Warming puts the squeeze on photosynthesis – lessons from tropical trees

Mirindi Eric Dusenge1 and Danielle A. Way1,2,*

1 Department of Biology, University of Western Ontario, London, ON N6A 5B7, Canada
2 Nicholas School of the Environment, Duke University, Durham, NC 27708, USA
* Correspondence: dway4@uwo.ca

Tropical forests are regions of relative thermal stability and so, although equatorial regions are expected to experience less climate warming than the global average in coming years, tropical trees might be more vulnerable to change. But are they? In this issue of Journal of Experimental Botany, Slot and Winter (2017) provide one of the most comprehensive studies on thermal acclimation of tropical trees to date.

Climate change will increase global temperatures by 2–4 °C in the next 85 years. While this represents an enormous shift in the Earth’s climate, warming is not expected to be uniform over the globe, with equatorial regions warming by ‘only’ 1–2 °C by 2050 (IPCC, 2013). This might lead to the conclusion that tropical forests are therefore less at risk from climate warming than other biomes (Sala et al., 2000). However, tropical forests are regions of thermal stability: on a geological timescale, they have avoided the repeated glaciations and associated climate extremes experienced by higher latitudes. On much shorter timescales, diurnal temperatures may fluctuate by only 5 °C, while monthly mean temperatures may differ by just 1–4 °C across the year (Trewin, 2014), an enormous contrast to the broad temperature swings that temperate and boreal trees experience on a daily and yearly basis.

It has thus long been thought that tropical species may be adapted to a narrow thermal niche and that the ability to tolerate and acclimate to temperatures outside this temperature range may be much more limited than it is in higher latitude species (Janzen, 1967). If this is true, then the relatively small increases in temperatures expected in low latitudes may actually cause greater thermal stress in tropical forests than the larger degree of warming will in temperate and tropical trees. Indeed, increased growth temperatures decrease tree growth in tropical species in almost every study (Way and Oren, 2010). Given that tropical forests contain more than 50% of the carbon found in forests (Pan et al., 2011) and that the majority of the world’s biodiversity is in the tropics (Lewis, 2006), declines in the growth, carbon sequestration and survival of tropical tree species in a warmer world would have dire consequences.

Thermal acclimation capacity of tropical tree species

While we have considerable data on how temperate species respond to increased growth temperatures, there are only a handful of studies looking at the thermal acclimation capacity of tropical tree species, and this paucity of information impedes our ability to predict how low-latitude forests will respond to a future, warmer world. The new paper by Slot and Winter (2017) provides one of the most comprehensive studies on thermal acclimation of tropical trees to date. They grew seedlings of three common lowland tropical species at 25 °C, 30 °C and 35 °C and assessed how photosynthesis, respiration and growth were affected by the different temperature regimes.

The good news is that all the species acclimated to the warmer temperatures: the thermal optimum of photosynthesis ($T_{\text{opt}}$, the temperature at which carbon uptake is maximized) increased with increasing growth temperature, and respiration rates were lower in plants from warmer treatments (indicating a reduction in carbon losses). But there was also bad news. The shift in $T_{\text{opt}}$ was smaller than the shift in growth temperature, net photosynthetic rates at the growth temperature ($P_{\text{growth}}$, the most ecologically relevant measurement of CO$_2$ uptake) were reduced in plants grown at the warmest temperature, and the photosynthetic capacity of leaves showed little plasticity to growth temperature. Most strikingly, one of the three species (Calophyllum longifolium) grew so poorly at 35 °C that Slot and Winter had to use a 33 °C treatment to provide enough leaves to collect their data. Even under this lower, ‘severe’ warming treatment, the late-successional C. longifolium showed substantial reductions in photosynthesis compared to seedlings grown at 25 and 30 °C, and also compared to the other species in the study, Ficus insipida and Ochroma pyramidale, which are both early-successional. Overall, the results indicate that while photosynthesis in the study species shows some plasticity to increasing temperatures, acclimation cannot keep pace with warming, and this failure to acclimate successfully may be worse in late-successional species, as also seen in Cheesman and Winter (2013).
High-temperature CO₂ compensation point

One of the most interesting parts of the work by Slot and Winter (2017) was their assessment of the high-temperature CO₂ compensation point, the upper leaf temperature at which net CO₂ assimilation rates were zero (T_{max}; see Box 1). Recent work has explored how thermal acclimation affects photosynthetic traits such as T_{opt} and P_{growth} (Way and Yamori, 2014; Yamori et al., 2014). Also, Yamori et al. (2014) noted that the span of leaf temperatures that realizes 80% of the maximum photosynthetic rate was invariant with growth temperature, implying that the temperature response of net photosynthesis is not narrowed or broadened by warming. However, there is almost nothing known about how T_{max} is affected by changes in growth temperature. In their study, Slot and Winter (2017) found that a 10 °C change in growth temperature had no effect on T_{max}, but T_{max} did vary between species: while T_{max} was 45 °C in C. longifolium (the late-successional species with pronounced mortality at 35 °C), T_{max} was 50 °C for both F. insipida and O. pyramidale. The combination of a shift in T_{opt} without a corresponding shift in T_{max} in plants grown at warmer temperatures resulted in a narrowing of the temperature-response curve of photosynthesis.

To further explore the extent to which T_{max} changes in response to an increase in growth temperature, we collated data from 34 published studies (Box 2; Table 1) that reported temperature-response curves of net photosynthesis for plants grown at two or more different thermal regimes. Only papers with measurements that included points of declining net CO₂ assimilation rates above the T_{opt} were used, ensuring a robust estimate of T_{max}. We then estimated T_{max} for both control and warm-grown plants for each reported species using a second-order polynomial fit to the temperature-response curve of net photosynthesis. Although there is considerable variation in the relationship between the degree of warming and the shift in T_{max}, overall, a 1 °C increase in growth temperature led to a 0.4 °C increase in T_{max}. Unfortunately, there is insufficient data to determine if there are significant differences in the thermal acclimation of T_{max} between plant functional types, but in 25% of the cases assessed, T_{max} actually decreased with increasing growth temperature (Box 2). Based on these findings, the inability of the tropical species investigated in Slot and Winter (2017) to shift their T_{max} is uncommon, and may be related to the high values for T_{max}, which are close to temperatures that can cause irreversible damage to leaves (Krause et al., 2010; 2015).

**Perspectives**

Although Slot and Winter (2017) provide critical data on how carbon fluxes in tropical species acclimate to warming, there is a pressing need to move beyond gas exchange measurements in these types of studies. Many papers on thermal acclimation measure traits such as leaf nitrogen concentrations and specific leaf area, but future studies should delve more deeply into the biochemical and physiological mechanisms underlying photosynthetic (and respiratory)
acclimation. Recent studies in tropical tree species have highlighted the importance of within-leaf N allocation as a strong determinant of variation in photosynthetic capacity (Coste et al., 2005; Dusenge et al., 2015). Specifically, Scafaro et al. (2016) demonstrated that accounting for changes in N allocation to the CO₂-fixing enzyme Rubisco in response to growth temperature explained the measured variation in photosynthetic capacity in a range of temperate and tropical species. Shifts in N allocation between the Calvin cycle and electron transport may represent a major theme for thermal acclimation of carbon gain (Hikosaka et al., 2006), but we still lack a predictive model of photosynthetic acclimation to temperature that could explain the variation we see between plant functional types (as described in Yamori et al., 2014, and Way and Yamori, 2014). While this is not a problem unique to tropical systems, building such a model will require a much more extensive understanding of how changes in temperature affect photosynthesis in a broad range of species and ecosystems. This represents a significant challenge, but it would be an important step forward for predicting future carbon fluxes in vegetation.

Key words: Carbon uptake, climate change, dark respiration, global warming, photosynthetic acclimation, temperature-response curve, thermal acclimation, tropical forest.

Journal of Experimental Botany, Vol. 68 No. 9 pp. 2073-2077, 2017 doi: 10.1093/jxb/erx114

References

Cheesman AW, Winter K. 2013. Growth response and acclimation of CO₂ exchange characteristics to elevated temperatures in tropical tree seedlings. Journal of Experimental Botany 64, 3817–3828.
Chi Y, Xu M, Shen R, Yang Q, Huang B, Wan S. 2013. Acclimation of foliar respiration and photosynthesis in response to experimental warming in a temperate steppe in northern China. PLoS One 8, e56482.

Coste S, Roggy JC, 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.

Cowling SA, Sage RF. 1998. Interactive effects of low atmospheric CO₂ and elevated temperature on growth, photosynthesis and respiration in Phaseolus vulgaris. Plant, Cell & Environment 21, 427–435.

Crous KY, Quentin AG, Lin YS, Medlyn BE, Williams DG, Barton CV, Ellsworth DS. 2013. Photosynthesis of temperate Eucalyptus globulus trees outside their native range has limited adjusted to elevated CO₂ and climate warming. Global Change Biology 19, 3790–3807.

Dillaway DN, Kruger EL. 2010. Thermal acclimation of photosynthesis: a comparison of boreal and temperate tree species along a latitudinal transect. Plant, Cell & Environment 33, 889–899.

Dusenge ME, Wallin G, Gårdenström J, Niyonzima F, Adolfsson L, Nsabimana D, Uddling J. 2015. Photosynthetic capacity of tropical montane tree species in relation to leaf nutrients, successional strategy and growth temperature. Oecologia 177, 1183–1194.

Ferrar PJ, Slattery RO, Vranic JA. 1989. Photosynthetic temperature acclimation in Eucalyptus species from diverse habitats, and a comparison with Nemiera oleander. Australian Journal of Plant Physiology 16, 217–199.

Forseth IN, Ehleringer JR. 1982. Ecophysiology of two solar-tracking desert winter annuals. I. Photosynthetic acclimation to growth temperature. Australian Journal of Plant Physiology 9, 321–332.

Graves JD, Taylor K. 1988. A comparative study of Geum rivale L. and G. urbanum L. to determine those factors controlling their altitudinal distribution. II. Photosynthesis and respiration. New Phytologist 108, 297–304.

Gunderson CA, O’Hara KH, Campion CM, Walker AV, Edwards NT. 2015. Comparative responses to temperature of the major canopy species of Tasmanian cool temperate rain-forest and their ecological significance II. net photosynthesis and climate analysis. Australian Journal of Botany 38, 185–205.

Rosenthal DM, Ruiz-Vera UM, Siebers MH, Gray SB, Bernacchi CJ, Ort DR. 2014. Biochemical acclimation, stomatal limitation and precipitation patterns underlie decreases in photosynthetic stimulation of soybean (Glycine max) at elevated [CO₂] and temperatures under fully open air field conditions. Plant Science 226, 136–146.

Sala OE, Chapin FS 3rd, Amundson JJ, et al. 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774.

Scarafo AP, Xiang S, Long BM, Bahar NHA, Weerasinghe LK, Creek D, Evans JR, Reich PB, Atkin OK. 2016. Strong thermal acclimation of photosynthesis in tropical and temperate wet-forest tree species: the importance of altered Rubisco content. Global Change Biology doi: 10.1111/gcb.13566.

Shen H, Klein JA, Zhao X, Tang Y. 2009. Leaf photosynthesis and simulated carbon budget of Gentiana straminea from a decade-long warming experiment. Journal of Plant Ecology 2, 207–216.

Shen H, Wang S, Tang Y. 2013. Grazing alters warming effects on leaf photosynthesis and respiration in Gentiana straminea, an alpine forb species. Journal of Plant Ecology 6, 418–427.

Sheu B-H, Lin C-K. 1999. Photosynthetic response of seedlings of the sub-tropical tree Schima superb with exposure to elevated carbon dioxide and temperature. Environmental and Experimental Botany 41, 57–65.

Silm SN, Ryan N, Kubien DS. 2010. Temperature responses of photosynthesis and respiration in Populus balsamifera L.: acclimation versus adaptation. Photosynthesis Research 104, 19–30.

Slot M, Winter K. 2017. Photosynthetic acclimation to warming in tropical forest tree seedlings. Journal of Experimental Botany 68, 2275–2284.

Toft NL, Pearcy RW. 1982. Gas exchange characteristics and temperature relations of two desert annuals: A comparison of a winter-active and a summer-active species. Oecologia 55, 170–177.

Tranquillini W, Havranek WM, Ecker P. 1986. Effects of atmospheric humidity and acclimation temperature on the temperature response of photosynthesis in young Larix decidua Mill. Tree Physiology 1, 37–45.

Trewin B. 2014. The climates of the tropics, and how they are changing. State of the Tropics 2014 Report 39–57.

Veres JS, Williams GJ III. 1984. Time course of photosynthetic temperature acclimation in Carex eleanorica Bailey. Plant, Cell & Environment 7, 545–547.

Wardlaw IF, Begg JE, Bagnall D, Dunstone RL. 1983. Jojoba: temperature adaptation as expressed in growth and leaf function. Australian Journal of Plant Physiology 10, 299–312.

Way DA, Oren R. 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 DA, Sage RF. 2008a. Elevated growth temperatures reduce the carbon gain of black spruce [Picea mariana (Mill.) B.S.P.]. Global Change Biology 14, 624–636.

Way DA, Sage RF. 2008b. Thermal acclimation of photosynthesis in black spruce [Picea mariana (Mill.) B.S.P.]. Plant, Cell & Environment 31, 1250–1262.

Way DA, Yamori W. 2014. Thermal acclimation of photosynthesis: on the importance of adjusting our definitions and accounting for thermal acclimation of respiration. Photosynthesis Research 119, 89–100.

Xiong FS, Mueller EC, Day TA. 2000. Photosynthetic and respiratory acclimation and growth response of Antarctic vascular plants to contrasting temperature regimes. American Journal of Botany 87, 700–710.
Insight

Translational switching from growth to defense – a common role for TOR in plant and mammalian immunity?

Maria Eugenia Zanetti1,* and Flavio A. Blanco1

1 Instituto de Biotecnología y Biología Molecular, Facultad de Ciencias Exactas, Universidad Nacional de La Plata, CCT-La Plata, CONICET, La Plata, Argentina
*Correspondence: ezanetti@biol.unlp.edu.ar

Characterization of mRNA populations associated with the translational machinery (translatome) is shedding light on the molecular mechanisms of plant environmental responses. The work presented by Meteignier et al. (2017) describes how selective changes in translation modulate the transition from growth to defense responses in Arabidopsis, revealing new similarities between plant and animal immunity.

Plants have developed sophisticated mechanisms to adjust their developmental programs in response to changes in their environment. This adaptation largely depends on transcriptional and post-transcriptional control. Transcriptional changes provide a long-term response and, usually, are triggered by a signaling pathway initiated by signal perception that culminates in the activation of transcription factors in the nucleus. Transcriptome (the population of total cellular mRNAs) studies have enabled the identification of genes that are crucial for adaptation in numerous plant species. However, mRNA abundance and protein levels do not always correlate due to co- and post-transcriptional mechanisms controlling gene expression. Among such post-transcriptional mechanisms, mRNA translation plays a crucial role in controlling the amount of protein present in a cell or tissue. Translational control has been observed in a number of developmental processes in plants, as well as in response to environmental cues.

During the past decade, an increasing number of studies have focused on changes in the translatome (the population of actively translating mRNAs) during phase-transitions or perturbation caused by endogenous or exogenous signals. From these studies we know that translational control can be global, affecting all cellular mRNAs, or selective, affecting just a subset. Global translational repression has been observed during stresses that produce a cellular ‘energy crisis’, such as hypoxia (Branco-Price et al., 2005; Branco-Price et al., 2008; Mustroph et al., 2009), heat (Yanguez et al., 2013), and drought (Kawaguchi and Bailey-Serres, 2002; Kawaguchi et al., 2004; Lei et al., 2015). On the other hand, selective translational regulation has been associated with dark/light transitions (Juntawong and Bailey-Serres, 2012), photomorphogenesis (Liu et al., 2013), daily clock cycles (Missra et al., 2015), and symbiosis with nitrogen-fixing bacteria (Reynoso et al., 2013).

Meteignier et al. (2017) show that selective translational control also occurs during plant immunity. A remarkable characteristic of translational regulation is that it enables rapid adjustment of the proteome using the existing transcriptome, thus providing cells or tissues with a fast and flexible response for adapting to changes in their environment, as in the case of the hypersensitive response triggered by some plant pathogens. This rapid response is frequently achieved by controlling the initiation step of translation, i.e. by increasing or decreasing the number of molecules of individual transcripts that are recruited to the translational machinery without a change in transcript abundance or even, in some cases, with an opposite change in transcript abundance.