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REVIEW

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Characteristics of the temperature coefficient, Q_{10}, for the respiration of non-photosynthetic organs and soils of forest ecosystems

Abstract The temperature coefficient, Q_{10} (fractional change in rate with a 10°C increase in temperature) describes the temperature sensitivity of soils, roots, and stems, as well as their possible performance in global warming processes. It is also a necessary parameter for the estimation of total CO_2 efflux from each element. A number of studies have focused on Q_{10} values to date; however, their conclusions are not universal and do not always agree. A review of these reported Q_{10} values therefore becomes necessary and important for a global understanding of the temperature sensitivity of different forest types and elements. The aims of our present paper are, first, to find the frequency distribution pattern of soils, roots, and stems (branches) and compare their temperature sensitivity; then, to find the Q_{10} differences between conifer and deciduous tree species and the effect of methodology on Q_{10} values; finally we want to give a perspective on future Q_{10}-related studies. We found that most Q_{10} values of each element were concentrated in a relatively narrow range despite a total data distribution over quite a wide range. For soil respiration, the median Q_{10} value was 2.74 and the center of the frequency distribution was between 2.0 and 2.5 with a percentage of 23%. Most of the data (>80%) were within the range from 1.0 to 4.0. The median Q_{10} value for root respiration was 2.40 and the center of the frequency distribution was from 2.5 to 3.0 with a percentage of 33%. Most of the results (>80%) ranged from 1.0 to 3.0. For stem respiration, the median Q_{10} value was 1.91 and the frequency distribution was concentrated between 1.5 and 2.0. Over 90% of the data ranged from 1.0 to 3.0. Obvious differences in Q_{10} value were found between different elements, stem < root < soil including root < soil excluding root. The differences between woody organisms of stems, roots, and soils excluding roots were statistically significant (p<0.05), indicating that heterotrophic respiration from microorganism activity may be more sensitive to global warming. The duration of the period with leaves slightly affects the temperature sensitivity of woody organisms since the Q_{10} values for root and stem of coniferous evergreen trees did not differ significantly from deciduous trees (p>0.10). CO_2 analytical methods (soda lime absorption method, IRGA (Infra-read gas analysis), and chromatograph analysis) and root separation methods (excised root and trenched box) slightly affected the Q_{10} values of soil and root respiration (p>0.10), but an *in vitro* measurement of stem respiration yielded a significantly higher Q_{10} value than an *in vivo* method (p<0.05). In general, although the Q_{10} values of non-photosynthetic organisms stayed within a relatively conservative range, considerable variation between and within elements were still detectable. Accordingly, attention should be paid to the quantitative estimation of total CO_2 efflux by Q_{10}-related models. In future studies, the biochemical factors and the environmental and biological factors controlling respiration should be emphasized for precise estimation of total CO_2 efflux. The difficulty is how to clarify the underlying mechanism for fluctuations of Q_{10} values for one specific habitat and element (e.g. temperature acclimation or adaptation of Q_{10} values) and then allow the Q_{10} values to be more conservative for representation of temperature sensitivity in global warming processes.

Keywords non-photosynthetic organisms of forest, soil respiration, stem respiration, root respiration, Q_{10}, frequency distribution

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1 Introduction

The temperature coefficient, Q_{10}, is an important base for

estimating the total CO_2 efflux from non-photosynthetic organs of a forest ecosystem. The prevailing equation for describing the relation between temperature and respiration is the exponential equation $R = ae^{bT}$ (Lloyd and Taylor, 1994; Fang and Moncrieff, 2001). The Q_{10} value, as a parameter to describe the temperature sensitivity, can be computed as $Q_{10}=e^{10b}$ (Boone et al., 1998; Tjoelker et al., 2001; Rey et al., 2002). Generally, Q_{10} value is quite stable for a specific chemical reaction; so we can calculate the reaction rate at any temperature when we know this value and the reaction rate at any given temperature. The respiration rate from non-photosynthetic organs and forest soils are usually simplified as a simple chemical reaction, $R = R_{T_1}(Q_{10})^{(T-T_1)/10}$, where, R_{T1} is respiration rate at temperature T_1 (Edwards and Hanson, 1996). The total CO_2 flux is the mathematical integral to temperature and time. Currently, many studies on Q_{10} values for respiration of forest soils, roots, and stems have enhanced our understanding of the sensitivity of temperature differences. However, different opinions among the various authors make it difficult to scale up from organisms to ecosystems (Wang et al., 2001a, 2001b).

The possible performance of non-photosynthetic organs facing global warming has become a worldwide hot issue, of which the Q_{10}-related studies are important because these values act as indicators of the respiratory temperature sensitivity of the studied material (Kirschbaum, 1995; Boone et al., 1998). Quite a few comparative studies among forest soils and other non-photosynthetic organs have been reported. For example, Kirschbaum (1995) found that the Q_{10} value for the decomposition of soil organic matter at low temperature is much higher than that of NPP (Net Primary Productivity). Although this tendency was somewhat mitigated at high temperatures, it still can enhance soil respiratory activity and induce much more CO_2 efflux from soils and finally reduce the content of soil organic matter. However, Gifford (1992) argued that soil organic matter cannot be reduced at all. Some authors also discussed the temperature sensitivity of respiration from soil microbes and roots in various forests (Boone et al., 1998; Rey et al., 2002; Singh et al., 2003), but their findings were not consistent and even contradictory. This has largely restricted our complete understanding of questions, such as: how about the temperature sensitivity of soil (microbes), roots and stems on a regional scale? What are the ranges of Q_{10} of respiration for different forest soils, roots and stems? Moreover, methods for respiration measurement are different for different materials (Wang, 2004) and the question then arises whether there are methodological influences on the estimation of Q_{10}. To answer these questions, a synthesis of previously published data will be beneficial and important.

Given this background, decades old, existing references were collected to discuss the temperature sensitivity of different non-photosynthetic organs and forest soils in the forthcoming global warming scenarios.

2 Data collection and analytical methods

2.1 Data collection

All data were collected from published papers and our own results. In most of the references for soil and root respiration, IRGA (infra-red gas analysis) techniques, together with dynamic chambers were used to measure respiration. Some measurements were made by a static soda lime absorption method or gas chromatographic analysis of sampling gas. Root respiration measurements were mainly made by root separation methods and some of them were done by a trenched box method. Stem respiration was mainly measured on intact stems but some on *in vitro* (isolated) stems.

2.2 Data analysis

In order to find the probable region for the Q_{10} volues of soil, root, and stem respiration, frequency distributions of all the data were analyzed. Four types of mean value, the arithmetic mean, the harmonic mean, the geometric mean, and the median value of the collected data were computed. The arithmetic mean is calculated as $Y_{\text{arith}}=\frac{1}{n}\sum_{i=1}^{n}Y_i$, which is the most commonly used average in data analysis; the harmonic mean is calculated as $\frac{1}{Y_{\text{harm}}}=\frac{1}{n}\sum_{i=1}^{n}\frac{1}{Y_{\text{i}}}$, which is fitted to data when the interval between their reciprocals are approximately equidistant; the geometric mean is calculated as $Y_{\text{geom}}=\sqrt[n]{Y_1Y_2\cdots Y_n}$, which is suitable to ratio data or variation rates. All three types of mean values mentioned, are so-called numeric means describing the averages of samples from different aspects. The median is a kind of position mean reflecting the center of a frequency distribution, which eliminates the influences of extreme data points.

Duncan post hoc multiple comparisons and one-way ANOVA (Analysis of Variance) were used to analyze the data. SPSS 11.0 (SPSS, USA) and Microsoft Excel were used to perform these analyses.

3 Frequency distribution of the Q_{10} value for soil respiration

Table 1 shows the data from different authors. Respiration from different forest soils showed different temperature sensitivity and large temporal variation in Q_{10} was observed, even in the same soil. Frequency analysis of Q_{10} values for soil respiration (including and excluding root systems) showed that the distribution center ranged from 2.0 to 2.5 and Q_{10} values in this region accounted for about 23% of

total data. Generally, in 42% of the data found, Q_{10} for soil respiration ranged from 2.0 to 3.0, while 82% of the Q_{10} data ranged from 1.0 to 4.0 (Fig. 1). The median value for these data was 2.74. Raich and Schlesinger (1992) have reviewed 46 Q_{10} values measured by static soda lime absorption methods from references published by Monteith in 1968 to Yoneda in 1987, and found that most Q_{10} values ranged from 1.70 to 2.90 with a median of 2.40. The 119 Q_{10} values in this paper, from more recent publications, were measured mainly by IRGA techniques. The median value was somewhat higher than that of Raich and Schlesinger (1992). Also, the range of Q_{10} values was much larger than before. However, the distribution center is quite similar (2.0–3.0 in this study, while 1.7–2.9 in their report).

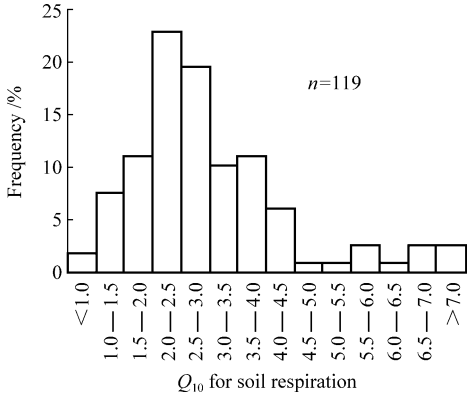

Fig. 1 Frequency distribution for the Q_{10} values for forest soil respiration (both including and excluding roots)

Table 1 Reported Q_{10} values for root respiration

Species	Q_{10} value	Method	References
Coniferous evergreen trees			
Pinus radiata	2.80	Excised roots seedlings	Sprugel et al., 1995
	1.50, 2.00	Excised roots, tree	Ryan et al., 1996
	2.30	Excised roots, tree	Benecke, 1985
Pinus taeda	1.60	Excised roots, seedlings	Ryan, 1994b
	1.30	Excised roots, seedings	Ryan, 1994b
	2.00	Excised roots seedlings	Sprugel et al., 1995
Pinus elliotti	1.94	Trenching, mature forest	Cropper and Gholz, 1991
	2.50+	Excised roots, tree	Burton et al., 2002
Pinus balsamifera	2.35	Excised roots, seedlings	Lawrence and Oechel, 1983
Pinus resinosa	3.00+	Excised roots, tree	Burton et al., 2002
Picea abies and *Pinus sylvestris*	5.00	Excised roots, tree	Widén and Majdi, 2001
Picea glauca	2.90+	Excised roots	Burton et al., 2002
Picea engelmannii	2.00	1 cm excised root segments, small tree	Sowell and Spomer, 1986
Abies lasiocarpa	1.90	1 cm excised root segments, small tree	Sowell and Spomer, 1986
Pseudotsuga menziesii	2.70	Excised roots, seedlings	Sprugel et al., 1995
	3.00	Excised soil blocks, mature forest	Sprugel et al., 1995
Deciduous trees			
Acer saccharum	2.70+	Excised roots	Burton et al., 2002
Juniperus monosperma	2.60+	Excised roots	Burton et al., 2002
Liriodendron tulipifera	2.70	Excised roots	Hanson et al., 2000
	2.60+	Excised roots	Burton et al., 2002
Mixed oak hardwood	2.40+	Excised roots	Burton et al., 2002
Mixed hardwood forest	4.60	Trenching, mature forest	Boone et al., 1998
Quercus cerris	2.20	Trenching, mature forest	Rey et al., 2002
Populus balsamifera	2.40+	Excised roots, tree	Burton et al., 2002
Quercus-Carya	3.10+	Excised roots, tree	Burton et al., 2002
Shrubs (Herb)	1.60+	Excised roots	Loveys et al., 2003

+: measured by root separation method according to O_2 changes; others were measured by IRGA or soda lime adsorption method.

4 Frequency distribution of the Q_{10} value for root respiration

In the process of global warming, it is believed that more photosynthates will be transported to underground parts of plants (Tingey et al., 2000). This forces us to pay more attention to the possible performance of root and soil respiration as a consequence of temperature increases. Our results found that Q_{10} values of root respiration were concentrated in the region from 2.5 to 3.0 (33%) although we note the large range of Q_{10} values observed by different authors (Fig. 2 and Table 2). In general, about 82% of published data found that Q_{10} values for root respiration ranged from 1.5 to 3.0 (Fig. 2) and the median value was 2.40 (Table 4).

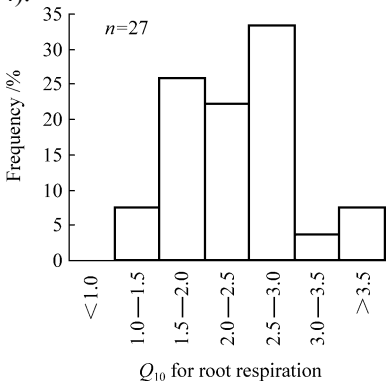

Fig. 2 Frequency distribution for the Q_{10} values of root respiration

The root respiration used in Q_{10} calculations in this paper was mainly made on isolated roots (Table 2). These isolated measurements may affect the precision of root respiration measurements (Table 2) since a recent study has shown that at least 65% of root respiration is from newly formed photosynthates (Ekblad and Högberg, 2001). When we separate roots from soil or cut roots by trenched boxes, it not only affects the nutrient and water absorption by roots and photosynthates transportation to roots, but also affects the exudation from roots to soil microbes, which finally affect the respiration from soil microbes (Hanson et al., 2000). The possibility of differences in Q_{10} values caused by the methods of Q_{10} estimation will be discussed in section 6. One difficulty in soil respiration studies is how to discriminate between root respiration and soil respiration, although some new methods, such as isotope labeling methods, have improved our ability to discriminate. This method can only used to find the ratio between root respiration or respiration from root exudates to total soil respiration, while to date, no study has used this kind of method in Q_{10} calculation (Hanson et al., 2000).

5 Frequency distribution of the Q_{10} value for stem respiration

The analysis of 136 Q_{10} values from stem respiration (Table 3) showed that most of the published data were concentrated in the region from 1.5 to 2.0 (42%), while over 90% of the data ranged from 1.0 to 3.0 (Fig. 3). The median of these data was 1.91 (Table 4). Thus, the most likely region of Q_{10} value from stem respiration was ranged from 1.0 to 3.0.

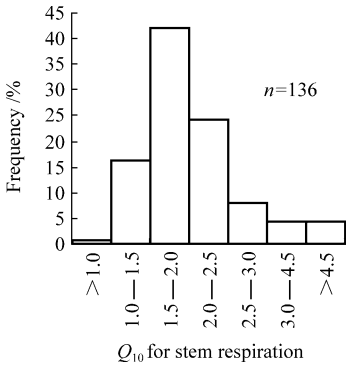

Fig. 3 Frequency distribution for the Q_{10} values of stem respiration

When we classified total tree species in this paper into two groups, deciduous and coniferous evergreen trees, we found that Q_{10} values for stem respiration of coniferous evergreen trees were higher than those of deciduous trees, although this difference was statistically insignificant (Fig. 4). Burton et al. have measured 11 forest types and found that Q_{10} values for root respiration of coniferous (gymnosperm) trees (2.7) are almost similar to those of deciduous (angiosperm) trees (2.6) (Burton et al., 2002). Similarly, we found no significant differences in Q_{10} value for root respiration between coniferous evergreen and deciduous trees in this paper, although deciduous trees had, on average, a higher Q_{10} value than coniferous evergreen trees (Fig. 4). These findings may indicate that the length of the leafless period seems to affect slightly the respiratory temperature sensitivity of the non-photosynthetic organs, although the photosynthates formed by these leaves strongly affect respiration from non-photosynthetic organs (Ekblad and Högberg, 2001; Högberg and Högberg, 2002).

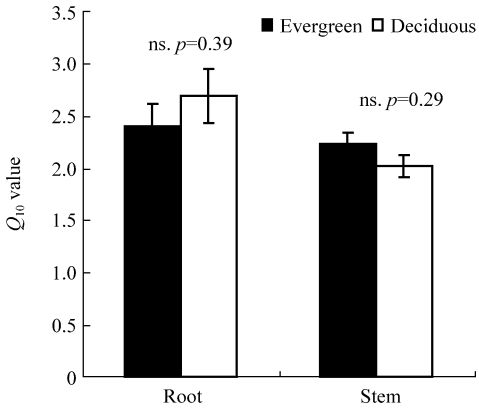

Fig. 4 Difference in Q_{10} values for stem respiration of coniferous evergreen and deciduous trees. The vertical bar on columns indicates the standard error of the mean; ns mean the difference is insignificant.

Table 2 Reported Q_{10} of respiration of intact soil and soil excluding root

Species	Q_{10} value	Method	References
Respiration of soil including root			
Median value for different soils	2.40	Mainly soda lime absorption	Raich and Schlesinger, 1992
Pinus sylvestris	2.92-3.84	Sampling gas and gas chromatograph analysis	Borken et al., 2002
	3.30, 6.29, 2.94, 3.72	Sampling gas and IRGA method	Pumpanen et al., 2003
Picea abies	2.50–3.48	Sampling gas and gas chromatograph analysis	Borken et al., 2002
	2.30–4.10	IRGA method	Buchmann, 2000
	3.90–5.70	Sampling gas and gas chromatograph analysis	Borken et al., 1999
Pinus abies	2.41, 2.34, 2.34, 3.22, 4.11, 4.11, 2.87, 3.27, 3.27, 2.39, 2.82, 2.82	IRGA method	Buchmann 2000
Pinus ponderosa	1.40, 1.80	IRGA method	Xu and Qi, 2001
	1.80	IRGA method	Law et al., 1999
Fagus sylvatica	2.71-3.57	Sampling gas and gas chromatograph analysis	Borken et al., 2002
Mixed hardwood	3.50,2.50	IRGA method	Boone et al., 1998
	3.50, 4.10, 3.40, 5.60, 4.50, 4.00, 3.90	IRGA analysis	Davidson et al., 1998
Calluna vulgaris	2.53, 2.35, 2.34, 2.44, 2.68, 2.57, 2.20, 2.12, 2.09, 2.32, 2.47, 2.24	Soda lime absorption	Chapman, 1979
Abies balsamea	2.15, 1.66, 2.22, 2.76, 1.68, 3.45, 3.49, 2.86, 2.50, 3.00, 2.78	IRGA method	Lavigne et al., 2003
Larix kampferi	1.40, 1.60, 1.80, 4.20, 7.00, 3.00, 2.98	IRGA method	Wang et al., 2001a ; 2001b
Agricultural soil	2.31	IRGA method	Fang and Moncrieff 2001
	2.80	IRGA method	Wang et al., 2001b
	1.70–2.30	IRGA method	Koizumi et al., 1999
Fagus sylvatica	4.00, 4.59, 4.07	IRGA method	Janssens and Pilegaard., 2003
Picea sitchensis	3.09	IRGA method	Fang and Moncrieff, 2001
Quercus cerris	2.32	IRGA method	Rey et al., 2002
Betula pubescens	39.4, 7.6, 0.7	IRGA method	Sjögersten and Wookey, 2002
Mixed sub-tropical forests	1.25, 1.37, 1.46 (based on air temperature)	Soda lime absorption	Yi et al., 2003
Quercus lisotungensis	2.56	IRGA method	Liu et al., 1998
	1.40, 1.50, 1.70 (based on air temperature)	IRGA method	Jiang et al., 1997
Quercus glauca	2.55 (based on air temperature)	IRGA method	Huang et al., 1999
Phyllostachys pubescens	2.11 (based on air temperature)	IRGA method	Huang et al., 1999
Camellia sinensis	1.75 (based on air temperature)	IRGA method	Huang et al., 1999
Taiga forests	0.98, 1.30, 1.30, 1.90	Sampling gas and gas chromatograph	Gulledge and Schimel, 2000
Respiration of soil excluding root			
Pinus taeda	1.70–1.90	Soda lime absorption	Winkler et al., 1996
Picea abies and *Pinus sylvestris*	2.10	IRGA method	Widén and Majdi, 2001
Betula pubescens	2.80, 6.70, 2.40, 5.30, 2.80, 6.90, 3.70, 3.60, 2.60, 14.00, 3.60, 3.60, 5.70, 3.60, 3.80	IRGA method	Sjögersten and Wookey, 2002
Tropical forest soil	2.10	IRGA method	Bekku et al., 2003
Abandoned soil	2.90	IRGA method	Bekku et al., 2003
Arctic forest soil	3.40	IRGA method	Bekku et al., 2003
Fagus sylvatica	1.71	IRGA method	Granier et al., 2000
Hardwood forests	3.10	IRGA method	Boone et al., 1998
Quercus cerris	2.89	IRGA method	Rey et al., 2002

Table 3 Reported Q_{10} values for stem and branches

Species	Q_{10}	Method	Reference
Coniferous evergreen trees			
Pinus ponderosa	1.90–2.90	*in vivo*; IRGA	Xu et al., 2000; 2001
	1.40	*in vivo*; IRGA; maintenance respiration	Ryan et al., 1995
	2.20, 2.60, 1.50, 5.80, 1.40, 1.40, 6.30, 1.20, 1.50, 5.60, 1.40, 1.50	*in vitro*; stem segments; gas chromatograph	Pruyn et al., 2002b
	2.40, 2.30,1.60, 1.90	*in vivo*; IRGA	Carey et al., 1997
	1.70	*in vivo*; IRGA	Carey et al., 1996
Pinus taeda	2.90*	*in vitro*; soda lime absorption	Kinerson, 1975
	1.68, 1.62, 2.34, 2.48, 1.57, 1.57, 1.58, 1.58, 1.84, 1.80, 1.77, 1.92, 1.40, 1.49, 1.21, 1.24, 1.25, 1.34, 1.55, 1.67, 1.77, 1.90, 1.67, 1.80, 1.92, 2.05	*in vivo*; IRGA; maintenance respiration	Maier, 2001
	1.88, 1.79	*in vivo*; IRGA; maintenance respiration	Maier et al., 1998
Pinus cembra	1.80, 2.20	*in vivo* ; IRGA	Ryan et al., 1994b
Pinus resinosa	1.30	*in vivo*; IRGA; maintenance respiration	Ryan et al., 1995
Pinus elliottii	1.90		Ryan et al., 1995
Pinus radiata	1.40 (branches)	*in vivo*; IRGA	Ryan et al., 1996
Pinus engelmannii	3.30, 2.30, 2.80	*in vivo*， IRGA	Ryan, 1990
Pinus contorta	1.80, 2.00, 2.30	*in vivo;* IRGA	Ryan, 1990
Pinus banksiana	1.20-3.00	*in vivo;*IRGA; maintenance respiration	Lavigne et al., 1996
Pinus sylvestris	2.00*	*in vivo*; soda lime absorption	Linder and Troeng, 1981
Pinus pinaster	1.83, 2.13, 2.38	*in vivo*; IRGA	Bosc et al., 2003
Abies balsamea	1.56, 2.01, 2.14, 2.68, 2.00, 2.10, 2.30, 2.50	*in vivo*; IRGA	Lavigne 1987 ; Lavigne et al., 1996
Abies amabilis	2.00*	*in vivo*; IRGA	Sprugel, 1990
Picea abies	2.60, 2.30, 2.00, 1.90, 1.90, 2.20, 2.10, 2.00	*in vivo*; IRGA	Stockfors and Linder, 1998; Stockfors, 2000
Picea mariana	1.50, 1.80, 2.20	*in vivo*; IRGA	Lavigne and Ryan, 1997
Chamaecyparis obtuse	1.50, 2.00, 2.20, 2.80, 3.20*	*in vivo*; IRGA	Paembonan et al., 1991, 1992
Tsuga heterophylla	1.80	*in vivo*; IRGA; maintenance respiration	Ryan et al., 1995
Pseudotsuga menziesii	2.20, 4.50, 2.40, 4.50, 5.30, 2.00, 4.80, 1.90, 7.60, 1.90	*in vitro*; stem segment; gas chromatograph	Pruyn et al., 2002a
Deciduous trees			
Larix gmelini	2.22–3.53	*in vivo*; IRGA	Wang et al., 2003
Larix kaempferi	2.60–3.80*	*in vivo*; IRGA	Wang et al., 2001b
Fagus sylvatica	1.70, 1.70, 1.80, 1.60, 2.40, 2.70	*in vivo*; IRGA	Damesin et al., 2002 ; Damesin, 2003
	1.60, 1.70, 1.80	*in vivo*; IRGA	Granier et al., 2000
	2.00–3.00 (branches)	*in vivo*; IRGA	Granier et al., 2000
Simarouba amara and *Minquartia guianensis*	2.20, 2.10*	*in vivo*; IRGA	Ryan et al., 1994a
Tropical rain forest (23 sp.)	1.60, 1.80	*in vivo*; IRGA	Meir and Grace, 2002
Guiera senegalensis	2.17	*in vivo* ; IRGA	Levy and Jarvis, 1998
Combretum nigricans	1.64	*in vivo*; IRGA	Levy and Jarvis, 1998
Populus tremuloides	1.00, 1.20-1.30	*in vivo*; IRGA	Lavigne and Ryan, 1997
Prunus persica	1.50, 2.00*	*in vivo*; IRGA	Grossman and Dejong, 1994
Quercus prinus	2.40*	*in vivo* ; IRGA	Edwards and Hanson, 1996
Quercus alba	2.40*	*in vivo* ; IRGA	Edwards and Hanson, 1996
Acer rubrum	1.70*	*in vivo* ; IRGA	Edwards and Hanson, 1996
	1.70*	*in vivo* ; IRGA	Edwards and Hanson, 1996
Liquidambar styraciflua	1.90, 2.20, 2.10, 1.70	*in vivo* ; IRGA	Edwards et al., 2002

*: calculation was based on air temperature, others were based on stem temperature.

Table 4 Different mean Q_{10} values for soil and stem respiration

	Arithmetic mean	Harmonic mean	Geometric mean	Median
Q_{10} for stem respiration	2.18	1.93	2.03	1.91
Q_{10} for root respiration	2.50	2.30	2.40	2.40
Q_{10} for root+soil respiration	3.24	2.42	2.70	2.57
Q_{10} for soil respiration	3.74	2.97	3.27	3.00

6 Comparison of Q_{10} values for respiration from soil, roots, and stems

Whether or not there are differences in respiratory temperature sensitivity, this sensitivity is important as an indicator of their performance under conditions of global warming. However, few studies have been concerned with this. Statistics of our results showed a general tendency in the arithmetic mean, the harmonic mean, the geometric mean, and the median value, i.e., Q_{10} values of soil without roots >Q_{10} values of soil together with roots >Q_{10} values of roots>Q_{10} values of stems (Table 4). Multiple comparison of these data showed that the differences of Q_{10} values for roots and stems were insignificant, while Q_{10} values for soil without roots was significantly higher than that of roots and stems (p<0.05) (Fig. 5). The respiration from soil without roots is mainly due to the activity of soil microbes, while respiration from roots and stem is due to the autotrophic respiratory activity for maintenance and growth of their body. Our findings indicate that soil microbes are more sensitive to temperature changes than those of non-photosynthetic organs of roots and stems. Therefore, in the process of global warming, CO_2 from the heterotrophic decomposition of soil microbes may be higher than that from autotrophic activities of trees.

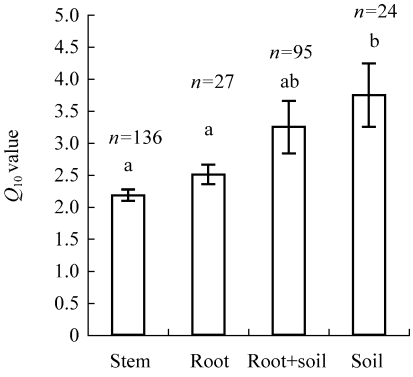

Fig. 5 Differences in Q_{10} values for respiration of stem, root, intact soil of root and soil and soil excluding root

Furthermore, comparisons between different types of mean values showed that arithmetic means were generally higher than other mean values, while harmonic means and geometric means showed relatively small differences with the median. Given that the median of the data can stand for the mean status of observed values since the median excludes the influence from extreme values (Chen et al., 1992), our findings indicate that the harmonic and geometric means represent the mean level of all data better than the arithmetic mean.

There are no consistent conclusions based on the temperature sensitivity of different forest elements. Singh et al. (2003) found that roots are not sensitive to ambient temperature variation from the stem girdling method, while Rey et al. (2002) found that Q_{10} values for root respiration of coniferous trees are slightly lower than those of respiration from soil microbes by a trenched box method. These findings are the same as ours. However, by a similar trenched box method, Boone et al. (1998) found that Q_{10} values of root respiration are much higher than those of respiration from soil microbes, implying that roots are more sensitive than soil microbes. Compared to the stem girdling method, the trenched box method always increases the soil moisture (Hanson et al., 2000). This moisture change strongly influences soil respiration measurements (Davidson et al., 1998). The study in our university forests of Laoshan station has proved that Q_{10} values for both control and trenched soils are quite similar when trenched boxes are located at ridges. However, Q_{10} values for control soil (soil + roots) were much higher than those of trenched soils when trenched boxes were located at flat sites, where water easily accumulates. Thus, the large differences in Q_{10} values calculated from trenched box methods are due to soil moisture differences. Stem girdling methods do not change soil moisture very much, since they do not change the water transportation system from soil to canopy. Therefore, a key question for precise estimation of Q_{10} value for root respiration is the choice of methodology.

The vertical bars on each column indicate the standard error of the mean value. Duncan Post Hoc tests were used in the analysis. Different letters on the columns indicate that the differences are significant. The number in each column indicates the number of data points.

7 Methodological influences on Q_{10} values for respiration of soil, roots, and stems

According to the method for CO_2 measurement, soil respiration can be classified as infra-red gas analysis, IRGA method, soda lime absorption method, and chromatographic detection method for sampling gas and other methods. According to the isolation of roots and soil, root respiration can be classified as root separation method, trenched box method, root exclusion method, forest gap method, stem girdling

method, and isotope labeling method. The first two methods can be used to calculate Q_{10} values of root respiration. According to the status of measured stems, stem respiration can be classified as *in vivo* and *in vitro* methods. Although these methods have well been reviewed (Hanson et al., 2000; Wang, 2004), no document has reported on their effect on Q_{10} values. Table 5 is analyzed from Table 1 to 3. It can be seen from this table, in the case of soil respiration, Q_{10} values measured by IRGA and chromatographic detection methods did not significantly differ from those measured by the soda lime absorption method, although Q_{10} values measured by the soda lime absorption method were relatively lower (p>0.10). In the case of root respiration, Q_{10} values measured by the trenched box method did not significantly differ from that measured by root separation (excised root) either, (p>0.10). In the case of stem respiration, however, Q_{10} values estimated by *in vitro* methods were significantly higher than those of *in vivo* methods (p<0.05). Comparing the respiration values measured by *in vitro* and *in vivo* methods, we found that values by in vitro methods were 56 times higher than those of *in vivo* methods (Hanson et al., 2000).

Table 5 The effect of methodology on the estimation of Q_{10} values of soil respiration, root respiration and stem respiration

Item and method	Soil respiration			Root respiration		Stem respiration	
	Soda lime absorption	IRGA	Chromatographic detection method	Trenched box	Excised root	*in vivo*	*in vitro*
Q_{10} value	2.14(0.43)a	3.69(4.26)a	2.84(1.36)a	2.94(1.20)a	2.43(0.75)a	1.98(0.49)a	3.15(1.93)b
Sample size	18	89	12	4	23	113	23

Values in parentheses are standard deviations. In each respiration measurements, the same letter indicates non-significant differences (p>0.05), whereas different letters indicate significant differences (p<0.05).

8 Prospective on the Q_{10} study in future

Since it is easy for respiration scaling up by temperature alone, the variation of Q_{10} values do not affect their wide utilization in temperature-dependent models (Edwards and Hanson, 1996; Boone et al., 1998; Rey et al., 2002). CO_2 flux studies in China are just being initiated (Wang et al., 2003). It is necessary to do more studies on the respiratory features of non-photosynthetic organs, in order to be able to scale up precisely to a Q_{10}-based model. Synthesis of internal physiological and external environmental factors and strengthening Q_{10}-based respiration estimations may become a pressing issue in future studies. It has been reported that the external environmental and ontogenetic factors, such as temperature, moisture and ambient CO_2 concentration (Clinton and Vose, 1999; McDowell et al., 1999), root size and distribution depth (Pregitzer et al., 1998), microbes and mycorrhizal (Waring and Running, 1998) can strongly affect soil and root respiration. In the case of stem and branch respiration, many parameters such as temperature, size, and growth rate (Paembonan et al., 1992; Covey-Crump, 2002; Meir and Grace, 2002), ambient CO_2 concentration and sap CO_2 concentration and its stem flows (Teskey and Mcguire, 2002), live cell distribution on stem and temperature variation on the same stem (Stockfors, 2000) can strongly influence the individual differences and differences within the same stem (Pruyn et al., 2002a). Although many factors affecting respiration have been found, their effects on Q_{10} values are still uncertain. Some attempts have been made. Xu et al. (2001) have introduced moisture in the one-element temperature exponential equation: $F = \beta_0 e^{\beta_1 T} W^{\beta_2}$; Granier et al. (2000) also introduced a moisture factor into their scaled-up model: $Rs = 1.13\theta_v e^{0.136T_{-10}} (r^2 = 0.86; n = 20)$, while the effect of other factors has seldom been considered to date.

Many studies also have tried to elucidate the effects of internal biochemical aspects on respiratory activity. Stockfors and Linder found that soluble sugar enhancement in stems is directly correlated with changes in stem respiration after fertilization treatment (Stockfors and Linder, 1998). Matyssek *et al.* reported that the microscopic structure of stem, including xylem cell division and activity of phloem cells are closely correlated with respiratory activity (Matyssek et al., 2002). Although the metabolism-related nitrogen in plants only accounts for 30%–40% of the maintenance and growth of cells, the nitrogen content in non-photosynthetic organs is positively correlated with respiration in general (Amthor, 2000; Cannell and Thornley, 2000). This correlation is organ specific (different between different organs) (Ryan et al., 1996). Phytohormones broadly affect the growth and division of cells (Sundberg et al., 2000), so they may also affect growth and maintenance respiration, although this needs to be confirmed by direct proofs from further studies. Although the above-mentioned biochemical parameters are expected to affect respiration of non-photosynthetic organs, a few studies have managed to include them into Q_{10}-related models; e.g., Maier has introduced nitrogen into the temperature-dependent model $R=(b_0+b_1N)e^{aT}$ (Maier, 2001), while other factors have not been included as yet to date.

Respiratory temperature coefficients ranged widely (Tables 1–3), although our analyses have provided the most likely region for their distribution (Figs.1–3) and their organ-specific differences (Fig. 4). In an environment of global warming, we still generally use Q_{10} as an indicator for describing the temperature sensitivity of the respiration of studied material (Boone et al., 1998). A difficulty in future studies then is how to overcome this large variation in Q_{10} for the same material. Existing documents found that

the adaptation of plants to temperature variation can change the temperature sensitivity of its respiration. Kirschbaum has reported the temperature adaptation of Q_{10} values for soil and litter respiration (Kirschbaum, 1995), i.e., Q_{10} values negatively correlated with temperature ($b = e^{[-3.764+0.204T(1-\frac{0.5T}{36.9})]}$, R^2=0.50; n=43) where the b value can be used to calculate $Q_{10}=e^{10b}$; no consideration was given to the temperature adaptation of Q_{10} values for non-photosynthetic organs. Similar to Kirschbaum, Tjoelker et al. (2001) found that unbiased estimates can be achieved as long as the temperature-dependent Q_{10} value is used in the estimation of respiration from individual plants, soil, and ecosystems. Janssens and Pilegaard (2003) found that Q_{10} values for soil respiration in winter are much higher than those observed in summer. However, the Q_{10} values calculated from the data of an entire year can be used to estimate precisely the total CO_2 flux from the soil on an annual basis. Through modeling analysis, Atkin et al. (2000) found that the adaptation of Q_{10} values to temperature is determined by soil carbon storage. The rapid adaptation controlled by purine nucleotide-related compounds slightly affect the estimation of soil carbon storage, while long-term adaptation caused by respiratory enzyme changes can induce more soil carbon efflux to the atmosphere. Others have reported that the adaptation of non-photosynthetic organs to temperature changes is much slower than that of leaves (Bostad et al., 2003) and are not even sensitive to temperature treatment in the case of Q_{10} values of root respiration (Burton and Pregitzer, 2003). Therefore, there is no unique conclusion to draw of how to explain the Q_{10} changes for the respiration of non-photosynthetic organs in the seasonal changes of the field environment. It is necessary to consider internal and external factors and make a comprehensive view on the temperature sensitivity of these organs and their performances in the coming environment of global warming.

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