Collaboration occurs when people envision an outcome that is greater than any one person can accomplish alone. In science, researchers collaborate so that they can complement existing disciplinary expertise, gain access to specialized equipment, or expand the depth and breadth of datasets that can be used to derive new knowledge. Motivated by this latter objective, Atkin et al. (2015; this issue of New Phytologist, pp. 614–636) compiled a global database (GlobResp) that details rates of leaf dark respiration and associated traits from sites that span Arctic tundra to tropical forests. This compilation builds upon earlier research (Reich et al., 1998; Wright et al., 2006) and was supplemented by recent field campaigns and unpublished data. In keeping with other trait databases, GlobResp provides insights on how physiological traits, especially rates of dark respiration, vary as a function of environment and how that variation can be used to inform terrestrial biosphere models and land surface components of Earth System Models. Although an important component of plant and ecosystem carbon (C) budgets (Wythers et al., 2013), respiration has only limited representation in models. Seen through the eyes of a plant scientist, Atkin et al. (2015) give readers a unique perspective on the climatic controls on respiration, thermal acclimation and evolutionary adaptation of dark respiration, and insights into the covariation of respiration with other leaf traits.

Atkin et al. (2015) show that changes in leaf respiration were less than expected given the range of growth temperatures; that is, a typical doubling of dark respiration associated with a 10°C increase in temperature was not observed. On the contrary, rates of dark respiration that were adjusted to a common temperature were higher for plants at colder compared to warmer sites. Such a dependency of dark respiration on growth temperature, although not consistently observed in previous analyses, is an intriguing observation. It is one that is supported by various lines of evidence, including the fact that rates of dark respiration at a given leaf nitrogen (N) concentration, and at a given leaf mass per unit leaf area, are also higher in plants growing at cold compared to warm sites. This suggests that thermal history of a plant, especially for cold-adapted species, may drive the allocation of N to metabolic as opposed to structural components. Atkin et al. (2015) speculated that this could reflect either phenotypic (acclimation) or genotypic (adaptation) differences in dark respiration across gradients in growth temperature. Although this topic is debated, it is widely observed that increases in dark respiration upon an instantaneous change in temperature are not necessarily maintained, but can change in response to thermal acclimation, biogeochemical feedbacks, or evolutionary adaptation (Fig. 1). This presents a dilemma in terms of how respiration is related to short-term prevailing temperatures or long-term averages in growth temperature. Processes related to acclimation can change not only basal rates of respiration, but also the sensitivity of respiration to temperature (Atkin et al., 2008). This issue of thermal sensitivity (i.e. Q10) and whether it differs in a predictable manner across species and sites further complicates interpretation of broad geographic patterns of dark respiration. How best to handle this source of uncertainty in models is also of concern. Moreover, in addition to the process of thermal acclimation, longer term changes in dark respiration rates may also reflect adaptation due to genotypic differences. Unfortunately, while the global database

**Climatic controls on dark respiration and the importance of thermal acclimation**

Soil water availability and temperature vary across biomes, and through regulation of resources, both have the potential to impact leaf respiration. The GlobResp database includes a wide geographical range of sites whose mean annual precipitation differ by more than an order of magnitude, and whose mean annual temperature differ by almost 40°C. Across these contrasting environments,
presented in Atkin et al. (2015) is more than sufficient to highlight the importance of thermal acclimation and adaptation of plant respiration, it is not sufficient to identify underlying mechanisms related to these processes. Similarly, and admittedly to a lesser extent than temperature, aridity also has the potential to impact dark respiration. This might occur through poorly understood effects of drought on carbohydrate status, substrate availability, and enzyme kinetics. Atkin et al. (2015) point out, however, that the response of respiration to soil water availability is inconsistent, sometimes increasing and sometimes decreasing in response to drought. Whether this represents a true cause-and-effect relationship remains an open question. Future studies should explore this dependency and identify the mechanisms that underlie possible variability of leaf respiration across aridity gradients.

Dark respiration and trait covariation

The GlobResp database provides a compilation of leaf respiration that can, by design, be readily linked to key leaf traits across biomes. Previous research has shown that leaf structural, chemical or physiological traits, such as leaf mass per area, concentration of leaf N or phosphorus (P), and photosynthetic rate, are strongly linked to leaf respiration (Reich et al., 1997). Analysis of the GlobResp database showed that including the carboxylation capacity of Rubisco ($V_{cmax}$) as an explanatory variable improved predictions of dark respiration; more so than leaf N or P concentration. Similar results, albeit from a narrower distribution of traits, were reported for tropical forest trees and lianas (Slot et al., 2013). These results provide support for the simplifying association of leaf traits (i.e. trait covariation) that has important implications for how processes can be represented in models. In addition, leaf traits linked to dark respiration were shown by Atkin et al. (2015) to vary broadly across species and sites, reflecting a close link to plant growth strategy. A key conclusion made by these authors is that despite a wide range in dark respiration rates across species and sites, the plant functional type (PFT) concept widely used in modeling the terrestrial biosphere (Wullschleger et al., 2014) works quite well. It remains to be seen whether bivariate trait relationships will hold within, as well as across, PFTs. Future refinements to the PFT concept and to the trait covariation approach, with extension to below-ground traits (Iversen et al., 2015; Warren et al., 2015) have the potential to improve model simulations and therein usher in a new era in modeling land surface processes, especially C flux estimation.

Models and equations that predict global variability in leaf respiration

One of the overarching goals behind compiling the GlobResp database was to provide modelers with a resource that could be used to inform terrestrial biosphere models. As such, Atkin et al. (2015) analyze data in keeping with the UK Hadley Center model JULES (Clark et al., 2011) and ask whether the GlobResp database can provide equations that improve representation of leaf respiration given the PFT framework of this model. Although JULES includes only a limited number of PFTs, it was shown that predictions of dark respiration could be made using PFT, growth temperature, and leaf physiology and chemistry. Interestingly, Atkin et al. (2015) show that replacing the JULES model with the more extensive PFT characterizations used in the LPJ model (Sitch et al., 2003) did not improve the quality of the predictive model. This adds confidence to the utility of the GlobResp database and to the simplifying assumptions of floristic complexity through the PFT

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**Fig. 2** A traditional interpretation of observed relationships among leaf nitrogen (N) concentration, photosynthetic potential ($V_{cmax}$), and leaf respiration ($R$) defines a family of curves connecting $V_{cmax}$ to N on the basis of broad vegetation groups (plant functional types (PFTs)), with a single relationship between $R$ and $V_{cmax}$ for all PFTs. This approach is based on a priori definitions of the PFTs, and does not allow for transitions over time due to acclimation processes. An alternative approach allows for the emergence of multiple variance clusters by considering dynamic responses of leaf traits ($R$ and $V_{cmax}$, for example) to shifting environmental factors (such as growth temperature).
concept. By including analysis of the GlobResp database on the basis of both leaf area and mass, Atkin et al. (2015) make their conclusions relevant to a broad spectrum of current modeling approaches. Demonstrating the strength of the global-scale relationship between dark respiration and $V_{\text{cmax}}$ should lead to a new generation of modeling approaches which consider both leaf nutrient concentration and the fractional deployment of leaf nutrients to a variety of structural and functional roles when estimating dark respiration rates (Fig. 2). GlobResp and the analysis provided by Atkin et al. (2015) mark an important step from the current use of static PFT classifications towards new modeling approaches based on probabilistic trait associations with distribution functions that are responsive to environment on multiple timescales (Verheijen et al., 2013). It is in this regard that the GlobResp database, like others, will continue to inform model development even as concepts change and model structures evolve.

Conclusions and future directions

While the successful application of the Atkin et al. (2015) database will improve representation of leaf respiration in models, it also provides motivation towards a larger goal of developing a mechanistic model of plant respiration (Atkin et al., 2008). Much research remains, however, before that goal can be realized. More data will be needed to resolve leaf respiration in the context of specific molecular, biochemical, and physiological controls operating at a variety of scales. In addition, despite having field observations from > 100 sites, Atkin et al. (2015) note that several PFTs remain poorly represented (e.g. C₄ plants, boreal deciduous observations from data will be needed to resolve leaf respiration in the context of mechanistic model of plant respiration (Atkin will improve representation of leaf respiration in models, it also US Department of Energy under Contract Number DE-Ridge National Laboratory is managed by UT-Battelle, LLC for the Research supported by the Office of Biological and Environmental

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References


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