

# Temperature Sensitivity of Respiratory Processes Vary Across Scales

Xuhui Zhou\* and Lingyan Zhou

Research Institute for the Changing Global Environment, Coastal Ecosystems Research Station of Yangtze River Estuary, Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, The Institute of Biodiversity Science, Fudan University, 220 Handan Road, Shanghai 200433, China

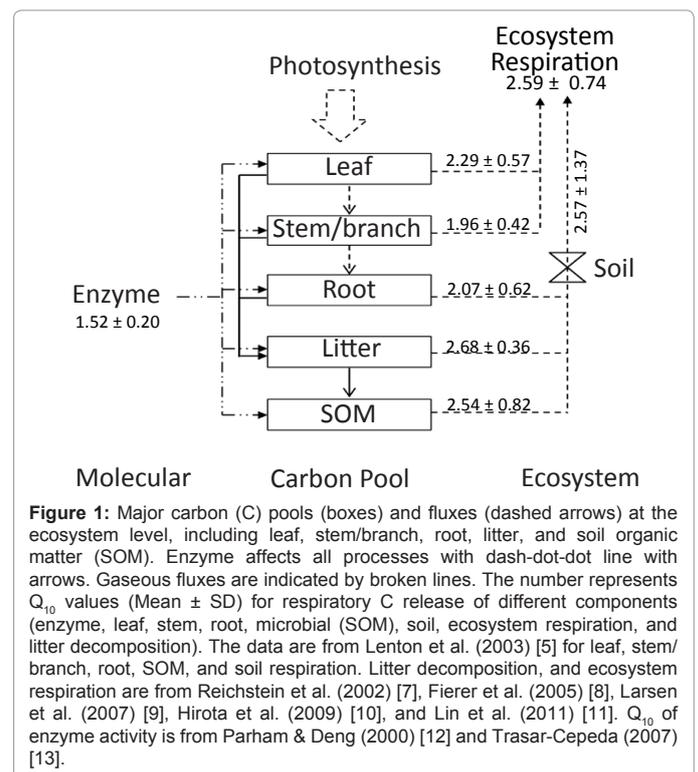
Predictions of terrestrial feedbacks to climate change from coupled climate-carbon (C) models differ remarkably in the magnitude and even the direction of soil and plant C responses [1,2]. These differences likely reflect the uncertainties inherent in how models parameterize temperature dependence of respiratory processes (i.e. temperature sensitivity), when the theoretical understanding of photosynthesis is well-established [3]. The sensitivity of respiratory processes to temperature is commonly described by  $Q_{10}$ , which is a proportional change in respiration rate for a 10°C increase in temperature [4]. A majority of models usually assume a globally constant  $Q_{10}$  value of 2 to generate C dynamics based on biochemical and physiological studies, independent of temporal and spatial scales with changing environmental conditions and vegetation types [2,5]. However, modeling studies have found that even a small deviation of the  $Q_{10}$  values could significantly exacerbate or mitigate the buildup of atmospheric CO<sub>2</sub> [5,6], with consequent feedbacks to climate change [1,2]. Temperature sensitivity of respiratory processes will largely determine the global pattern and magnitude of the predicted climate change. Therefore, understanding the sensitivity of respiratory processes to temperature is a critical step to quantify the climate-C cycle feedback in the future.

Carbon (C) enters the ecosystem via a single process, photosynthesis, but is returned back to the atmosphere via a variety of respiratory processes (Figure 1). At the biochemical level, a respiratory system involves numerous enzymes that drive glycolysis, the tricarboxylic acid (TCA) cycle and the electron transport train [4]. It is very difficult to measure the temperature sensitivity of each respiratory process individually. The  $Q_{10}$  values are often derived from its temperature variation at a specific period (e.g. weekly, seasonal or annual), dependent of the research need. The estimated  $Q_{10}$  values are thus the product of multiple processes in response to changes in temperature. In practice, respiratory processes include leaf, stem, root, microbial (or heterotrophic) respiration, litter decomposition, soil and ecosystem respiration (Figure 1).

Based on data compiled nearly 30 years ago, the global median values of  $Q_{10}$  for leaf, stem/branch, root, microbial, soil, ecosystem respiration and litter decomposition are  $2.29 \pm 0.57$  (SD, standard deviation),  $1.96 \pm 0.42$ ,  $2.07 \pm 0.62$ ,  $2.54 \pm 0.82$ ,  $2.57 \pm 1.37$ ,  $2.59 \pm 0.74$  and  $2.68 \pm 0.36$ , respectively (Figure 1) [5,7-11]. Temperature sensitivity of enzyme activity is  $1.52 \pm 0.20$ , which is relatively low compared to other respiratory processes (Figure 1) [12,13]. However, past research have shown that the  $Q_{10}$  values of respiratory processes vary widely from little more than 1 (low sensitive) to more than 10 (even 30, high sensitive) across temporal and spatial scales [8,14-16]. For example, Fierer et al. [8] found that the range in  $Q_{10}$  values of microbial respiration was from 2.2 to 4.6 in the continental USA. Within one year in a beech forest, Zealand, the  $Q_{10}$  values of soil respiration were from 2.0 to 32.7 for 4-7 days windows [14]. But considerable uncertainties remain associated with the temperature sensitivity of respiratory processes across scales and its controlling processes.

What are temporal and spatial patterns of  $Q_{10}$  values for different respiratory processes? Few studies have examined the temporal and spatial patterns of  $Q_{10}$  values for microbial and ecosystem respiration

to date. For example, Zhou et al. [16] found that the  $Q_{10}$  values for microbial respiration are spatially heterogeneous and largely vary with environmental factors, which tend to be high in the high-latitude regions (e.g. tundra) and low in arid ecosystems (e.g. deserts). Although Mahecha et al. [17] found that short-term temperature sensitivity of ecosystem respiration does not differ among biomes across 60 FLUXNET sites, apparent and/or long-term temperature sensitivity may be highly variable among sites. Large variation in the  $Q_{10}$  values also occurred for soil respiration on the regional and global scales [15,18,19]. Moreover, roots and leaves can also differ in their  $Q_{10}$  values as can other respiratory processes [20]. Therefore, more studies should concentrate on the spatial and temporal variations in  $Q_{10}$  values of respiration to modify the ecosystem Rs model. Such variable  $Q_{10}$  values need to be fully explored in global C modeling.



**Figure 1:** Major carbon (C) pools (boxes) and fluxes (dashed arrows) at the ecosystem level, including leaf, stem/branch, root, litter, and soil organic matter (SOM). Enzyme affects all processes with dash-dot-dot line with arrows. Gaseous fluxes are indicated by broken lines. The number represents  $Q_{10}$  values (Mean ± SD) for respiratory C release of different components (enzyme, leaf, stem, root, microbial (SOM), soil, ecosystem respiration, and litter decomposition). The data are from Lenton et al. (2003) [5] for leaf, stem/branch, root, SOM, and soil respiration. Litter decomposition, and ecosystem respiration are from Reichstein et al. (2002) [7], Fierer et al. (2005) [8], Larsen et al. (2007) [9], Hirota et al. (2009) [10], and Lin et al. (2011) [11].  $Q_{10}$  of enzyme activity is from Parham & Deng (2000) [12] and Trasar-Cepeda (2007) [13].

\*Corresponding author: Xuhui Zhou, Research Institute for the Changing Global Environment, Fudan University 220 Handan Road, Shanghai 200433, China. E-mail: zxuhui14@fudan.edu.cn

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What are the controlling factors for temporal and spatial patterns of temperature sensitivity of respiratory processes? The local patterns of temperature, light and water availability have both short- and long-term effects on individual organisms and then potentially influence temperature sensitivity of respiratory processes. For example, many studies have shown that the temperature sensitivity of soil respiration negatively correlated with temperature and positively correlated with soil moisture [14,15,18,19]. For a fine scale of enzyme, the  $Q_{10}$  values of extracellular enzymes changed seasonally, although temperature sensitivity of intracellular enzymes has a relative uniform inner environment [21]. However, it is largely unclear what controls temperature sensitivity of respiratory processes on regional and global scales as well as the interannual and longer-scale variability of the  $Q_{10}$  values.

Respiratory acclimation to temperature is very common in the long term, which in effect reduces the temperature sensitivity [20,22-24]. In the short-term, changes in temperature sensitivity of respiratory processes may result from physical or chemical reaction to substrate, enzyme and environmental changes. The variation in the degree of acclimation may result from the interactive effects of temperature and other abiotic factors (e.g. irradiance, drought and nutrient availability) and passive responses to change in respiratory substrate availability [20]. Much remains unclear what the underlying mechanisms are responsible for respiratory acclimation to temperature with decreased  $Q_{10}$  values and what determines the degree of acclimation? In addition, the sensitivity of respiratory processes to temperature has often been modeled based on thermodynamic principles by using simple, first-order exponential equations with temperature (e.g. Arrhenius or Van't Hoff's equation). This simple temperature-dependency poorly reflects the complex nature of the numerous respiratory processes, which is currently being questioned [25]. Therefore, new insights are needed to improve the estimated methods for the sensitivity of respiratory processes to temperature, especially using integrated methods with both experiments and models.

The sensitivity of respiratory processes to temperature is one of the major uncertainties in predicting climate-C cycle feedback. In this essay, we simply review temporal and spatial patterns of temperature sensitivity of multiple respiratory processes and identify four important questions to be answered: What are spatial patterns of the  $Q_{10}$  values, what are the controlling factors, what are the underlying mechanisms responsible for respiratory acclimation to temperature and how to improve the estimated methods of the  $Q_{10}$  values? These questions will guide our research to improve the understanding on projecting climate change in the future.

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