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Plant responses to climate warming: physiological adjustments and implications for plant functioning in a future, warmer world

Kristine Y. Crous[1,2]

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[1] Hawkesbury Institute for the Environment, Western Sydney University, Locked Bag 1797, Penrith, NSW, Australia

[2] Author for correspondence (e-mail: K.Crous@westernsydney.edu.au)

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The Earth's average temperatures have been rising since the start of the Industrial Revolution, in major part driven by rising concentrations of carbon dioxide. Correlated with the rise of atmospheric CO_2 from ~280 ppm (before the start of the Industrial Revolution) to the current 410 ppm, the average temperature has warmed by about 1°C since 1880 (Ciais et al., 2013). However, as CO_2 concentrations continue to rise, the Earth will experience further warming, although how much warming will also depend on political will and human capacity to reduce carbon emissions in the near future. As such, rising temperatures will create new climate conditions in many places, affecting species' functioning and their current geographical distributions.

Terrestrial plants across the globe have played an important role in mitigating climate change by absorbing some of the CO_2 emitted by fossil fuels into the atmosphere. Currently, plants absorb 30% of CO_2 emissions annually (Ciais et al., 2013), slowing the rate of climate warming. But plants are dynamic and can adjust to environmental change such as different growth temperatures (see below). Given the key role of forests in global terrestrial productivity, it is particularly important to quantify the response of forest trees to warming to predict future climate conditions more accurately. Studying the response of forest trees includes measuring what physiological adjustments trees may make as temperatures increase. Unfortunately, physiological responses of forest trees to temperature are one of the largest uncertainties in Earth System Models (Mercado et al., 2018), affecting our understanding of the carbon cycle and predictions on the magnitude of future increases in atmospheric CO_2. These physiological adjustments are not included in most models at present, and there is a risk that net ecosystem productivity may be overestimated, if plant physiological adjustments to warming are not accounted for (Smith et al., 2016). Given that photosynthesis and respiration represent the largest fluxes of carbon uptake and carbon loss respectively, the ability of a species to physiologically adjust their plant metabolism is a first line of evidence for how they will cope with warmer temperatures.

PLANT RESPONSES TO CLIMATE WARMING

Temperature is a central regulator of tree growth and many physiological processes. The rate of warming currently experienced by many species is unprecedented in evolutionary history with predictions of 2–5°C warming likely to occur this century. Given that plants are sessile and have a longer lifespan, especially trees, relative to the current pace of increasing temperatures, they may need to make physiological adjustments to warmer temperatures. Most plants do have considerable capacity to adjust to warmer conditions

and tend to do so in a way that maintains or enhances carbon gain. In response to warming, these adjustments can include reduced respiration rates (Atkin and Tjoelker, 2003), an increase in total leaf area (Way and Oren, 2010) and sometimes increased assimilation rates at a warmer growth temperature, increasing carbon uptake and growth (Way and Sage, 2008). Most species can also shift their thermal optimum of photosynthesis upward in response to warming (Way and Oren, 2010; Crous et al., 2013) (Fig. 1). These physiological adjustments to changes in growth temperature are termed "thermal acclimation". The thermal optimum of photosynthesis can shift, typically by one third to one half the number of degrees as the shift in growth temperature (Berry and Bjorkman, 1980). Increasing the temperature optimum of photosynthesis could significantly reduce the negative impact of warming, allowing plants to operate at higher temperatures without reduced photosynthetic rates (Fig. 1). Similarly, reduced respiration rates with warmer temperatures curb carbon loss compared to respiration rates that did not adjust to warming (Atkin et al., 2015) (Fig. 1). Given that plants affect the global and regional climate, large-scale alterations in plant fluxes of photosynthesis and respiration will affect the degree of climate warming experienced in the future (Dusenge et al., 2019).

Different species have shown different acclimation capacities, in part dependent on the climate to which they are adapted. In cooler climates, species often exhibit a positive growth response to warming along with increased rates of photosynthetic capacity (Way and Sage, 2008; Gunderson et al., 2010). By contrast, evidence from studies in warmer climates indicated reduced tree growth and carbon gain in species that grow in warmer low-latitude climates along with reduced photosynthetic capacity (Feeley et al., 2007; Cheesman and Winter, 2013; Crous et al., 2013). This evidence points to a limited capacity to physiologically adjust to warmer temperatures in warmer-grown species. Equatorial species may have less capacity to adjust to warmer temperatures because they have adapted to stable thermal conditions year-round compared to species from cooler climates (higher latitudes) where temperature fluctuates strongly among the seasons. In addition, species at lower latitudes tend to operate closer to their thermal optimum (Doughty and Goulden, 2008; Crous et al., 2018). Therefore, further warming in lower latitudes could have a large effect on plant growth via reduced carbon uptake in tropical regions, thereby reducing the carbon sink of the most productive ecosystem on Earth, the tropical rainforests.

Other factors such as elevated [CO_2], nutrient availability and altered precipitation patterns can interact with plant responses to warming. Patterns of more variable rainfall combined with the increased frequency and intensity of heatwaves are likely to increase drought stress, reinforcing the negative effects of warmer temperatures. Reduced growth due to warmer temperatures can also affect seed production and dispersal, leading to less seedling establishment and forest dieback at larger scales (Allen et al., 2010). The various effects of temperature and precipitation patterns can ultimately lead to a reduced

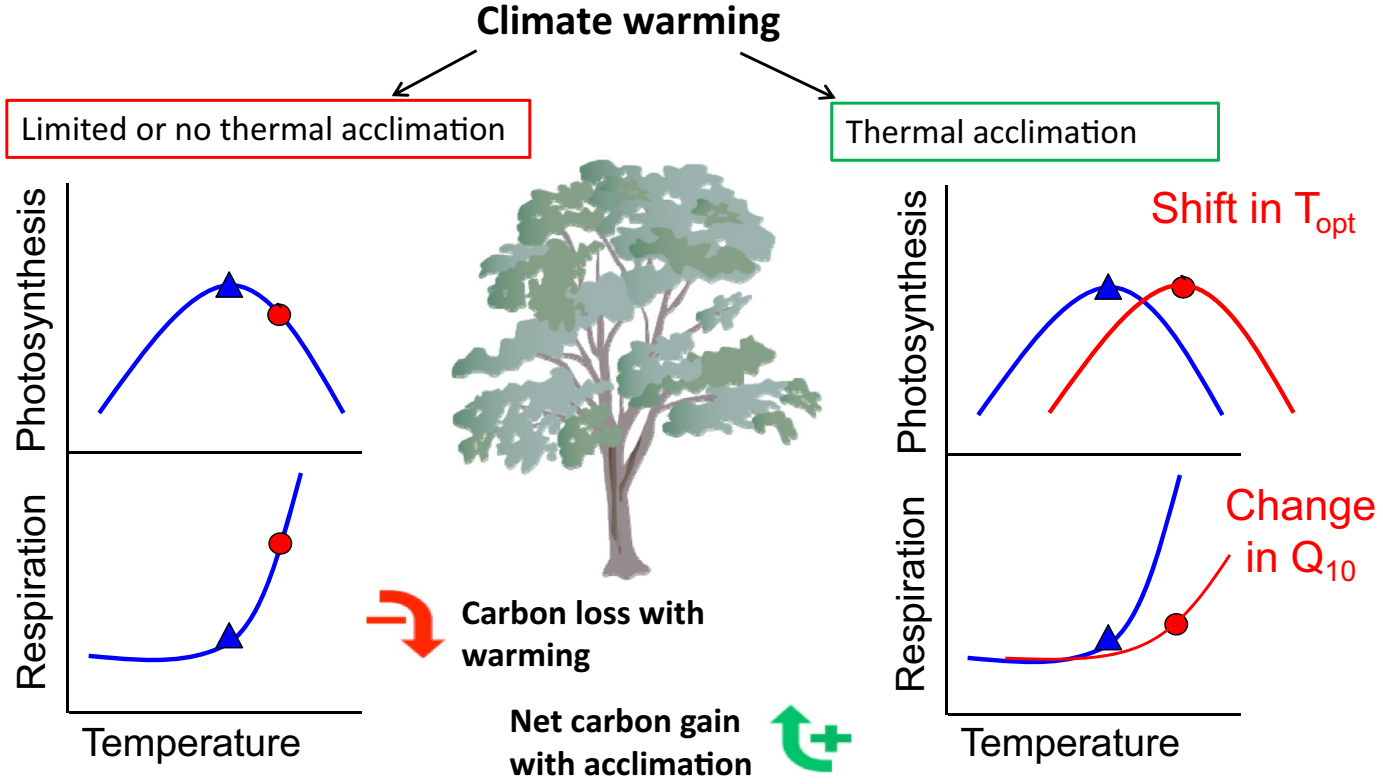

FIGURE 1. Simplified version of physiological adjustments plants can make over time in response to climate warming (i.e., thermal acclimation). The left figure shows decreased photosynthesis rates and increased respiration rates with warming (red dots) compared to ambient conditions, resulting a reduced carbon gain. The right figure shows an example of common adjustments to warming in photosynthesis via a shift toward a higher temperature optimum (Shift in T_{opt}), resulting in similar photosynthesis rates at the warmer growth temperature (compare red with blue lines in upper right panel). A reduced slope is one example of thermal acclimation in respiration (Change in Q_{10}) curbing carbon loss at warmer temperatures such that respiration is similar at the new growth temperature compared to ambient conditions (compare red with blue lines in bottom right panel).

or shifted distribution ranges in many plant species (Harsch and HilleRisLambers, 2016), as well as changes in community composition.

FUTURE DIRECTIONS

Tropical rainforest species may be especially vulnerable when these species show reduced capacity to cope with warming. However, data on temperature responses of photosynthesis on tropical rainforest species has been relatively scarce, despite rainforests currently contributing 30% of the global net primary productivity (Ciais et al., 2013). Understanding the physiological limits in tropical rainforests and how much capacity they have to adjust to warmer temperatures is a knowledge gap that should be filled because of their large contribution of CO_2 exchange with the atmosphere (Cavaleri et al., 2015). Net photosynthesis is influenced by three underpinning processes: the biochemical capacity for Rubisco carboxylation and electron transport, the amount of leaf respiration, and stomatal and mesophyll conductance for CO_2 transfer from air to leaf. Each of these processes has its own temperature dependencies and contribute to a mechanistic understanding of the temperature response of photosynthesis. These processes underlying photosynthesis are now used in most large-scale models via the photosynthesis model (Farquhar et al., 1980); therefore, these parameters are important to quantify, including in rainforests. If we have a clear understanding of the temperature responses for each of these processes, both in the short and longer term, then we can improve our ability to predict photosynthetic responses to future climate conditions. Ultimately, this mechanistic understanding can be incorporated into Earth System Models, including acclimation processes, improving the accuracy of the carbon balance and future climate projections.

Given that temperature responses of plants to warming are fundamental in any environment, how are plant function and metabolism linked to seasonal variations and climate? Recently, Crous et al. (2018) found that two widely distributed *Eucalyptus* species had reduced photosynthetic capacity in trees from tropical provenances compared to those from temperate provenances, which was linked to reduced nitrogen investment in photosynthetic capacity in tropical trees. Linking physiological characteristics with ecological plant traits would further improve our understanding of the response of different plant groups or biomes to changing climate conditions. Much more research is needed if we are to understand how plant warming responses vary over large geographical scales and how climate factors can affect physiological flexibility (Breza et al., 2012). For example, studying the same species in different environments (both within and outside their current native distribution) can yield insight into how different climatological conditions shape the temperature response. Understanding how temperature dependence of physiological processes is related to climate variation is critical to predict how species will adjust to warmer temperatures, what their thermal tolerances are, and ultimately lead to understanding how future species distributions may change.

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LITERATURE CITED

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259: 660–684.

Atkin, O. K., and M. G. Tjoelker. 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science* 8: 343–351.

Atkin, O. K., K. J. Bloomfield, P. B. Reich, M. G. Tjoelker, G. P. Asner, D. Bonal, G. Bonisch, et al. 2015. Global variability in leaf respiration in relation to climate, plant functional types and leaf traits. *New Phytologist* 206: 614–636.

Berry, J., and O. Bjorkman. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology and Plant Molecular Biology* 31: 491–543.

Breza, L. C., L. Souza, N. J. Sanders, and A. T. Classen. 2012. Within and between population variation in plant traits predicts ecosystem functions associated with a dominant plant species. *Ecology and Evolution* 2: 1151–1161.

Cavaleri, M. A., S. C. Reed, W. K. Smith, and T. E. Wood. 2015. Urgent need for warming experiments in tropical forests. *Global Change Biology* 21: 2111–2121.

Cheesman, A. W., and K. Winter. 2013. Growth response and acclimation of CO_2 exchange characteristics to elevated temperatures in tropical tree seedlings. *Journal of Experimental Botany* 64: 3817–3828.

Ciais, P., C. Sabine, G. Bala, L. Bopp, V. Brovkin, J. Canadell, A. Chhabra, et al. 2013. Carbon and Other Biogeochemical Cycles. *In* T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, et al. [eds.], Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Crous, K. Y., A. G. Quentin, Y.-S. Lin, B. E. Medlyn, D. G. Williams, C. V. M. Barton, and D. S. Ellsworth. 2013. Photosynthesis of temperate *Eucalyptus globulus* trees outside their native range has limited adjustment to elevated CO_2 and climate warming. *Global Change Biology* 19: 3790–3807.

Crous, K. Y., J. E. Drake, M. J. Aspinwall, R. E. Sharwood, M. G. Tjoelker, and O. Ghannoum. 2018. Photosynthetic capacity and leaf nitrogen decline along a controlled climate gradient in provenances of two widely distributed *Eucalyptus* species. *Global Change Biology* 24: 4626–4644.

Doughty, C. E., and M. L. Goulden. 2008. Are tropical forests near a high temperature threshold? *Journal of Geophysical Research-Biogeosciences* 113: G00B07, https://doi.org/10.1029/2007JG000632.

Dusenge, M. E., A. G. Duarte, and D. A. Way. 2019. Plant carbon metabolism and climate change: elevated CO_2 and temperature impacts on photosynthesis, photorespiration and respiration. *New Phytologist* 221: 32–49.

Farquhar, G. D., von Caemmerer S., and J. A. Berry. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 plants. *Planta* 149: 78–90.

Feeley, K. J., S. J. Wright, M. N. N. Supardi, A. R. Kassim, and S. J. Davies. 2007. Decelerating growth in tropical forest trees. *Ecology Letters* 10: 461–469.

Gunderson, C. A., K. H. O'Hara, C. M. Campion, A. V. Walker, and N. T. Edwards. 2010. Thermal plasticity of photosynthesis: the role of acclimation in forest responses to a warming climate. *Global Change Biology* 16: 2272–2286.

Harsch, M. A., and J. HilleRisLambers. 2016. Climate warming and seasonal precipitation change interact to limit species distribution shifts across Western North America. *Plos One* 11: 17.

Mercado, L. M., B. E. Medlyn, C. Huntingford, R. J. Oliver, D. B. Clark, S. Sitch, P. Zelazowski, et al. 2018. Large sensitivity in land carbon storage due to geographical and temporal variation in the thermal response of photosynthetic capacity. *New Phytologist* 218: 1462–1477.

Smith, N. G., S. L. Malyshev, E. Shevliakova, J. Kattge, and J. S. Dukes. 2016. Foliar temperature acclimation reduces simulated carbon sensitivity to climate. *Nature Climate Change* 6: 407–411.

Way, D. A., and R. Oren. 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiology* 30: 669–688.

Way, D. A., and R. F. Sage. 2008. Thermal acclimation of photosynthesis in black spruce *Picea mariana* (Mill.) BSP. *Plant Cell and Environment* 31: 1250–1262.