American Journal of Botany

Botanical Society of America
leading scientists and educators
since 1893

NEWS & VIEWS

ON THE NATURE OF THINGS: ESSAYS

New Ideas and Directions in Botany

Small flux, global impact: Integrating the nuances of leaf mitochondrial respiration in estimates of ecosystem carbon exchange

Mary A. Heskel[1,2]

Manuscript received 12 December 2017; revision accepted 31 January 2018.

[1] The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543, USA

[2] Authors for correspondence (e-mail: mheskel@gmail.com)

Citation: Heskel, M. A. 2018. Small flux, global impact: Integrating the nuances of leaf mitochondrial respiration in estimates of ecosystem carbon exchange. *American Journal of Botany* 105(5): 1–4.

doi:10.1002/ajb2.1079

The balance of photosynthesis and respiration, their responses to a changing environment, and predictive models of these responses continue to be an active body of research. While photosynthesis is robustly described by a long-standing, scalable biochemical model (Farquhar et al., 1980), a similar mechanistic model of respiration remains an ongoing challenge. Respiration encompasses multiple cellular processes in the mitochondria and cytosol that drive energy and carbon skeleton production for plant growth and maintenance. Through glycolysis (cytosol), the tricarboyxlic acid (TCA) cycle (mitochondrial matrix), the electron transport chain/oxidative phosphorylation (mitochondrial inner membrane), and other associated pathways, metabolic products of photosynthesis are transformed into energy in the form of ATP, oxygen is consumed, and carbon dioxide is produced. Unlike its metabolic foil, photosynthesis, mitochondrial respiration takes place in all plant tissues, in all cells, at all times. Its ubiquity as an energy source in plants, its role promoting and maintaining efficient photosynthesis, and its contribution to the terrestrial carbon cycle warrant accurate quantification for scaling leaf-level fluxes of carbon.

New strategies for measuring and modeling plant respiration across systems and scales are necessary to robustly characterize how carbon flows through terrestrial environments. Developments in measurement techniques, comprehensive field-based data sets, and cross-scale research collaborations are directly addressing environmental sensitivities and biochemical nuances and, in turn, advancing how respiration is considered at the leaf and ecosystem levels. This essay covers current areas of plant respiration research and their integration into the broader terrestrial carbon cycle.

LIGHTS, CARBON, INHIBITION!

Mitochondrial respiration is often termed “dark respiration” because leaves must be darkened for measurement of carbon efflux to eliminate the co-occurring signal of photosynthetic carbon assimilation. However, leaves not only continue to respire during daylight, but many of the cellular pathways of respiration are altered by light and result in inhibition of oxygen uptake and carbon release. This phenomenon, first reported in algal suspensions in the mid-20th century (Kok, 1948), has recently been the focus of increased attention due to its potential to impact calculations of ecosystem primary productivity (Wehr et al., 2016). For example, ecosystem estimates of respiration are often based on above-canopy eddy covariance measurements made at night or made in darkened chambers that eliminate a photosynthetic signal. Applying these approaches equates daytime and nighttime respiration fluxes, neglecting the known inhibition of respiration by light, and in turn, overestimating the gross flux of carbon into the ecosystem (Fig. 1). The degree of this overestimation may vary across systems. For example, overestimation may be greater in ecosystems with high

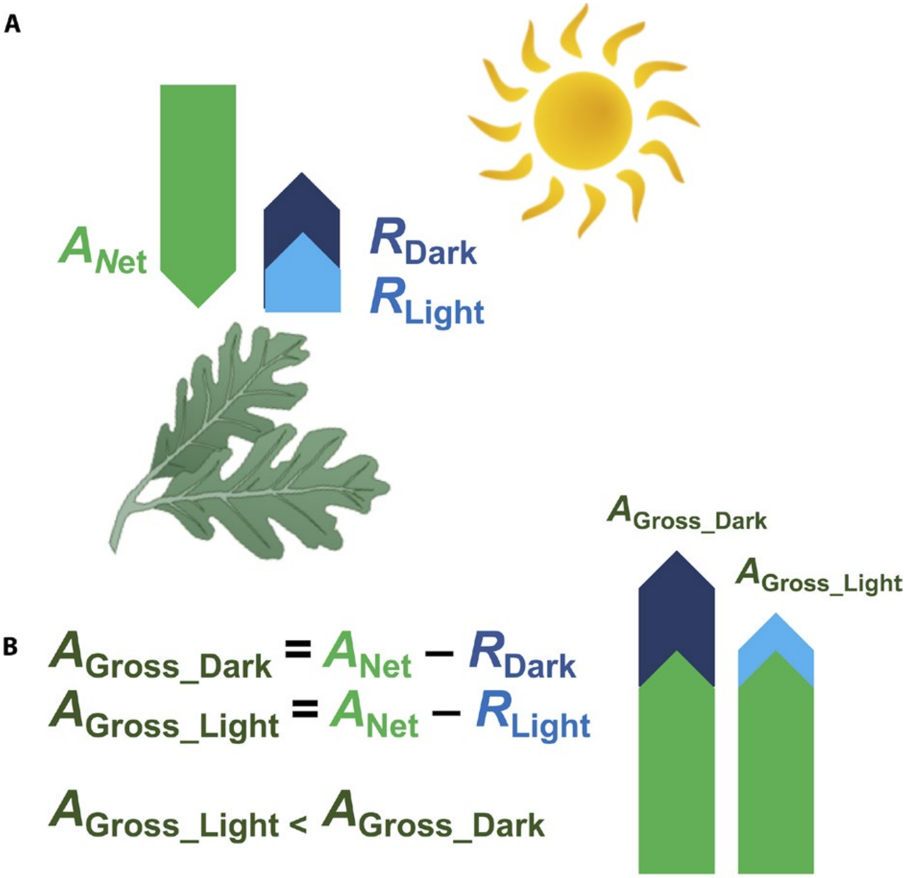

FIGURE 1. Carbon is assimilated into leaves via photosynthesis and released via respiration (A); the difference of these rates is referred to as net photosynthesis (or A_{Net}). In the light, the rate of respiration is inhibited, so that respiration in the light (R_{Light}) is less than respiration in the dark (R_{Dark}). The total amount of carbon assimilated (B), or A_{Gross}, is calculated by subtracting the value of respiration (measured as a negative flux) from net photosynthesis. In the light, neglecting the observed phenomena of light inhibition and applying an uninhibited value of R_{Dark} can lead to overestimations of A_{Gross}.

values of canopy leaf area index (i.e., tropical rainforests), where leaf respiration is likely to comprise a large proportion of total ecosystem respiration.

The sources of the light inhibitory effect and the controls of the degree of inhibition are complex and include environmental, developmental, and biochemical signals (Tcherkez et al., 2017a). Studies at the subcellular level have identified a reorganization of the TCA cycle in light and link inhibition of mitochondrial respiration with the co-occurring process of photorespiration (Tcherkez et al., 2008). In field and greenhouse studies, variability in the degree of inhibition is also associated with environmental growth conditions of atmospheric CO_2, temperature, and soil nitrogen availability (Crous et al., 2017). Leaf developmental age and seasonality can also impact the inhibition of leaf respiratory fluxes; inhibition increases with the progression of the growing season in evergreen and deciduous species in arctic tundra (Heskel et al., 2014), though it is unaltered in a Mediterranean forest (Turnbull et al., 2017).

With overlapping, and sometimes inextricable, biological and environmental controls regulating the daytime respiratory flux, minimizing other sources of variation and potential measurement error is critical. Within the past year, two studies delved into the methodological complexity of capturing accurate measurements of respiration in the light while accounting for sensitivity to cellular carbon dioxide concentrations (Buckley et al., 2017; Farquhar and Busch, 2017). Overall, the study of the light inhibition of respiration—for many decades considered a niche within a niche of plant physiological research—is rapidly expanding at both the biochemical and canopy scales and exemplifies the importance and need of cross-scale collaborations for accurate ecosystem and global carbon accounting.

THE LONG AND THE SHORT OF TEMPERATURE RESPONSE

The amount of carbon respired by leaves increases with temperature in an exponential-like response within the normal growth temperature range (<45°C) in the time frame of seconds to days (Heskel et al., 2016). As leaf temperatures exceed ~50°C, respiration rates increase at a slower rate, eventually reach a maximum rate, and plummet at higher temperatures. The inherent shape of this response, the derivative of which exhibits a declining rate of change (often termed Q_{10}) as temperatures increase, is conserved across functionally and climactically diverse species (Heskel et al., 2016). This apparently universal response suggests a deeply phylogenetically shared metabolic response to temperature, which may be explained by enzyme thermodynamics (Liang et al., 2017). A consistent and quantitatively (relatively) simple short-term temperature response of respiration across broad plant functional types provides great utility for regional and global carbon models, which generally rely on the oft-applied, yet inaccurate, fixed Q_{10} of 2.

The apparent universal shape of the short-term response of respiration to temperature allows for easy calculation of leaf carbon efflux across a wide range of temperatures when a reference value of respiration exists. A recently assembled global database of leaf respiration values, GlobResp, comprised of nearly 900 species' values of respiration representing 100 climactically diverse terrestrial sites that span the globe, provides an extensive library of reference respiration values for those seeking to model fluxes (Atkin et al., 2015). This collection of leaf respiration values, along with trait, climate, and plant functional group information, creates opportunities for empirically driven improvements of how respiration is represented in dynamic global vegetation models. Field-based values of leaf respiration can have significant impacts on estimated carbon fluxes from leaves—substituting GlobResp values in place of standard respiration parameters may increase estimates of whole-plant respiration by up to 30% (Huntingford et al., 2017). In agreement with meta-analyses where data spans diverse species and ecosystems, GlobResp data reveal thermal acclimation responses to growth temperatures, where leaves grown at colder temperatures respire at higher rates than leaves grown at warmer temperatures (when measured at a common reference temperature) (Vanderwel et al., 2015).

In many plant species, the long-term response of respiration to warmer growth temperatures results in thermal acclimation, the decreasing adjustment of metabolic rates that occurs on the timescale of days to years (Atkin and Tjoelker, 2003). When acclimated, a leaf grown under elevated temperatures will release less carbon through respiration compared to a leaf grown under ambient conditions when measured at the same reference temperature. By contrast, photosynthesis often acclimates to elevated growth temperature by increasing its optimum temperature, and over longer-term warming, could result in more carbon assimilation and less carbon efflux at higher temperatures (Fig. 2). Integrating thermal acclimation observed at the leaf level into Earth Systems Models has shown a reduction in carbon efflux to the atmosphere and an increase in carbon stored in plants and soils (Lombardozzi et al., 2015). However, acclimation should not be hailed as a potential "silver-lining" to plants experiencing warmer growth temperatures due to climate change; the interactive impacts of individual species, drought, and soil nutrient variability, as well as acclimation of photosynthesis and plant hydraulic processes will factor greatly in the future carbon exchange of terrestrial ecosystems. These interactions and their resulting effects on respiratory acclimation and whole-plant carbon storage is an area of expanding, active leaf-level research from the tropics to the tundra (Slot et al., 2014). Modeling the variability in spatial, species-level, and environmental controls on long-term temperature responses of respiration and integrating these responses into Earth System Models will further refine our understanding of how carbon flows through ecosystems under current and future conditions.

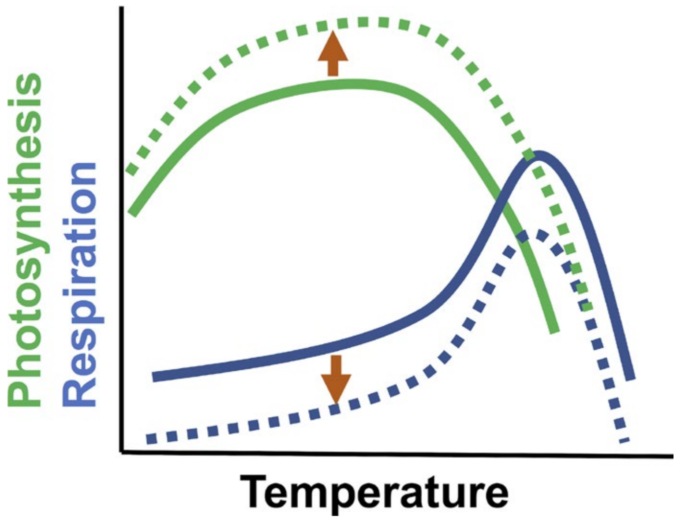

FIGURE 2. Under short-term (seconds to days) temperature increases, respiration increases in an exponential-like form, reaches a maximum rate, and rapidly decreases thereafter. Photosynthesis under the same warming conditions reaches an optimum value at a more moderate temperature. Under longer-term warming, both processes acclimate: respiration adjusts with a downward shift in rates, and photosynthesis generally increases its rates and the temperature at which the optimum rate occurs. The solid lines represent rates at ambient temperatures, and the dashed lines represent warm-acclimated rates. Orange arrows mark the shift in rates at the same reference temperature.

So, what is next? Will a robust, predictive model of respiration emerge from empirical studies on environmental and biological controls and become anchored in Earth System Models? The past few years' expansive collection of field and lab studies, novel analyses, available databases, and cross-scale collaborations suggest a productive and insightful future for the study of leaf respiration and its impact on whole-plant and ecosystem carbon fluxes. Momentum from recent New Phytologist Workshops (Atkin et al., 2014; Tcherkez et al., 2017b), increased dialogue between ecosystem, organismal, leaf, and systems scientists, and inclusive cross-scale collaborations that promote and encourage new perspectives on this "small flux" will drive research forward toward a more complete understanding of plant respiration and its role in the global carbon cycle.

ACKNOWLEDGEMENTS

I thank the Rosenthal Family Foundation and The Ecosystems Center of the Marine Biological Laboratory for sponsoring my postdoctoral fellowship and the reviewers for their comments on this essay.

LITERATURE CITED

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

Atkin, O. K., P. Meir, and M. H. Turnbull. 2014. Improving representation of leaf respiration in large-scale predictive climate–vegetation models. *New Phytologist* 202: 743–748.

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.

Buckley, T. N., H. Vice, and M. A. Adams. 2017. The Kok effect in *Vicia faba* cannot be explained solely by changes in chloroplastic CO_2 concentration. *New Phytologist* 216: 1064–1071.

Crous, K. Y., G. Wallin, O. K. Atkin, J. Uddling, and A. A. Ekenstam. 2017. Acclimation of light and dark respiration to experimental and seasonal warming are mediated by changes in leaf nitrogen in *Eucalyptus globulus*. *Tree Physiology* 37: 1069–1083.

Farquhar, G. D., and F. A. Busch. 2017. Changes in the chloroplastic CO_2 concentration explain much of the observed Kok effect: a model. *New Phytologist* 214: 570–584.

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

Heskel, M. A., D. Bitterman, O. K. Atkin, M. H. Turnbull, and K. L. Griffin. 2014. Seasonality of foliar respiration in two dominant plant species from the Arctic tundra: response to long-term warming and short-term temperature variability. *Functional Plant Biology* 41: 287–300.

Heskel, M. A., O. S. O'Sullivan, P. B. Reich, M. G. Tjoelker, L. K. Weerasinghe, A. Penillard, J. J. G. Egerton, et al. 2016. Convergence in the temperature response of leaf respiration across biomes and plant functional types. *Proceedings of the National Academy of Sciences, USA* 113: 3832–3837.

Huntingford, C., O. K. Atkin, A. Martinez-de la Torre, L. M. Mercado, M. A. Heskel, A. B. Harper, K. J. Bloomfield, et al. 2017. Implications of improved representations of plant respiration in a changing climate. *Nature Communications* 8: 1602.

Kok, B. 1948. A critical consideration of the quantum yield of *Chlorella* photosynthesis. *Enzymologia* 13: 1–56.

Liang, L. L., V. L. Arcus, M. A. Heskel, O. S. O'Sullivan, L. K. Weerasinghe, D. Creek, J. J. G. Egerton, et al. 2017. Macromolecular rate theory (MMRT) provides a thermodynamics rationale to underpin the convergent temperature response in plant leaf respiration. *Global Change Biology* 24: 1538–1547.

Lombardozzi, D. L., G. B. Bonan, N. G. Smith, J. S. Dukes, and R. A. Fisher. 2015. Temperature acclimation of photosynthesis and respiration: a key uncertainty in the carbon cycle–climate feedback. *Geophysical Research Letters* 42: 8624–8631.

Slot, M., C. Rey-Sánchez, S. Gerber, J. W. Lichstein, K. Winter, and K. Kitajima. 2014. Thermal acclimation of leaf respiration of tropical trees and lianas: response to experimental canopy warming, and consequences for tropical forest carbon balance. *Global Change Biology* 20: 2915–2926.

Tcherkez, G., R. Bligny, E. Gout, A. Mahe, M. Hodges, and G. Cornic. 2008. Respiratory metabolism of illuminated leaves depends on CO_2 and O_2 conditions. *Proceedings of the National Academy of Sciences, USA* 105: 797–802.

Tcherkez, G., P. Gauthier, T. N. Buckley, F. A. Busch, M. M. Barbour, D. Bruhn, M. A. Heskel, et al. 2017a. Leaf day respiration: low CO_2 flux but high significance for metabolism and carbon balance. *New Phytologist* 216: 986–1001.

Tcherkez, G., P. Gauthier, T. N. Buckley, F. A. Busch, M. M. Barbour, D. Bruhn, M. A. Heskel, et al. 2017b. Tracking the origins of the Kok effect, 70 years after its discovery. *New Phytologist* 214: 506–510.

Turnbull, M. H., R. Ogaya, A. Barbeta, J. Peñuelas, J. Zaragoza-Castells, O. K. Atkin, F. Valladares, et al. 2017. Light inhibition of foliar respiration in response to soil water availability and seasonal changes in temperature in Mediterranean holm oak (*Quercus ilex*) forest. *Functional Plant Biology* 44: 1178–1193.

Vanderwel, M. C., M. Slot, J. W. Lichstein, P. B. Reich, J. Kattge, O. K. Atkin, K. J. Bloomfield, et al. 2015. Global convergence in leaf respiration from estimates of thermal acclimation across time and space. *New Phytologist* 207: 1026–1037.

Wehr, R., J. W. Munger, J. B. McManus, D. D. Nelson, M. S. Zahniser, E. A. Davidson, S. C. Wofsy, and S. R. Saleska. 2016. Seasonality of temperate forest photosynthesis and daytime respiration. *Nature* 534: 680–683.