

## Commentary

### Clues for our missing respiration model

Gregory (Scotland Yard detective): 'Is there any other point to which you would wish to draw my attention?' Holmes: 'To the curious incident of the dog in the night-time.' Gregory: 'The dog did nothing in the night-time.' Holmes: 'That was the curious incident.'

Arthur Conan Doyle (1892) from *The Adventure of Silver Blaze* in *The Memoirs of Sherlock Holmes*

Respiration is as essential to plants as it is to animals. Because respiration increases exponentially in response to temperature in the short term, models predict that higher temperatures would lead to higher plant respiration losses, yielding less carbohydrate supply for growth and reproduction. Also because the short-term temperature response is exponential, respiration has been suggested as the cause of slower growth in warmer conditions in field studies (Clark *et al.*, 2003). However, many studies have shown acclimation of respiration, where respiration rates of plant tissues at a common temperature decline after longer exposure to warmer temperatures, becoming close to their original rate before the temperature was increased (Atkin & Tjoelker, 2003). Respiration also shows this acclimation response in roots and soil microbial communities (Luo *et al.*, 2001). Evidence of acclimation is accumulating (Slot & Kitajima, 2015), but questions remain on whether acclimation is a general response for different species, soils, tissues and for the whole plant and the ecosystem. Questions also remain about incomplete acclimation – if the response of respiration to higher temperatures is lower than estimated from short-term responses, but greater than no change at all. We cannot have a useful, powerful model of respiration until these issues are addressed with strong evidence. Obtaining strong evidence depends on the challenging task of precisely measuring the components of the whole-tree carbon (C) balance. In this issue of *New Phytologist*, Drake *et al.* (2019a, pp. 1298–1312) present an elegant solution to this challenge to answer questions about partitioning of photosynthesis. Their whole-tree chambers (Fig. 1) provided nearly continuous measurements of above-ground respiration, belowground C flux, and growth for *Eucalyptus tereticornis* trees as they grew from 1 to c. 9 m tall under control and c. +3°C warming. Also in this issue of *New Phytologist*, Drake *et al.* (2019b, pp. 1313–1324) expand on the first study by using carbon-13 ( $^{13}\text{C}$ ) labelling to determine if the



**Fig. 1** Whole-tree chambers near Hawkesbury, New South Wales, Australia. (a) Closer view of a chamber and the air-handling and control equipment. (b) Chambers used in the Drake *et al.* (2019a,b) experiments in the context of the surrounding plantation. Photographs © Sebastian Pfautsch, used with permission.

This article is a Commentary on Drake *et al.* (2019a), **222**: 1298–1312 and Drake *et al.* (2019b), **222**: 1313–1324.

fraction of photosynthesis used for respiration changes in response to the  $\approx +3^\circ\text{C}$  warming treatment.

*'These results will give experimentalists and modellers much to contemplate.'*

The first study found that  $+3^\circ\text{C}$  warming increased partitioning to aboveground growth and respiration and reduced belowground flux, which led to more leaf area, aboveground biomass and greater canopy photosynthesis (Drake *et al.*, 2019a). Warming did not affect the maintenance respiration rate or the relationship between growth respiration and biomass growth. The second study found that  $+3^\circ\text{C}$  warming did not alter the fraction of canopy photosynthesis used for respiration and growth, or the residence time of C in various tree components (Drake *et al.*, 2019b). Thus, warmer chambers grew larger trees that captured more C and grew more, with no change in carbon use efficiency (CUE,  $1 - \text{respiration/}$  photosynthesis, or the ratio of growth to photosynthesis).

The results on respiration are striking for showing complete acclimation at the whole-tree level, supporting previous studies on the acclimation of respiration at leaf-level (Slot & Kitajima, 2015). Clearly the temperature responses of trees are not well represented with exponential short-term responses (Huntingford *et al.*, 2017). Leaf-level acclimation allows respiration rates to maintain homeostasis under sustained changes in temperature, and results from alterations in respiratory enzyme capacity, the supply of photosynthetic substrates, or the demand of respiratory products (O'Leary *et al.*, 2019). Acclimation may dampen the increase in respiration rate with temperature predicted by short-term temperature response if it occurs at whole-tree level across many species (Reich *et al.*, 2016). Drake *et al.* (2019b) produced strong evidence that respiration indeed acclimates at the whole-tree level in response to warming. This result emphasizes the need for advances in models of respiration, with realistic acclimation functions, to predict the response of respiration to environmental change. It also highlights the need for a better conceptual understanding of respiration, from a description of a phenomenon to the underlying set of processes each with its own controls.

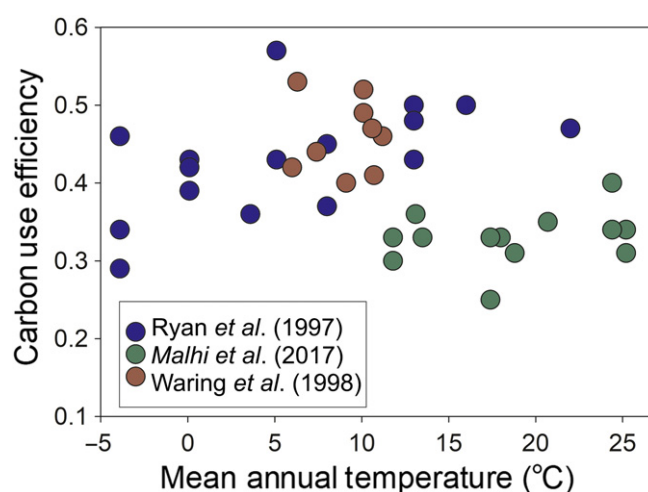
The Farquhar *et al.* (1980) model of photosynthesis has been remarkably useful and predictive – why do we not have similarly strong models of respiration? The Farquhar *et al.* (1980) photosynthesis model succinctly linked equations describing the kinetics of the photosynthetic enzyme Rubisco with those describing the limitations of electron transport and C reduction to estimate photosynthesis by which of the two was most limiting. Most approaches to modelling respiration are empirical, based on a paradigm that partitions respiration to components of growth and maintenance (Amthor, 2000). Growth respiration is modelled as a percentage of growth rate or canopy level photosynthesis, and maintenance respiration is modelled as respiration capacity adjusted by temperature response. Respiration capacity is modelled as a percentage of photosynthetic capacity in leaves, using tissue-specific rates, or with

the nitrogen (N) content of the live tissue, and the temperature response is modelled using exponential or Arrhenius functions. Acclimation of respiration is modelled by adjusting one of the parameters of the temperature response function using an empirical relationship (Smith & Dukes, 2013; Huntingford *et al.*, 2017).

A very attractive simplification, that respiration is a constant fraction of photosynthesis (Waring *et al.*, 1998), has also been proposed and used in models. The results from the Drake *et al.* (2019b) study show no difference in CUE in response to higher temperature at the whole tree level. CUE did not vary with site mean annual temperature for sites that compared CUE across sites (Fig. 2, Ryan *et al.*, 1997; Waring *et al.*, 1998; Malhi *et al.*, 2017), but there is a high variability in CUE sites even at the same temperature (Fig. 2, from 0.25 to 0.57) for all of the cross-site studies. We do not yet understand the cause of that variability.

The Drake *et al.* (2019a,b) experiments, and the earlier cross-site studies raise two important questions. First, is respiration really so finely tied to the supply of carbohydrates from photosynthesis that we can conclude that we have found a respiration model (respiration = some constant fraction of photosynthesis)? Second, what are the mechanisms that promoted a stable CUE in the Drake *et al.* (2019a,b) experiments when respiration comes from many different tissues and supports many different processes, with some tissues experiencing different temperatures?

A constant CUE may be useful for modelling only if we have no better information, and then only at the annual timescale where the CUE estimates in the literature were developed. Respiration occurs continuously in all tissues while photosynthesis occurs only in leaves under light. Modelling respiration for the whole tree and at night or in winter for deciduous trees will require knowledge of the mechanisms linking carbohydrate storage to respiration rates. Linking respiration to carbohydrate supply will require modelling carbohydrate transport and storage and a mechanism for partitioning carbohydrates to various tissues. For reasons not yet



**Fig. 2** Carbon use efficiency (CUE) versus mean annual temperature from Ryan *et al.* (1997, Table 8), Waring *et al.* (1998, Tables 1 and 2), Malhi *et al.* (2017, Tables 1 and 2). The relationship of CUE with mean annual temperature was not significant ( $P = 0.15$ ,  $R^2 = 0.06$ , mean = 0.41). Points common to Ryan *et al.* (1997) and Waring *et al.* (1998) were only used once.



understood, annual CUE is variable across sites and species, with generally lower values observed in the tropics and at high latitudes (Ryan *et al.*, 1997; Malhi *et al.*, 2017), thus arguing against the analysis in Waring *et al.* (1998). A model that assumed a constant CUE would forgo learning anything about the role of respiration and metabolism in plant function. As Cannell & Thornley (2000) argued, a stable CUE should be an outcome or a diagnostic criterion of a model with appropriate mechanisms, and not a foundational assumption of a model.

Given what we know about respiration, it is interesting that CUE did not vary with a + 3°C temperature increase for the Drake *et al.* (2019b) study and also did not vary with temperature across sites in other studies. Respiration at the level of cellular biochemistry results from the activities of numerous enzymes along the glycolysis and oxidative pentose phosphate pathways, the citric acid cycle and the activity of the mitochondrial electron transport chain. The enzyme activities are occurring at all times, under changing cellular conditions, and each of the pathways has multiple control points with alternative routes. Both substrate supply and product demand exert control over respiratory processes (reviewed in O'Leary *et al.*, 2019). Carbon dioxide (CO<sub>2</sub>) is a product of cellular respiration, but CO<sub>2</sub> efflux measured for a leaf is aggregated over a range of cell types; CO<sub>2</sub> efflux measured for the whole tree is aggregated over a range of plant components. Using the growth and maintenance paradigm in modelling respiration at leaf and whole plant level aggregates the complexity into two broad categories, and arose in part out of ease of use in linking respiration to growth rate and biomass, both of which are relatively easy to measure (Amthor, 2000), particularly for the annual herbs for which it was first proposed. The growth and maintenance paradigm predicts that CUE would decline through the course of the Drake *et al.* (2019b) experiment as trees accumulate biomass in nonphotosynthetic tissues that require increasing proportion of canopy level photosynthesis for maintenance. That CUE was constant shows that the growth and maintenance paradigm requires modification or replacement. Another mechanism is needed to reproduce the acclimation response to temperature also seen in this study.

For plant ecophysiology, the task for the Sherlock Holmes in us will be to discern the appropriate mechanisms to represent in the models. Modelling approaches based on optimization may be instructive. They reference evolution as a guiding principle and use a governing equation that optimizes a fitness proxy. One of the most prominent models is based on optimization, that for stomatal conductance, where plants maximize C gain while minimizing water loss (Cowan & Farquhar, 1977). Optimization approaches are also used to model C allocation, where plants maximize growth, and growth is then linked to photosynthesis, respiration, and partitioning of C to various plant compartments (Franklin *et al.*, 2012). Acclimation of soil respiration to changes in temperature may be an outcome of selection pressure by temperature that forces a trade-off in enzyme activity against the stability of enzymes and membranes (Bradford *et al.*, 2019). The optimization models offer advantages in explaining behaviour (of stomata, allocation, acclimation and perhaps respiration) in terms of benefits and costs arising from select few mechanisms, without the complexities required in a full description of underlying mechanisms. Just as

with any other models, they benefit from clear distinction of system boundary – under what conditions and time frame – as it dictates which mechanisms to represent. Just where that boundary lies remains unclear for most models.

The results from the two Drake *et al.* (2019a,b) papers are stunning and unexpected, and these studies have shown the field an important new tool and important findings. It is difficult to understand or even contemplate how the many changes induced by the elevated temperature treatment came together to a result in no change in CUE or the ratio of respiration to photosynthesis. These results will give experimentalists and modellers much to contemplate. We eagerly await more of these experiments with different species and treatments to inform the next generation of respiration models.

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