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Soil moisture effect on the temperature dependence of ecosystem respiration in a subtropical *Pinus* plantation of southeastern China

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Abstract

Variation in temperature accounts for most of the seasonal fluctuation of terrestrial ecosystem respiration. However, other factors, such as soil moisture, also influence ecosystem respiration. In this study, continuous measurement of carbon dioxide exchange was made over a subtropical *Pinus* plantation of southeastern China using the eddy covariance (EC) technique. The effect of soil water content on ecosystem respiration and its sensitivity to temperature (Q_{10}) were examined during the unusual dry summer of 2003. The results indicate that soil water content significantly affected the dynamics of respiration rate and its relationship with temperature in the drought-stressed ecosystem. The effect of soil water content on the Q_{10} value of ecosystem respiration is described best by a quadratic function, instead of the commonly used multiplicative model. The regression model analysis revealed that ecosystem respiration was more sensitive to soil water content than is estimated by the multiplicative model. The multiplicative model led to an overestimation of response of the respiration to warming under the dry soil condition. Sensitivity of the ecosystem respiration to temperature was found to vary with air temperature and soil water content. This, to a considerable extent, precludes accurate estimates of the seasonal dynamics of ecosystem respiration.

Keywords: Carbon cycle; Climate change; Eddy covariance; Q_{10} value; Drought effects

1. Introduction

Considerable debate has focused on the response of terrestrial ecosystem respiration to environmental conditions, such as temperature, moisture and nutrient availability, as well as how it will respond to future climate change (Valentini et al., 2000; Giardina and Ryan, 2000; Grace and Rayment, 2000; Janssens et al., 2001). Temperature sensitivity of respiration is often expressed by Q_{10}, the factor by which respiration rate increases with every 10 °C increment of temperature. The Q_{10}-based formulation has been used commonly to calculate soil or ecosystem respiration from local to global scales (e.g. Cox et al., 2000; Fang and Moncrieff, 2001; Falge et al., 2002). However, the temperature response of respiration has been questioned recently (e.g., Luo et al., 2001; Tjoelker et al., 2001). It is suggested that the terrestrial ecosystem respiration rate

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has been overestimated in global carbon cycles (Cox et al., 2000). So far, it still remains unknown regarding how Q_{10} is affected by factors other than temperature (Tjoelker et al., 2001; Fang and Moncrieff, 2001). It has been documented that effects of temperature and moisture on Q_{10} are of critical importance in assessing the impacts of changing climate on ecosystem carbon fluxes (Betts, 2000; Cox et al., 2000). A few studies have recently shown that seasonal values of Q_{10} are negatively correlated with temperature, but positively related to soil water content over a limited range of soil water content (Xu and Qi, 2001; Reichstein et al., 2002; Qi et al., 2002; Janssens and Pilegaard, 2003). Currently, when temperature and moisture effects on soil or ecosystem respiration are described simultaneously, e.g., in models of global change, it is assumed that effect of individual factors may be multiplicative (e.g. Fang and Moncrieff, 1999). This hypothesis has not been well tested and may lead to an overestimation of the respiration response of ecosystem to warming under dry soil conditions (Cox et al., 2000; Reichstein et al., 2002). Unfortunately, varying sensitivity of soil or ecosystem respiration to temperature and moisture has not been explicitly considered in the ecosystem models that are commonly used in the studies of global climate change. This may result in a significant missing link in the current ecosystem models (Qi et al., 2002). Simulating soil or ecosystem respiration without a sufficient understanding of variation in temperature sensitivity will undoubtedly limit a model's utility (Fang and Moncrieff, 2001; Qi et al., 2002).

Of special interest are the influences of temperature and soil moisture on temperature sensitivity (Q_{10}) of respiration. It has long been recognized that the Q_{10} value is temperature-dependent (Lloyd and Taylor, 1994; Janssens and Pilegaard, 2003), but the effect of soil moisture on Q_{10} has rarely been studied. We have taken advantage of an unusual drought to investigate the effects of soil water content on the temperature sensitivity (Q_{10}) of whole-ecosystem respiration (as measured by eddy covariance) in an Asian monsoon climate. The objectives of this study were to (1) determine how soil moisture affects ecosystem respiration and its temperature sensitivity (Q_{10}); (2) evaluate the assumptions of the current models, which describe ecosystem respiration as a simple multiplicative function of temperature and moisture; (3) characterize effect of severe drought on seasonal variation of nighttime ecosystem respiration in the subtropical *Pinus* plantation of southeastern China.

2. Materials and methods

2.1. Site description

The study site, established in late August of 2002, is located at Qianyanzhou Experimental Station of Chinese Ecosystem Research Network (CERN) and ChinaFLUX network in southeastern China (26°44′52″N, 115°03′47″E, elevation 102 m). The mean annual air temperature is 17.9 °C, and mean annual precipitation is 1485.1 mm (1985–2004). The plantation, which was planted in 1985, around the site is on gently undulating terrain with slopes between 2.8° and 13.5° (Wen et al., 2005). The plantation is dominated by *Pinus elliottii*, *Pinus massoniana* and *Cunninghamia lanceolata*. A survey made in 2005 around the flux tower indicates that the mean tree height, diameter at breast height, and density of *P. elliottii* were about 12.6 m, 17.0 cm and 745 stems ha^{-1}, respectively, and were about 10.5 m, 13.4 cm and 880 stems ha^{-1} for *P. massoniana*, respectively, and were about 10.8 m, 13.5 cm and 102 stems ha^{-1} for *C. lanceolata*, respectively.

2.2. Measurements and instrumentation

The above-canopy flux system mounted at 39.6 m on a tower consists of model CSAT-3 3-axis sonic anemometer (Campbell Scientific Inc., Logan, UT) and model LI-7500 fast response CO_2/H_2O infrared gas analysers (Licor Inc., Lincoln, NB). The signals of these instruments were recorded at 10 Hz by a CR5000 datalogger (Model CR5000, Campbell Scientific) and then block-averaged over 30 min for analysis and archiving.

Additional meteorological measurements included radiation measurements were made at 41.6 m height using a four-component net radiometer (Model CNR-1, Kipp & Zonen), a pyranometer (Model CM11, Kipp & Zonen) and a quantum sensor of photosynthetically active radiation (LI190SB, Licor Inc.). Air temperature and relative humidity sensors (Model HMP45C, Vaisala Inc.) were mounted in ventilated mounts (Model 41002, RM Young Inc.) at heights of 1.6, 7.6, 11.6, 15.6, 23.6, 31.6 and 39.6 m above the ground. Wind speed sensors (A100R, Vector Inc.) were also mounted at the same levels with the HMP45C sensors. Soil temperatures were measured at five depths (2, 5, 20, 50 and 100 cm) with thermocouples (105T and 107-L, Campbell Scientific). Soil water contents were recorded with three TDR probes (Model CS615-L, Campbell Scientific) at depths of 5 cm (hereafter, referred to the upper soil layer), 20 and 50 cm. Rainfall was monitored with a rain gauge (Model 52203, RM Young, Inc.). Three CR10X dataloggers (Model CR10XTD, Campbell Scientific) and a CR23X datalogger (Model CR23XTD, Campbell Scientific) with a 25-channel solid-state multiplexer (Model AM25T, Campbell Scientific) were used for data collection.

2.3. Flux calculation and correction

Carbon dioxide, water vapour and heat fluxes were measured from 1 September 2002 to 31 October 2003 using the eddy covariance (EC) technique (Baldocchi et al., 1988). Nighttime ecosystem respiration (R_{eco}, mg CO_2 m^{-2} s^{-1}) was calculated with:

$$R_{\mathrm{eco}} = \overline{w'\rho_c'(z_r)} + \int_0^{z_r} \frac{\partial \bar{\rho}_c}{\partial t}\,\mathrm{d}z \qquad (1)$$

where the first term on right-hand side is the eddy flux for carbon dioxide, the second term is the storage below the height of observation (z_r). Note that positive sign represents CO_2 release into the atmosphere, and vice versa.

Three-dimensional rotation of the coordinate was applied to the wind components to remove the effect of instrument tilt or irregularity on the airflow (Tanner and Thurtell, 1969; Kaimal and Finnigan, 1994; Aubinet et al., 2000). Correction was made for the effect of fluctuations of air density on the fluxes of CO_2 and water vapour (Webb et al., 1980; Liebethal and Foken, 2003; Leuning, 2004). The characteristics of the instrument and the quality and reliability of the flux measurements were examined by calculation of power- and co-spectra (Wen et al., 2005; Sun et al., 2006).

Spurious data were removed from the dataset if the instrument performance and experimental condition were abnormal. The problems were largely related to rainfall, water condensation, or system failure (20.1% of the study site half-hourly data). To avoid possible underestimation of the fluxes under stable conditions during the night, the effect of friction velocity u_* was examined (Wen et al., 2005; Yu et al., 2006). When the value of u_* was less than 0.2 m s^{-1}, a decreasing trend in the flux was observed. In this case, the values observed in the night (global radiation < 1 W m^{-2}) were excluded (32.8% of the half-hourly data), since storage and advection are likely to reduce gas fluxes through the measurement plane of the EC instruments under these conditions. Likewise, negative fluxes at night (i.e. apparent photosynthesis) were also taken out of the database.

2.4. Ecosystem respiration models

The importance of temperature and water availability in determining ecosystem CO_2 emissions has long been recognized (Lloyd and Taylor, 1994; Davidson et al., 1998, 2000; Xu and Qi, 2001; Reichstein et al., 2002). The response of soil or ecosystem respiration to temperature is commonly described using the equations of Van't Hoff, Arrhenius or Lloyd & Taylor (LT), each with a different theoretical basis (Lloyd and Taylor, 1994; Fang and Moncrieff, 2001). As reported, these equations may underestimate the thermal response of soil or ecosystem respiration at low temperature (Fang and Moncrieff, 2001) when moisture is adequate (Xu and Qi, 2001; Reichstein et al., 2002), but overestimate in the dry season.

In all equations, air temperature at the EC measurement level was taken as input for predicting ecosystem respiration. Parameterizations were made using the nighttime EC data, resulting in a nighttime ecosystem respiration term (R_{eco}) that combines leaf, bole and soil respirations, as well as a site-specific fitted parameter of the simulated ecosystem respiration term ($R_{\mathrm{eco,ref}}$) at reference temperature (T_{ref}).

The Van't Hoff equation is given as

$$R_{\mathrm{eco}} = R_{\mathrm{eco,ref}}\,\mathrm{e}^{B(T_K - T_{\mathrm{ref}})} \qquad (2)$$

where B is a fitted site-specific parameter and T_K is the air temperature in K. This equation can be re-written as a Q_{10} relationship with $B = \ln(Q_{10})/10$. The Arrhenius equation is expressed as

$$R_{\mathrm{eco}} = R_{\mathrm{eco,ref}}\,\mathrm{e}^{(E_a/R)(1/T_{\mathrm{ref}} - 1/T_K)} \qquad (3)$$

where E_a is the activation energy in J mol^{-1}, which is a fitted site-specific parameter, R is the gas constant (8.314 J K^{-1} mol^{-1}). The Lloyd & Taylor (LT) equation is written as

$$R_{\mathrm{eco}} = R_{\mathrm{eco,ref}}\,\mathrm{e}^{E_0(1/(T_{\mathrm{ref}} - T_0) - 1/(T_K - T_0))} \qquad (4)$$

In the application, the parameter E_0 is set as 309 K, whereas T_0 is a fitted temperature parameter.

To examine the dependence of ecosystem respiration on soil moisture, we normalized all the data after excluding the influence of temperature by rearranging the Van't Hoff, Arrhenius and LT equations:

$$R'_{\mathrm{eco,ref}} = R_{\mathrm{eco,obs}}\,\mathrm{e}^{-B(T_K - T_{\mathrm{ref}})} \qquad (5)$$

$$R'_{\mathrm{eco,ref}} = R_{\mathrm{eco,obs}}\,\mathrm{e}^{-(E_a/R)(1/T_{\mathrm{ref}} - 1/T_K)} \qquad (6)$$

$$R'_{\mathrm{eco,ref}} = R_{\mathrm{eco,obs}}\,\mathrm{e}^{-E_0(1/(T_{\mathrm{ref}} - T_0) - 1/(T_K - T_0))} \qquad (7)$$

where $R'_{\mathrm{eco,ref}}$ is the normalized ecosystem respiration at reference temperature (T_{ref}), and $R_{\mathrm{eco,obs}}$ is the measured nighttime ecosystem respiration.

To quantify the coupled effect of temperature and soil moisture on ecosystem respiration, data of both air temperature at the EC measurement level and soil water content in the upper soil layer (5 cm) were used in the prediction. In the multiplicative model, ecosystem respiration is described by the product of functions $f(T_{\mathrm{K}})$ and $f(S_{\mathrm{w}})$ of air temperature (T_{K}) and soil water content (S_{w}). $f(T_{\mathrm{K}})$ is the LT function and $f(S_{\mathrm{w}})$ is a quadratic function:

$$R_{\mathrm{eco}} = R_{\mathrm{eco,refs}}\, f(T_{\mathrm{K}})\, f(S_{\mathrm{w}}) \tag{8}$$

$$f(T_{\mathrm{K}}) = \mathrm{e}^{309(1/(T_{\mathrm{ref}}-T_0)-1/(T_{\mathrm{K}}-T_0))} \tag{9}$$

$$f(S_{\mathrm{w}}) = \mathrm{e}^{aS_{\mathrm{w}}^2+bS_{\mathrm{w}}+c} \tag{10}$$

where $R_{\mathrm{eco,refs}}$ denotes the ecosystem respiration at reference temperature (T_{ref}) and optimal soil water content, and S_{w} is soil water content in $\mathrm{m}^3\,\mathrm{m}^{-3}$.

The multiplicative model implies that the temperature sensitivity (Q_{10}) of ecosystem respiration is independent of soil water content. This assumption is challenged by a modeling approach that includes the effect of soil water content on the Q_{10} coefficient. In the Q_{10} models I and II, the ecosystem respiration is described by a simple Van't Hoff function:

$$R_{\mathrm{eco}} = R_{\mathrm{eco,refs}}\, \mathrm{e}^{\ln(Q_{10})(T_{\mathrm{K}}-T_{\mathrm{ref}})/10} \tag{11}$$

Q_{10} models I and II differ in the form of the Q_{10} functions. In the Q_{10} model I, dependence of Q_{10} on temperature and soil moisture was expressed as (e.g. Xu and Qi, 2001):

$$Q_{10} = a - bT_{\mathrm{K}} + cS_{\mathrm{w}} \tag{12}$$

where positive b and c mean that the Q_{10} of ecosystem respiration decreases with increasing temperature and decreasing soil water content, respectively, over a limited range of soil water content (Xu and Qi, 2001; Reichstein et al., 2002; Qi et al., 2002). In the Q_{10} model II, a quadratic relationship of Q_{10} with soil water content was suggested to be

$$Q_{10} = a - bT_{\mathrm{K}} + cS_{\mathrm{w}} + dS_{\mathrm{w}}^2 \tag{13}$$

where a, b, c and d are fitted site-specific parameters. This function implies that ecosystem respiration is restrained under dry or wet condition that only allows a small Q_{10}.

3. Results

3.1. Seasonal air temperature, soil moisture and ecosystem respiration

Impacted by Asian monsoon climate, the study site frequently experiences extreme heat stress during growing season, with the maximum daily temperature in excess of 40 °C. Temperature was found to be negatively correlated with soil volumetric water content across seasons (Fig. 1). For the study year, the annual average nighttime air temperature was 18.3 °C, ranging from −2.2 to 32.7 °C (Fig. 1a). The soil water content was closely related to precipitation, with an unusual drought during the summer of 2003 (Fig. 1b). The annual average nighttime soil water content was $0.21\ \mathrm{m}^3\,\mathrm{m}^{-3}$, varying from 0.09 to $0.35\ \mathrm{m}^3\,\mathrm{m}^{-3}$. In July 2003, the combined effect of high air temperature and low soil water content resulted in decrease of the nighttime ecosystem respiration (Fig. 6).

3.2. The relationship between ecosystem respiration and temperature

EC measurements of nighttime ecosystem respiration are highly scattered. Thus, a bin width of 2 K with a minimum bin size of $n = 10$ was used in the fitting procedure to reduce effect of heteroscedasticity and to

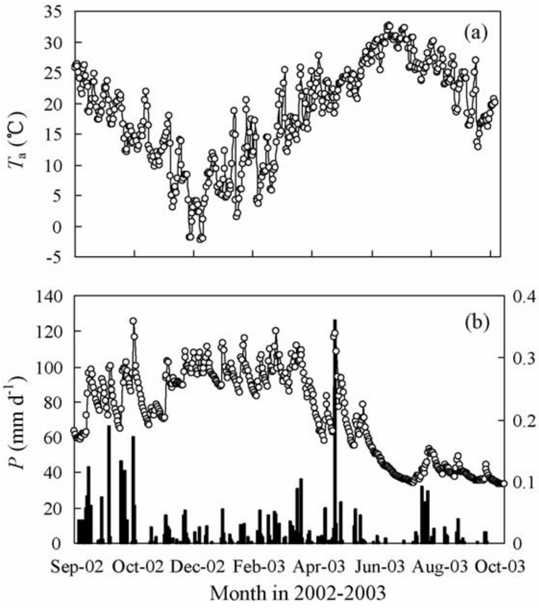

Fig. 1. (a) Daily mean nighttime air temperature at the EC measurement level, and (b) soil water content in the upper soil layer with daily precipitation, from September 2002 to October 2003, in a subtropical *Pinus* plantation of southeastern China.

provide equal weighting in the parameter estimate (e.g. Griffis et al., 2003). When air or soil temperature was taken as input for predicting ecosystem respiration, the ecosystem respiration predicted by air temperature was about 9% higher than that by soil temperature with different temperature response equations during the study year (Yu et al., 2005) since soil respiration could only account for about 40% of whole-ecosystem respiration at the study site (Yu et al., 2006). In fact the best variable should be those which best characterize the temperature of the respiration elements. Therefore, Table 1 only lists the parameters of the different equations, which are fitted using the data of nighttime ecosystem respiration and air temperature at the EC measurement level. In spite of the good fits, the Q_{10} values derived from the equations exhibit different trends with respect to temperature. They are conceptually invariable with temperature in the most commonly used Van't Hoff equation, whereas the Q_{10} values fitted with Arrhenius and LT equations decrease with increasing temperature. Such relationship are commonly accepted (e.g. Lloyd and Taylor, 1994; Fang and Moncrieff, 2001; Tjoelker et al., 2001). Among the three equations, the LT equation predicts the most rapid response of respiration to change of temperature, because the resultant Q_{10} was larger at low temperature but smaller at high temperature (Table 1). Nevertheless, these equations might still, to some extent, underestimate the thermal response of ecosystem respiration at low temperature, but overestimate at high temperature due to ignoring soil moisture effects (Fig. 2a).

3.3. Effects of soil moisture on ecosystem respiration and its Q_{10}

To examine the effect of soil moisture on ecosystem respiration, we normalized all the data for temperature dependence using Eqs. (5)–(7) and examined the residual dependence on soil moisture. As described by Eq. (10), a strong correlation was observed, between the normalized ecosystem respiration at the reference temperature (283.16 K) and soil water contents for the three temperature equations (Fig. 3).

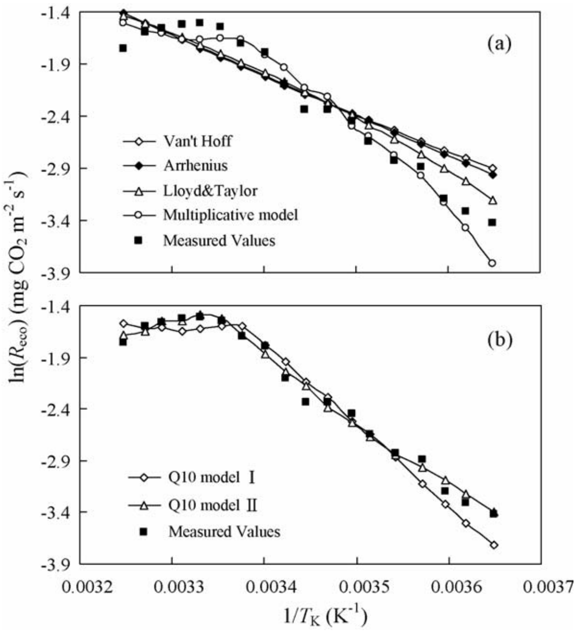

Fig. 2. The natural logarithm of nighttime ecosystem respiration, $\ln(R_{eco})$, where R_{eco} is in mg CO_2 m^{-2} s^{-1}, against the reciprocal of absolute temperature, T_K. Bin widths of 2 K with a minimum bin size of $n = 10$ (total $n = 1253$) was used in the fitting procedure to reduce the effects of heteroscedasticity ($n = 18$, referred to measured values).

By considering the coupled effect of temperature and moisture on ecosystem respiration, the multiplicative and Q_{10} models significantly improved the regression fit (Table 2) and the residual value (not shown here). The multiplicative model, which assumes that Q_{10} is independent of soil water content, contrasts to the Q_{10} model, in which the soil water effect on Q_{10} is considered.

Table 1
Nonlinear regression results of nighttime ecosystem respiration vs. air temperature at EC measurement level with the Van't Hoff, Arrhenius and Lloyd & Taylor equations

Equation	Fitted parameters		Q_{10} at			R^2
	$R_{eco,ref}$	$B/E_a/E_0$	10 °C	20 °C	30 °C	
Van't Hoff	0.082	0.044	1.553	1.553	1.553	0.801
Arrhenius	0.081	3.21×10^4	1.591	1.543	1.501	0.818
Lloyd & Taylor	0.077	212.207	1.712	1.521	1.4	0.857

Bin widths of 2 K with a minimum bin size of $n = 10$ (total $n = 1253$) was used in the fitting procedure to reduce the effects of heteroscedasticity and to provide equal weighting in the parameter estimate ($n = 18$). Reference temperature for R_{eco} was 283.16 K.

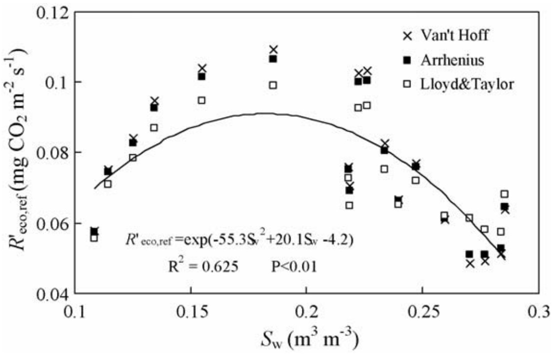

Fig. 3. Relationship between nighttime ecosystem respiration normalized to 283.16 K by Eqs. (5)–(7) and soil water content for the Van't Hoff, Arrhenius and Lloyd & Taylor equations.

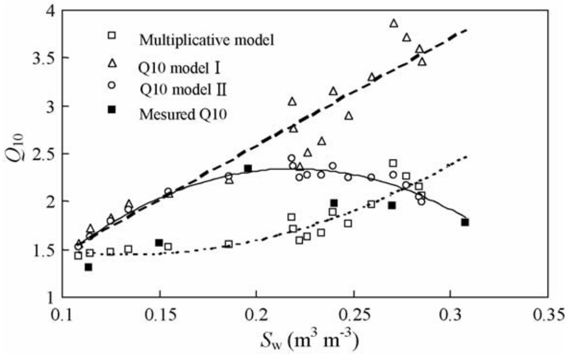

Fig. 4. Q_{10} values of the multiplicative model (dashed line), Q_{10} models I (long dashed line) and II (solid line), as well as measured values as a function of soil water content. All the night ecosystem respiration data were classified into six moisture levels, and for each moisture level the temperature sensitivity of ecosystem respiration was described using a simple Van't Hoff function so that six-measured Q_{10} values can be derived.

Worth noting is that the parameter c in Q_{10} model I may have a negative value, which implies that temperature sensitivity (Q_{10}) increases with decreasing soil water content. This, however, contradicts previous reports (Xu and Qi, 2001; Reichstein et al., 2002).

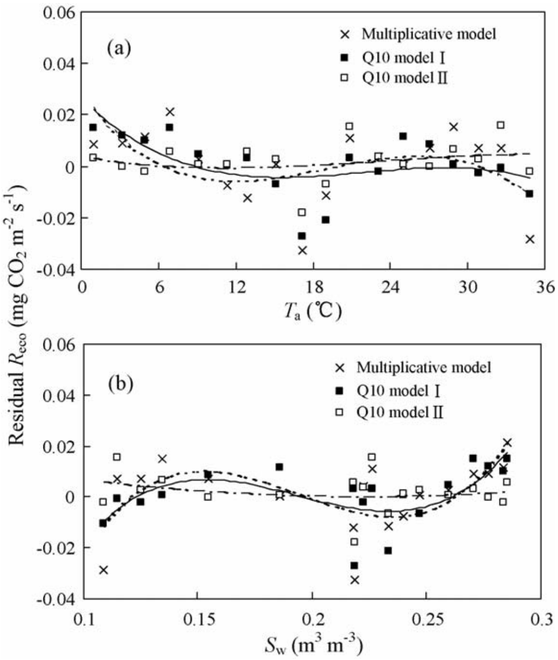

Fig. 5. Residual difference of the measured and simulated nighttime ecosystem respiration by the multiplicative model (dashed line), Q_{10} models I (solid line) and II (dot dashed line) against (a) temperature and (b) soil water content. The cubic polynomial relationship is significant for multiplicative model and Q_{10} model I, but not for Q_{10} model II.

The nighttime ecosystem respiration datasets were classified into six moisture levels, and the data were fitted with the Van't Hoff function (Fig. 4). Dependence of Q_{10} on soil water content was identified when Q_{10} was expressed as a quadratic function of soil moisture (Q_{10} model II, Eq. (13)). Residual analysis suggested that Q_{10} model II did not show a systematic variation between the simulated and measured ecosystem respiration against temperature (Fig. 5a) and soil water content (Fig. 5b). By taking into account the soil water effect, the Q_{10} model II describes the response of ecosystem respiration to temperature very well (Fig. 2b).

Table 2

Nonlinear regression results of nighttime ecosystem respiration vs. air temperature at the EC measurement level and soil water content in the upper soil layer with the multiplicative model, Q_{10} models I and II

	Fitted parameter					R^2
	$R_{eco,refs}$	a	b	c	Others	
Multiplicative model	0.042	−72.263	27.578	−1.939	T_0 = 219.456	0.959
Q_{10} model I	0.06	3.941	0.068	−0.043		0.973
Q_{10} model II	0.062	−0.165	0.018	29.409	d = −75.082	0.99

Bin widths of 2 K with a minimum bin size of n = 10 (total n = 1253) was used in the fitting procedure to reduce the effects of heteroscedasticity and to provide equal weighting in the parameter estimate (n = 18). Reference temperature for R_{eco} was 283.16 K.

3.4. Drought effect on the seasonal variation of nighttime ecosystem respiration

In the drought-stressed ecosystem, nighttime ecosystem respiration changed seasonally, with low rates during dry period and in winter (Fig. 6). This was mainly attributed to soil water effects, because soil water content could exert significant influence on the ecosystem respiration under dry soil conditions. As shown in Fig. 6a, most of the seasonal variation of nighttime ecosystem respiration was described well by the LT equation, especially in the seasons with water adequacy. Fig. 6b indicates that the multiplicative model and Q_{10} model II behaved similarly in predicting the seasonal variation of nighttime ecosystem respiration. Although Table 2 and Fig. 7 showed that the multiplicative model and Q_{10} model II kept good fits, Fig. 6b revealed that ecosystem respiration under dry soil condition was more sensitive to soil moisture than was predicted by the frequently used multiplicative model.

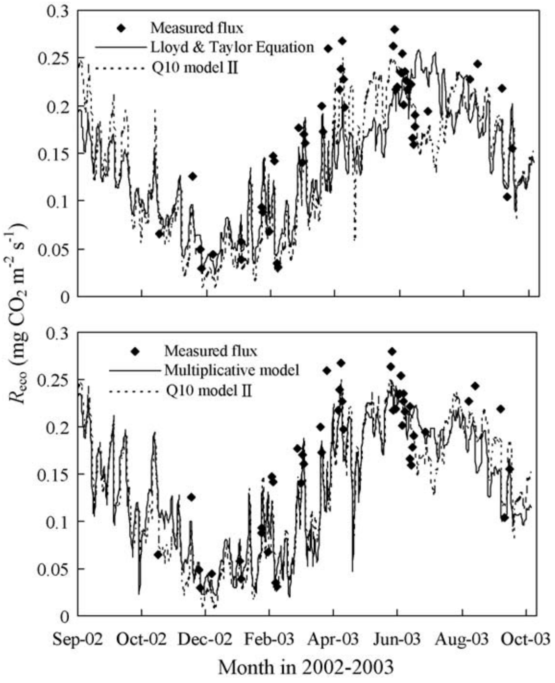

Fig. 6. Seasonal variation of nighttime ecosystem respiration based on the Lloyd & Taylor equation, multiplicative model and Q_{10} model II over a subtropical *Pinus* plantation in southeastern China. Bin widths of 1 day with a minimum bin size of $n = 10$ (total $n = 1253$) was used in the fitting procedure to reduce the effects of heteroscedasticity and to provide equal weighting in the parameter estimate ($n = 48$). Reference temperature for R_{eco} was 283.16 K.

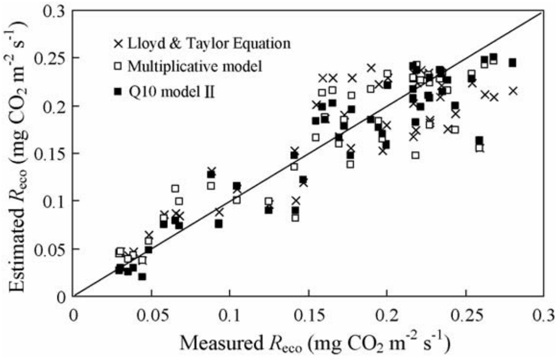

Fig. 7. Comparison of values of nighttime ecosystem respiration, R_{eco}, measured and estimated by means of the Lloyd & Taylor equation, multiplicative model and Q_{10} model II. Refer to Table 2 for the regression statistics. The solid line represents a line of 1:1.

4. Discussion

4.1. Effect of soil water content

Due to the influence of Asian monsoon climate, the site for this study is frequently subject to extreme heat stress in the summer. At this site, the effect of soil moisture on the Q_{10} of whole-ecosystem respiration was studied. In contradiction to the assumption that respiration can be described by a simple multiplicative function of temperature and moisture, the Q_{10} was found to depend on soil moisture. The Q_{10} values decreased with decreasing moisture content when soil water content was less than its optimum value (Xu and Qi, 2001; Reichstein et al., 2002; Qi et al., 2002), but an opposite trend was shown when soil retained water at contents higher than the optimum water content (Fig. 4). Several mechanisms were responsible for the Q_{10} variation with moisture condition. First of all, soil drying can decrease the activities of roots and soil microorganisms and inhibit their respiration, since sufficient water is essential for normal root and microbial function. It is demonstrated that labile substrates are often associated with the coarse fraction (litter), and they do not respire under dry conditions (Reichstein et al., 2002). Second, soil dehydration can partially inactivate the rhizosphere activity, which usually contributes a significant fraction to the total ecosystem respiration (Boone et al., 1998). This is mainly ascribed to the reduced transport of assimilates toward rhizosphere (Reichstein et al., 2002). As known, carbon assimilation by the canopy decreases remarkably as soil dries up, and consequently supply of the carbohydrates to the below-ground bio-community is reduced accordingly. On the other hand, soil water

Table 3
Increasing rates (Q_{10}) of whole-ecosystem respiration with each 10 °C increment

Forest type	Q_{10}	Reference	Forest type	Q_{10}	Reference
Maple-tulip polar	1.9	Schmid et al. (2000)	Pine	2.6	Lindroth et al. (1998)
Black spruce	2.0	Jarvis et al. (1997)	Douglas fir	2.8	Aubinet et al. (2001)
Black spruce	2.0	Goulden et al. (1997)	Maple-aspen	2.9	Lee et al. (1999)
Oak-maple	2.1	Goulden et al. (1996)	Douglas-fir	4.5	Jork et al. (1998)
Beech	2.2	Valentini et al. (1996)	Aspen	5.5	Black et al. (1996)
Spruce-hemlock	2.4	Hollinger et al. (1999)	Beech	6.0	Pilegaard et al. (2001)
Pinus plantation	1.6	Our annual value			

content sometimes exceeds the optimal moisture condition for ecosystem respiration. The optimum for soil respiration is usually found at intermediate water contents, and the respiration decreases at water contents either higher or lower than the optimum (Davidson et al., 2000). In very wet soil, limitation of soil-atmosphere gas exchange can lead to low concentration of oxygen in soil. As a result aerobic respiration of soil bio-community is restrained. Therefore, both dry and wet soil conditions can lower the sensitivity of ecosystem respiration to temperature (Q_{10}). A consequence of ignoring soil water effects is to over-emphasize the dominance of warming to ecosystem respiration, particularly under water-stressed conditions (Fig. 6b) (e.g. Cox et al., 2000; Reichstein et al., 2002). Since water contents of most soils are not in their optimal ranges under most natural conditions, consideration of soil water effect in the relationships between respiration and environmental elements is critical for accurate prediction of global climate change scenarios.

4.2. Q_{10} values

The Q_{10} value derived from our annual datasets with the Van't Hoff function is lower than those reported in literature (Table 3). This might be caused by the consideration of the seasonal changes in soil water content, root biomass, litter inputs, microbial populations and other seasonally fluctuating conditions or processes when the Q_{10} value was estimated from the annual datasets (Davidson et al., 1998; Yuste et al., 2004). Moreover, the presence of relatively stable materials, which have a lower Q_{10} and usually contribute most to the ecosystem respiration may be another reason for the lower value of Q_{10} under dry conditions. Seasonal features of biotic processes (e.g. phenology) could also influence the annual course of ecosystem respiration, and changes in fine roots and microbial population due to variation of the temperature might be masked (Greco and Baldocchi, 1996; Black et al., 1996; Griffis et al., 2003; Yuste et al., 2004). Root respiration, which accounts for a large fraction of soil respiration and exerts a strong influence on the temperature sensitivity of soil respiration, may be partly responsible for the small value of Q_{10} coefficient (Black et al., 1996; Boone et al., 1998). All the above factors have been documented to correlate with the seasonal variation of temperature (Davidson et al., 2000). However, their effects on the Q_{10} value remain to be further characterized.

4.3. Ecosystem respiration

The use of the annual respiration values derived from nighttime EC data may not be suitable for studies where heterogeneity and fetch limitation exist. Given the potential problems associated with nighttime EC measurement, such as inadequate turbulent mixing, advection, extended flux footprints, and so on, the potential difference in physiological behavior between daytime and nighttime (Falge et al., 2002; Griffis et al., 2003), and the consistency of annual ecosystem respiration, which was derived from daytime light-response analyses and nighttime EC estimates (Table 4),

Table 4
Annual ecosystem respiration estimated by the daytime light-response analysis (Dagneli, 1991) and nighttime ecosystem respiration with different models

Model	Annual ecosystem respiration (g C m^{-2} yr^{-1})			
	Nighttime	% Q_{10} model II	Daytime	% Daytime
Van't Hoff	1244.6	105.9	1271.3	97.9
Arrhenius	1243.5	105.8	1262.2	98.5
Lloyd & Taylor	1221.8	104.0	1261.9	96.8
Multiplicative model	1203.3	102.4	1158.0	103.9
Q_{10} model I	1166.1	99.2	1169.5	99.7
Q_{10} model II	1175.2	100	1168.2	100.6

Bin widths of 1 day with a minimum bin size of $n = 10$ (total $n = 1253$) was used in the fitting procedure to reduce the effects of heteroscedasticity and to provide equal weighting in the parameter estimate ($n = 48$). Reference temperature for R_{eco} was 283.16 K.

suggest that our study site was not significantly affected by heterogeneity or fetch problems (Griffis et al., 2003). The annual ecosystem respiration calculated with functions that were derived from EC measurements during nighttime was 1166–1244 g C m^{-2} yr^{-1} (Table 4). Under similar temperature and precipitation conditions, estimates of annual ecosystem respiration in this study are consistent with the results of other planted forests (Law et al., 2002).

5. Conclusions

The importance of temperature and soil moisture in determining ecosystem CO_2 emissions are highlighted based on a large volume of observed data. Soil moisture affected not only ecosystem respiration but also its temperature sensitivity or Q_{10} value. The results revealed that a quadratic function best described the temperature sensitivity of ecosystem respiration on soil water content. The multiplicative model, which treats the temperature and moisture dependence of respiration as independent factors, might lead to an overestimation of ecosystem respiration under dry soil conditions.

The seasonal variation of ecosystem respiration could be described without bias when Q_{10} of ecosystem respiration is expressed as a simple function of soil water content and temperature. The function predicted a higher temperature sensitivity at low water contents compared to the multiplicative model. The summer drought and heat wave were two major climatic factors that had a critical effect on annual carbon balance of the subtropical *Pinus* plantation of southeastern China.

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