

Short communication

## Modelling respiration of vegetation: evidence for a general temperature-dependent $Q_{10}$

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### Abstract

Temperature responses of rates of respiratory  $\text{CO}_2$  efflux from plants, soils, and ecosystems are frequently modelled using exponential functions with a constant  $Q_{10}$  near 2.0 (fractional change in rate with a  $10^\circ\text{C}$  increase in temperature). However, we present evidence that  $Q_{10}$  declines with short-term increases in temperature in a predictable manner across diverse plant taxa. Thus, models using a constant  $Q_{10}$  are biased, and use of a temperature-corrected  $Q_{10}$  may improve the accuracy of modelled respiratory  $\text{CO}_2$  efflux in plants and ecosystems in response to temperature and predicted global climate changes.

**Keywords:** biome, boreal tree species, dark respiration, elevated carbon dioxide,  $Q_{10}$ , temperature response function

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### Introduction

Biologists have long used  $Q_{10}$  to describe the temperature dependence of rates of biological processes, a concept originating in the 19th century physical-chemistry models of Arrhenius (1889) and Van't Hoff (1896). The  $Q_{10}$  function assumes an exponential relationship with temperature in which  $Q_{10}$  is the ratio of the rate at one temperature to that at a temperature  $10^\circ\text{C}$  lower. Yet, it has long been known that short-term temperature responses of many biological processes, including respiration of plants (Belehrádek 1930; Wager 1941) and soils (Lloyd & Taylor 1994), often fail to accurately fit an exponential  $Q_{10}$  model over a broad range of temperatures. In plants, dark respiration (see reviews by James 1953; Forward 1960; Berry & Raison 1981) and respiratory enzymes (ap Rees *et al.* 1988; Farrar & Williams 1991) often exhibit declining values of  $Q_{10}$  with increasing measurement-temperature intervals. However, it remains unclear whether the temperature dependence of respiratory  $Q_{10}$  is a general phenomenon. The evidence suggests that respiratory  $Q_{10}$  is likely not constant, but

dependent on both the shape of the temperature-response curve and range of measurement temperatures used in its determination.

Despite these and other limitations, a simple exponential function (see equation in Materials and methods section) using a fixed  $Q_{10}$  of 2.0 has gained wide acceptance in modelling leaf- to ecosystem-scale respiration responses to temperature and global vegetation responses to climate change (Ryan 1991; Aber & Federer 1992; Melillo *et al.* 1993; Schimel *et al.* 1997; Cramer *et al.* 1999). Respiratory  $Q_{10}$  values are often reported near 2.0 (e.g. Amthor 1984; Collier & Cummins 1990). In a literature review,  $Q_{10}$  ( $10$ – $20^\circ\text{C}$ ) averaged 2.3 among 125 alpine, lowland, and crop species (Larigauderie & Körner 1995). However, few studies report  $Q_{10}$  values over a range of environmentally relevant temperatures for modelling temperature responses in contrasting climatic conditions.

Herein an experiment on the temperature dependence of respiratory  $Q_{10}$  for five boreal tree species is reported. In order to test further the temperature dependence of respiratory  $Q_{10}$ , literature data on the temperature responses of dark respiration of plants of

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diverse biomes are also analysed and a general function that describes the short-term temperature dependence of  $Q_{10}$  for foliar respiration is presented.

### Materials and methods

Five tree species common to the North American boreal forest were selected: quaking aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), tamarack (*Larix laricina* [Du Roi] K. Koch), black spruce (*Picea mariana* [Mill.] B.S.P.), and jack pine (*Pinus banksiana* Lamb.). Plants were grown from seed in 2.7 dm<sup>3</sup> pots in sand and fertilized daily with a complete nutrient solution. As part of a larger study, we grew the seedlings at three growth temperatures 18/12, 24/18, and 30/24 °C (16-h light/dark period) and two CO<sub>2</sub> concentrations of 580 and 370 µmol mol<sup>-1</sup>. The CO<sub>2</sub> and temperature treatments were applied as a complete factorial in a set of six identical growth

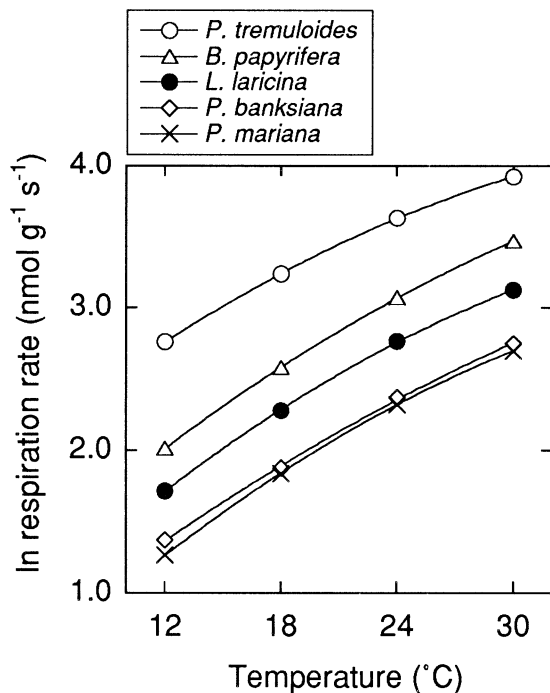
chambers with high-intensity-discharge lighting, providing 1200 µmol m<sup>-2</sup> s<sup>-1</sup> PPFD (Conviron E15, Controlled Environments, Inc., Winnipeg, Manitoba, Canada). Plants of each species grew separately in 10–15 pots in each growth chamber and treatments lasted 97 days (Tjoelker *et al.* 1998a).

The objective of this study is to examine the  $Q_{10}$  of respiration in relation to measurement temperature. The larger study explored growth, photosynthesis, and respiration responses to the treatments (Tjoelker *et al.* 1998a,b; Tjoelker *et al.* 1999a,b). The analysis here is based on temperature-response functions for dark respiration determined for each species throughout the experiment (Tjoelker *et al.* 1999b). Specific rates of dark net CO<sub>2</sub> efflux were determined for fully developed foliage at measurement temperatures of 12, 18, 24 and 30 °C using portable infra-red gas analysers and cuvettes (LCA-3 and PLC-C, Analytical Development Co. Ltd, Hoddesdon, UK). The temperature responses for three replicate shoots, consisting of leaves or needles and attached stem, were determined for each species and treatment combination.

Because the determination of the temperature responses involved multiple measures on individual plants, we used a statistical analysis of variance that included both between and within plant variation. To this end we conducted a repeated-measures analysis of variance for each species. The full general linear model included the fixed effects of CO<sub>2</sub> (1 d.f.), temperature treatment (2 d.f.) and their interaction, and the random effect of shoot nested within treatment combination (12 d.f.). Measurement temperature was included in the model as a nested and fixed effect (3 d.f.) and partitioned into single-degree-of-freedom contrasts for linear and quadratic effects.

Inspection of model fits to natural-log transformed rates revealed a consistent departure from linearity in each species. Quadratic contrasts consistently showed the temperature response (on a log scale) to be a second-order polynomial (Fig. 1). In contrast to a linear fit, a second-order polynomial fit means that the slope (i.e. temperature coefficient) varies as a linear function of temperature. By definition, the temperature coefficient multiplied by 10 is equivalent to the natural log of the  $Q_{10}$ . Thus, the temperature coefficient or  $Q_{10}$  are dependent upon measurement temperature.

Given the widespread usage of  $Q_{10}$  in modelling and to facilitate comparisons across published studies, we show  $Q_{10}$  values to describe the temperature sensitivity of respiration. We calculated  $Q_{10}$  values separately for each of the three measurement temperature intervals (12–18, 18–24, and 24–30 °C) based on the equation:



**Fig. 1** Short-term temperature response of foliar dark respiration for seedlings of five boreal tree species. Least squares means of natural log-transformed specific respiration rates are shown averaged across treatment combinations for each species (see Materials and methods). Quadratic polynomial fits for each species indicate a declining slope and  $Q_{10}$  with increasing measurement temperature. Standard errors of the least squares means are: *Populus tremuloides*, 0.024; *Betula papyrifera*, 0.022; *Larix laricina*, 0.026; *Pinus banksiana*, 0.022; and *Picea mariana*, 0.030.

$$R_{s(t)} = R_0 Q_{10}^{\left(\frac{t-t_0}{10}\right)}$$

where respiration rate,  $R_{s(t)}$ , at temperature  $t$ , is a function of  $R_0$ , the specific respiration rate at a reference temperature  $t_0$  (12, 18, or 24 °C), and  $Q_{10}$ , the ratio of rates given a 10 °C change in temperature. In order to equalize variances, the interval values of  $Q_{10}$  were transformed using the natural logarithm and the repeated-measures model was used to test the effect of measurement temperature.

## Results and discussion

Decreasing slopes of natural log-transformed rates of respiration were found that were a function of increasing measurement temperature for each species (Fig. 1). The quadratic contrasts of the measurement temperature effect were statistically significant ( $P \leq 0.002$ ). Therefore, for each of the five boreal tree species, calculated values of  $Q_{10}$  declined with increasing measurement-temperature intervals (Table 1). Similar declines in  $Q_{10}$  values were observed in plants in all temperature or CO<sub>2</sub> treatment combinations (Table 1). Moreover, the respiratory  $Q_{10}$  for five boreal tree species was independent of the temperature or CO<sub>2</sub> concentration at which the seedlings were grown (Tjoelker *et al.* 1999b).

**Table 1** Temperature effect on calculated  $Q_{10}$  of dark respiration of five common tree species of the boreal forest biome grown at two CO<sub>2</sub> concentrations\*

Species	Growth [CO <sub>2</sub> ] <sup>†</sup>	Q <sub>10</sub> of dark respiration Measurement temperature interval		
		12–18 °C	18–24 °C	24–30 °C
<i>Populus tremuloides</i>	370	2.26	1.95	1.62
	580	2.23	1.97	1.63
<i>Betula papyrifera</i>	370	2.48	2.27	2.01
	580	2.77	2.37	1.88
<i>Larix laricina</i>	370	2.68	2.34	1.81
	580	2.49	2.44	1.96
<i>Pinus banksiana</i>	370	2.48	2.37	1.88
	580	2.26	2.26	1.91
<i>Picea mariana</i>	370	2.61	2.18	1.93
	580	2.88	2.38	1.95

\*Rates of dark net CO<sub>2</sub> efflux of foliage were determined at measurement temperatures of 12, 18, 24 and 30 °C to obtain short-term temperature responses and estimates of  $Q_{10}$  which differed among measurement temperature intervals in each species ( $P \leq 0.017$ ).

<sup>†</sup>Growth CO<sub>2</sub> concentration (μmol mol<sup>-1</sup>), growth temperature (18/12, 24/18, and 30/24 °C), and the interaction term had no effect on  $Q_{10}$  in any species ( $P \geq 0.15$ ).

These findings were corroborated by a synthesis of published results of  $Q_{10}$  for foliar respiration rates consisting of 238 data points for 56 plant species (Table 2). The present literature data analysis included species of diverse taxa, including grasses, forbs, and woody plants of tropical, temperate, boreal, and arctic biomes. Measures included those of field- and laboratory-grown plants in a variety of thermal environments. Regardless of the thermal environment or species, the  $Q_{10}$  of respiration was dependent upon the range of measurement temperatures in a simple linear relationship (slope =  $-0.046 \pm 0.0033$  SEM) that was consistent among the biomes (Fig. 2). In addition, a dataset ( $n = 32$ ) of respiration rates of roots was examined that revealed a comparable slope relating  $Q_{10}$  to measurement temperature ( $-0.042 \pm 0.011$  SEM), but lower intercept (2.85) compared to foliage (data not shown).

A declining  $Q_{10}$  indicates that the temperature sensitivity of respiration is reduced with increasing measurement temperature. For example, a 10 °C increase in measurement temperature at low measurement temperatures from 5 to 15 °C results in an approximate 2.8 fold increase in respiration rate, whereas an increase in temperature from 25 to 35 °C results in a less than two-fold (1.8) increase in rate. In practice, the use of a  $Q_{10}$  at 2.0 could lead to over-predictions of respiration with warming at higher temperatures (e.g. >27 °C, where  $Q_{10} < 2.0$ ) and under-predicting increases in respiration with warming at lower measurement temperatures (e.g. <27 °C). Predicted temperature responses using a fixed vs. temperature-corrected  $Q_{10}$  will differ in magnitude and direction depending upon both the measurement and prediction temperatures. For example, using a fixed  $Q_{10}$  of 2.0 for a respiration rate determined at 10 °C results in predicted rates that are 17% larger at 5 °C and 15% lower at 15 °C compared to a model with a temperature-corrected  $Q_{10}$  of 2.8 for 10 °C. In the absence of a measured  $Q_{10}$  or if  $Q_{10}$  is known at a given temperature, it is suggested that the general linear relationship (or slope) may be used to select a temperature-corrected  $Q_{10}$  for the relevant temperature range for modelling. For example, the linear relationship of  $Q_{10}$  with measurement temperature (Fig. 2) could be substituted for the  $Q_{10}$  term in the temperature-response function. Consequently, climate data could be used to generate daily or seasonally adjusted  $Q_{10}$  values.

The temperature dependence of  $Q_{10}$  calls into question the widespread use of a constant  $Q_{10}$  in modelling rates of respiration and perhaps the accuracy of those predictions, including global estimates of terrestrial carbon balance. For example, a fixed  $Q_{10}$  of 2.0 is used in biogeochemical models such as Biome-BGC and Century (Schimel *et al.* 1997) as well as PnET (Aber & Federer 1992). In comparison, the TEM model does recognize a need to

**Table 2** Literature survey of temperature coefficients ( $Q_{10}$ ) of the short-term response of foliar dark respiration to measurement temperatures from 5 to 35 °C

	Temperature class midpoint (°C)*							
Species	5	10	15	20	25	30	35	Reference and notes
Arctic								
<i>Antennaria alpina</i>	4.2	–	3.3	–	2.0	–	1.6	Wager (1941)
<i>Cassiope hypnoides</i>	2.1	–	2.2	–	2.2	–	2.1	
<i>Cassiope tetragona</i>	3.3	–	2.9	–	2.2	–	1.7	
<i>Diapensia lapponica</i>	3.8	–	3.4	–	2.1	–	2.1	
<i>Empetrum nigrum</i>	3.5	–	2.7	–	2.3	–	2.0	Lab
	3.6	–	2.7	–	2.2	–	–	Field
<i>Oxyria digyna</i>	3.1	–	1.6	–	–	–	–	
<i>Poa</i> spp.	2.7	–	2.3	–	–	–	–	
<i>Polygonum viviparum</i>	3.0	–	2.0	–	–	–	–	
<i>Ranunculus glacialis</i>	3.6	–	1.4	–	–	–	–	
<i>Ranunculus pygmaeus</i>	2.8	–	3.1	–	2.1	–	–	
<i>Salix herbacea</i>	3.5	–	2.5	–	–	–	–	
<i>Saxifraga cernua</i>	2.3	–	3.2	–	–	–	–	
<i>Saxifraga oppositifolia</i>	3.9	–	2.5	–	2.1	–	1.8	Lab
	3.0	–	2.7	–	2.2	–	1.9	Field
<i>Viscaria alpina</i>	2.8	–	2.2	–	2.0	–	2.0	
<i>Chamaenerium latifolium</i>	2.2	–	2.45	–	–	–	–	Müller (1928)‡
<i>Salix glauca</i>	3.17	–	1.79	–	–	–	–	
Boreal †								
<i>Betula papyrifera</i>	–	–	–	–	–	1.78	–	Ranney & Peet (1994)
<i>Picea abies</i>	–	2.5	2.0	–	–	–	–	Stockfors & Linder (1998)
Temperate								
<i>Betula nigra</i>	–	–	–	–	–	1.37	–	Ranney & Peet (1994)
<i>Chamaecyparis obtusa</i>	3.14	2.69	2.30	1.97	1.69	–	–	Paembonan <i>et al.</i> (1991)
<i>Eucalyptus pauciflora</i>	–	–	2.6	–	–	1.9	–	Kirschbaum & Farquhar (1984)
<i>Helianthus annuus</i>	–	–	–	–	2.4	–	1.7	Brown & Escombe (1925)#
	3.3	–	2.2	–	–	–	–	Kidd <i>et al.</i> (1921)#
<i>Lupinus</i> spp.	2.5	2.5	2.4	1.7	2.0	–	–	Clausen (1890)§
<i>Pisum sativum</i>	3.3	–	2.5	–	1.7	1.3	1.2	Fernandes (1923)#
	3	2.8	2.4	2.3	1.8	1.6	1.4	Kuijper (1910)¶
<i>Prunus laurocerasus</i>	–	–	2.2	–	2.3	–	–	Matthaei (1905)#
<i>Prunus persica</i>	–	–	–	–	2.11	–	2.03	Grossman & DeJong (1994)
<i>Solanum tuberosum</i>	3.3	2.1	1.9	2.2	2.1	1.8	2.1	Lundegårdh (1924)
<i>Triticum sativum</i>	2.9	2.4	2.1	1.9	1.6	1.2	1.1	Clausen (1890)¶
	3.5	–	–	–	1.5	–	–	Mayer (1876)#
	–	3.0	2.4	1.8	1.7	1.6	1.7	Rischavi (1876)#
	2.6	2.4	2.3	1.9	1.8	1.3	1.1	Kuijper (1910)¶
<i>Vicia faba</i>	–	–	2.5	–	2.1	–	–	Winter: Breeze & Elston (1978)
	–	–	1.7	–	1.5	–	–	Summer:
<i>Acer pennsylvanicum</i>	–	–	2.64	2.83	2.67	–	–	Bolstad <i>et al.</i> (1999), Mitchell <i>et al.</i> (1999) (and unpublished data)
<i>Acer rubrum</i>	–	–	2.83	2.82	2.63	–	–	
<i>Betula</i> spp.	–	–	3.57	2.98	2.62	–	–	
<i>Carya</i> spp.	–	–	2.75	2.59	2.40	–	–	
<i>Cornus florida</i>	–	–	3.05	3.07	2.60	–	–	
<i>Fraxinus</i> spp.	–	–	2.79	2.70	2.30	–	–	
<i>Liriodendron tulipifera</i>	–	–	2.58	2.30	2.10	–	–	
<i>Magnolia fraseri</i>	–	–	2.52	2.13	2.17	–	–	
<i>Nyssa sylvatica</i>	–	–	2.70	2.49	2.26	–	–	
<i>Oxydendron arboreum</i>	–	–	4.11	3.05	2.98	–	–	
<i>Platanus occidentalis</i>	–	–	2.46	2.38	2.11	–	–	
<i>Quercus alba</i>	–	–	2.36	2.30	2.17	–	–	
<i>Quercus coccinea</i>	–	–	2.37	2.49	2.40	–	–	

Table 2 Continued

Species	Temperature class midpoint (°C)*							Reference and notes
	5	10	15	20	25	30	35	
<i>Quercus prinus</i>	–	–	2.27	2.22	2.27	–	–	
<i>Quercus rubra</i>	–	–	2.41	2.48	2.37	–	–	
<i>Rhododendron maximum</i>	–	–	2.98	2.59	2.57	–	–	
<i>Robinia pseudoacacia</i>	–	–	2.85	2.67	2.50	–	–	
<i>Tilia americana</i>	–	–	2.55	2.46	2.27	–	–	
<i>Dactylus glomerata</i>	–	–	–	1.4	1.3	–	–	15 °C, growth temperature: Ziska & Bunce (1994)
	–	–	–	1.6	1.5	–	–	20
	–	–	–	1.9	1.7	–	–	25
	–	–	–	2.5	1.6	–	–	30
<i>Medicago sativa</i>	–	–	–	1.8	1.6	–	–	15
	–	–	–	1.8	1.6	–	–	20
	–	–	–	2.0	1.7	–	–	25
	–	–	–	2.2	1.8	–	–	30
<b>Tropical</b>								
<i>Calophyllum inophyllum</i>	–	–	1.8	–	1.9	–	1.9	Stocker (1935)
<i>Cassia fistula</i>	–	–	2.0	–	2.0	–	2.1	Shade leaf
	–	–	2.0	–	2.0	–	2.6	Sun leaf
<i>Stelechocarpus burahol</i>	–	–	3.0	–	2.0	–	1.7	Shade leaf
	–	–	2.7	–	2.8	–	1.8	Sun leaf
Mean	3.12	2.55	2.50	2.28	2.05	1.54	1.79	
Upper 95% C.I.	3.32	2.78	2.62	2.40	2.13	1.74	1.96	
Lower 95% C.I.	2.91	2.32	2.39	2.16	1.96	1.34	1.62	
N	27	8	65	43	65	9	21	

\*Values are tabulated based on temperature class midpoints (measurement range typically 10 °C)

†The boreal data and summary statistics include the five species examined in this study (Table 1)

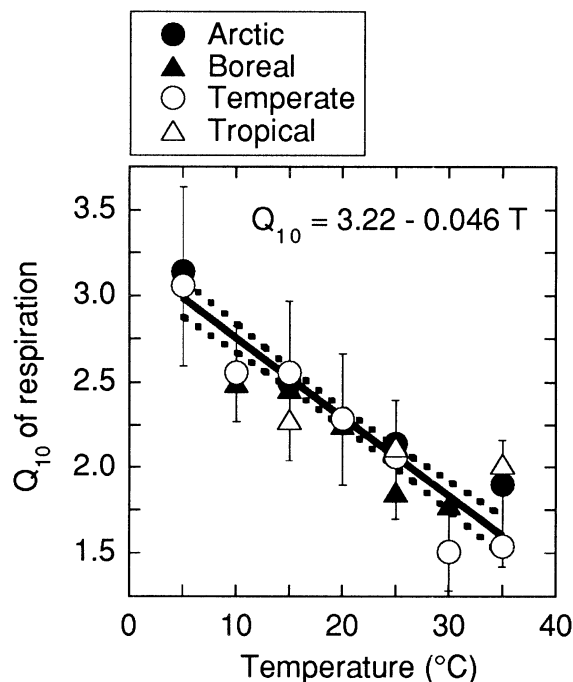
Based on data shown in: ‡Stocker 1935; #Wager 1941; ¶James 1953; §Forward 1960

adjust  $Q_{10}$ . In modelling the temperature dependence of respiration, TEM incorporates a linear decrease in  $Q_{10}$  from 2.5 to 2.0 between 0 and 5 °C, a constant value of 2.0 between 5 and 20 °C, and a linear decrease from 2.0 to 1.5 between 20 and 40 °C (McGuire *et al.* 1992). However, these values are lower overall and do not capture the linear response of the general relationship between temperature and respiratory  $Q_{10}$ . The consequences of using a fixed vs. temperature-dependent  $Q_{10}$  for integrated carbon budgets await testing and evaluation in these and other models.

In addition, it is suggested that care should be taken when comparing  $Q_{10}$  values across diverse thermal environments. In the present literature analysis, mean  $Q_{10}$  values across all temperatures were 2.14 for tropical, 2.26 for temperate, 2.20 for boreal, and 2.56 for arctic biomes. However, adjusting the means for the three biomes that shared a common covariate relationship with short-term measurement temperature ( $P = 0.50$  for homogeneity of slopes test) revealed similar  $Q_{10}$  values at 19 °C

of 2.31 for temperate, 2.22 for boreal, and 2.42 for arctic biomes. An analysis of the limited tropical data ( $n = 3$  species in one study) biome showed no relationship with temperature; however, more data are needed for a robust comparison with the other biomes. This analysis suggests that apparent biome differences in  $Q_{10}$  may, in part, be a result of measurement temperature differences. Studies at common temperatures are needed to distinguish the effect of measurement temperature from potential adaptive or acclimation responses of vegetation of contrasting climate zones. For example, the  $Q_{10}$  values of arctic and tropical lichens were comparable at common measurement temperatures (Scholander *et al.* 1952). In contrast, temperature coefficients of respiration were found to vary with climate of origin among woody species, but not among annuals or herbaceous perennials compared at common measurement temperatures (Criddle *et al.* 1994).

A temperature-dependent  $Q_{10}$  may complicate interpretation of annual variation in respiration in seasonal



**Fig. 2**  $Q_{10}$  of respiration rates of plants as a function of measurement temperature. Symbols are the mean  $Q_{10}$  of species of arctic (16 species), boreal (6 species), temperate (31 species), and tropical (3 species) biomes plotted at the midpoints in 5 °C classes. Error bars indicate  $\pm 1$  SD of the class means of all observations. Data are of 56 species from 23 studies, including our experiment with five boreal tree species (Table 1,2). Based on covariance analysis, neither slopes ( $P=0.50$ ) nor intercepts ( $P=0.07$ ) of linear regressions differed among the arctic, boreal, and temperate biome groups, evidence for a common relationship across these biomes. The  $Q_{10}$  of the tropical species showed no relationship with temperature ( $P=0.33$ ). A single linear regression was fit ( $\pm 95\%$  C.I., dashed lines) to all data points ( $R^2=0.45$ ,  $n=238$ ,  $P<0.0001$ ).

climates. A three-year record of aboveground night-time respiration of *Chamaecyparis obtusa* (Paembonan *et al.* 1991) revealed that  $Q_{10}$  varied as a function of annual variation in mean monthly night temperature, declining linearly with increasing ambient air temperatures. Although interpreted as temperature acclimation of  $Q_{10}$  (Paembonan *et al.* 1991; Larcher 1995), the linear response of long-term (seasonal) variation in  $Q_{10}$  with temperature was similar to the short-term response to measurement temperature shown in the present study. Furthermore, seasonal variation in  $Q_{10}$  based on measures at ambient temperatures alone is insufficient evidence of thermal acclimation, unless accompanied by measurements at standard temperatures. In comparison, the present authors' laboratory data of five boreal tree species suggest that  $Q_{10}$  may not acclimate to temperature (Tjoelker *et al.* 1999b). However, field studies of foliar

respiration of *Picea abies* (Stockfors & Linder 1998) and *Eucalyptus pauciflora* (Atkin *et al.* 2000b) each showed increased  $Q_{10}$  in autumn or winter than summer. These reports suggest that  $Q_{10}$  may acclimate to seasonal changes in temperature by increasing at lower temperatures in a pattern similar to that of the short-term temperature-response demonstrated here. It is apparent that both measurement-temperature and thermal environment together may influence respiratory  $Q_{10}$ . Further studies employing standard measurement temperatures are needed to discern daily or seasonal acclimation responses of respiratory metabolism from those of short-term temperature-responses (Atkin *et al.* 2000b).

Realized respiration rates are not only a function of short-term temperature responses, but respiration may also acclimate to thermal environment. Respiratory carbon exchange rates in plants are known to acclimate with time (hours to days) to prevailing temperatures (Larigauderie & Körner 1995; Tjoelker *et al.* 1999a,b; Atkin *et al.* 2000b). In effect, thermal acclimation to warmer environments results in a downward adjustment in respiration rates determined at a standard measurement temperature. Consequently, long-term responses of plant respiration to climate warming will differ from predictions based solely on short-term response functions (Atkin *et al.* 2000a,b). However, acclimation of the temperature-response function to thermal environment may occur largely through adjustment in the intercept ( $R_0$ ) and less so through changes in the temperature coefficient or  $Q_{10}$  (Butler & Landsberg 1981; Tjoelker *et al.* 1999b; but see Atkin *et al.* 2000b). Although respiratory  $Q_{10s}$  (Table 2) and specific respiration rates differ markedly among plant species (Reich *et al.* 1998) and their growth environments, the short-term sensitivity of  $Q_{10}$  to measurement temperature appears to be a general phenomenon, apparently reflecting a consistent bias in the standard exponential  $Q_{10}$  model.

At the global scale, climatic controls appear important in limiting the productivity of biomes (Churkina & Running 1998). Biogeochemical models of combined effects of elevated atmospheric  $CO_2$  concentrations and climate changes on terrestrial net primary productivity generally predict increases in production and carbon stocks (Cao & Woodward 1998; Pan *et al.* 1998). However, a positive feedback between temperature and the release of  $CO_2$  to the atmosphere by terrestrial respiration could significantly reduce the magnitude of terrestrial carbon accumulation (Houghton *et al.* 1998). Respiration is a major determinant of the carbon balance of forests (Valentini *et al.* 2000). In boreal forest ecosystems, for example, annual carbon losses to autotrophic respiration were about 60% of the carbon fixed in photosynthesis (Ryan *et al.* 1997). Therefore, accurate modelling of respiration will be critical in estimating global carbon

balance. Given the major role of respiratory  $\text{CO}_2$  efflux as a component of the net carbon balance of plants and ecosystems and its strong dependence on temperature, the use of a temperature-corrected  $Q_{10}$  as presented here may improve the accuracy of predictions of respiration from leaf to global scales.

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