



Commentary

On the role of ecological adaptation and geographic distribution in the response of trees to climate change

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Predicting how increases in surface temperature will modulate the response of plants to rising atmospheric CO₂ concentrations is an increasingly urgent aspect of climate change research. Plant responses to elevated CO₂ have been well documented over the last 40 years, and the mechanisms underlying these responses are well understood. Elevated CO₂ affects plants mainly by increasing photosynthesis and decreasing stomatal conductance (Ainsworth and Rogers 2007). However, the scaling up of these primary, leaf-level CO₂ responses to the whole plant and canopy levels is moderated by the plant's growth characteristics (e.g., sink strength, biomass partitioning), and the availability of soil water and nutrients (Long et al. 2004).

Unlike elevated CO₂, temperature has effects that extend beyond direct leaf-level responses. Temperature affects plant growth through a number of processes at varying scales, including photosynthesis, respiration, meristem initiation, cell division, water transport and phenology (Berry and Björkman 1980, Atkin and Tjoelker 2003, Thomas et al. 2007, Way 2011). Importantly, the response of biological activity to temperature is not linear, and it has long been known that photosynthetic thermal responses depend on the plant's ecological adaptation (Percy and Harrison 1974). Consequently, the response of plant growth to increasing temperature alone (not to mention its interaction with elevated CO₂) is complicated by ecological adaptation of the species or genotype examined. This, in turn, will determine the thermal optima of temperature-sensitive processes and their potential for acclimation.

Nevertheless, a survey of the literature indicates that growth in most tree species responds positively to warmer growth temperature, with deciduous species showing a greater positive response than evergreen trees (Way and Oren 2010).

However, this generalization does not always hold; for example, Ghannoum et al. (2010) found that evergreen eucalypts (*Eucalyptus saligna* and *Eucalyptus sideroxylon*) had a strong positive growth response to higher temperatures. In this issue, Wertin et al. (2011) demonstrate that the deciduous, temperate species *Quercus rubra* (northern red oak) showed a negative growth response to elevated temperature, which was strong enough to negate growth enhancements of high CO₂. While elevated CO₂ alone increased total biomass by 38% relative to the ambient CO₂ and ambient temperature (control) treatment, plants grown at elevated CO₂ and a 3°C warming had similar biomass to their control counterparts, and plants exposed to elevated CO₂ and a 6°C warming had 12% less biomass than control plants (Wertin et al. 2011). Declines in growth were associated with reduced net photosynthetic rates and photosynthetic capacity at higher temperatures, as well as higher dark respiration rates (Wertin et al. 2011). Since respiration usually acclimates to temperature more strongly and quickly than photosynthesis (Gunderson et al. 2000, Campbell et al. 2007, Ow et al. 2008, Way and Sage 2008a, 2008b, Way and Oren 2010), this result is surprising. These recent warming studies highlight the gaps in our understanding and the need to synthesize alternative hypotheses that can form the basis of future experiments in this field.

One potential explanation for the diversity in results from warming experiments is presented by Wertin et al. (2011): populations from the equatorial distribution limit of a species may be more prone to warming-related growth declines than populations from the poleward distribution limit. While poleward range limits have received more research attention, equatorial range limits are where negative impacts of climate

warming are likely to occur (Jump et al. 2010). Southern populations (in the Northern Hemisphere) may be more prone to heat stress or less able to physiologically acclimate to higher temperatures (Mägi et al. 2011, Figure 1). Accordingly, Way and Sage (2008a, 2008b) and Werten et al. (2011) found negative growth effects of high temperature on tree seedlings from southern populations of boreal evergreen and temperate deciduous species, respectively. Latitudinal differences in seed source could account for some of the variability in studies where the individuals are assumed to represent the 'species' as a whole. Southern populations may experience a narrower range of temperature variability relative to their central and northern counterparts; this could limit the acclimation potential of southern individuals to warming (Cunningham and Read 2003a, 2003b). Thus, increases in temperature may result in little or no thermal acclimation of source (photosynthesis) or sink (e.g., respiration, cell division) processes (Figure 1, southern population), either of which could suppress growth. While natural selection may favour genotypes with higher thermal optima for a suite of processes at the range edge, gene flow from cooler populations in the centre of the species' range can slow or prevent local adaptation in range margins (Hardie and Hutchings 2010).

While growth responses to temperature can be underlain by many physiological processes, papers studying plant growth responses to temperature often link their results to changes in photosynthesis and respiration and divergences in the degree of thermal acclimation between these two processes (Atkin et al. 2007, Way and Sage 2008a, Werten et al. 2011). At the larger scale, stand-level carbon fluxes and forest biomass are the results of these same physiological processes and their respective responses to temperature (Anderson-Teixeira et al. 2011). While the ratio of photosynthesis to respiration in woody plants is higher in species from cool regions compared with warm, dry regions (Chu et al. 2011), indicating variation in the baseline value of this ratio, we do not understand how this ratio acclimates within a species in response to warming. In a meta-analysis of 58 tree species, Way and Oren (2010) found little evidence for acclimation of photosynthetic capacity to increases in growth temperature, although respiration tended to acclimate strongly; this should increase the ratio of carbon fixation to carbon loss in leaves as temperature increases, allowing for greater growth. Consistent with this result, two meta-analyses found that warming generally increased tree biomass (Way and Oren 2010, Lin et al. 2010). However, Werten et al. (2011) found no thermal acclimation of respiration,

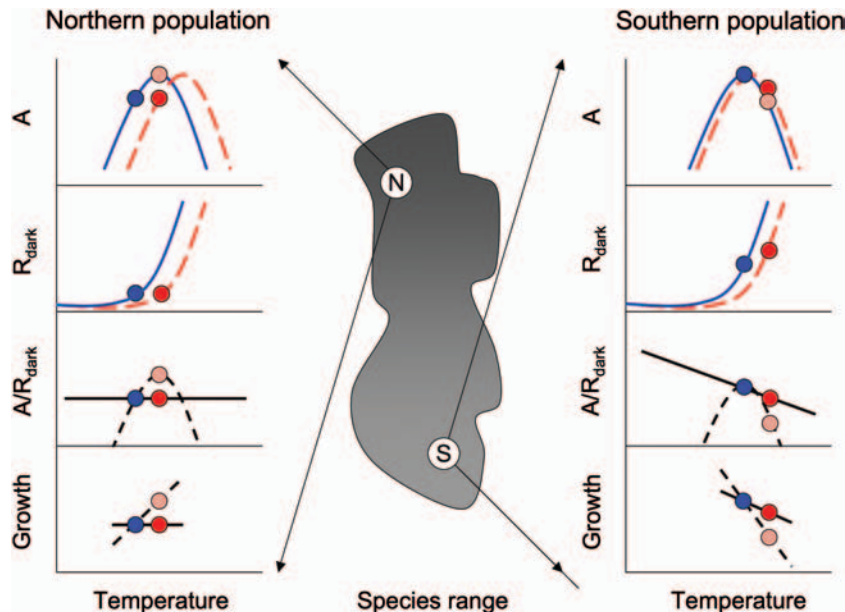


Figure 1. Conceptual figure of potential temperature responses of photosynthesis (A), dark respiration (R_{dark}), the ratio of A to R_{dark} (A/R_{dark}) and potential effect on growth in trees from the northern or central range (northern population) or from the southern range limit (southern population) in a species from the Northern Hemisphere. Blue lines indicate temperature response curves under current growth temperatures, with blue circles showing the value at current growth conditions; red lines indicate temperature response curves of plants acclimated to elevated temperature, with red circles showing the value at the warmer growth temperature. Trees from northern and central populations may show significant thermal acclimation for both photosynthesis and respiration, such that there is no change in measured A or R_{dark} at the warmer growth temperature. Thus, A/R_{dark} is constant as growth temperature changes (black line). If growth reflects A/R_{dark} , growth shows little change as temperature increases (blue and red dots are similar). If A does not acclimate (as shown for many trees in Way and Oren 2010), measured A can still increase with temperature (red striped circle), leading to higher A/R_{dark} and higher growth at warmer conditions. In southern populations, if processes do not acclimate as strongly as in central or northern populations, A is likely to decrease under warmer temperatures while R_{dark} may increase (compare red and blue circles). This reduces A/R_{dark} and potential growth. If A does not acclimate (red striped circle), a similar growth response can be seen if A is reduced and/or R_{dark} increased at higher temperatures (compare red striped and blue circles).

an unusual result, and little acclimation of photosynthesis, which might indicate low acclimation potential in general in trees from this southern population. There is little research on whether acclimation potential to high temperatures varies within species in relation to range distribution and the results from the few studies looking at intra-specific variation in thermal acclimation are contradictory (Billings et al. 1971, Gunderson et al. 2000, Lee et al. 2005, Tjoelker et al. 2009). But the implications for shifts in the balance of photosynthesis to respiration can be seen in the increasing relative importance of respiration over photosynthesis with decreasing elevation (and increasing temperature) and the consequent reduction in net ecosystem exchange and carbon storage on the landscape in the south-western USA (Anderson-Teixeira et al. 2011).

In conclusion, studies examining high-temperature acclimation responses of trees from populations varying in latitudinal origin are crucial. Provenance trials provide an excellent study system for these questions (Tjoelker et al. 2009), but these studies rarely involve conditions outside the natural distribution of the species where higher temperatures are found. While the southern range limit of a species may be set largely by competitive interactions with faster growing, more southerly species (MacArthur 1972, Loehle 1988), this does not preclude physiologically based growth declines south of the species' range. Consequently, the key questions that need to be systematically addressed in future studies include: how do co-occurring species and geographically separated genotypes of the same species differ in their growth response to increased temperature; to what extent can differential acclimation of photosynthesis and respiration explain differences in growth responses to increased temperature; and how does elevated CO₂ interact with these responses? These questions need to be tested in experiments that explicitly explore the southern/northern (polar/equatorial) ranges of species distribution.

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