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Temperature Sensitivity in Individual Components of Ecosystem Respiration Increases along the Vertical Gradient of Leaf–Stem–Soil in Three Subtropical Forests

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Received: 7 December 2019; Accepted: 22 January 2020; Published: 25 January 2020

Abstract: Temperature sensitivity (Q_{10}) of ecosystem respiration (ER) is a crucial parameter for predicting the fate of CO_2 in terrestrial ecosystems under global warming. Most studies focus their attention in the variation of Q_{10} in one or two components of ER, but not in the integration or comparison among Q_{10} in major components of ER. Vertical and seasonal variations in individual components, including leaf respiration, stem respiration and soil respiration, of ER were observed synchronously along the gradient of leaf–stem–soil over a 2 year period in three forest stands dominated by masson pine, loblolly pine and oak, respectively, in a subtropical forest ecosystem of central China. We found that Q_{10} in individual components of ER increased along the vertical gradient of leaf–stem–soil. The vertical pattern of Q_{10} in individual components of ER was ascribed to variations of diurnal temperature range (DTR) and activation energy (ΔH_a). These results suggest that a vertical pattern of Q_{10} in individual components of ER along the gradient of leaf–stem–soil should be taken into consideration in process-based models that simulate respiratory carbon flux in terrestrial ecosystems.

Keywords: climate change; leaf respiration; Q_{10} ; soil respiration; stem respiration; temperature acclimation

1. Introduction

Temperature sensitivity (Q_{10}) of ecosystem respiration (ER) is a crucial parameter for linking respiratory carbon flux to global warming in terrestrial ecosystems [1]. A constant Q_{10} value of 2 for ER is often used to generate carbon dynamics in Earth system models (ESMs) [2]. Nonetheless, a mean Q_{10} value of 1.6 for ER is found based on the FLUXNET database built from a global collection of eddy covariance CO_2 flux observations [3]. Moreover, there are increasing evidences that Q_{10} of ER is not constant instead varying with change in air temperature [4], precipitation [5], atmospheric CO_2 [6] and atmospheric nitrogen deposition [7]. ER, a major flux in the global carbon cycle, drives biosynthesis, cellular maintenance and active transport in plants [8]. A GPP of 80% or more is respired by autotrophs and heterotrophs and released back into the atmosphere [9]. In addition, disturbance event, such as harvest, fire, bark beetle outbreak, windthrow, defoliation by insects, fungal attack, and droughts, strongly influences the overall Q_{10} of ER, as it alters leaf area and coarse woody debris (CWD) [10]. Thus, the inaccurate parameterization in Q_{10} of ER limits abilities of process-based models to accurately simulate the magnitude of climate–carbon feedbacks [11].

Q_{10} in individual components of ER has received increased attention [12]. For example, a systematic review on the dynamic response of leaf respiration to temperature proposes that Q_{10} of leaf respiration is associated with maximum enzyme activity and substrate availability [8]. Likewise, Q_{10} of stem respiration is linked to canopy photosynthesis and carbohydrates supply [13]. Q_{10} of soil respiration is correlated with soil moisture, soil microbe activity, soil organic carbon degradability, root maintenance and growth activities [14,15]. Although the eddy covariance technique has provided a useful tool to continuously measure ER, tower-based flux measurements do not provide direct information on component fluxes [11]. Integrative studies of Q_{10} in individual components of ER have rarely been reported. Therefore, comparison among Q_{10} in major components of ER is pivotal for reducing model uncertainties and accurately predicting carbon dynamics.

Vertical variations of abiotic and biotic factors along the gradient of leaf–stem–soil potentially lead to differences among Q_{10} in individual components of ER [16,17]. On the one hand, diurnal temperature range of air (DTR_{air}) is wider than diurnal temperature range of soil (DTR_{soil}) although mean daily temperature in air showed the similar seasonal pattern with that of soil [18,19]. It has been hypothesized that respiratory metabolism in environments with wider temperature fluctuations may exhibit an increased capacity in temperature acclimation, that may be manifest in altered Q_{10} , than those in constant environments [20]. On the other hand, substrate quality in respiratory metabolism changes from labile such as sugars to recalcitrant such as lignin along the vertical gradient of leaf–stem–soil [21,22]. It is well known that recalcitrant substrates require higher activation energy than labile substrates [23]. On the basis of fundamental principles of enzyme kinetics associated with the Arrhenius equation, the carbon-quality temperature (CQT) hypothesis predicts that the Q_{10} of respiratory metabolism should increase with increasing activation energy of a reaction [12,24]. However, there has been a lack of direct measurements of activation energy that can be used to assess differences among Q_{10} in individual components of ER.

The subtropical forest ecosystem in East Asian region exhibits high net ecosystem productivity (NEP) of $362 \pm 39 \text{ g C m}^{-2} \text{ year}^{-1}$ derived from measurements of 106 flux sites, which is higher than that of Asian tropical and temperate forests, and is also higher than that of forests at the same latitudes in Europe, Africa and North America [25]. ER, one component of NEP, is more sensitive to temperature change than gross primary productivity (GPP), the other component of NEP, based on an integration of eddy covariance observations in this area [26]. Despite the ecological importance of ER in this area, pattern of Q_{10} in individual components of ER along the vertical leaf–stem–soil gradient is unclear. To address this knowledge gap, vertical and seasonal variations in individual components, including leaf respiration, stem respiration and soil respiration, of ER were measured synchronously over a 2 year period in three forest stands dominated by masson pine, loblolly pine and oak, respectively. Specifically, we hope to explain the following research questions: (1) How different is the Q_{10} among individual

components, including leaf respiration, stem respiration and soil respiration, of ER? (2) What are the regulatory mechanisms underlying differences among Q_{10} in individual components of ER?

2. Materials and Methods

2.1. Study Site

The study was conducted in the Jigongshan National Nature Reserve (31.46° N–31.52° N, 114.01° E–114.06° E), located at the south of Henan Province in central China. The climate is subtropical monsoon climate, characterized by hot and rainy summer and mild and rainless winter. The mean annual temperature (MAT) is 15.2 °C, with mean monthly temperature ranging from 1.9 °C in January to 27.5 °C in July. The mean annual precipitation (MAP) is 1063 mm, with 45% falling in the summer and only 9% in the winter [27]. The soil is classified as Haplic Luvisols based on International Society of Soil Science classification or as yellow-brown soil based on Chinese classification. The dominant tree species consist of masson pine (*Pinus massoniana* Lamb.), loblolly pine (*Pinus taeda* Linn.) and oak (*Quercus acutissima* Carr.). Masson pine forest is dominant native species planted around 1980s with stand density of 592 trees ha⁻¹ and an average DBH of 28.5 cm measured in 2010, while loblolly pine forest is dominant introduced species planted around 1980s with stand density of 428 trees ha⁻¹ and an average DBH of 25.2 cm, and oak forest is a secondary natural forest regenerated in 1970s with stand density of 452 trees ha⁻¹ and an average DBH of 29.1 cm. Woody shrubs include *Lindera glauca* (Sieb. et Zucc.) Bl., *Vitex negundo* L., and *Symplocos chinensis* (Lour.) Druce. Understory herbaceous plants include *Lygodium japonicum* (Tunb.) Sw., *Eriophorum comosum* Nees, and *Corydalis edulis* Maxim.

2.2. Experimental Design

The field experiments were conducted in three forest stands dominated by masson pine, loblolly pine and oak, respectively, in August 2008. All three forest stands (30 × 30 m each) were fenced to minimize anthropogenic and herbivore disturbances. The distance between any two forest stands was less than 5 km, which decreased differences in climate condition and soil type. Four replicate plots (15 × 15 m each) were established in each forest stand and one tree per plot (4 trees per forest stand) was selected randomly to measure individual components of ER synchronously (Figure 1).

Figure 1. Field measurements of individual components, including leaf respiration, stem respiration and soil respiration, of ecosystem respiration (ER) in subtropical forest ecosystem of central China.

2.3. Leaf Respiration

Leaf respiration was measured using a LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA) between 9:00 to 11:00 a.m. on clear sunny day once a quarter in 2009 and 2010. Branches about 30 cm long with sun-facing leaves were excised from the middle of the crown with the help of a professional tree climber, stored immediately in a bottle with fresh water, recut under water after being placed in the bottle, and measured on the ground. Dark treatments of 20 min were performed through covering an opaque cloth on the branch samples prior to measurements.

Leaves were put into a $2 \times 3 \text{ cm}^2$ leaf cuvette sealed with plasticine to prevent leakage. Measurements of leaf respiration were taken when gas exchange had equilibrated (taken to be when the coefficient of variation for the CO_2 partial pressure differential was below 1% between the sample and reference analysers). This condition was typically achieved within 1–2 min after a stable CO_2 concentration had been reached. Leaf respiration of oak was not measured in January and December 2009 and January 2010 because oaks are deciduous. A total of 84 data points of leaf respiration were collected (i.e., 3 forest stands $\times$ 4 plots per forest stand $\times$ 8 times per plot—1 forest stand $\times$ 4 plots per forest stand $\times$ 3 times per plot = 84 data across two years). All measurements were carried out under ambient temperature and a CO_2 concentration of $400 \mu\text{mol mol}^{-1}$. LI-6400 portable photosynthesis system was zeroed using H_2O and CO_2 free air before the respiration measurements. Leaf area enclosed in the cuvette was measured with a LI-3100 area meter (LI-COR Inc., USA). Leaf temperature was measured simultaneously using a thermocouple built in the leaf cuvette. The temperature range of leaf respiration measurements during each sampling period was an average value of 1.75°C .

2.4. Stem Respiration

Stem respiration was measured with a horizontally oriented chamber technique between 9:00 to 11:00 a.m. on clear sunny day once a quarter in 2009 and 2010. Briefly, a custom-built polyvinyl chloride (PVC) collar (inside diameter of 10 cm) was attached to the stem at a height of 1.3 m to permit connection between the stem and a LI-6400-09 CO_2 efflux chamber (LI-COR Inc., USA). One end of the PVC collar was cut to match the approximate stem curvature, and the other end was cut to match the LI-6400-09 CO_2 efflux chamber. LI-6400-09 CO_2 efflux chamber connected to a LI-6400 portable photosynthesis system for data collection and storage. A test of gas leakage was conducted prior to measurement and the LI-6400-09 CO_2 efflux chamber was held in place with bungee cords during the measurement.

A total of 96 data points of stem respiration were collected (i.e., 3 forest stands $\times$ 4 plots per forest stand $\times$ 8 times per plot = 96 data across two years). Stem temperature at a depth of 0–3 cm was measured simultaneously using a probe with a temperature sensor connected to LI-6400 portable photosynthesis system. A depth of 0–3 cm was the appropriate measuring depth of stem temperature for evaluating the Q_{10} of stem respiration because nearly no hysteresis occurs between stem respiration and temperature at this depth according to work by Yang et al. (2012) [27]. The temperature range of stem respiration measurements during each sampling period was an average value of 1.42°C .

2.5. Soil Respiration

Soil respiration was measured with an LI-6400-09 CO_2 efflux chamber between 9:00 to 11:00 a.m. on clear sunny day once a quarter in 2009 and 2010. A PVC collar with 10 cm in diameter and 3 cm in height was inserted 2 cm into the soil in each stand at random locations. The distance between collars and trees was more than 1 m. Plants inside the soil rings were removed at monthly intervals. A total of 96 data points of soil respiration were collected (i.e., 3 forest stands $\times$ 4 plots per forest stand $\times$ 8 times per plot = 96 data across two years). Soil temperature at a depth of 0–5 cm was measured simultaneously using a probe with a temperature sensor connected to LI-6400 portable photosynthesis system. A depth of 0–5 cm was the appropriate measuring depth of soil temperature for evaluating the Q_{10} of soil respiration because nearly no hysteresis occurs between soil respiration

and temperature at this depth according to work by Li et al. (2019) [28]. The temperature range of soil respiration measurements during each sampling period was an average value of 0.98 °C. Volumetric soil moisture at the depth of 0–10 cm was measured using TDR 2000 portable soil moisture probe (Spectrum Technologies Inc., Plainfield, IL, USA) when each soil respiration measurement was taken. The quarterly measurements covered the annual variation in temperature range from 4.86 to 32.50 °C for leaf and 1.51 to 27.04 °C for soil.

2.6. Leaf, Stem and Soil Characteristics

Leaf, stem and soil characteristics were measured in the middle of the growing seasons (late July to early August) in 2010. A total of 4 replicate individuals were measured in each forest stand. Typical A_n/C_i curves (light-saturated net CO_2 assimilation rate versus intercellular CO_2 concentrations) were measured at leaf temperature of 25 °C and photosynthetic photon flux density of $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$. The CO_2 concentrations were initially set to range from 400 to 50 $\mu\text{mol mol}^{-1}$ and then to range from 400 to 1200 $\mu\text{mol mol}^{-1}$ with a total of 9 points (400, 200, 100, 50, 400, 600, 800, 1000, 1200 $\mu\text{mol mol}^{-1}$). V_{cmax} (the maximum rate of Rubisco carboxylation) and J_{max} (the maximum rate of photosynthetic electron transport) were estimated by fitting the A_n/C_i curves using a spreadsheet-based software developed by Sharkey et al. (2007) [29]. A_n was obtained based on the A_n/C_i curves at CO_2 concentration of 400 $\mu\text{mol mol}^{-1}$.

Leaves were removed from branches after gas exchange measurements, and then the area was measured with a LI-3100 area meter (LI-COR Inc., USA). Leaf samples were dried at 65 °C for 48 h, and leaf carbon concentration (C) and leaf nitrogen concentration (N) were measured with a CN analyser (CE Inc., Hamburg, Germany). The leaf C/N ratio was calculated based on leaf C and leaf N, and specific leaf area (SLA) was calculated based on the leaf area and dry biomass.

A diameter at breast height (DBH) was measured with a specially calibrated diameter tape that displays the diameter measurement when wrapped around the circumference of a tree. Stand density was estimated by counting the number of trees in each plot. Stand age was measured by counting the annual rings of wood growth after extracting an increment core from the sample trees. Leaf area index (LAI) of each plot was determined at 1.5 m above the ground using LAI-2000 plant canopy analyzer (LI-COR Inc., USA).

Soil samples were collected by taking three soil cores with a 7 cm diameter at a depth of 0–10 cm in each plot. Three soil cores from each plot were mixed in situ to form one composite sample. After removal of roots and gentle homogenization, the moist soil was sieved through 2 mm mesh and was air dried. Then the dry samples were ground to powder for measuring soil C and soil N with a CN analyzer. Soil pH was measured with an Accumet Excel XL60 pH meter (Fisher Scientific, Hampton, NH, USA) at a soil to water ratio of 1:2.5.

2.7. Ecosystem Respiration

Ground-based leaf respiration was a product of LAI multiplied by measured leaf respiration. Ground-based stem respiration was estimated with stem surface area and measured stem respiration similar to study of Tang et al. (2008) [11]. Specifically, stem and branch biomass were functions of DBH:

$$M = a\text{DBH}^b$$

where M is the oven-dry weight of the biomass component of a tree (kg), DBH is the diameter at breast height (cm), and a and b are parameters. Table 1 reports the parameters in allometric biomass equation for the three tree species. Biomass was converted to volume based on wood mass density with 0.40 g cm^{-3} for masson pine and loblolly pine, and 0.63 g cm^{-3} for oak, which assumes no heartwood in the young trees.

Table 1. Parameters in allometric biomass equation for the three tree species.

Species	Stem		Branch		References
	a	b	a	b	
Masson pine	0.1730	2.1540	0.0630	2.5690	Xiang et al. 2016 [30]
Loblolly pine	0.0725	2.5074	0.0016	3.0786	Gonzalez-Benecke et al. 2018 [31]
Oak	0.2486	2.1350	0.0112	2.7353	Ozdemir et al. 2019 [32]

2.8. Air Temperature, Soil Temperature and Soil Moisture

Air temperature at the height of 1.5 m, soil temperature at the depth of 5 cm, and volumetric soil moisture at a depth of 0–10 cm were monitored at 30 min intervals using an EM50 datalogger (Decagon Devices Inc., Pullman, WA, USA) in masson pine stand during the entire year in 2009 and 2010.

2.9. Data Analysis

The temperature dependence in individual components of ER was assessed by an exponential model [33]:

$$R = R_5 Q_{10}^{\left(\frac{T-5}{10}\right)}$$

where R is the individual components, such as leaf respiration, stem respiration and soil respiration, of ER ($\mu\text{mol m}^{-2} \text{s}^{-1}$); T is the measurement temperature ($^{\circ}\text{C}$) in individual components of ER; R_5 is the estimated base respiration based on surface area ($\mu\text{mol m}^{-2} \text{s}^{-1}$) at the reference temperature of 5°C ; Q_{10} is a constant fitted by the least-square technique and describes the proportional increase in rate with a 10°C increase in temperature. A total of 36 temperature response curves were taken and analyzed (i.e., 3 forest stands $\times$ 3 components per forest stand $\times$ 4 plots per component = 36 curves across two years).

The activation energy in individual components of ER was calculated by fitting the temperature response curves using the equation [34]:

$$R = e^{\left(c - \frac{\Delta H_a}{R_g T_k}\right)}$$

where c is a scaling constant; ΔH_a is the activation energy (kJ mol^{-1}); R_g is the molar gas constant ($8.314 \text{ J mol}^{-1} \text{ K}^{-1}$); T_k is the absolute measurement temperature (K).

Kolmogorov-Smirnov and Levene's tests were used to test the normality and homogeneity of variances, respectively. One-way ANOVA was used to evaluate the differences among the three stands in leaf traits, leaf photosynthesis, stem characteristics and soil properties. If the difference was significant, then post-hoc multiple comparisons were conducted using the least significant difference tests. Repeated Measures ANOVA (RMANOVA) were performed to examine the main and interactive effects of the vertical position and forest stand on individual components of ER. Between-subject effects were evaluated as vertical position and forest stand; within-subject effects were sample date. The missing data for oak leaves was interpolated by the existing measurements and an exponential model. Two-way ANOVAs were used to analyze the main and interactive effects of the vertical position and forest stand on Q_{10} , ΔH_a and R_5 in individual components of ER. All statistical analyses were conducted using SPSS Version 17.0 (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Leaf, Stem and Soil Characteristics of the Three Forest Stands

The masson pine forest has the highest leaf A_n ($p = 0.017$), stand density ($p < 0.001$) and soil C/N ($p = 0.001$) among the three forest stands, while the loblolly pine forest has the highest leaf J_{max}

($p = 0.002$), soil C ($p < 0.001$) and soil N ($p < 0.001$), and the oak forest has the highest SLA ($p < 0.001$) and leaf N ($p < 0.001$) (Figure 2).

Figure 2. Leaf (blue, (a,b,e,f,i,j,m,n)), stem (grey, (c,g,k,o)) and soil (red, (d,h,l,p)) characteristics for masson pine, loblolly pine and oak forests in subtropical forest ecosystem of central China. SLA ($\text{cm}^2 \text{g}^{-1}$), specific leaf area; leaf C concentration (%), leaf carbon concentration; leaf N concentration (%), leaf nitrogen concentration; A_n ($\mu\text{mol m}^{-2} \text{s}^{-1}$), light-saturated net CO_2 assimilation rate; V_{cmax} ($\mu\text{mol m}^{-2} \text{s}^{-1}$), maximum rate of Rubisco carboxylation; J_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$), maximum rate of photosynthetic electron transport; DBH (cm), diameter at breast height; LAI, leaf area index; soil C concentration (%), soil carbon concentration; soil N concentration (%), soil nitrogen concentration. Values are means $\pm$ SE ($n = 4$). Different lowercases represent significant differences among forest stands ($p < 0.05$).

3.2. Vertical and Seasonal Variations in Individual Components of ER

The effects of the vertical position and sample date were significant for individual components of ER (both $p < 0.001$), while individual components of ER did not differ among forest stands ($p = 0.091$) (Table 2). The individual components of ER exhibited apparent vertical gradients, showing lowest mean values across forest stands and sampling dates in leaf respiration ($1.02 \pm 0.07 \mu\text{mol m}^{-2} \text{s}^{-1}$), intermediate in stem respiration ($1.04 \pm 0.09 \mu\text{mol m}^{-2} \text{s}^{-1}$) and highest in soil respiration ($1.66 \pm 0.12 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Figure 3a–c). The seasonal dynamics in individual components of ER exhibited bell-shaped curves, showing lowest mean values in early January (winter) and highest in late July (summer) (Figure 3a–c).

Table 2. Effects of the vertical position, forest stand, sampling date and their interactions on individual components of ecosystem respiration (ER) by repeated measures ANOVA analysis.

	d.f.	F	P
Vertical position	2	13.03	<0.001
Forest stand	2	2.62	0.091
Vertical position × Forest stand	4	3.62	0.017
Sampling date	7	178.81	<0.001
Sampling date × Vertical position	14	17.40	<0.001
Sampling date × Forest stand	14	3.36	<0.001
Sampling date × Vertical position × Forest stand	28	3.64	<0.001

Figure 3. Seasonal variations (top panels), temperature dependence (middle panels), and soil moisture dependence (bottom panels) in individual components, including leaf respiration (blue), stem respiration (grey) and soil respiration (red), of ecosystem respiration (ER) for masson pine (a,d,g), loblolly pine (b,e,h) and oak (c,f,i) forests over a 2 year period. Values are means ± SE (*n* = 4). Leaf respiration of oak forest was not measured in January and December 2009 and January 2010 because oaks are deciduous.

3.3. Temperature Dependence and Soil Moisture Dependence in Individual Components of ER

The individual components of ER exhibited close exponential relationships with individual measurement temperatures, which explained 29–80% of the seasonal variation in individual components

of ER (Figure 3d,e,f). Soil moisture dependence explained just 1–19% of the seasonal variation in individual components of ER (Figure 3g,h,i). The effects of the vertical position were significant for Q_{10} in individual components of ER ($p < 0.001$), while Q_{10} in individual components of ER did not differ among forest stands ($p = 0.230$) (Table 3 and Figure 4a–c). ΔH_a in individual components of ER showed a similar pattern with Q_{10} (Table 3 and Figure 4d–f). R_5 in individual components of ER exhibited an interactive effect of the vertical position and forest stands ($p = 0.024$) (Table 3 and Figure 4g,h,i).

Table 3. Effects of the vertical position, forest stand and their interactions on temperature sensitivity (Q_{10}), activation energy (ΔH_a), and base respiration (R_5) in individual components of ecosystem respiration (ER) by two-way ANOVA analysis.

	Q_{10}			ΔH_a			R_5		
	d.f.	F	p	d.f.	F	p	d.f.	F	p
Vertical position	2	12.29	<0.001	2	14.23	<0.001	2	2.38	0.112
Forest stand	2	1.55	0.230	2	1.13	0.338	2	1.20	0.316
Vertical position×Forest stand	4	2.57	0.060	4	2.36	0.079	4	3.34	0.024

Figure 4. Temperature sensitivity (Q_{10} , a–c), activation energy (ΔH_a , d–f), and base respiration (R_5 , g–i) in individual components, including leaf respiration (blue), stem respiration (grey) and soil respiration (red), of ecosystem respiration (ER) for masson pine (left panels), loblolly pine (middle panels) and oak (right panels) forests. Values are means $\pm$ SE ($n = 4$).

3.4. Overall ER per Ground Area from Specific Components during the Temperatures Peak

Total ecosystem respiration averaged $11.20 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the masson pine stand, $12.45 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the loblolly pine stand, and $7.41 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the oak stand during the growing season when temperatures peak (Table 4). Maximum of ecosystem respiration was estimated as $10.36 \mu\text{mol}$

$\text{m}^{-2} \text{s}^{-1}$ from the three stands when temperatures peak in a subtropical forest ecosystem of central China (Table 4).

Table 4. Ecosystem respiration, ground-based component respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and percentage (%) in three stands during the growing season when temperatures peak.

Respiration	Masson Pine		Loblolly Pine		Oak		Average
	2009	2010	2009	2010	2009	2010	
Leaf respiration	6.03 (55%)	6.86 (60%)	6.58 (60%)	9.17 (66%)	3.03 (44%)	2.91 (37%)	5.76 (54%)
Stem respiration	2.18 (20%)	2.01 (17%)	0.66 (6%)	0.84 (6%)	0.89 (13%)	1.09 (14%)	1.28 (13%)
Soil respiration	2.71 (25%)	2.62 (23%)	3.80 (34%)	3.86 (28%)	3.04 (44%)	3.86 (49%)	3.32 (34%)
Ecosystem respiration	10.92 (100%)	11.49 (100%)	11.04 (100%)	13.87 (100%)	6.96 (100%)	7.86 (100%)	10.36 (100%)

3.5. Vertical and Seasonal Variations of Temperature

The diurnal temperature range of air (DTR_{air}) was significantly greater than the diurnal temperature range of soil (DTR_{soil}) ($p < 0.001$), although the mean daily temperature in air showed the similar seasonal pattern with that in soil (Figure 5).

Figure 5. Daily maximum temperature, daily minimum temperature in air (blue) and soil (red) (a), diurnal temperature range (DTR) in air (DTR_{air}) and soil (DTR_{soil}) (b), and soil moisture (c) over a 2 year period in subtropical forest ecosystem of central China. DTR is the difference between maximum and minimum temperature within one calendar day. The arrows mark the timing of field campaigns when the measurements of respiration were initiated.

4. Discussion

4.1. Q_{10} in Individual Components of ER Increased along the vertical gradient of Leaf–stem–soil

Our study reported that Q_{10} in individual components of ER increased along the vertical leaf–stem–soil gradient in subtropical ecosystem of central China (Figure 4). In other words, soil respiration was more sensitive to temperature change than leaf respiration. Higher Q_{10} values in soil respiration while lower Q_{10} values in leaf respiration have been observed in other studies [35,36]. For example, Q_{10} of soil respiration range of 2.6–3.3 has been found in a meta-analysis based on 818 studies constituting 3379 records at global scale [36]. A study based on a multichannel automated measurement system shows Q_{10} of 2.81 for soil respiration in subtropical evergreen forest ecosystems [26]. However, Q_{10} of leaf respiration range of 2.1–2.6 has been observed in a synthesis of published results consisting of 238 data points in 56 plant species [35]. It has been proposed that even a small shift in Q_{10} of ER may cause a great change in CO_2 efflux [37,38]. Therefore, our observations suggest that differences among Q_{10} in individual components of ER should be taken into consideration in process-based models that simulate respiratory carbon flux in terrestrial ecosystems.

4.2. Mechanisms Underlying Differences among Q_{10} in Individual Components of ER

Vertical pattern of Q_{10} in individual components of ER along the gradient of leaf–stem–soil may be ascribed to different degree of temperature acclimation induced by temperature fluctuations in individual components. In current study, DTR_{air} was found to be significantly wider than DTR_{soil} , although mean daily temperature in air showed the similar seasonal pattern with that in soil (Figure 5). Wider temperature fluctuations may result in greater degree in temperature acclimation of respiratory metabolism compared with constant environments [39]. According to the mechanisms underlying temperature acclimation of respiration proposed by Atkin and Tjoelker (2003) [8], the degree in temperature acclimation of respiration is manifest primarily through the magnitude in reduction of Q_{10} . In addition, higher degrees in temperature acclimation of leaf respiration but lower degrees in temperature acclimation of soil respiration have been reported in previous studies [40,41]. For instance, temperature acclimation of leaf respiration is remarkably uniform across biomes and plant functional types based on a comprehensive database of 231 species spanning seven biomes [41]. Nonetheless, there is limited evidence for temperature acclimation of soil respiration based on a global synthesis of 27 experimental warming studies spanning nine biomes [40]. Thus, the determining role of vertical variations of DTR observed here, together with mechanisms underlying temperature acclimation of respiration, jointly indicates the importance of temperature fluctuations in governing the vertical pattern of Q_{10} in individual components of ER.

Variations of ΔH_a in individual components of ER also contribute to vertical pattern of Q_{10} in individual components of ER along the gradient of leaf–stem–soil. Activation energy, reflecting the energy required to initiate a reaction, is associated with substrate quality in respiratory metabolism [23]. The breakdown of more recalcitrant substrates—that is, those that require higher activation energy—generally should be more sensitive to changes in temperature than the decomposition of more labile substrates [42]. It is well known that substrate quality in respiratory metabolism changes from labile such as sugars to recalcitrant such as lignin along the vertical leaf–stem–soil gradient [21,22]. In the current study, the ΔH_a in individual components of ER was found to increase along the vertical leaf–stem–soil gradient (Figure 4). Moreover, higher ΔH_a values in soil respiration while lower ΔH_a values in leaf respiration have been observed in other studies [43,44]. For instance, a global dataset on the distribution of organic carbon shows up to 154 kJ mol^{-1} of activation energy for soil respiration [44]. However, activation energy of leaf respiration with a range of just $70\text{--}105 \text{ kJ mol}^{-1}$ has been observed in a study of *Eucalyptus grandis* in a differing nitrogen supply [43]. Therefore, vertical patterns of Q_{10} in individual components of ER along the gradient of leaf–stem–soil may be ascribed to variations of ΔH_a induced by substrate quality in individual components.

4.3. Uncertainty Analysis

There were three issues worthy of note. First, the air temperature was measured under the canopy at the height of 1.5 m above the ground, because the installment of the air temperature sensor is difficult within the canopy. Our study ignored the difference between air temperature and leaf temperature. Second, only one soil temperature sensor was used in masson pine stand. Our study ignored the spatial variability in climate condition within plots and among stand types. Third, because of the lack of respiratory temperature response curves within the quarterly measurements, this study could not evaluate the seasonal dynamics of Q_{10} or ΔH_a . Therefore, our conclusions should be treated with some caution and need to be confirmed by future experiments.

Our comparison between chamber and eddy covariance measurements of respiration showed larger Q_{10} in individual components of ER than overall Q_{10} of ER (Table 5). The lower Q_{10} of ER from eddy covariance measurements is probably due to underestimation of nocturnal respiration when turbulence is weak and drainage is significant [11]. Eddy covariance methods need to be complemented and compared to component fluxes when studying forest carbon dynamics from stand to regional scale.

Table 5. Q_{10} values of ecosystem respiration from eddy covariance measurements in subtropical forests in the literature.

Site	Longitude	Latitude	Q_{10}	Forest Type	References
Dinghushan	112°34' E	23°10' N	1.25	Evergreen broad-leave forest	Cui et al. 2018 [45]
Qianyanzhou	115°03' E	26°44' N	1.26	Evergreen coniferous forest	Cui et al. 2018 [45]
Qianyanzhou	115°03' E	26°44' N	1.54	Evergreen coniferous forest	Wen et al. 2006 [46]
Qianyanzhou	115°03' E	26°44' N	1.57	Evergreen coniferous forest	Yu et al. 2004 [47]

5. Conclusions

Taken together, our study found that Q_{10} in individual components of ER increased along the vertical leaf–stem–soil gradient based on synchronous observation of leaf respiration, stem respiration and soil respiration in three forest stands over a 2 year period in the subtropical forest ecosystem of central China. The vertical pattern of Q_{10} in individual components of ER may be ascribed to different degree of temperature acclimation induced by temperature fluctuations, or to variations of ΔH_a induced by substrate quality. The finding of a vertical pattern of Q_{10} in individual components of ER along the gradient of leaf–stem–soil suggests that warmer climate will enhance the magnitude of respiratory carbon efflux from soil relative to that from canopy.

Author Contributions: Y.C., Q.Y., L.Z. and M.X. conceived and designed the research. Y.C., Q.Y. and R.S. collected and processed the data. Y.C., L.Z., Z.Z. (Zhaoyang Zhang), Z.Z. (Zhenzhen Zhang), C.W., X.L. and J.J. analyzed the data. Y.C., Q.Y., L.Z., R.S. and S.Z. wrote the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by National Key Research and Development Program of China (2017YFB0504000 and 2016YFB0501501), National Natural Science Foundation of China (41871084, 41671046 and 31400393), Zhejiang Provincial Natural Science Foundation of China (LY19C030004), and a grant from State Key Laboratory of Resources and Environmental Information System.

Conflicts of Interest: The authors declare no conflict of interest.

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