Warming puts the squeeze on photosynthesis – lessons from tropical trees

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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_{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_{opt} was smaller than the shift in growth temperature, net photosynthetic rates at the growth temperature (P_{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 CO_2 compensation point

One of the most interesting parts of the work by Slot and Winter (2017) was their assessment of the high-temperature CO_2 compensation point, the upper leaf temperature at which net CO_2 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 CO_2

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)

Box 1. Temperature response of net photosynthesis to increasing growth temperature

The solid, blue line represents a cool-grown leaf and the dashed, red line represents a warm-grown leaf. Plants grown at higher temperatures usually exhibit an increased photosynthetic thermal optimum (T_{opt}, shown as a point on each curve), but there is little data on how T_{max} (the upper temperature at which net CO_2 assimilation rates are zero, i.e. carbon gain balances carbon loss) responds to warming. If T_{opt} increases but T_{max} remains constant, as in Slot and Winter (2017), the temperature response of net photosynthesis is 'squeezed' and becomes narrower.
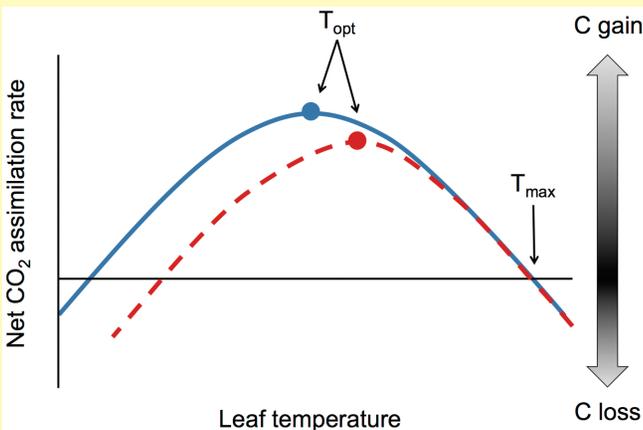
Box 2. Increasing growth temperatures alter the high-temperature CO_2 compensation point

Change in T_{max} (ΔT_{max}) of net CO_2 assimilation rate as a function of the increase in growth temperature (ΔT_{growth}) in plant species from four plant functional types (see key). Each point plotted represents a comparison between cool and warm-grown plants from a single study (Table 1). The dotted line shows the regression for all data taken together ($y = -1.29 + 0.40x$; $r^2 = 0.13$; $P = 0.0002$).
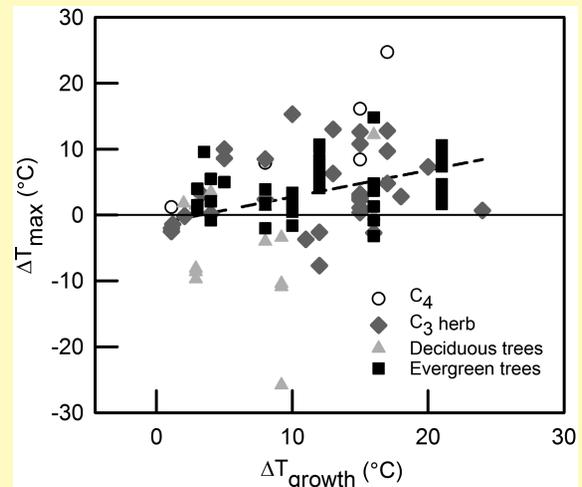
Table 1. Species/functional types used in the high-temperature CO_2 compensation point analysis

Species	Functional type	Source
Agropyron smithii	C_3 herb	Monson *et al.*, 1983
Albutilon theophrasti	C_3 herb	Ziska, 2001
Amaranthus retroflexis	C_4	Pearcy *et al.*, 1981
Ambrosia psilostachya	C_3 herb	Zhou *et al.*, 2007
Aster ericodes	C_3 herb	Zhou *et al.*, 2007
Atherosperma moschatum F700	Evergreen tree	Read and Busby, 1990
Athrotaxis selaginoides F980	Evergreen tree	Read and Busby, 1990
Betula payrifera	Deciduous tree	Dillaway and Kruger, 2010
Bouteloua gracilis	C_4	Monson *et al.*, 1983
Buchloe dactyloides	C_4	Monson *et al.*, 1983
Calamagrostis canadensis	C_3 herb	Kubien and Sage, 2004
Carex eleocharis	C_3 herb	Monson *et al.*, 1983
Carex eleocharis	C_3 herb	Veres and Williams III, 1984
Chenopodium album	C_3 herb	Pearcy *et al.*, 1981
Colobanthus quitensis	C_3 herb	Xiong *et al.*, 2000
Deschampia antarctica	C_3 herb	Xiong *et al.*, 2000
Dicoria canescens	C_3 herb	Toft and Pearcy, 1982
Eucalyptus camaldulensis (Qld)	Evergreen tree	Ferrar *et al.*, 1989
Eucalyptus camaldulensis (Vic)	Evergreen tree	Ferrar *et al.*, 1989
Eucalyptus globulus	Evergreen tree	Crous *et al.*, 2013
Eucalyptus incrassata	Evergreen tree	Ferrar *et al.*, 1989
Eucalyptus miniata	Evergreen tree	Ferrar *et al.*, 1989
Eucalyptus pauciflora (PS)	Evergreen tree	Ferrar *et al.*, 1989
Eucalyptus pauciflora (WP)	Evergreen tree	Ferrar *et al.*, 1989
Eucryphia lucida F700	Evergreen tree	Read and Busby, 1990
Gentiana straminea	C_3 herb	Shen *et al.*, 2009, 2013
Geraea canescens	C_3 herb	Toft and Pearcy, 1982
Geum rivale	C_3 herb	Graves and Taylor, 1988
Geum urbanum	C_3 herb	Graves and Taylor, 1988
Glycine max	Evergreen tree	Rosenthal *et al.*, 2014
Helianthus mollis	C_3 herb	Zhou *et al.*, 2007
Lagarostrobos franklinii P80	Evergreen tree	Read and Busby, 1990
Larix decidua	Deciduous tree	Tranquillini *et al.*, 1986
Liquidambar styraciflua	Deciduous tree	Dillaway and Kruger, 2010
Lupinus arizonicus	C_3 herb	Forseth and Ehleringer, 1982
Malvastrum rotundifolium	C_3 herb	Forseth and Ehleringer, 1982
Mucuna pruriens	C_3 herb	Monson *et al.*, 1992
Nothofagus cunninghamii F700	Evergreen tree	Read and Busby, 1990
Nothofagus cunninghamii F980	Evergreen tree	Read and Busby, 1990
Nothofagus cunninghamii P80	Evergreen tree	Read and Busby, 1990
Nothofagus gunnii F980	Evergreen tree	Read and Busby, 1990
Oryza sativa	C_3 herb	Nagai and Makino, 2009
Phaseolus vulgaris	C_3 herb	Cowling and Sage, 1998
Phyllocladus aspleniifolius F700	Evergreen tree	Read and Busby, 1990
Picea abies	Evergreen tree	Kroner and Way, 2016
Picea koraiensis	Evergreen tree	Zhang *et al.*, 2015
Picea likiangensis var. *linzhiensis*	Evergreen tree	Zhang *et al.*, 2015

Table 1. *Continued*

Species	Functional type	Source
Picea likiangensis var. *rubescens*	Evergreen tree	Zhang *et al.*, 2015
Picea mariana	Evergreen tree	Way and Sage, 2008*a*,b
Picea meyeri	Evergreen tree	Zhang *et al.*, 2015
Plantago asiatica (Sendai)	C_3 herb	Ishikawa *et al.*, 2007
Plantago asiatica (Shimada)	C_3 herb	Ishikawa *et al.*, 2007
Plantago asiatica (Tomakomai)	C_3 herb	Ishikawa *et al.*, 2007
Populus balsamifera (cool)	Deciduous	Silim *et al.*, 2010
Populus balsamifera (warm)	Deciduous	Silim *et al.*, 2010
Populus deltoides	Deciduous	Dillaway and Kruger, 2010
Populus tremula × *Populus tremuloides*	Evergreen	Rasulov *et al.*, 2015
Populus tremuloides	Deciduous	Dillaway and Kruger, 2010
Quercus rubra	Deciduous	Gunderson *et al.*, 2009
Schima superba	Evergreen	Sheu and Lin, 1999
Simmondsia chinensis	Evergreen	Wardlaw *et al.*, 1983
Sorghastrum nutans	C_4	Zhou *et al.*, 2007
Spinacia olearacea	C_3 herb	Yamori *et al.*, 2006
Stipa krylovii	C_3 herb	Chi *et al.*, 2013
Triticum aestivum	C_3 herb	Nagai and Makino, 2009
Triticum aestivum	C_3 herb	Yamasaki *et al.*, 2002

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 CO_2-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.

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Insight

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

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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 selective changes in gene expression, which include 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 most 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.