

Seasonal patterns and environmental control of ecosystem respiration in subtropical and temperate forests in China

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Abstract Continuous measurement of carbon dioxide exchange using the eddy covariance (EC) technique was made at two ChinaFLUX forest sites including the young subtropical *Pinus* plantation (Qianyanzhou) and old temperate broad-leaved Korean pine mixed forest (Changbai Mountains) as part of the ChinaFLUX network. Seasonal patterns and environmental control of ecosystem respiration in the subtropical and temperate forests were evaluated by the often-used multiplicative model and Q_{10} model as a function of temperature and soil water content. The results suggested that (i) temperature was found to be a dominant factor in the ecosystem respiration, and most of the temporal variability of ecosystem respiration was explained by temperature. However, in the drought-stressed ecosystem, soil water content controlled the temporal variability of ecosystem respiration other than temperature effects, and soil water content became a dominant factor when severe drought affected the ecosystem respiration; (ii) the regression models analysis revealed that in the drier soil, ecosystem respiration was more sensitive to soil moisture than was expressed by the often-used multiplicative model. It was possible to accurately estimate the seasonal variation of ecosystem respiration based on the Q_{10} model; and (iii) annual ecosystem respiration derived from the often-used multiplicative model was 1209 g C m^{-2} and 1303 g C m^{-2} , and was consistently a little higher than the Q_{10} model estimates of 1197 g C m^{-2} and 1268 g C m^{-2} for Qianyanzhou and Changbai Mountains, respectively.

Keywords: ChinaFLUX, eddy covariance, Q_{10} , drought effects, temperature effects.

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The terrestrial ecosystem respiration is defined as the sum of soil microbial, root, leaf and stem respiration. Large amount of carbon fixed by vegetation was lost through respiration. The quantity of carbon fixed by vegetation, the gross ecosystem productivity, is estimated to be 120 Pg C a^{-1} with approximately 60 Pg C a^{-1} lost by plant (autotrophic) respiration and

another 60 Pg C a^{-1} lost through microbial (heterotrophic) respiration or decomposition. Small differences in these large biospheric fluxes account for year-to-year difference in carbon storage by terrestrial ecosystem^[1–3]. To predict long-term trends in carbon sequestration by ecosystems, it is necessary to understand the response of terrestrial ecosystem respiration

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to environmental factors such as temperature, moisture and substrate properties and the response of terrestrial ecosystem respiration to the environment is a key global change issue that scientists are investigating by means of measurements and models on short- and long-term scales^[3–6].

Interest in the factors that control ecosystem respiration is growing because of the potential for changing climate, including temperature and precipitation, to affect net ecosystem productivity and exchange of CO₂ between terrestrial ecosystem and the atmosphere^[7–9]. Lots of field experiments will be of benefit to understanding the factors/process controlling respiration and also has implication to improve our understanding on how net ecosystem CO₂ exchange and gross ecosystem productivity respond to environmental conditions diurnally, seasonally and interannually. An exponential increase in respiration with respect to temperature is commonly accepted and was observed for biological systems over a limited range of temperature^[10,11]. It has been debated which temperature (soil or air) to use for calculation of the relationship. As we know, the choice of soil temperature is the most common^[12–14]. In addition, air temperature^[15,16], a weighted mean of soil and air temperature^[17], bole temperature^[18] are also taken as a reference. Less consistent results have been recorded with respect to soil moisture on respiration, so that different functions describing the dependence have been applied^[8]. There are several examples of empirical relationships between field measurement of respiration and temperature and soil moisture^[6–8]. However, when describing temperature and soil moisture effects on soil or ecosystem respiration simultaneously, for example in models of global change, it has been assumed that the effects of individual factors may be multiplicative^[19,20]. However, this assumption was not well tested and might lead to an overestimation of the respiration response to warming under the dry soil conditions^[8,21]. Direct and long-term measurements of canopy-scale carbon dioxide fluxes are needed over various ecosystems to quantify the effect of environmental and physiological forcing factors on ecosystem respiration and its seasonal patterns, and to provide

data for the establishing and testing of ecosystem carbon and water balance models^[6,15].

At present, relatively few long-term studies of carbon dioxide and water vapour fluxes by the eddy covariance (EC) technique have been made in China, especially over forests^[22], before Chinese Terrestrial Ecosystem Flux Research Network (ChinaFLUX) had been established since late August in 2002, which applies the EC technique of microclimatology as a main research method to studying fluxes of carbon dioxide, water and heat between vegetation and the atmosphere. Motivated in larger part by the need to address the seasonal patterns and environmental control of ecosystem respiration over the ChinaFLUX forests, we presented ecosystem respiration data of the whole year of 2003 at two ChinaFLUX forest sites including the young subtropical *Pinus* plantation (Qianyanzhou) and old temperate broad-leaved Korean pine mixed forest (Changbaishan), in order to analyze the role of soil moisture using the often-used multiplicative model and Q_{10} model as a function of temperature and soil water content.

1 Materials and methods

1.1 Site description

An overview over the site characteristics of Qianyanzhou subtropical *Pinus* plantation and Changbai Mountains temperate broad-leaved Korean pine mixed forest in 2003 is given in table 1. See Wen et al.^[22], Li et al.^[23], Liu et al.^[24] and Guan et al.^[25] for a more extensive description of the two sites.

1.2 Data collection and treatment

The EC technique was used to estimate the flux of carbon dioxide between forest ecosystem and the atmosphere. Wind speed and temperature fluctuations were measured with three-dimensional sonic anemometers (Model CSAT-3, Campbell Scientific) mounted on the tower. CO₂ and water vapour density fluctuations were measured with CO₂/H₂O analyzers (Model LI-7500, Licor Inc.). All data were recorded at 10 Hz by CR5000 dataloggers (Model CR5000, Campbell Scientific) and then block-averaged over 30 minutes for analysis and archiving. Our measurement

Table 1 Characteristics and data collection at the subtropical *Pinus* plantation (Qianyanzhou) and temperature broad-leaved Korean pine mixed forest (Changbai Mountains) of two ChinaFLUX forest sites in 2003

	Qianyanzhou	Changbai Mountains
Location, altitude and terrain	26°44'N, 115°03'E, 102 m, hilly region	42°24' N, 128°05'E, 738 m, flat plateau
Climate	Typical subtropical monsoon climate	Temperate continental monsoon climate
Annual mean temperature/°C	17.9	4.1
Annual precipitation/mm	855	496
Canopy species	<i>Pinus elliotii</i> , <i>Pinus massoniana</i> , <i>Cunninghamia lanceolata</i> , etc.	<i>Pinus koraiensis</i> , <i>Tilia amurensis</i> , <i>Quercus mongolica</i> , <i>Fraxinus mandshurica</i> , <i>Acer mimo</i> , etc.
Leaf area index/m ² m ⁻²	3.6	5.8
Stand height/m	12	26
Soil type	Typical red earth	Upland dark brown forest soil
Stand age	20	200
Data collection		
Flux measurement height	39.6 m	40 m
Soil conditions	TDR at three locations: 5, 20 and 50 cm; soil temperature at five locations: 2, 5, 20, 50 and 100 cm	TDR at three locations: 5, 20 and 50 cm; soil temperature at five locations: 2, 5, 20, 50 and 100 cm
Meteorological variables	Air temperature/humidity at seven locations: 1.6, 7.6, 11.6, 15.6, 23.6, 31.6 and 39.6 m	Air temperature/humidity at seven locations: 2.5, 8.0, 22.0, 26.0, 32.0, 50.0 and 61.8 m

system produced the above-canopy eddy fluxes of carbon dioxide at 30-min intervals and numerically rotated wind velocity axes by triple rotation to compute flux covariance that were aligned normal to the mean streamlines^[26]. Correction was made on carbon dioxide flux for density effects due to heat and water vapour transfer^[27]. Three common tests were applied in order to check the validity of the measurement including spectral analysis, integral turbulence test and energy balance closure^[28–30]. Although the land-surface conditions cannot fully meet the demand by the EC technique, our measurements are valid and representative of the two ChinaFLUX forest sites^[25,30].

The nighttime net ecosystem CO₂ exchange, which results only from ecosystem respiration, was defined as ecosystem respiration (R_{eco} , mg m⁻² s⁻¹)

$$R_{\text{eco}} = \overline{w'\rho'_c(z_r)} + \int_0^{z_r} \frac{\partial \bar{\rho}_c}{\partial t} dz, \quad (1)$$

where the first term on the 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 CO₂ release into the atmosphere, and *vice versa*.

We limited ourselves to remove spurious values when their causes were clearly identified, which frequently occurred at night. The problems were, in most

cases, related to rainfall or water condensation. The below algorithms were applied to genuine nighttime EC fluxes. All nighttime (Global radiation <1 W m⁻²) EC data with friction velocity <0.2 m s⁻¹ were excluded from the analysis^[25,30,31], as it is likely that under these conditions storage and advection can reduce gas fluxes through the boundary layer. Similarly, negative night fluxes (i.e. with night uptake) were excluded.

1.3 Ecosystem respiration models

The importance of temperature and water availability in determining ecosystem CO₂ emissions has long been recognized. The response of ecosystem respiration to temperature is commonly described using the Van't Hoff (eq.(2)), Arrhenius (eq.(3)) and Lloyd & Taylor (eq.(4)) equations with different theoretical bases^[10,11].

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

$$R_{\text{eco}} = R_{\text{eco,ref}} e^{\left\{ \frac{E_a}{R} \left(\frac{1}{T_{\text{ref}}} - \frac{1}{T_K} \right) \right\}}, \quad (3)$$

$$R_{\text{eco}} = R_{\text{eco,ref}} e^{E_0 \left(\frac{1}{T_{\text{ref}} - T_0} - \frac{1}{T_K - T_0} \right)}, \quad (4)$$

where $R_{\text{eco,ref}}$ is the ecosystem respiration (mg m⁻² s⁻¹) at reference temperature (T_{ref}); B is a fitted

site-specific parameter ($B = \ln(Q_{10})/10$). Therefore we excluded the Q_{10} function from the analysis; T_K is air temperature in K; E_a is the activation energy in J mol^{-1} , which is a fitted site-specific parameter; R is the gas constant ($8.134 \text{ J K}^{-1} \text{ mol}^{-1}$). In the application, the parameter E_0 is set to 309 K, whereas T_0 is a fitted temperature parameter.

When describing temperature and moisture effects on ecosystem respiration simultaneously, the ecosystem respiration datasets were analyzed with the two types of models, each with different and partly mutually exclusive assumptions. In two types of models, air/soil temperature and soil water content in the upper soil layer (5 cm in depth) were taken as predictors of ecosystem respiration.

In the multiplicative model (Multiplicative model), ecosystem respiration was described as being multiplicatively dependent on temperature (T) and soil water content (S_w), $f(T)$ is the function of Lloyd & Taylor function^[10] and $f(S_w)$ is a quadratic type function.

$$R_{\text{eco}} = R_{\text{eco,refs}} f(T) f(S_w), \quad (5)$$

$$f(T) = e^{309 \left(\frac{1}{T_{\text{ref}} - T_0} - \frac{1}{T_K - T_0} \right)}, \quad (6)$$

$$f(S_w) = e^{bS_w + cS_w^2}, \quad (7)$$

where $R_{\text{eco,refs}}$ is the ecosystem respiration ($\text{mg m}^{-2} \text{ s}^{-1}$) at reference temperature (T_{ref}) and optimal soil water content. S_w is soil water content in $\text{m}^3 \text{ m}^{-3}$. b and c are fitted site-specific parameters.

Multiplicative model implies that the temperature sensitivity (Q_{10}) of ecosystem respiration is independent of soil water content. This assumption is challenged by using a modeling approach that includes the effects of soil water content on the Q_{10} (Q_{10} model). In the Q_{10} model, the ecosystem respiration was described by a simple Van't Hoff function.

$$R_{\text{eco}} = R_{\text{eco,refs}} e^{\ln(Q_{10})(T_K - T_{\text{ref}})/10}. \quad (8)$$

Lots of studies showed that the seasonal changes in Q_{10} could be related to changing temperature and/or

soil moisture conditions because they were negatively correlated with temperature, and positively with soil water content over a limited range of soil water content^[8,11,32,33]. However, ecosystem respiration will be restrained under dry or wet conditions^[34], which only allow a lower Q_{10} both above and below the optimum soil moisture condition. Thus,

$$Q_{10} = a - bT_a + cS_w + dS_w^2, \quad (9)$$

where a , b , c and d are fitted site-specific parameters, in which $b > 0$ and $d \leq 0$.

2 Results

2.1 Response of ecosystem respiration to temperature

As we know, a consensus exists with respect to the importance of seasonal variation of temperature and soil water content in determining the seasonal patterns of ecosystem respiration. First of all, the ecosystem respiration datasets were analyzed with different temperature response functions in order to accurately estimate the seasonal patterns of ecosystem respiration and its annual magnitude. However, nighttime ecosystem respiration (as measured by the EC technique) scattered greatly because respiration measurements, average over 30 minutes, have relatively low magnitudes and sampling errors are large at night. Time averaging significantly reduced nighttime EC flux variability because it was mostly stochastic reflecting the generally Gaussian nature of turbulence^[35]. A bin width of 1 day with a minimum bin size of $n > 3$ was used in the fitting procedure to reduce the effects of heteroscedasticity and random errors.

The annual average of surface air temperature near the ground (2.5 m) at Changbai Mountains was $4.1 \pm 12.0^\circ\text{C}$ (-24.7 to 22.5°C), while the annual average of surface air temperature (1.6 m) at Qianyanzhou was $17.9 \pm 8.9^\circ\text{C}$ (-2.1 to 32.5°C). The annual average of soil temperature of surface layer (2 cm) at Changbai Mountains was $6.4 \pm 7.8^\circ\text{C}$ (-3.7 to 19.8°C), while the annual average of surface soil temperature (2 cm) at Qianyanzhou was $17.7 \pm 8.9^\circ\text{C}$ (2.0 to 29.6°C). Despite of larger difference in magnitude, the two sites

have a similar seasonal pattern of soil and air temperature. Table 2 shows that ecosystem respiration of Qianyanzhou would be expressed by both air and soil temperature well, but surface air temperature at best (fig. 1(a)). Of the variance in ecosystem respiration, 69%—71% was expressed with the Van't Hoff, Arrhenius and Lloyd & Taylor equations when surface air temperature was taken as a predictor of ecosystem respiration at Qianyanzhou, but only 60%—63% was expressed when surface soil temperature was taken as a predictor. In comparison, ecosystem respiration of

Changbai Mountains was expressed as 84%—86% when surface soil temperature was taken as a predictor, but only 69%—71% was expressed when surface air temperature was taken as a predictor. The Lloyd & Taylor equation for temperature dependence of ecosystem respiration performed well (table 2). Compared with the Van't Hoff and Arrhenius equations, the Lloyd & Taylor equation does have faster response at low and high temperature as the Lloyd & Taylor equation has larger Q_{10} at low temperature but smaller at high temperature.

Table 2 Nonlinear regression results of ecosystem respiration versus air/soil temperature with different temperature equations in the subtropical *Pinus* plantation (Qianyanzhou) and temperate broad-leaved Korean pine mixed forest (Changbai Mountains)

Equation	Height/m (Air/soil temperature)	$R_{eco,ref}$ (283.16K)	$B/E_a/T_0$	Q_{10}			R^2	
				10°C	20°C	30°C		
Qianyanzhou	Van't Hoff	39.6 (Air)	0.091	0.046	1.584	1.584	1.584	0.622
		1.6 (Air)	0.085	0.055	1.733	1.733	1.733	0.690
		0.02 (Soil)	0.092	0.054	1.716	1.716	1.716	0.603
		0.05 (Soil)	0.089	0.055	1.733	1.733	1.733	0.597
	Arrhenius	39.6 (Air)	0.089	3.336×10^4	1.622	1.571	1.526	0.633
		1.6 (Air)	0.084	3.967×10^4	1.777	1.711	1.653	0.697
		0.02 (Soil)	0.090	3.882×10^4	1.755	1.691	1.635	0.609
		0.05 (Soil)	0.088	3.957×10^4	1.774	1.708	1.651	0.603
	Lloyd & Taylor	39.6 (Air)	0.084	2.139×10^2	1.756	1.548	1.417	0.656
		1.6 (Air)	0.079	2.192×10^2	1.922	1.645	1.479	0.712
		0.02 (Soil)	0.086	2.181×10^2	1.883	1.623	1.465	0.626
		0.05 (Soil)	0.083	2.190×10^2	1.914	1.641	1.477	0.619
Changbai Mountains	Van't Hoff	32 (Air)	0.175	0.092	2.509	2.509	2.509	0.708
		2.5 (Air)	0.163	0.091	2.694	2.694	2.694	0.694
		0.02 (Soil)	0.158	0.115	3.158	3.158	3.158	0.841
		0.05 (Soil)	0.153	0.123	3.421	3.421	3.421	0.840
	Arrhenius	32 (Air)	0.177	6.140×10^4	2.434	2.296	2.177	0.711
		2.5 (Air)	0.165	6.149×10^4	2.437	2.298	2.170	0.698
		0.02 (Soil)	0.160	7.736×10^4	3.068	2.849	2.665	0.845
		0.05 (Soil)	0.155	8.261×10^4	3.390	3.059	2.848	0.842
	Lloyd & Taylor	32 (Air)	0.184	2.256×10^2	2.214	1.803	1.576	0.719
		2.5 (Air)	0.170	2.264×10^2	2.260	1.828	1.590	0.705
		0.02 (Soil)	0.169	2.321×10^2	2.694	2.038	1.710	0.857
		0.05 (Soil)	0.164	2.338×10^2	2.871	2.118	1.753	0.850

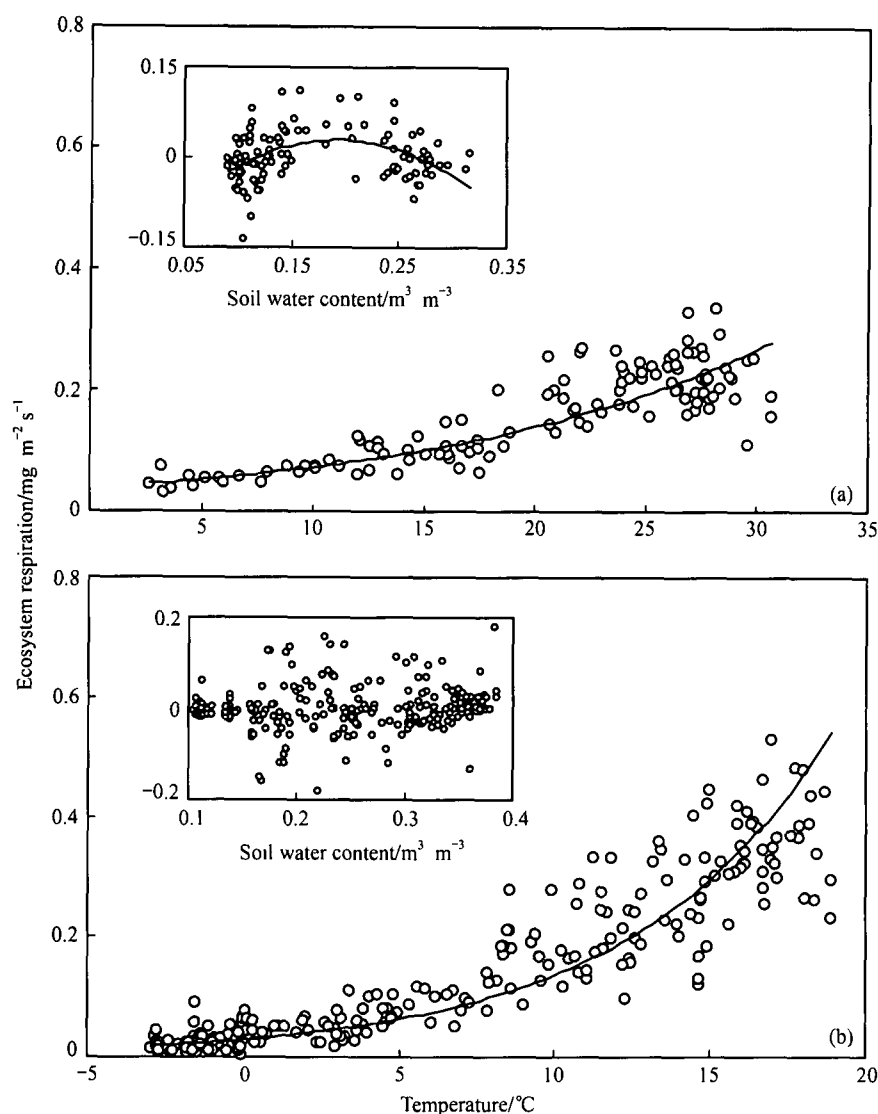


Fig. 1. Relationship between ecosystem respiration and surface air temperature (1.6 m, a) at the Qianyanzhou subtropical *Pinus* plantation and surface soil temperature (2 cm, b) at the Changbai Mountains temperature broad-leaved Korean pine mixed forest. The nonlinear regression curve was modeled by Lloyd & Taylor function. The insets show the relationship between the residuals between measured and simulated ecosystem respiration and soil water content.

2.2 Effects of soil water content on ecosystem respiration

The annual average of soil water content in the upper soil layer (5 cm) at Qianyanzhou was $0.179 \pm 0.079 \text{ m}^3 \text{ m}^{-3}$ and ranged from 0.091 to $0.349 \text{ m}^3 \text{ m}^{-3}$, experiencing an unusual drought during the summer of 2003. Soil water contents in the upper and deeper soil layer were severely depleted during the drought period at Qianyanzhou (fig. 2(a)). In comparison, the annual

average of soil water content in the upper soil layer (5 cm) at Changbai Mountains was $0.234 \text{ m}^3 \text{ m}^{-3}$ (0.105 to $0.443 \text{ m}^3 \text{ m}^{-3}$). However, soil water content in the deeper soil layer kept higher level during the whole year of 2003 (fig. 2(b)). The upper soil water content of the two ChinaFLUX forest sites was closely related to precipitation (fig. 2). The two sites differ substantially with respect to water availability, although having a similar seasonal pattern of temperature.

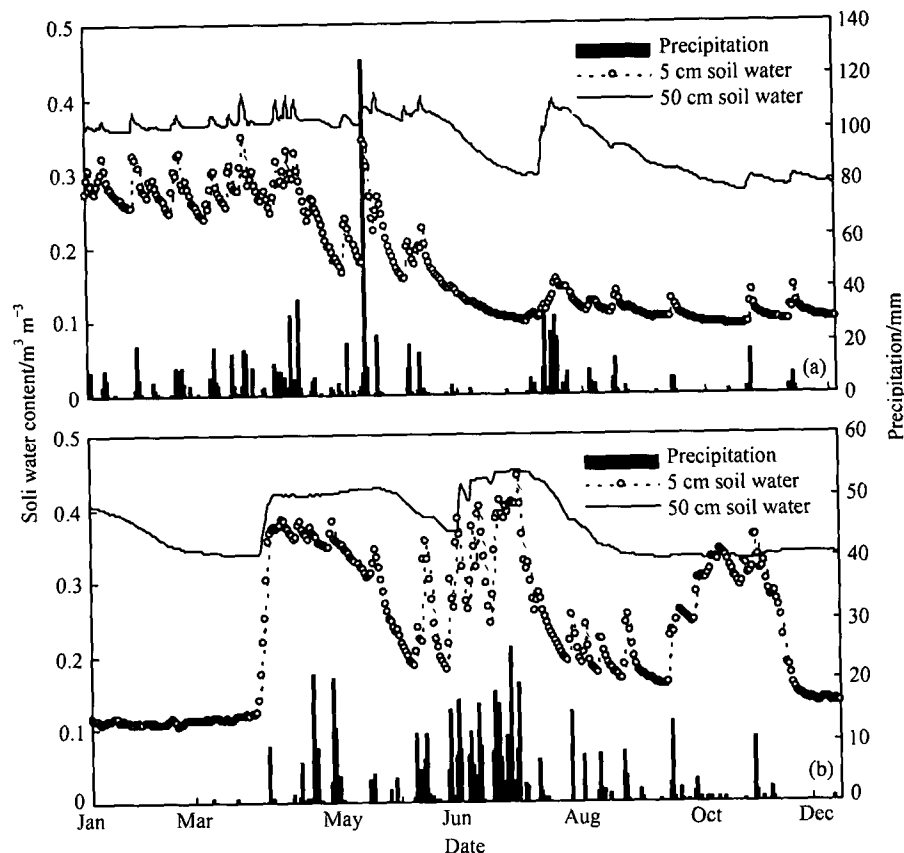


Fig. 2. Daily mean soil water content in the upper (5 cm) and deeper (50 cm) soil layer with daily sum precipitation at the Qianyanzhou subtropical *Pinus* plantation (a) and Changbai Mountains temperature broad-leaved Korean pine mixed forest (b) in 2003.

Although the Lloyd & Taylor equation does have faster response at lower and higher temperature, residual analysis shows that it might somewhat underestimate the response of ecosystem respiration at optimum soil water content, and overestimate ecosystem respiration both below and above the optimum soil water content (fig. 1(a)). There existed an obvious quadratic relationship between the residuals between measured and simulated ecosystem respiration and soil water content at Qianyanzhou, which could be well described by eq. (7). However, there was no obvious relationship between the residuals between measured and simulated ecosystem respiration and soil water content at Changbai Mountains (fig. 1(b)), that is to say, soil water content did not become an obvious influence in the ecosystem respiration.

When soil water content was also taken as a pre-

dictor in the ecosystem respiration models, the Multiplicative model (eqs. (4)–(7)) and Q_{10} model (eqs. (8) and (9)) were evaluated to describe the effects of soil water content on ecosystem respiration. Table 3 also shows that soil water content did not become an obvious influence factor in the ecosystem respiration at Changbai Mountains, but not the case at Qianyanzhou. Although both the multiplicative model and the Q_{10} model could describe the response of ecosystem respiration to temperature and soil water content, the regression models analysis revealed that ecosystem respiration was more sensitive to soil moisture than was expressed by the current multiplicative model (fig. 3(a)). The multiplicative model might lead to an overestimation of the respiration response to warming, for example July in 2003 in fig. 3(a), under the dry soil condition.

Table 3 Nonlinear regression results of ecosystem respiration with the often-used multiplicative model and Q_{10} model as a function of soil water content and temperature at the Qianyanzhou subtropical *Pinus* plantation and Changbai Mountains temperature broad-leaved Korean pine mixed forest

Model parameter	Qianyanzhou		Changbai Mountains	
	Multiplicative model	Q_{10} model	Multiplicative model	Q_{10} model
$R_{eco,ref}$ (283.16K)	0.019	0.067	0.138	0.177
a		2.016		4.741
b	18.196	0.07	0.818	0.178
c	-48.241	23.407	-0.021	3.405
T_0/d	215.376	-64.281	231.891	
R^2	0.784	0.806	0.863	0.868

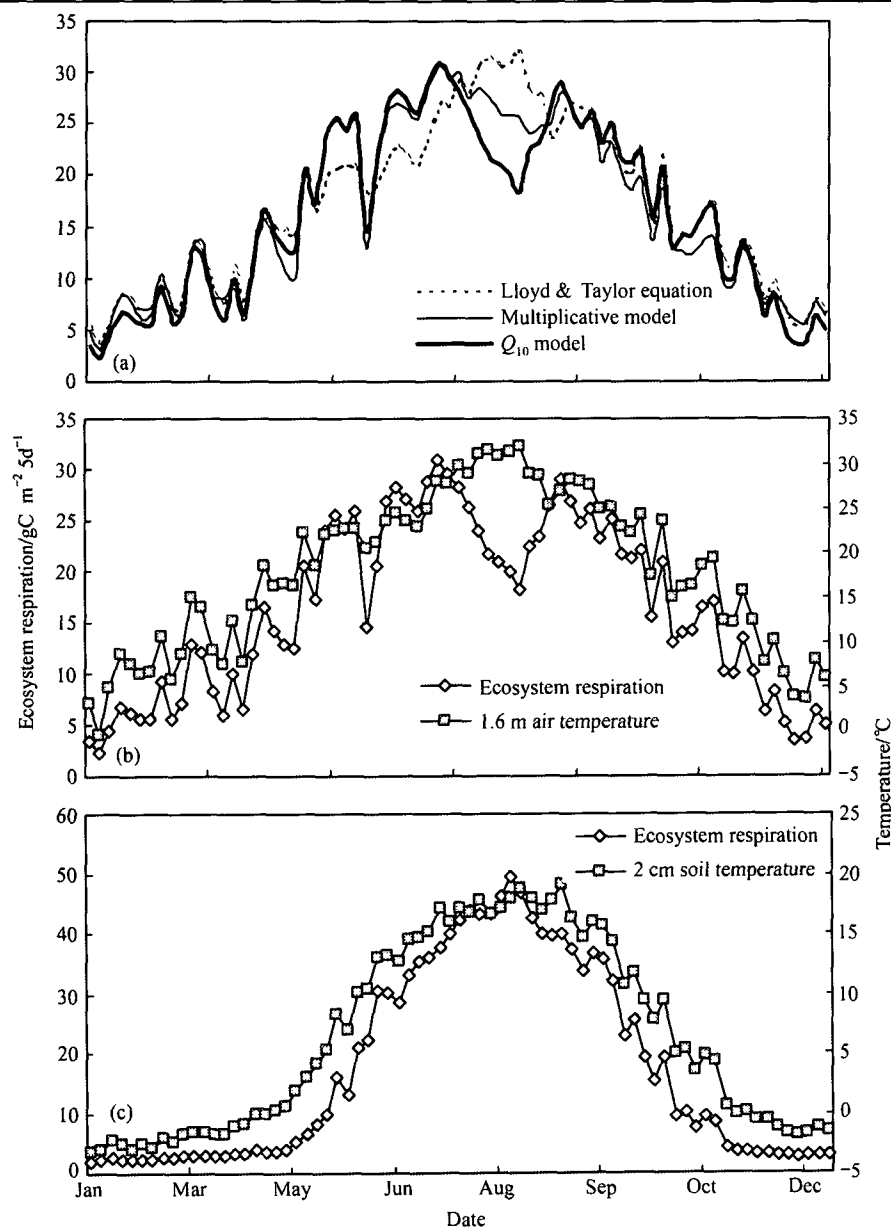


Fig. 3. Effects of soil water content on the seasonal variation of ecosystem respiration based on the Lloyd & Taylor equation, multiplicative model and Q_{10} model at Qianyanzhou subtropical *Pinus* plantation (a), and seasonal variation of ecosystem respiration estimated by the Q_{10} model and its corresponding temperature predictor at the subtropical *Pinus* plantation (Qianyanzhou, b) and temperature broad-leaved Korean pine mixed forest (Changbai Mountains, c) (in 2003).

2.3 Seasonal variation of ecosystem respiration and its annual estimate

Since temperature was found to be a dominant factor in the flux observed, it is not surprising that the seasonal variation of ecosystem respiration at Changbai Mountains was consistent with the seasonal patterns of soil temperature (fig. 3(c)), but would be of no effect at the dry soil conditions when soil water content turned into a dominant factor on ecosystem respiration (fig. 3(b)). The seasonal variation of ecosystem respiration of Qianyanzhou showed obviously different patterns compared with the seasonal variation of surface air temperature (fig. 3(b)). In this drought-stressed ecosystem (fig. 2(a)), ecosystem respiration showed a clear seasonality, with low rates during drought and in winter.

Annual ecosystem respiration derived from the often-used multiplicative model was 1209 g C m^{-2} and 1303 g C m^{-2} , and was consistently a litter higher than the Q_{10} model estimates of 1197 g C m^{-2} and 1268 g C m^{-2} for Qianyanzhou and Changbai Mountains, respectively. Compared with the annual estimates of Q_{10} model, annual ecosystem respiration derived from the Van't Hoff equation was 5.9% and 4.9% higher for Qianyanzhou and Changbai Mountains, respectively. Not considering the differences of annual ecosystem respiration, it was worthy to discern the different seasonal variation patterns derived from the different temperature equations and models. Especially while in the drought-stressed ecosystem, soil water content became a dominant influence in the ecosystem respiration (fig. 3(a)).

3 Discussion

It has long been recognized that an exponential increase in soil or ecosystem respiration with respect to temperature is commonly accepted and was observed for biological systems over a limited range of temperature^[10,11]. The response of soil or ecosystem respiration to temperature is commonly described using the Van't Hoff, Arrhenius or Lloyd & Taylor equation with different theoretical bases^[6,11,36]. Considerable debate has been focused on the role of air and soil temperature in determining the carbon balance of for-

est ecosystems and how they will control the ecosystem respiration^[12–18]. These factors, however, have been challenging to quantify because of their strong autocorrelation among the seasonal variation of air temperature and soil temperature. However, in fact the best variable should be those which best characterize the temperature of the respiration elements. Plant respiration can account for most of ecosystem respiration of Qianyanzhou subtropical *Pinus* plantation since the plantation was planted in 1985, while soil respiration by soil autotrophs and heterotrophs can account for most of ecosystem respiration of Changbai Mountains temperate broad-leaved Korean pine mixed forest because it is an about 200-year-old growth forest. Thus, air temperature should be the best variable at Qianyanzhou and soil temperature at Changbai Mountains, and our assumption was proved by the nonlinear regression results of ecosystem respiration versus air/soil temperature with different temperature equations (table 2).

A consensus exists with respect to the importance of temperature and soil water content in determining ecosystem respiration^[9]. Recently, of special interest is the confounding influences of temperature and soil moisture on the temperature sensitivity (Q_{10})^[8,33,37,38]. However, when describing temperature and moisture effects on soil or ecosystem respiration simultaneously, for example in models of global change, it has been assumed that the effects of individual factors may be multiplicative^[8,19,20], which implies that Q_{10} of ecosystem respiration is independent of soil water content. This assumption is challenged by using a modeling approach that includes the effects of soil water content on the Q_{10} . However, a quadratic dependent of Q_{10} on soil water content was suggested in our Q_{10} model. Fig. 3(a) shows that although multiplicative model and Q_{10} model could describe similar seasonal patterns of ecosystem respiration, in the drought-stressed conditions, the multiplicative model might lead to an overestimation of the respiration response to warming. Compared with the annual estimates of Q_{10} model, annual ecosystem respiration derived from the multiplicative model was about 1% and 2.7% higher at Qianyanzhou and Changbai Mountains, respectively (table 4). The discrepancies might not have explicitly

Table 4 Annual ecosystem respiration estimated by the different temperature equations, multiplicative model and Q_{10} model at the Qianyanzhou subtropical *Pinus* plantation and Changbai Mountains temperate broad-leaved Korean pine mixed forest

	Annual ecosystem respiration	
	Qianyanzhou/ $\text{g C m}^{-2} \text{ a}^{-1}$	Changbai Mountains/ $\text{g C m}^{-2} \text{ a}^{-1}$
Van't Hoff equation	1267.2	1330.2
Arrhenius equation	1268.9	1324.2
Lloyd & Taylor equation	1245.4	1287.9
Multiplicative model	1208.5	1302.5
Q_{10} model	1196.9	1267.9
Averages (standard deviation)	1237.4 ± 33.2	1302.5 ± 25.7

considered the varying sensitivity of ecosystem respiration to temperature and moisture, which may be a significant missing link in the current ecosystem models^[8,37]. Although the different regression models did not result in significant differences in the total annual ecosystem respiration, inappropriate models may introduce significant errors in the seasonal patterns of estimated fluxes. Fig. 3(b) shows large deviation on the seasonal variation of ecosystem respiration during the studied year at Qianyanzhou. This multiplicative assumption is not well tested and might lead to an overestimation of the respiration response to warming under the dry soil conditions^[8,21]. Direct and long-term measurement of canopy-scale carbon dioxide flux is needed over various ecosystems to quantify the effect of environmental and physiological forcing factors on ecosystem respiration, and experiment and field-based mechanistic understanding of interaction between terrestrial ecosystem respiration and dry and warm soil conditions need to be fully understood and modeled^[8,9,33,35,37].

Of the variance in ecosystem respiration, 78%—81% was explained with the empirical model as a function of temperature and soil water content at Qianyanzhou subtropical *Pinus* plantation, while 84%—86% was expressed at Changbai Mountains temperate broad-leaved Korean pine mixed forest. The unexplained variability may be due to several reasons. At present, the EC measurements are most trustworthy when they come from micrometeorologically ideal sites, extensive canopies on flat terrain. However, the land-surface conditions cannot fully meet the demand by the EC technique. There are lots of uncertainties in estimating the annual carbon balance of forest ecosys-

tems resulting from the transfer of carbon by non-turbulent exchange processes, which are not detected by the EC technique and more serious at night^[39,40]. By weighting the relative underestimation with the frequency distribution of the friction velocity, a relative loss of CO_2 efflux can be estimated. Even when the component of the flux due to storage is included, a relative loss of CO_2 efflux was estimated at between 4% and 36%^[29]. The threshold of friction velocity u_* (used as a measure for turbulent mixing) and CO_2 efflux during the night was determined according to the method mentioned by Blanken et al.^[31] at Qianyanzhou and Changbai Mountains, respectively. All nighttime EC data with $u_* < 0.2 \text{ m s}^{-1}$ were excluded from the analysis, as it is likely that under these conditions storage and advection can reduce gas fluxes through the boundary layer^[25,30,31]. More importantly, seasonality of biotic process influences the annual course of ecosystem respiration and changes in fine roots and microbial population following the temperature were masked^[12,15,35]. Fig. 4 shows that there existed an obviously exponential relationship between ecosystem respiration and leaf area index during the growing season at Changbai Mountains, but residual analysis showed that the exponential relationship disappeared when temperature effect was excluded by the Lloyd & Taylor equation. The apparent phenomena might result from their strong autocorrelation between temperature and leaf area index (correlation coefficient: 0.825). The residuals between measured and simulated ecosystem respiration by the Q_{10} model showed clearly seasonal variability at Changbai Mountains, which might be due to temporal changes of the fluctuating root and microbial biomass^[6]. The annual pat-

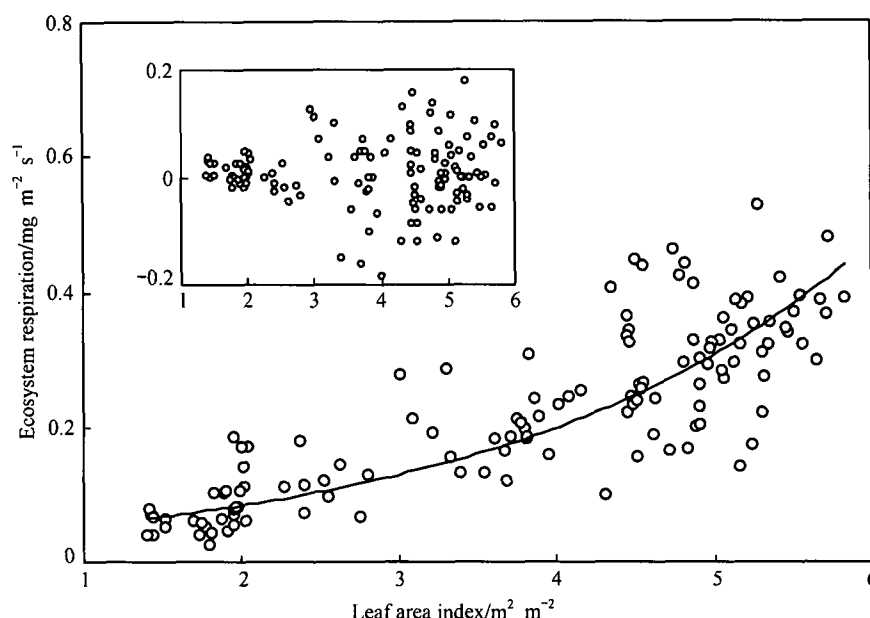


Fig. 4. The relationship between ecosystem respiration and leaf area index at Changbai Mountains temperate broad-leaved Korean pine mixed forest (April to October in 2003). The inset shows the relationship between the residuals between measured and simulated ecosystem respiration by the Lloyd & Taylor equation and leaf area index.

terms of root and microbial biomass might, therefore, be unrelated to that of temperature and soil water content, and increase the scatter in the relationship between ecosystem respiration and temperature and soil water content. Other factors that may have confounded the relation with temperature and soil water content are difference in vegetation cover, site productivity, soil acidity and texture, quality and quantity of soil organic.

Whereas there are very few flux sites between 20°–30°N, therefore no relevant finding was reported in the literature. However, having the similar temperature and precipitation conditions, estimates of annual ecosystem respiration at Qianyanzhou provided here are comparable with the results of other planted forest (table 5). The annual ecosystem respiration at Changbai Mountains was higher than the yearly ecosystem respiration reported in Law et al.^[9]. It might be

Table 5 Comparison of annual ecosystem respiration as derived from FLUXNET forests measurements^[9] with our results of Qianyanzhou subtropical *Pinus* plantation and Changbai Mountains temperate broad-leaved Korean pine mixed forest

Site Name	Location	Climate	$T_{\text{grow}}/^{\circ}\text{C}$	P/mm	Age/a	$\text{LAI}/\text{m}^2 \text{ m}^{-2}$	$R_{\text{eco}}/\text{g C m}^{-2} \text{ a}^{-1}$
Qianyanzhou, China	26°44'N, 115°03'E	Subtropical monsoon	17.9	855	20	3.6	1197
Duke, USA	36°2'N, 79°8'W	Oceanic	17.2	748	17	5.2	941
Bordeaux, France	44°05'N, 0°05'W	Temperate	17	995	30	2.8	1638
Changbai Mountains, China	42°24'N, 128°05'E	Temperature continental	14.2	496	200	5.8	1268
Willow Creek, USA	45°47'N, 90°3'W	Temperature continental	19.2	694	35–70	4.2	769
			17.1	1092			865
Park Falls, USA	45°56'N, 90°16'W	Temperature continental	15.1	525	60–80	4	1081
			18.1	706			829
Hesse, France	48°40'N, 7°05'E	Temperature continental	13.7	924	30	6	1009
Braschaat, Belgium	51°18'N, 4°31'E	Temperature continental	17.5	662	67	3	1033
			17.0	1042			1218

Site characteristics, including growing season temperature (T_{grow}), annual precipitation (P), leaf area index (LAI) and ecosystem respiration (R_{eco}).

expected that annual cumulative carbon losses from the forest floor should be larger than others because of a large amount of accumulated substrate for heterotrophic respiration. Accuracy of estimates for the seasonal variation of ecosystem respiration is needed for short-term periods of drought while the soil water content effect is crucial. Canopy-scale CO_2 flux measurement will be of benefit to understanding the factors/process controlling respiration and also has implication to improve our understanding on how net ecosystem exchange and gross ecosystem productivity respond to environmental conditions diurnally, seasonally and interannually^[21,37]. Because whole-ecosystem respiration was studied here, we emphasize the importance of effects such as varying Q_{10} at the ecosystem level. We need more information on how temperature and drought affect ecosystem respiration. These results have implications for future climate change scenarios^[8,21,37].

4 Conclusions

Ecosystem respiration of Qianyanzhou subtropical *Pinus* plantation and Changbai Mountains temperature broad-leaved Korean pine mixed forest showed clear seasonality, with a lower rate during the drought periods and in winter. At the ecosystem level, temperature was found to be a dominant factor in controlling the ecosystem respiration. The importance of soil water content in determining the ecosystem respiration was confirmed other than temperature effects. In the drought-stressed ecosystem, soil water content may overwhelm the temperature effects and become a dominant factor on ecosystem respiration.

Of the variance in ecosystem respiration, 78%—81% was explained with the empirical models as a function of temperature and soil water content at Qianyanzhou, while 84%—86% was explained at Changbai Mountains. The regression models analysis revealed that in drier soil, ecosystem respiration was more sensitive to soil moisture than was expressed by the often-used multiplicative model. It was possible for accuracy of estimates for the seasonal variation of ecosystem respiration based on the Q_{10} model.

Annual ecosystem respiration derived from the

often-used multiplicative model was 1209 g C m^{-2} and 1303 g C m^{-2} , and was consistently a little higher than the Q_{10} model estimates of 1197 g C m^{-2} and 1268 g C m^{-2} for Qianyanzhou subtropical *Pinus* plantation and Changbai Mountains temperature broad-leaved Korean pine mixed forest, respectively.

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