortable reading some of the major conclusions of the work here, such as speculation that large canopy trees are most vulnerable to warming when water is limited, but understory trees may be more vulnerable [to warming] when well-watered. This is not consistent with my knowledge of ‘preponderance of available data’. Perhaps the authors implying that understory trees will succumb to warming earlier in a heat wave than large canopy trees? Is this based on the T50 evidence (l. 542-548) which is from 2 studies, or from one tree-ring study (l. 674-676), or both? An intriguing thought, but these studies and the corresponding author’s study have weaknesses and no clean experiment on this has been set up and done. I recommend that the more cautious language on l. 676-678 should in fact be repeated in the conclusions relevant to this point. It’s less stimulating and sober, but true, that it’s difficult to say so with strength of evidence and remains for further testing with good experimental design. An objective of such a review can stimulate further and better research.

**We agree that more caution is warranted on comparing canopy vs understory responses to warming, particularly because understory responses are highly uncertain. We have reworded relevant text as follows:**

* **“Implications: Global Change Responses : Warming” section, 4th par (previous lines 793-797: “While it is currently difficult to predict whether canopy or understory photosynthesis will be more severely affected by warming (see section 4.2), *limited tree-ring evidence* indicates that understory trees *can* exhibit greater reductions in growth during unusually hot growing seasons (section 5.1, Fig 4b, Rollinson *et al.*, 2020).”**
* **“Implications: Global Change Responses : Warming” section, final par (previous lines 803-806: “We expect that the tallest trees will be increasingly prone to hydraulic failure and damaging or lethal ’s, *while much larger uncertainty remains surrounding the resoponses of understory trees*.”**
* **Conclusions section, first part (text specifically cited in the comment above): “Similarly, much remains unknown about how crown exposure influences the temperature sensitivity of woody stem growth. While most available data suggest that large canopy trees are the most vulnerable to warming when water is limited, far less is known about the responses of understory trees, which might be more vulnerable to chronic warming stress under relatively mesic conditions (Fig. 4).”**

### Details

There are a few dense sentences or run-ons that could be revised. Lines 192-196 and lines 201-204, for instance. Please revise.

**We revised the following lines:**

* **Lines 192-196: Notably, this pattern can be reversed in open forests, where below-canopy maximum can be warmer than canopy due to turbulent air mixing and the thermal radiative flux from the soil and the canopy that is intercepted by lower-canopy layers, analogous to a ‘canopy greenhouse effect’**
* **Notably, buffering against high maximum daytime becomes weaker and can be reversed as canopies become more open (Curtis *et al.*, 2019; Meeussen *et al.*, 2021). Analogous to a ‘canopy greenhouse effect’, in open forests, below-canopy maximum can be warmer than canopy , due to turbulent air mixing and interception of thermal radiative flux from the soil and the canopy by lower-canopy layers.**
* **Lines 201-204: is strongly tied to , and is further influenced by other micrometeorological drivers (section 1) and by leaf traits and stomatal conductance (see sections 3-4), with leaves adjusting to their environment to approach, when possible, an optimal for carbon assimilation and metabolic processes (Drake et al., 2020; Perez & Feeley, 2020; Michaletz et al., 2015)**
* **is strongly tied to , and is further influenced by other micrometeorological drivers (section 1) and by leaf traits and stomatal conductance (see sections 3-4). Leaves adjust to their environment to approach, when possible, an optimal for photosynthesis and metabolism (Michaletz *et al.*, 2015 ).**

line52: ‘with decreases being more commonly documented across the world’s forests’

**We do not understand this comment, but have verified that this sentence is correct.**

line128: ‘… but understory leaf area density is often relatively high in the understory as well’ sounds redundant. Please reword.

**We removed the second ‘understory’ word here:** **“In tropical and temperate forests with dense broadleaf canopies, leaf area density is generally highest in the canopy layer (i.e., that formed by the crowns of dominant trees), but understory leaf area density is often relatively high ~~in the understory~~ as well”**

line140 ‘Light … decreases from the canopy top to the forest floor’ – why isn’t foliage clumping mentioned here amongst the other factors?

**We added foliage clumping into the list of factors influencing vertical light gradient here:** **“The intensity of visible and photosynthetically active radiation (PAR, 400-700nm) decreases from the canopy top to the forest floor, with a profile whose shape is modified by leaf area density, leaf clumping, canopy height, and vertical structure across species and forest types (Koike *et al.*, 2001; Fig. 2a-d, Supporting Information Figure S1, Béland & Baldocchi, 2021; Bin *et al.*, 2022).”**

line148: ‘Variability in the light environment decreases with height’ – I don’t see this except perhaps at z = 0 and even so seems tenuous. Explain.

**We revised the sentence to make it clearer:**

* **Previous sentences: Variability in the light environment decreases with height, with the shaded understory being highly influenced by sunflecks, or brief increases in solar radiation caused by small canopy gaps and wind-induced canopy movements (Way & Pearcy, 2012). Likewise, the mid-canopy experiences a highly variable light environment due to the sun’s passage across a dynamically structured canopy surface (Way & Pearcy, 2012).**
* **Changed sentences: Mid-canopies and understories experience a highly dynamic light environment due to sunflecks, or brief increases in direct solar radiation, caused by small canopy gaps, wind-induced canopy movements or the sun’s passage across a dynamically structured canopy surface (Way & Pearcy, 2012).**

Fig. 1: In the diagram, stomatal density, leaf angle are separate categories yet VAZ and VOC are not. As far as I know though, there is no biochemical link between VAZ and VOC, so these should be separate shouldn’t they?

**We agree with the suggestions. Therefore, to make it more clearer, we added photoprotection as one of the factors in Fig.1 and isoprene emission in a separate line instead of VAZ and VOC in the same line.**

Fig. 2 is a mix of computed and measured quantities. LAD and proportion of sun leaves are both computed quantities, and the basis of these should be clearer. Or at least state ‘modelled LAD’ and ‘calculated proportion of sun leaves’.

**Done**

line165-172: refixation of respired CO2 in the understory isn’t mentioned here, but there have been a number of studies, particularly involving 13C, that have looked at this. Please mention along with at least 1 reference.

**Vertical CO2 concentration gradients can drive gradients in the ratio of leaf intercellular CO2 to ambient CO2 () calculated from , and in rates of refixation of respired CO2 vertically, both of which tend to be higher at lower heights (Table 1).Particularly, understory seedlings benefit from elevated CO2 by having higher rates of CO2 refixation (Brooks *et al.*, 1997)."**

line185: Buffering again. I supposed what is ‘buffering’ for the authors would conventionally be thought of differently by meteorologists. Please consult with one of them, and consider using different wording.

**This passage now occurs after the new paragraph about turbulent transport within canopies. We have reworded the passage as, “Despite these complexities of within-canopy transport, wind speeds are generally much higher at the top of the canopy than within or beneath (Jiao-jun *et al.*, 2004; Jucker *et al.*, 2018).”**

line187: Where mentioning radiation fluxes, could I please ask the authors to use the phrase ‘and sensible heat emission’? I think this is really what the authors are referring to, so why not say so?

**Done**

line188: ‘dense canopies buffer understories’ is one perspective, that there is far less radiant energy received and therefore understories stay cool is another. Can the authors please consider reflecting this perspective? I’ve studies canopies for a a score of years and I just don’t think ‘buffering’ is at play so much!

**We were using the term “buffer” in a functional or biological sense, meaning “protect,” rather than as a description of the underlying physics; i.e., the canopy protects the understory from large diel swings in both air temperature and radiation. We have reworded this passage to clarify: “Typically, *diel temperature range is smaller beneath dense canopies than above, resulting from*~~dense canopies buffer understories from high maximum more than open canopies, i.e., dense canopy understories can have~~ lower maximum daytime and warmer nighttime minimum than beneath open canopies or in nearby clearings”**

line199 should end with something like ‘to shape Tleaf patterns within canopies’ rather than just drop at Tleaf.

**Done**

line206-207 ‘Leaves are typically warmer than air …’. That is not what is predicted in theory, proven by parts of the simulations in Fig. 3. Why not use ‘Leaves can be warmer …’? That would be more consistent.

**Done**

Figure 3: Variables in the inset table need to be stated. I can guess what they are, but this should be explicit.

**We added the description for the variables as part of the figure caption: Variables in the inset table are now described in the figure caption as: “Biohphysical constants in the the table include: shortwave radiation (swr), wind speed (ws), relative humidity (rh), leaf characteristic dimension (lcd), stomatal conductance (gs), air temperature (tair).”**

Figure 3: Humid and drought is not a straight comparison. Well-watered vs. drought would be clearer as there are some assumptions about gs in these conditions that underlie the modelling being done here.

**We changed to “humid” to “moist” (as opposed to “well-watered”). We chose the term “moist” because it conveys both high soil moisture and atmospheric humidity, which is what we aim to capture.**

Figure 3: why not put a point that represents the leaf values for top and bottom of the canopy?

**We have added points along each line to indicate the constants applied in the other modeling scenarios. These dots represent our best estimates of “typical” values.**

Table 1: What is here is not leaf gas exchange, and it seems that the authors have repeated the caption for Table 2 in error. Please fix this. Also don’t capitalise ‘leaf’.

**Done**

Lines 354-372 on sun versus shade leaves and Table 1. Most of what is here was known a long time ago, say in Vogel 1968 (cited) and Boardman 1977 (not cited) but pertains to within-canopy rather than between sun and shade plants. I would suggest that this would be improved if the authors started from these old studies that most readers will recognise, and state how we’ve advanced in understanding and progressed toward within-canopy work rather than between sun-and-shade habitats.

**Thank you for the suggestion. We have added additional information highlighting older work and recent advances in the paragraph below:**

**Anatomical, structural and biochemical leaf traits vary vertically across forest strata at anatomical, structural and biochemical levels (Table 1, Sack *et al.*, 2006; Niinemets *et al.*, 2015a; Chen *et al.*, 2020), shaping vertical profiles of leaf temperature, metabolism, and thermal sensitivity (Zwieniecki *et al.*, 2004; Michaletz *et al.*, 2015, 2016). Vertical variation in leaf structure and composition has been long recognized, with sun and shade leaf traits distinguished for more than 100 years (Haberlandt, 1914; Salisbury, 1928). Early work attributed differences among leaves to sun versus shade (Wylie, 1951; Vogel, 1968), and this tendency grew given the parallel differences observed for plants grown in sun versus shade (Boardman, 1977; Abrams & Kubiske, 1990). More recent work has extended the focus from light alone to leaf height in the canopy, as important in determining differences in leaf structure and function that can partially mitigate the effects of gravity and hydraulic pathlength on leaves higher up in the canopy (Koch *et al.*, 2004; Burgess *et al.*, 2006; Sack *et al.*, 2006). For example, leaf mass per area (LMA), photosynthetic capacity ( per area) and have been observed to increase with height, independently of light (Cavender-Bares & Bazzaz, 2000; Thomas & Winner, 2002; Houter & Pons, 2012; Bin *et al.*, 2022). Thus, leaves develop differently according to the irradiance and hydraulic stress associated with their canopy location, height and evaporative load, with additional potential influences of branch ontogenetic stage (Sack *et al.*, 2006; Niinemets, 2010; Casas *et al.*, 2011; Niinemets *et al.*, 2015b; Keenan & Niinemets, 2016; Chen *et al.*, 2020; Table 1, Carter *et al.*, 2021; Bin *et al.*, 2022). Plasticity throughout the canopy may emerge when development of new leaves is influenced by information from adjacent mature leaves or apical meristems, including (e.g., for deciduous species expanding leaves) a “memory” of previous conditions in that location, and may also acclimate during and after expansion to the current microclimate (Zwieniecki *et al.*, 2004). Overall, leaves may optimize their biochemistry, anatomy and structure for their local conditions (Niinemets, 2007; Lloyd *et al.*, 2010; Hikosaka, 2014; Kitao *et al.*, 2018; Buckley, 2021). Yet, while these studies have clarified many details of leaf differences throughout the canopy, no papers have integrated the many differences in leaf traits throughout the canopy in a cohesive framework. Rather, much of our understanding of trait coordination is based on the leaf economics spectrum concept developed across diverse species using sun leaves (Wright *et al.*, 2004; Keenan & Niinemets, 2016; Chen *et al.*, 2020). As canopy shade is known to alter these trait relationships (Osnas *et al.*, 2018), further research is needed to characterize trait relationships and responses vertically through the full range of canopy microenvironments.**

line382: ‘more frequent stomatal closure higher’ is awkward and does not follow the comparative. Higher than what?

**We agree that the comparison is not very clear here. We added “compared to shaded lower canopies” to the sentence: "Higher photosynthetic rates (per unit leaf area) and more frequent stomatal closure in sun exposed canopies** *compared to shaded lower canopies,***result in lower intercellular CO2 concentrations and higher C isotopic ratios in leaf tissues**

line383: d13C is NOT a concentration, it is an isotope ratio. Please revise.

**Done**

line404-405: A cause-effect for an earlier, juvenile understory tree leaf-out is implied here, and I;m not sure that is demonstrated. There are other phenomena underlying this e.g. turgor, hydraulics, hormones, etc.

**Thank you for pointing this out. In line 404-405, we are concentrated on interactions between microenvironments and function. We edited the text to emphasize the mechanisms for earlier bud break in the understory, including warmer temperatures, and the benefits of maximizing carbon gain before overstory closure reduces light availability (added ref. Lee & Ibáñez, 2021). We edited the rest of the paragraph to more clearly emphasize mechanisms of feedbacks between vertically structured microenvironments, leaf phenology, and forest function.**

line475: ‘because water supply often cannot meet the demands incurred …’. How do we know how frequent this is? Evidence?

**We have added references showing that stomatal conductance is often limited by imbalance of water supply and evaporative demand for leaves in more elevated or more sunlit canopy positions (Yoder *et al.*, 1994; Koch *et al.*, 2004; Sillett *et al.*, 2010).**

line478: ‘intracellular CO\_2’ needs to be fixed.

**Done**

line479: ‘In sun leaves, Tleaf thus further increases’. Further than what? Comparatives should have be clear what we’re comparing to.

**This sentence has been rewritten as, “Stomatal closure reduces transpirational cooling, thus amplifying the warming of sun leaves by high radiation loads.”**

line481 ‘is maximized’ or is maximal? Please correct.

**We have replaced “maximal” with “greatest”.**

line485-487: It seems that VPD and its effect on gs is ignored here. Please clarify? The well-known stomatal closure at high VPD alone would mean higher Tair would decrease gs in the upper canopy (not ‘canopy leaves’ as stated) compared to the lower canopy. See Grossiord et al. (2020) Tansley Review. VPD only gets mentioned in the section on photosynthesis (l. 496). Please do so earlier.

**We agree, and have modified the text in this section to emphasize the role of VPD in driving stomatal closure in sun leaves (new text italicized): “However, ~~because~~ water supply often cannot meet the demands incurred by the high irradiance and experienced by sun leaves *with fully open stomata, because of height-related constraints on water transport (e.g., Yoder et al. 1994, Koch et al. 2004, Sillett et al 2010) and/or because of increased evaporative demand (VPD) caused by leaf warming in sunlit canopy locations (Buckley et al. 2014)*. As a result, midday stomatal depression is more prevalent in sun leaves than shade leaves in closed-canopy forests (Table 2), which drives the lower intracellular CO2 and carbon isotope discrimination discussed in section 3.1 (Table 1). Stomatal depression reduces transpirational cooling, thus amplifying the warming of sun leaves by high radiation loads ~~In sun leaves, Tleaf thus further increases due to the lack of transpirational cooling.~~” We have also added the phrase** *“(driven by increased VPD)”***after “sun leaves in the upper canopy show a stronger decrease in gs in response to rising Tair”, and clarified that “high Tair should decrease gs of *upper canopy*leaves”.**

line510-525: There is a long discussion about whether Topt for gas exchange or its components differs between overstory and understory. Here the authors aren’t clear, but such a comparison only matters if the same species is measured in different canopy layers.

**Thank you for noting this, we revised the sentence to make it clear (please see below), where we specify that majority of the studies are within species between sun and shade leaves of the same trees. Carter *et al.* (2021) is one of the only studies comparing between overstory and understory.**

* **We have very little evidence as to how the temperature sensitivity of photosynthesis compares between sun and shade leaves, and existing studies, which compare sun and shade leaves of the same trees, reveal no pronounced overall trend with height in the optimum temperatures for photosynthetic processes**

The section on VOC emissions was interesting and informative.

**Thank you.**

line641: ‘tends to be greater in canopy trees’. Greater than what? Please state the comparison.

**This sentence has been revised to read, “In turn, the drought sensitivity of woody growth tends to be greater in canopy trees than in smaller trees with less exposed crowns.”**

line650: ‘In addition to lower drought resistance of growth, larger trees frequently exhibit lower ability to recover’. Having studied large overstory trees and young understory saplings, I have a very, very difficult time with this statement especially portraying it as categorically true even if consistent with the 4 cited studies. Very few researchers have studies the same species in this context, and in this review manuscript the authors cannot scientifically lay the effect on canopy position and microclimate rather than age or other confounding factors. I must challenge their assertion and ask a higher level of evidence to make these statements, which should be qualified.

**As the point about resilience was not critical, we have removed that part of the statement. The sentence now reads, “In addition to lower drought resistance of growth, larger trees frequently exhibit greater increases in mortality (Bennett *et al.*, 2015; Stovall *et al.*, 2019).”**

line946: ‘… how … temperature sensitivities of metabolism and woody growth vary across these vertical gradients’. I’m not sure why the authors are speculating on woody growth in this context, surely it would be extremely difficult to show that woody growth varied vertically in an individual? And that across-individual differences compound comparisons of individuals in different vertical strata? Shouldn’t these things be pointed out to readers?

**This has been reworded to read, “However, there remains a lot of uncertainty as to how temperature sensitivity of foliar gas exchange varies across these vertical gradients. Similarly, much remains to be learned about how crown exposure influences the temperature sensitivity of woody stem growth. While the preponderance of available data suggest that large canopy trees are the most vulnerable to warming when water is limited, far less is known about the responses of understory trees, which might be more vulnerable to chronic warming stress under relatively mesic conditions (Fig. 4).”**

## References

**Abrams MD, Kubiske ME**. **1990**. Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: Influence of light regime and shade-tolerance rank. *Forest Ecology and Management* **31**: 245–253.

**Bennett AC, McDowell NG, Allen CD, Anderson-Teixeira KJ**. **2015**. Larger trees suffer most during drought in forests worldwide. *Nature Plants* **1**: 15139.

**Béland M, Baldocchi DD**. **2021**. Vertical structure heterogeneity in broadleaf forests: Effects on light interception and canopy photosynthesis. *Agricultural and Forest Meteorology* **307**: 108525.

**Bin Y, Li Y, Russo SE, Cao H, Ni Y, Ye W, Lian J**. **2022**. Leaf trait expression varies with tree size and ecological strategy in a subtropical forest. *Functional Ecology* **n/a**.

**Boardman NK**. **1977**. Comparative Photosynthesis of Sun and Shade Plants. *Annual Review of Plant Physiology* **28**: 355–377.

**Breshears DD, Fontaine JB, Ruthrof KX, Field JP, Feng X, Burger JR, Law DJ, Kala J, Hardy GESJ**. **2021**. Underappreciated plant vulnerabilities to heat waves. *New Phytologist* **231**: 32–39.

**Brooks JR, Flanagan LB, Varney GT, Ehleringer JR**. **1997**. Vertical gradients in photosynthetic gas exchange characteristics and refixation of respired CO2 within boreal forest canopies. *Tree Physiology* **17**: 1–12.

**Buckley TN**. **2021**. Optimal carbon partitioning helps reconcile the apparent divergence between optimal and observed canopy profiles of photosynthetic capacity. *New Phytologist* **230**: 2246–2260.

**Burgess SSO, Dawson TE, Burgess SSO**. **2006**. Regressions of leaf traits.

**Carter KR, Wood TE, Reed SC, Butts KM, Cavaleri MA**. **2021**. Experimental warming across a tropical forest canopy height gradient reveals minimal photosynthetic and respiratory acclimation. *Plant, Cell & Environment* **44**: 2879–2897.

**Casas RR de, Vargas P, Pérez‐Corona E, Manrique E, García‐Verdugo C, Balaguer L**. **2011**. Sun and shade leaves of Olea europaea respond differently to plant size, light availability and genetic variation. *Functional Ecology* **25**: 802–812.

**Cavaleri MA**. **2020**. Cold-blooded forests in a warming world. *New Phytologist* **228**: 1455–1457.

**Cavender-Bares J, Bazzaz FA**. **2000**. Changes in drought response strategies with ontogeny in Quercus rubra: Implications for scaling from seedlings to mature trees. *Oecologia* **124**: 8–18.

**Chen X, Sun J, Wang M, Lyu M, Niklas KJ, Michaletz ST, Zhong Q, Cheng D**. **2020**. The Leaf Economics Spectrum Constrains Phenotypic Plasticity Across a Light Gradient. *Front. Plant Sci.* **11**.

**Curtis EM, Knight CA, Leigh A**. **2019**. Intracanopy adjustment of leaf-level thermal tolerance is associated with microclimatic variation across the canopy of a desert tree (Acacia papyrocarpa). *Oecologia* **189**: 37–46.

**de Castro F**. **2000**. Light spectral composition in a tropical forest: Measurements and model. *Tree Physiology* **20**: 49–56.

**De Frenne P, Lenoir J, Luoto M, Scheffers BR, Zellweger F, Aalto J, Ashcroft MB, Christiansen DM, Decocq G, Pauw KD, *et al.*** **2021**. Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology* **27**: 2279–2297.

**Fisher RA, Koven CD, Anderegg WRL, Christoffersen BO, Dietze MC, Farrior CE, Holm JA, Hurtt GC, Knox RG, Lawrence PJ, *et al.*** **2018**. Vegetation demographics in Earth System Models: A review of progress and priorities. *Global Change Biology* **24**: 35–54.

**García-Plazaola JI, Becerril JM, Hernández A, Niinemets Ü, Kollist H**. **2004**. Acclimation of antioxidant pools to the light environment in a natural forest canopy. *New Phytologist* **163**: 87–97.

**Goss R, Lepetit B**. **2015**. Biodiversity of NPQ. *Journal of Plant Physiology* **172**: 13–32.

**Haberlandt G**. **1914**. *Physiological Plant Anatomy*. Macmillan and Company, limited.

**Haesen S, Lembrechts JJ, De Frenne P, Lenoir J, Aalto J, Ashcroft MB, Kopecký M, Luoto M, Maclean I, Nijs I, *et al.*** **2021**. ForestTemp – Sub-canopy microclimate temperatures of European forests. *Global Change Biology* **27**: 6307–6319.

**Hikosaka K**. **2014**. Optimal nitrogen distribution within a leaf canopy under direct and diffuse light. *Plant, Cell & Environment* **37**: 2077–2085.

**Houter NC, Pons TL**. **2012**. Ontogenetic changes in leaf traits of tropical rainforest trees differing in juvenile light requirement. *Oecologia* **169**: 33–45.

**Jiao-jun Z, Xiu-fen L, Yutaka G, Takeshi M**. **2004**. Wind profiles in and over trees. *Journal of Forestry Research* **15**: 305.

**Jucker T, Hardwick SR, Both S, Elias DMO, Ewers RM, Milodowski DT, Swinfield T, Coomes DA**. **2018**. Canopy structure and topography jointly constrain the microclimate of human-modified tropical landscapes. *Global Change Biology* **24**: 5243–5258.

**Keenan TF, Niinemets Ü**. **2016**. Global leaf trait estimates biased due to plasticity in the shade. *Nature Plants* **3**: 1–6.

**Kitao M, Kitaoka S, Harayama H, Tobita H, Agathokleous E, Utsugi H**. **2018**. Canopy nitrogen distribution is optimized to prevent photoinhibition throughout the canopy during sun flecks. *Scientific Reports* **8**: 503.

**Koch GW, Sillett SC, Jennings GM, Davis SD**. **2004**. The limits to tree height. *Nature* **428**: 851–854.

**Koike T, Kitao M, Maruyama Y, Mori S, Lei TT**. **2001**. Leaf morphology and photosynthetic adjustments among deciduous broad-leaved trees within the vertical canopy profile. *Tree Physiology* **21**: 951–958.

**Krinner G, Viovy N, Noblet-Ducoudré N de, Ogée J, Polcher J, Friedlingstein P, Ciais P, Sitch S, Prentice IC**. **2005**. A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. *Global Biogeochemical Cycles* **19**.

**Lee BR, Ibáñez I**. **2021**. Spring phenological escape is critical for the survival of temperate tree seedlings. *Functional Ecology* **35**: 1848–1861.

**Leigh A, Sevanto S, Close JD, Nicotra AB**. **2017**. The influence of leaf size and shape on leaf thermal dynamics: Does theory hold up under natural conditions? *Plant, Cell & Environment* **40**: 237–248.

**Lloyd J, Patiño S, Paiva RQ, Nardoto GB, Quesada CA, Santos AJB, Baker TR, Brand WA, Hilke I, Gielmann H, *et al.*** **2010**. Optimisation of photosynthetic carbon gain and within-canopy gradients of associated foliar traits for Amazon forest trees. *Biogeosciences* **7**: 1833–1859.

**Martin TA, Hinckley TM, Meinzer FC, Sprugel DG**. **1999**. Boundary layer conductance, leaf temperature and transpiration of Abies amabilis branches. *Tree Physiology* **19**: 435–443.

**Matusick G, Ruthrof KX, Brouwers NC, Dell B, Hardy GStJ**. **2013**. Sudden forest canopy collapse corresponding with extreme drought and heat in a mediterranean-type eucalypt forest in southwestern Australia. *Eur J Forest Res* **132**: 497–510.

**Meeussen C, Govaert S, Vanneste T, Bollmann K, Brunet J, Calders K, Cousins SAO, De Pauw K, Diekmann M, Gasperini C, *et al.*** **2021**. Microclimatic edge-to-interior gradients of European deciduous forests. *Agricultural and Forest Meteorology* **311**: 108699.

**Michaletz ST, Weiser MD, McDowell NG, Zhou J, Kaspari M, Helliker BR, Enquist BJ**. **2016**. The energetic and carbon economic origins of leaf thermoregulation. *Nature Plants* **2**: 16129.

**Michaletz ST, Weiser MD, Zhou J, Kaspari M, Helliker BR, Enquist BJ**. **2015**. Plant Thermoregulation: Energetics, Trait–Environment Interactions, and Carbon Economics. *Trends in Ecology & Evolution* **30**: 714–724.

**Niinemets Ü**. **2007**. Photosynthesis and resource distribution through plant canopies. *Plant, Cell & Environment* **30**: 1052–1071.

**Niinemets Ü**. **2010**. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management* **260**: 1623–1639.

**Niinemets Ü, Bilger W, Kull O, Tenhunen JD**. **1998**. Acclimation to high irradiance in temperate deciduous trees in the field: Changes in xanthophyll cycle pool size and in photosynthetic capacity along a canopy light gradient. *Plant, Cell & Environment* **21**: 1205–1218.

**Niinemets Ü, Keenan TF, Hallik L**. **2015a**. A worldwide analysis of within-canopy variations in leaf structural, chemical and physiological traits across plant functional types. *New Phytologist* **205**: 973–993.

**Niinemets Ü, Kull O, Tenhunen JD**. **2015b**. Variability in Leaf Morphology and Chemical Composition as a Function of Canopy Light Environment in Coexisting Deciduous Trees. *International Journal of Plant Sciences*.

**Niyogi KK**. **2000**. Safety valves for photosynthesis. *Current Opinion in Plant Biology* **3**: 455–460.

**Osnas JLD, Katabuchi M, Kitajima K, Wright SJ, Reich PB, Van Bael SA, Kraft NJB, Samaniego MJ, Pacala SW, Lichstein JW**. **2018**. Divergent drivers of leaf trait variation within species, among species, and among functional groups. *Proc Natl Acad Sci USA* **115**: 5480–5485.

**Poorter L, Kwant R, Hernández R, Medina E, Werger MJA**. **2000**. Leaf optical properties in Venezuelan cloud forest trees. *Tree Physiology* **20**: 519–526.

**Rey-Sánchez A, Slot M, Posada J, Kitajima K**. **2016**. Spatial and seasonal variation in leaf temperature within the canopy of a tropical forest. *Climate Research* **71**: 75–89.

**Roberts J, Cabral OMR, Aguiar LFD**. **1990**. Stomatal and Boundary-Layer Conductances in an Amazonian terra Firme Rain Forest. *The Journal of Applied Ecology* **27**: 336.

**Rollinson CR, Alexander MR, Dye AW, Moore DJP, Pederson N, Trouet V**. **2020**. Climate sensitivity of understory trees differs from overstory trees in temperate mesic forests. *Ecology* **102**: e03264.

**Sack L, Melcher PJ, Liu WH, Middleton E, Pardee T**. **2006**. How strong is intracanopy leaf plasticity in temperate deciduous trees? *American Journal of Botany* **93**: 829–839.

**Salisbury EJ**. **1928**. On the Causes and Ecological Significance of Stomatal Frequency, with Special Reference to the Woodland Flora. *Philosophical Transactions of the Royal Society of London. Series B, Containing Papers of a Biological Character* **216**: 1–65.

**Scartazza A, Di Baccio D, Bertolotto P, Gavrichkova O, Matteucci G**. **2016**. Investigating the European beech (Fagus sylvatica L.) Leaf characteristics along the vertical canopy profile: Leaf structure, photosynthetic capacity, light energy dissipation and photoprotection mechanisms. *Tree Physiol* **36**: 1060–1076.

**Sellers PJ**. **1985**. Canopy reflectance, photosynthesis and transpiration. *International Journal of Remote Sensing* **6**: 1335–1372.

**Sillett SC, Van Pelt R, Koch GW, Ambrose AR, Carroll AL, Antoine ME, Mifsud BM**. **2010**. Increasing wood production through old age in tall trees. *Forest Ecology and Management* **259**: 976–994.

**Stovall AEL, Shugart H, Yang X**. **2019**. Tree height explains mortality risk during an intense drought. *Nature Communications* **10**: 4385.

**Suzuki N, Mittler R**. **2006**. Reactive oxygen species and temperature stresses: A delicate balance between signaling and destruction. *Physiologia Plantarum* **126**: 45–51.

**Teskey R, Wertin T, Bauweraerts I, Ameye M, Mcguire MA, Steppe K**. **2015**. Responses of tree species to heat waves and extreme heat events. *Plant, Cell & Environment* **38**: 1699–1712.

**Thomas SC, Winner WE**. **2002**. Photosynthetic differences between saplings and adult trees: An integration of field results by meta-analysis. *Tree Physiology* **22**: 117–127.

**Urban O, Kosvancová M, Marek MV, Lichtenthaler HK**. **2007**. Induction of photosynthesis and importance of limitations during the induction phase in sun and shade leaves of five ecologically contrasting tree species from the temperate zone. *Tree Physiol* **27**: 1207–1215.

**Vogel S**. **1968**. "Sun Leaves" and "Shade Leaves": Differences in Convective Heat Dissipation. *Ecology* **49**: 1203–1204.

**Vogel S**. **2009**. Leaves in the lowest and highest winds: Temperature, force and shape. *New Phytologist* **183**: 13–26.

**Way DA, Pearcy RW**. **2012**. Sunflecks in trees and forests: From photosynthetic physiology to global change biology. *Tree Physiology* **32**: 1066–1081.

**Wong SC, Cowan IR, Farquhar GD**. **1979**. Stomatal conductance correlates with photosynthetic capacity. *Nature* **282**: 424–426.

**Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, *et al.*** **2004**. The worldwide leaf economics spectrum. *Nature* **428**: 821–827.

**Wylie RB**. **1951**. Principles of Foliar Organization Shown by Sun-Shade Leaves from Ten Species of Deciduous Dicotyledonous Trees. *American Journal of Botany* **38**: 355–361.

**Yoder BJ, Ryan MG, Waring RH, Schoettle AW, Kaufmann MR**. **1994**. Evidence of Reduced Photosynthetic Rates in Old Trees. *Forest Science* **40**: 513–527.

**Zellweger F, Coomes D, Lenoir J, Depauw L, Maes SL, Wulf M, Kirby KJ, Brunet J, Kopecký M, Máliš F, *et al.*** **2019**. Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe (A Algar, Ed.). *Global Ecology and Biogeography* **28**: 1774–1786.

**Zwieniecki MA, Boyce CK, Holbrook NM**. **2004**. Hydraulic limitations imposed by crown placement determine final size and shape of Quercus rubra L. leaves. *Plant, Cell & Environment* **27**: 357–365.