Soil respiration of a Moso bamboo forest significantly affected by gross ecosystem productivity and leaf area index in an extreme drought event (#27113)

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Soil respiration of a Moso bamboo forest significantly affected by gross ecosystem productivity and leaf area index in an extreme drought event

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We analyzed the dynamics of soil respiration (Rs) and its relation to environmental factors in a Moso bamboo forest (Phllostachys heterocycla cv. pubescens). Annual average Rs was 44.07 tCO2·ha-1·a-1. Rs was significantly correlated with soil temperature ($P < 0.01$), which explained 69.7% of the variation of Rs. Soil moisture was correlated significantly with Rs outside of the winter on a daily scale indicating it affected Rs. A model including both soil temperature and soil moisture explained 93.6% of seasonal variations for Rs. The relationship between Rs and soil temperature during a day showed a clear hysteresis. Rs was in significant and positively ($P < 0.01$) related to gross ecosystem productivity and leaf area index during our study, illustrating the significance of biotic factors as crucial drivers of Rs.

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Abstract

We analyzed the dynamics of soil respiration (R_s) and its relation to environmental factors in a Moso bamboo forest (*Phllostachys heterocycla cv. pubescens*). Annual average R_s was 44.07 $tCO_2 \cdot ha^{-1} \cdot a^{-1}$. R_s was significantly correlated with soil temperature ($P < 0.01$), which explained 69.7% of the variation of R_s. Soil moisture was correlated significantly with R_s outside of the winter on a daily scale indicating it affected R_s. A model including both soil temperature and soil moisture explained 93.6% of seasonal variations for R_s. The relationship between R_s and soil temperature during a day showed a clear hysteresis. R_s was in significant and positively ($P < 0.01$) related to gross ecosystem productivity and leaf area index during our study, illustrating the significance of biotic factors as crucial drivers of R_s.

Keywords: Soil respiration; Moso bamboo forest; environmental determiners; gross ecosystem productivity; leaf area index

Introduction

Soils are important sources and sinks in the global carbon budget (*Sheng et al., 2010*). Soil respiration (R_s) presents a major source of CO_2 emissions from terrestrial ecosystem, as the second largest carbon flux between the atmosphere and ecosystems it is surpassed only by gross primary production (*Raich and Schlesinger, 1992*). Soils release approximately 68 ± 4 Pg C per year globally, nearly 10 times of the amount of CO_2 released annually by the combustion of fossil fuels (*Raich and Potter ,1995*). Hence, slight variations in R_s may cause profound changes in the atmospheric concentration of CO_2, the accumulation of soil carbon (*Schlesinger & Andrews, 2000*), and subsequently affect global climate.

Considering the importance of forest ecosystem in the terrestrial carbon cycle and their response to global climate, numerous studies have been conducted to explore R_s and its dependence on environmental drivers. For instance, the temperature and moisture of soils are two of the major environmental drivers regulating R_s (*Liu et al., 2016*). Additionally, disturbances (as e.g. fire, *Muñoz-Rojas et al., 2016*; *Köster et al., 2014*), harvesting (*Bahn et al., 2008*), artificial warming and precipitation changes (*Li et al., 2017a*) or land use changes *(Liu et al., 2011; Willaarts et al., 2016*) can also have large effects on R_s. R_s is a complex biogeochemical process highly related to ecosystem productivity, leaf area index and soil fertility (*Hibbard et al., 2005*). Recently, research has reported R_s to be also influenced by the amount of litter (*Oishi et al., 2013*; *Wu et al., 2017*), vegetation type, latitude (*Mahecha et al., 2010*; *Wang et al., 2011*), and composition of the soil microbial community (*Luo et al., 2016*). Furthermore, some biological factors (e.g. leaf area index and ecosystem productivity) are closely related to R_s, suggesting coupling between CO_2 assimilation by the vegetation and emissions from the soil (*Bahn et al., 2008*; *Hibbard et al., 2005*). However, many of the environmental drivers are correlated with each other and it is difficult to distinguish and quantity the contribution of each environmental factor.

Bamboo forests are widely distributed in warm temperate, subtropical and tropical zones between 46°N-47°S of the world (*McDowell et al., 2015*). Globally, bamboo forests cover 31.5 million ha (*FAO, 2010*). In the context of sustainable development, bamboo plays a significant role in substituting wood as well as in the terrestrial carbon cycle (*Song et al., 2011*). Well known as bamboo kingdom, China has 6.16 million ha bamboo forest, accounting for 2.97% of total forest area in China (*SFAPRC, 2015*). Appreciated for its rapid growth and high timber production (*Guan et al., 2017*), Moso bamboo (*Phllostachys heterocycla cv. pubescens*) forest is a major vegetation type of subtropical forests in subtropical China (*Song et al., 2013*). Currently, the area covered by Moso bamboo forest increases annually by about 3%, since it provides many benefits (including high income generation and other ecosystem services) to the forest owners.

Notably, Moso bamboo has high rates of carbon accumulation, sequestering 4.91 - 5.45 tC ha^{-1} each year (*Zhou and Jiang, 2004*), showing great potential for alleviating global warming by carbon fixation. Previous studies of Moso bamboo have concentrated on carbon storage, balance and its distribution in the ecosystem (*Li et al., 2013*), as well as on the productivity of bamboo forest (*Cheng et al., 2015*; *Isagi et al., 1997*), variation of soil organic carbon stocks (*Guan et al., 2015*). Previous studies reported a close relationship between R_s and biotic factors in other forest types (*Hibbard et al., 2005*) suggesting a coupling between forest canopy assimilation and carbon emissions from soil. However, comparatively little is known about bamboo forests. Thus, it is imperative to explore the relationship between biotic, abiotic factors and R_s in Moso bamboo forest. Also, it is necessary to explore the driving forces behind soil respiration in the forest.

In this study, we used soil respiration measurements from a Moso bamboo stand and combined these with measurements of abiotic as well as biotic factors. Our aims were to explore the temporal dynamics of soil respiration, and to identify the relative importance of biotic and abiotic factors.

Materials and Methods

Study site

A Moso bamboo stand, with a flux tower observation, was selected as study site at Anji County (30°28′34.5″N, 119°40′25.7″E, and elevation 380 m, Figure S1), located in northwestern of Zhejiang Province, southeast China. As the subtropical monsoon climate, according to Trewartha climate classification, the average annual air temperature and precipitation was 15.6°C and 1413.2 mm, respectively, according to meteorological measurements for 1981-2010 from weather stations of Anji. Effective accumulated temperature above 10°C is 4934.1°C. There are on average hours 2021 h of sunshine annually. Monthly average rainfall and air temperature in the study period were shown in Figure 1. The soil type of this area is yellow red soil (Chinese system of soil classification), equivalent to Hapludult in USDA Soil Taxonomy (*Soil Survey Staff of USDA, 1999*), with a pH ranging from 4.4 to 4.8 and a soil bulk density of 1.5 g·cm^{-3} (*Chen, 2016*).

The area of Moso bamboo forest was approximately 1687 hectares and 1km around the flux tower, it accounted for 86.1% (*Xu et al., 2013*) of the area, with stand density of 3235 culms per hectare. The average canopy height and diameter at breast height were 11 m and 9.3 cm, respectively. There was only a sparse understory in the stand. The main management activities were harvesting 6 or 7-year old bamboos, and a proportion of new bamboo shoots each year. No fertilization nor weeding were done in the forest. Further detailed information of the site can be found in Mao et al. (*2017*) . Moso bamboo has a biannual growth pattern. During “off years” (which are the even in our site) few new bamboo shoots are produced, there is leaf senescence of old leaves and vigorous growth of new leaves (*Qiu, 1984*). In “on years” which are uneven years more new bamboo shoots are produced and leaf senescence is limited.

Experimental design and measurement

Soil CO_2 flux measurement

The soil CO_2 flux was measured using the LI-8150 (LI-COR Inc., Lincoln, NE, USA) multiplexer automatic soil carbon flux measurement system, from January to December in

2013. Four 20 m ×20 m plots were established around the flux tower within the forest. Four sampling polyvinyl chloride (PVC) soil collars (20 cm inside diameter, 10 cm height, and 5 cm plugged in the soil from the ground surface) were randomly placed within each plot. All collars remained permanently in place throughout the study period. To reduce the disturbance-induced carbon dioxide emission, the first measurement started 24 h after insertion. Green plants growing inside every soil collar were cut off carefully using scissors. The data and the functioning of the equipment were checked regularly to ensure the experiment stability throughout the year. Soil water content (SWC, $m^3 \cdot m^{-3}$) and soil temperature (T_s, °C) were monitored simultaneously adjacent to each collar at 5 cm depth of the soil, with 2 theta probes (ML2x, Delta-T Inc., UK; Omega Inc., USA) provided with the system. Soil respiration measurements were done at 2-hourly intervals on selected sunny days (about two weeks) in every mid-month of 2013. We defined March through May as spring, June through August as summer, September through November as autumn, January, February and December as winter.

Measurements of environmental variables at the eddy covariance site

Provided with meteorological measurements, T_s and SWC were monitored by soil temperature sensors (109SS, Campbell, USA) and soil moisture sensors (CS616, Campbell, USA), at 5 cm, 50 cm and 100 cm depths, respectively. Air temperature and relative humidity were measured using HMP45C probes (Vaisala, Helsinki, Finland) at seven heights (1 m, 7 m, 11 m, 17 m, 23 m, 30 m, 38 m) above the ground. Ground-surface temperature was obtained using a SI-111 infrared temperature sensor (Apogee, USA). All the data were recorded by a data logger (CR1000, Campbell Inc., USA) and saved as 30-min averages.

Biological factors measurement

The biological factors we considered were gross ecosystem productivity (GEP) and leaf area index (LAI). GEP was obtained by eddy co-variance (EC) technique. LAI was measured using digital camera provided with a fish-eye lens then in combination with MODIS LAI following the methods of Li et al. (*2017b*). LAI is reported as the average of three sample points were chosen within the 20 m ×20 m plot on non-rainy days. The LAI data was reported as mean values ±SD (standard deviation). For EC technique, an open-path infrared gas analyzer LI-7500 (Li-Cor Inc., Lincoln, NE, USA), in conjunction with a 3-dimensional sonic anemometer CSAT3 (Campbell Scientific Inc., Logan, UT, USA) was placed at 38 m above the ground. All the raw flux data were sampled at 10 Hz, calculated and recorded by a CR1000 data logger (Campbell Inc., USA) as 30-min average values. Whilst daily carbon fluxes (net ecosystem exchange, NEE, ecosystem respiration, RE and gross ecosystem productivity, GEP) were estimated as described by Xu et al. (*2016*).

Data analysis

We analyzed the soil respiration as a function of soil temperature assuming an exponential Q_{10} type relationship.

$$R_s = ae^{bt} \qquad (1)$$

$$Q_{10} = e^{10b} \qquad (2)$$

Where R_s (μmol·m^{-2}·s^{-1}) is soil respiration, T is soil temperate at 5 cm depth, a and b are parameters, Eq.1 (*van't Hoff, 1884*). Whilst the temperature sensitivity parameter, Q_{10}, was calculated by Eq.2 (*Sheng et al., 2010*; *Song et al., 2013*).

One-way analysis of variance (ANOVA) were carried out to test the statistical significance of differences in soil respiration, environmental and biotic factors (Table 2) between seasons. Regression analysis was performed to analyze the relationship between soil respiration, biotic and abiotic variables. All analyses were conducted using the PASW Statistics 18.0 software.

Results

Seasonal dynamics of environmental and biotic factors in Moso bamboo forest

As can be seen from Figure 1, 2013 was drier and warmer than the long-term average, with average air temperature 1.2 °C higher and total precipitation 114.5 mm lower than the long-term average. Especially in July and August, T_a (30.7 and 30.3 °C) was as much as 7.9 and 2.8 °C higher than that of the long-term average. Whilst compared to the long-term average, precipitation was 57.2% and 31.5% of the mean, for July and August, respectively. The annual rainfall of 2013 was 1298.7 mm, and most occurred in the period from May to October. Additionally, July was the driest month (Figure 1), showing exceptionally hot and dry conditions (*Yuan et al., 2016*). Figure 2 showed seasonal dynamics of environmental variables and biotic factors during study period. Temperatures at different depths (soil temperature at 5 cm and 50 cm depth, T_{s5}, T_{s50}; air temperature at 1m height, T_a) presented a similar annual pattern (Figure 2A), it increased gradually from January to July, being maximal in July, and then decreased slowly till December. T_{s5} and T_{s50} changed more comparatively smooth and steadily than T_a. Soil water contents (SWC, at 5 cm and 50 cm depths, SWC_5 and SWC_{50}) were obviously affected by rainfall, and decreased greatly in July and August.

Seasonal variation of carbon flux (net ecosystem exchange, NEE, ecosystem respiration, RE, gross ecosystem productivity, GEP) showed several peaks during 2013, with lower value in August (0.76 $gC{\cdot}m^{-2}$ mean daily NEE) (Figure 2C), and maxima in June and September. Besides, NEE was positive on some rainy and cloudy days. Mean daily NEE, RE and GEP was -2.11 $gC{\cdot}m^{-2}{\cdot}day^{-1}$, 5.36 $gC{\cdot}m^{-2}{\cdot}day^{-1}$and 7.48 $gC{\cdot}m^{-2}{\cdot}day^{-1}$, respectively. Due to the impact of drought, GEP decreased significantly in July and August, being 59.9%, 80.0% of the values for 2011 (*Chen et al., 2016*). LAI remained at a lower value (about 3.6) in winter and spring, it increased gradually starting in March, and reached a maximum (5.92) in July. Thereafter, LAI decreased slowly (Figure 2D), exhibiting the typical growth characteristic of Moso bamboo in an "on year".

Diurnal variation of soil CO_2 fluxes and its response to temperature

R_s in our forest presented a similar diurnal cycle throughout the year (Figure 3A). After a daily minimum occurring between 5:00~7:00 o'clock, it increased slowly reaching a maximum value at about 14:00-16:00 o'clock, and then decreased gradually. There were, however, great differences in R_s during the different months. It (the mean instantaneous value at each time) ranged from 0.63 to 7.52 $\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$, with a mean value of 3.11 $\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$, and coefficient of variation (*CV*) of 4.5%~23.6%. The maximal measured R_s was in August, with a value of 7.52 $\mu mol \cdot m^{-2} \cdot s^{-1}$ followed by July. Monthly maximum values of R_s ranged from 0.85 to 7.52 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Table 2 showed the correlation coefficients between environmental factors and soil respiration. There was positive significant correlation between diurnal mean values of R_s and soil surface (T_{S5}) and air temperature (T_a) with the correlation with soil surface temperature being larger (Figure 3C and 3D). Furthermore, an exponential relationship was used to estimate R_s based on T_s (Table 1). T_s explained 69.7% variation of R_s at a diurnal scale. Whereas T_{s5} could explain 63.9% of R_s (not shown). Both regression models were statistically significant ($P < 0.01$). We plotted the diurnal variation of R_s against T_s, and T_{s5} (Figure 4). The relationship showed a clear hysteresis. Additionally, there was slight discrepancy in elliptic shape of T_s and T_{s5}. and subtle difference in both could explain the coefficient or determination (R^2) in an exponential relationship of T_s and T_{s5} (Table 1).

Seasonal dynamics of soil CO_2 fluxes and its affecting factors

The stand showed a clear seasonal pattern in soil respiration (Figure 3A, 3B), being highest in summer with 5.77 $\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$, followed by autumn (3.50 $\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$), spring (2.42 $\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$), and lowest in winter (0.76 $\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$). The average annual soil CO_2 flux was 3.11 $\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$, equating to annual R_s of 44.07 t $CO_2 \cdot ha^{-1} \cdot a^{-1}$.

Temperatures at different height and depths presented similar seasonal dynamics, being maximum in summer and minimum in winter (Figure 3E). Besides, values Q_{10} were small in summer and large in winter (Table 1).

Monthly mean values of LAI, soil temperature and GEP were all significantly related to soil respiration (Table 2 and Figure 5). Maximum Rs was significantly correlated with associated soil temperature (Figure 5E). Within each season, there was a complex relationship between SWC and R_s, with significant ($P < 0.01$) negative correlation in summer (R= -0.796, R_s = -19.101*SWC+10.368, whilst, soil temperature and soil moisture showed significant relationship, R= -0.939, T_s=-0.013*SWC+0.559, $P < 0.001$), and positive correlation in autumn ($P < 0.01$, R= 0.552, R_s = 47.663*SWC-7.012) and spring ($P < 0.05$, R= 0.331, R_s = 36.661*SWC-6.708), but no correlation ($P > 0.05$) in winter (R= 0.008), indicating that SWC played crucial role in R_s at the growing period of Moso bamboo. Whilst R_s was closely related (P<0.01) to T_s at all seasons (Figure 3C), with an R of 0.94 in spring, 0.72 in summer, 0.98 in autumn and 0.851 in winter.

Moreover, exponential equation model was used to fit the relationship between different temperatures (T_s, T_{s5}, T_{s50} and T_a) and soil respiration (Figure 3C, 3D). The equations of T_{s5}-Rs (R^2= 0.954) and T_{s50}-R_s (R^2= 0.929) both showed higher R^2 than that of T_s-R_s (R^2= 0.915), possible because of the relative stability of soil temperature profile measurement in eddy covariance system. Furthermore, due to the complex relationship between SWC and R_s, as well as considering combination of temperature and soil moisture, six models were compared that predict R_s based on soil temperature and soil moistures (Table 3). Based on root mean square (*RMSE*) and R^2, the model (R_s=a+b*exp(c*T_s) +d*T_s*SWC) showed the best result, suggesting T_s and SWC could explain 93.6% temporal variation of R_s in 2013. Compared with a soil temperature (T_s)-soil respiration (R_s) equation (Figure 3C, R^2=0.915), It showed a slight increase R^2(Table 3, R^2=0.936).

Discussion

Our work shows that there are three factors that affect soil respiration in Moso bamboo: temperature, soil humidity and either productivity or LAI. The importance and interactions of the factors will be discussed subsequently. Of the three factors, soil temperature was the dominant driver of soil respiration with an R^2 of over 0.8.

Seasonal change of R_s has been investigated in varying ecosystems. Soil temperature and soil water content are commonly to be two major determinants to give rise to seasonal variations in measured R_s (*Davidson et al., 1998*). In this study, soil respiration increased with the rising of soil temperature. Similar results were explored by Shi et al. (*2012*) on a global scale. However, soil temperature explained only 62.7% variation of soil respiration during summer (June, July and August). This was not only due to a lower variation of soil temperature during summer months, but also, as shown in Table 1, the temperature sensitivity of soil respiration was markedly lower in the summer. Indeed, plots of soil respiration against daily temperature patterns show a rather flat relationship for the summer with a strong hysteresis. Similar findings have been reported in Moso bamboo forest of subtropical China by Tang et al. (*2016*) and Song et al. (*2013*). Depth of the soil temperature measurement affected the explanatory power of soil temperature. The explanatory power of the temperature in the humus layer was highest and decreased with the depth of the measurements. This indicates that most of the respiration originates from the humus layer. Zhang et al. (*2016*) made similar observations in winter wheat ecosystems. While Dai et al. (*2004*) found soil respiration of wheat was highly correlated with soil temperature at 10 cm depth.

The relationship between soil carbon efflux and soil temperature showed a diurnal hysteresis (Figure 4). This indicates that there is a delayed effect between rapidly varying temperature and diurnal variation of soil respiration, similar to the study of Högberg et al. (*2008*). Furthermore, other research suggested that the length of the delay could vary among different species (*Raich & Schlesinger, 1992*). Since the depth of the measurements of soil temperature varies between studies, it might be difficult to compare the sensitivity of soil respiration to soil temperature between studies (*Zhang et al., 2016*). Previous research suggested diurnal variation of R_s was out of phase with corresponding T_s at 2 cm depth, resulting in significant hysteresis (*Gaumont-Guay et al., 2006*). As discussed above, there may be two possible reasons (1) effects of diurnal variations of root respiration supplied by newly produced photosynthetic products (*Bahn et al., 2008*) and (2) diurnal variations of soil water content near the critical value (*Bahn et al., 2008*).

The relationship between soil respiration and soil moisture was more complicated in our study. Soil moisture improved marginally our models of soil respiration with a better fit of the models particularly in the dry summer 2013. No significant correlation was found between soil respiration and soil moisture in 2013 (Figure 3F). Similar findings had been reported for Moso bamboo forest in Zhejiang province (*Song et al., 2013*). However, soil moisture had a negative statistically significant ($P < 0.001$, R= -0.796, $R_s = -19.101*SWC+10.368$) correlation with soil respiration in summer while correlation in the other seasons was positive. However, previous observation indicated a pronounced correlation between R_s and SWC in subtropical forests (*Sheng et al., 2010; Liu et al., 2011*). The negative correlation of soil respiration and soil moisture in our study was probably caused by a spurious correlation (R= -0.939, $P < 0.001$) of soil temperature and soil moisture during summer. When we fitted non-linear models to soil respiration using temperature and soil moisture we got only a small increase in the R^2 when soil moisture was included into the model. This indicates that soil moisture was, even in the dry year of 2013, not an important limitation of soil respiration. The models of soil respiration suggest that the temperature sensitivity of soil respiration declines when soil moisture is decreasing (*Almagro et al., 2009; Jassal et al., 2008; Wang et al., 2006*). Also, Q_{10} varied over the different seasons (Table 1) and we think that this variation is related to differences in soil moisture. This is supported plots of the relationship of soil respiration on temperature within a day. Due to smaller amplitude of soil temperature in deeper layers (*Pavelka et al., 2007*) tend Q_{10} values estimated from deeper soil layers tended to be larger than those of shallower layers. This can partly explain the discrepancy between T_a, T_s, and T_{s5}. Q_{10} was about 2.80 in our study, within range of 1.33~5.53 estimated for forests in China(*Chen et al., 2008*), lower than 4.09 in Moso bamboo forest of central

Taiwan (Hsieh et al., 2016), but higher than median of 2.0~2.4 (*Hashimoto, 2005*). Previous observation pointed out that annual Q_{10} value was not only an indicator of the response to soil temperature, but also a comprehensive response to variations of other factors (i.e. SWC, root biomass, root growth, amplitude of R_s, and other seasonal processes, *Yuste et al., 2004*).

Another driver of soil respiration is the growth pattern of Moso bamboo which shows a large variation in below ground activities. In the spring, carbon is allocated to the production of new bamboo shoots. After bamboo has completed its main growth period in summer and new leaves are fully-expanded, it accumulates nutrient substance and allocates its main growth to the rhizome. Then in autumn Moso bamboo starts to hatch bamboo shoots for the next year (*Chen et al., 2016*). In this growing phase, soil moisture was a key factor for soil respiration. Subsequently, the stand got into overwintering stage. Soil moisture became less important in this period. Consequently, the importance of soil moisture for soil respiration varies among seasons and was more important during the time of active growth of Moso bamboo. However, soil temperature rather than soil moisture remained the most important drivers of soil respiration (*Janssens & Pilegaard, 2003*).

Another explanation could be that the differences in soil respiration and Q_{10} values are driven by the annual pattern of gross primary production which drives substrate supply to the root and rhizosphere (e.g. *Bahn et al., 2008*). Currently several authors have reported productivity should be considered to improve the prediction of soil respiration (*Bahn et al., 2008*; *Hibbard et al., 2005*; *Zhang et al., 2016*). Numerous studies have shown close relations between soil respiration and canopy photosynthesis at different timescales. Högberg et al. (*2008*) reported that soil respiration was largely driven by recent primary production of the vegetation.

Monthly soil respiration was significantly related to LAI and GEP in our study (Figure 5A and 5C). The finding agreed with the view of a short-term coupling of photosynthesis and soil respiration. Likewise, Yuste et al. (*2004*) found that seasonal R_s was positively related to LAI. Bahn et al (*2008*) suggested R_s was closely related to LAI across grassland sites. In our study, LAI reflected the productivity of vegetation. There was similar monthly variation pattern of LAI and T_a in our study, which in turn increased the difficulty to detect relationships of R_s in relation to biological variable. Soil respiration is a complex biological process, composed of several processes from both autotrophic and heterotrophic organisms. Besides soil temperature and soil water content, it is known that soil respiration is partly explained by forest type, stand age and altitude in subtropical forests (*Wang et al., 2011*). Additionally, other variables such as management (i.e. fertilization, thinning and harvesting activities, *Gao et al., 2014*; *Liu et al., 2011*), litter, soil microbial (*Linn & Doran, 1984*) and physical properties, root biomass and extreme weather (e.g. warming, precipitation events, short-term drought events), all have indirect and direct effects on soil respiration. However, how these influence autotrophic and heterotrophic processes is not well understood and should be a subject of further research.

Conclusions

Soil respiration in the forest exhibited similar daily and seasonal dynamic patterns, with its highest values in summer and lowest values in winter, annual mean soil respiration was 44.1 $tCO_2 \cdot ha^{-1} \cdot a^{-1}$. Soil respiration indicated positive significantly correlation with soil temperature (*P* < 0.01), it can explain 69.7% of temporal variation for R_s. No obvious related with soil moisture on daily scale, but significant correlation with soil moisture during seasons except winter, implying soil moisture played a crucial role in different growth phase. The model compound by soil temperature and soil moisture, could explain 93.6% of seasonal variation for R_s. The correspondent relationship between R_s and different soil temperature exhibited an exhibited clear hysteresis. Soil respiration was significantly and positively ($P < 0.01$) in relation to gross ecosystem productivity and LAI during our study, illustrating the significance of biotic factors as crucial driving factors of soil respiration, and importance of future research revealing correspondence mechanism of canopy photosynthesis and soil CO_2 flux.

Acknowledgements

We thank Li Y for giving comments that greatly improved this manuscript. Tan Y provided field assistance. And we also would like to thank Professor Jiang Hong's team for their invaluable support with the flux data collection and anonymous reviews.

Additional information and declarations

Funding

This study was supported by the National Natural Science Foundation of China (31670644, 31370637), Natural Science Foundation of Zhejiang Province (LR14C160001), 973 Program of China (2011CB302705), Joint Research fund of Department of Forestry of Zhejiang Province and Chinese Academy of Forestry (No. 2017SY04), Zhejiang Provincial Collaborative Innovation Center for Bamboo Resources and High-efficiency Utilization, the Key Science and Technology Projects of Zhejiang Province (2015C03008), and the Key Discipline of Forestry of Creative Technology Project of Zhejiang Province (201510).

Competing Interests

The authors declare that there are no competing interests.

Author Contributions

Yuli Liu, Guomo Zhou and Huaqiang Du: conception and design; fieldwork; analysis and interpretation; statistical analysis and writing the paper. Frank Berninger, analysis and critical revision of the paper. Fangjie Mao, Xuejian Li and Liang Chen: fieldwork and statistical analysis; Lu Cui, Yangguang Li and Di'en, Zhu: field work; analysis and interpretation.

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Figure 1

Monthly variation of air temperature, precipitation (P, mm) at the study site in 2013 and long-term average.

The legend was shown as in the figure.

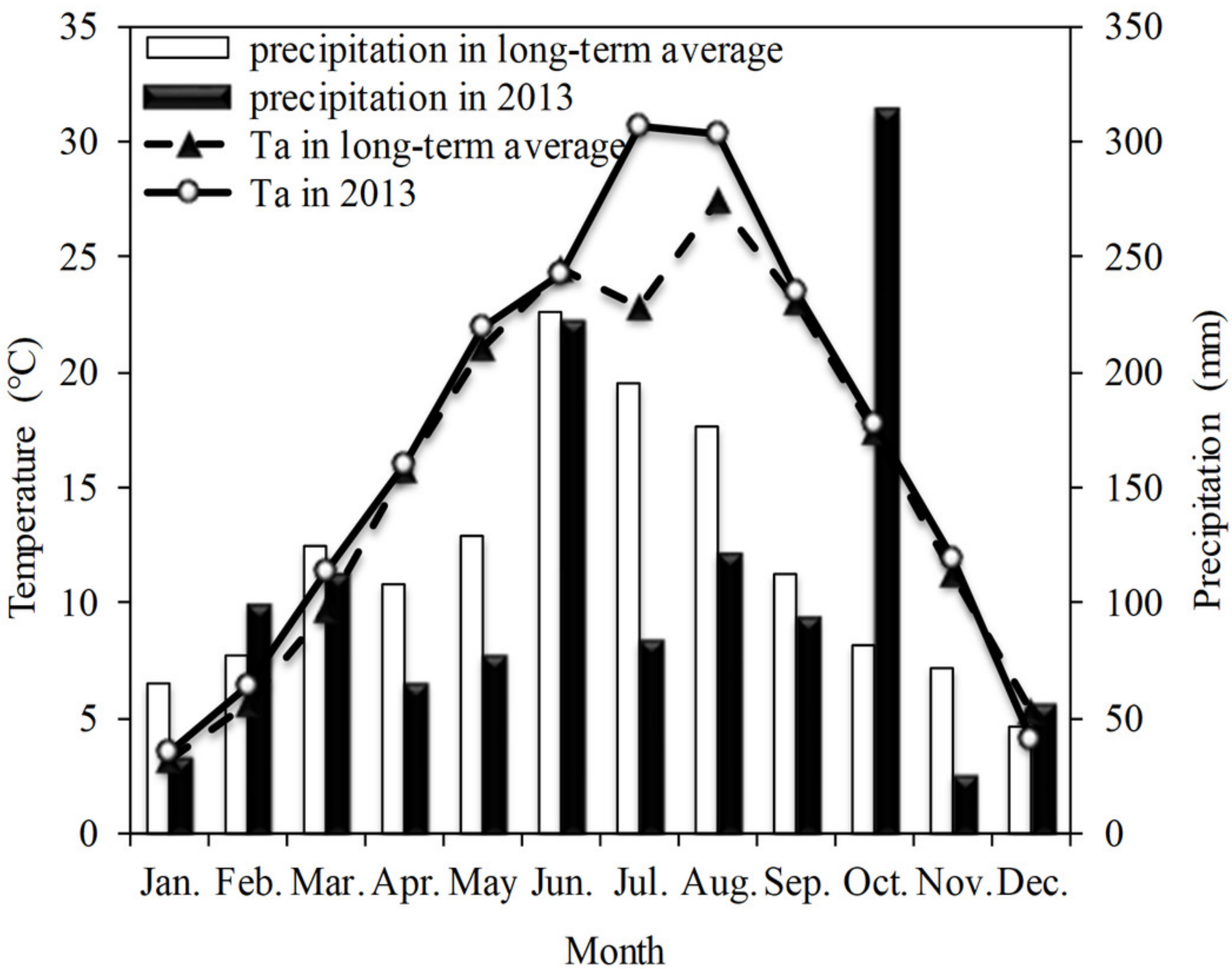


Figure 2

Seasonal variation of abiotic and biotic factors of Moso bamboo forest in 2013.

(A) daily temperature (℃) of air (Ta) and soil at 5 cm(Ts5),50cm(Ts50) depth, (B) Daily rainfall amount (mm) and soil water content (m3·m-3) at 5 cm depth (SWC5) and 50 cm depth (SWC50), (C) daily carbon fluxes (NEE, RE, GEP, gC·m-2), (D) mean monthly LAI (m2·m-2) during the study period Mean ± SD (n=3).

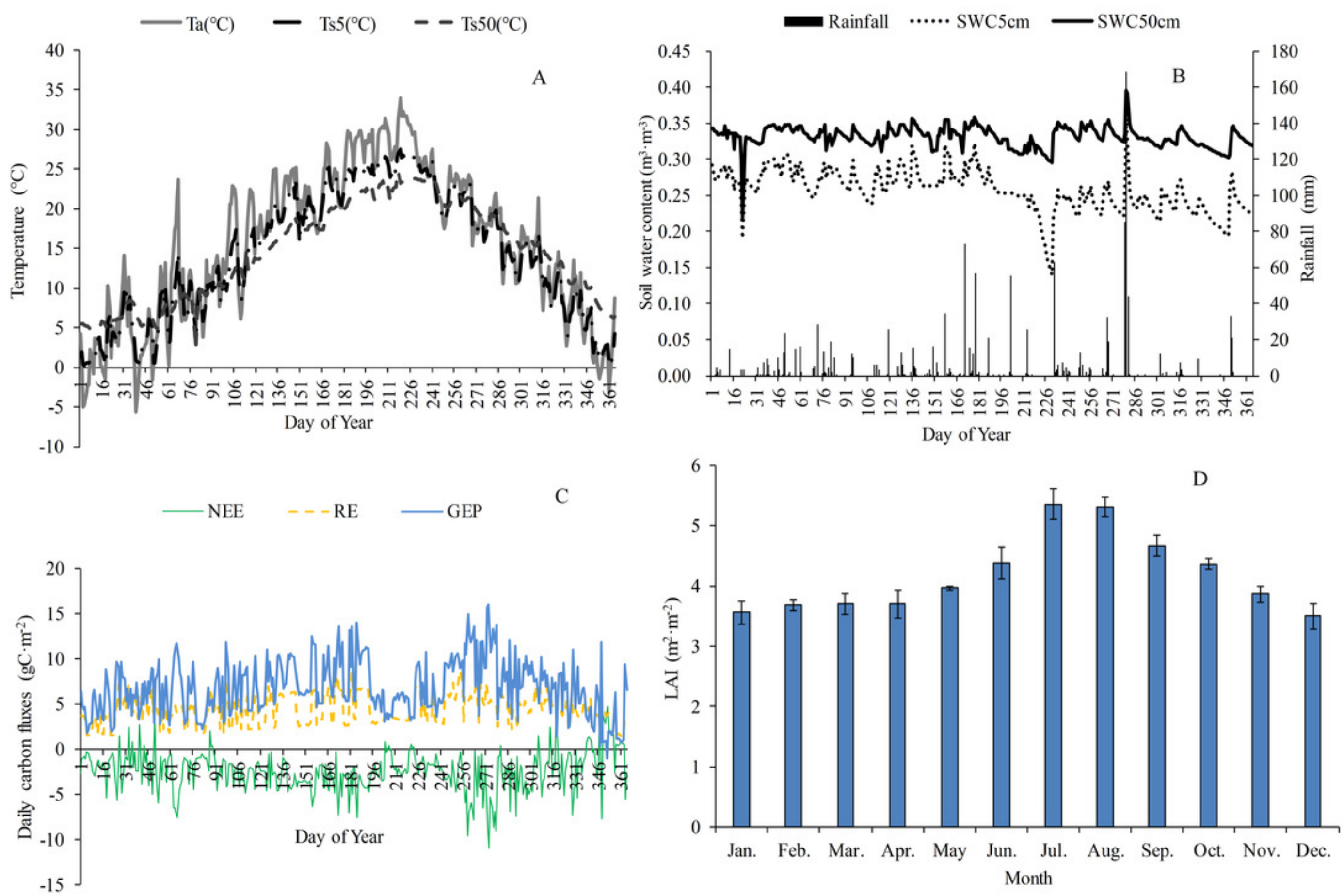
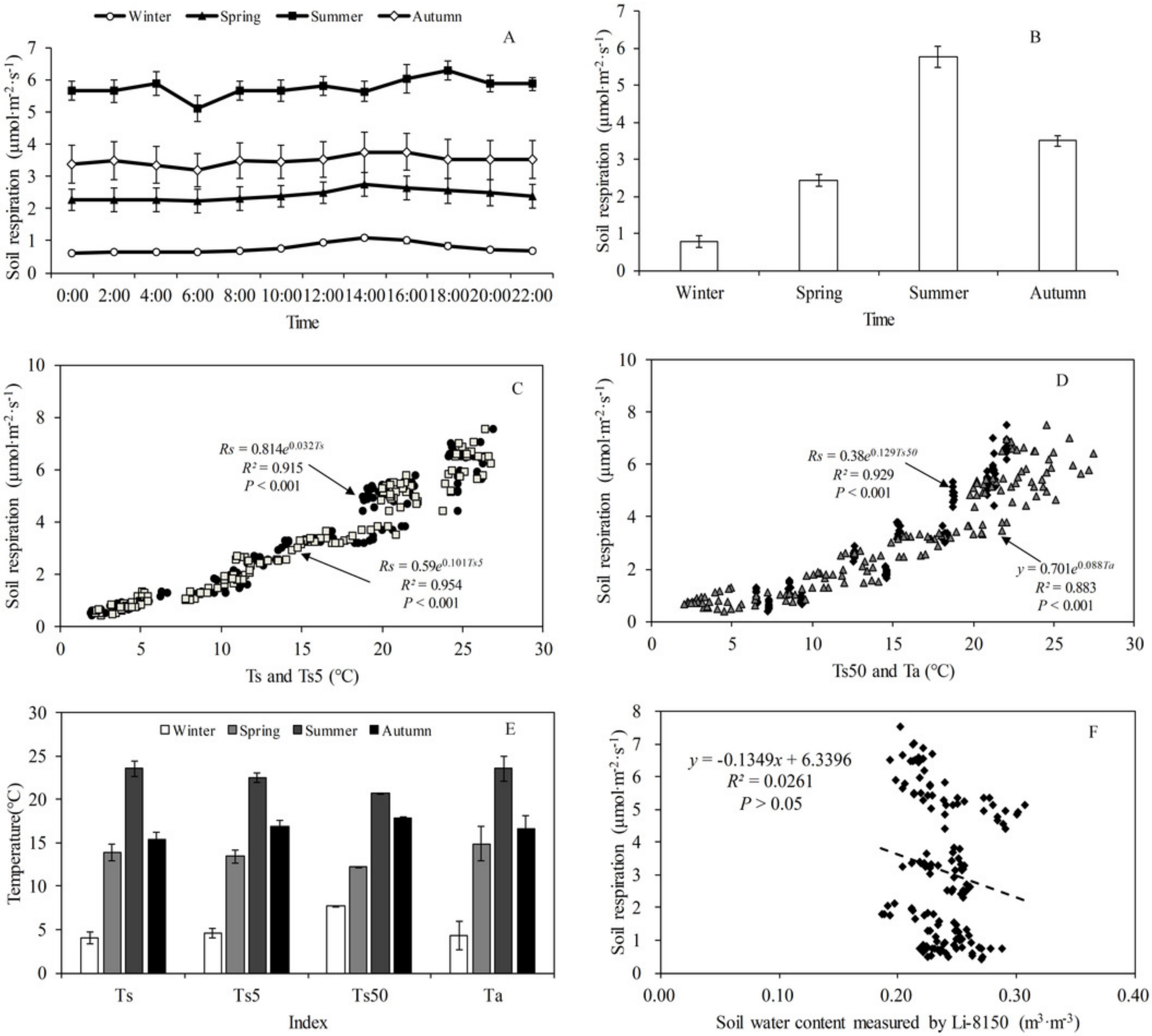


Figure 3

Diurnal, seasonal dynamic of soil respiration and the relationship between related factors and soil respiration in Moso bamboo forest.

(A, error bars denote standard error of means, n=12). Seasonal variation of soil respiration (b, error bars denote standard deviation of means, n=12). Seasonal relationship between soil respiration and different temperature (C and D, Ts, black circle, Ts5, white diamond, Ts50, black diamond, and Ta, grey triangular, n=144), and (E) their seasonal variation; (F) relationship between soil water content and soil respiration (n=144) error bars indicate standard deviation of the means (n=12).



Winter
Spring
Summer
Autumn
A
Soil respiration (μmol·m-2·s-1)
0:00 2:00 4:00 6:00 8:00 10:00 12:00 14:00 16:00 18:00 20:00 22:00
Time
B
Winter
Spring
Summer
Autumn
Time
C
Rs = 0.814e^0.032Ts
R² = 0.915
P < 0.001
Rs = 0.59e^0.101Ts5
R² = 0.954
P < 0.001
Ts and Ts5 (°C)
D
Rs = 0.38e^0.129Ts50
R² = 0.929
P < 0.001
y = 0.701e^0.088Ta
R² = 0.883
P < 0.001
Ts50 and Ta (°C)
E
Temperature(°C)
Ts
Ts5
Ts50
Ta
Index
F
y = -0.1349x + 6.3396
R² = 0.0261
P > 0.05
Soil water content measured by Li-8150 (m3·m-3)

Figure 4

Mean diurnal changes of R_s in response to T_s and T_{s5} in different months of Moso bamboo forest.

R_s denotes soil respiration, T_s denotes soil temperature measured by Li-8150, T_{s5} denotes soil temperature at 5 cm depth measured by eddy covariance technique. one month of the season was chosen.

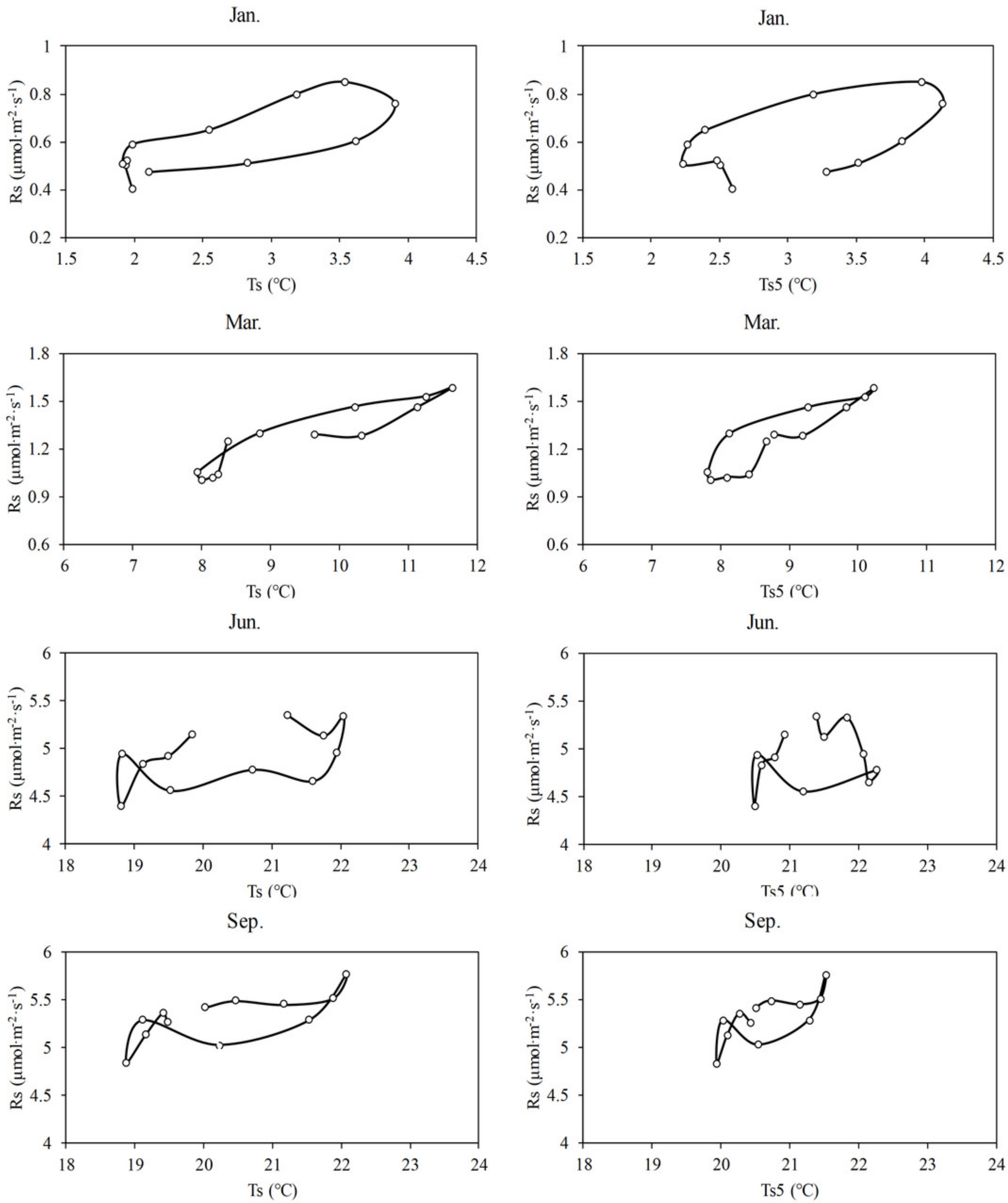

Jan.
Jan.
Mar.
Mar.
Jun.
Jun.
Sep.
Sep.
Rs (μmol·m-2·s-1)
Ts (°C)
Ts5 (°C)

Figure 5

Relationship between monthly soil respiration and leaf area index ,gross ecosystem productivity.

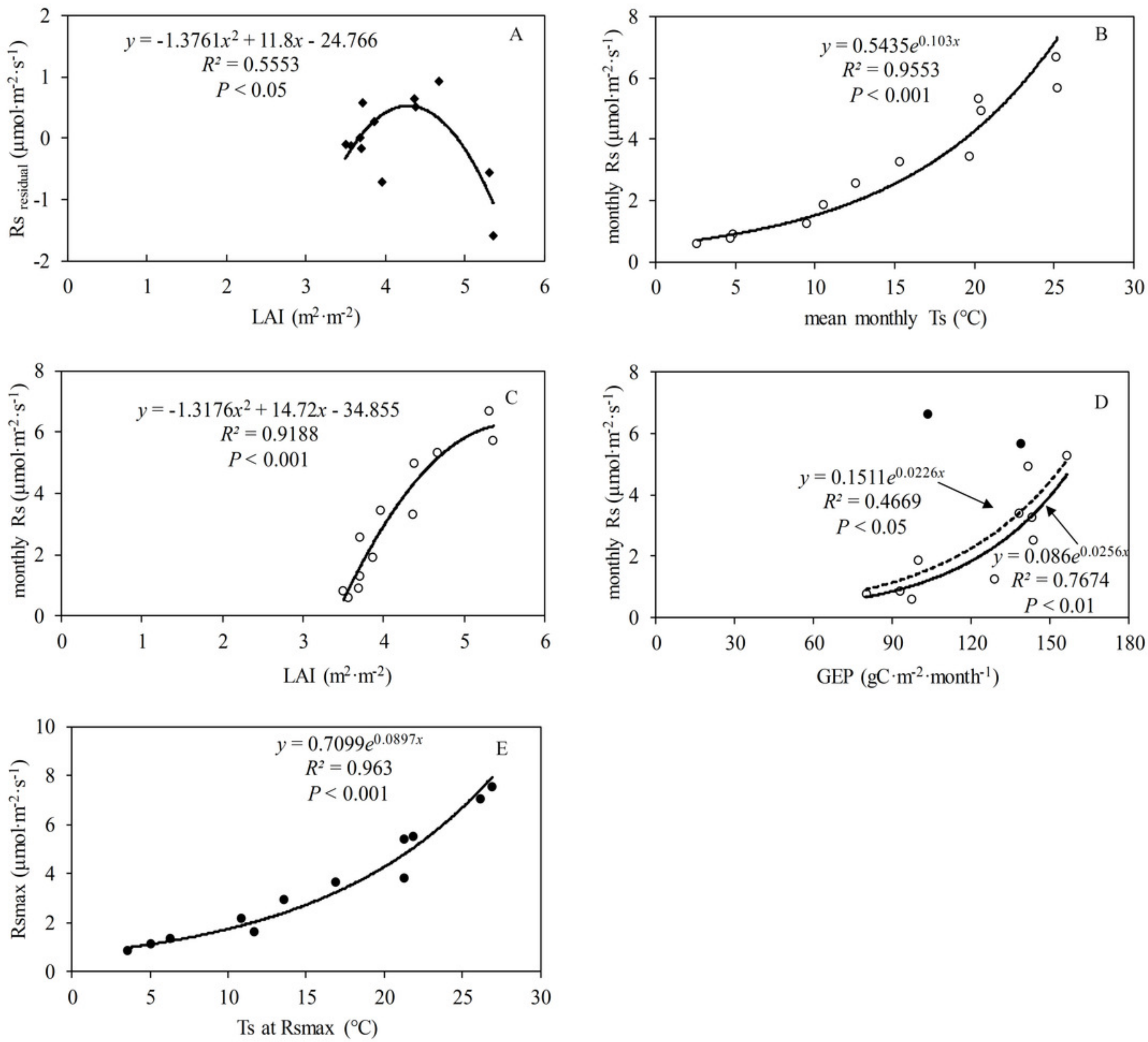


Table 1 (on next page)

Relationships between mean diurnal soil respiration (R_s) and soil temperature measured by Li-8150 (T_s) in 2013.

Rs is soil respiration, Ts is soil temperature measured by Li-8150.

Table. 1. Relationships between mean diurnal soil respiration (R_s) and soil temperature measured by Li-8150 (T_s).

Time	Equation	R^2	Q_{10}	*F*	*P*
Dec.~Feb.	R_s=0.279exp(0.241*T_s)	0.684	11.08	73.74	0.000
Mar.~May	R_s=0.629exp(0.095*T_s)	0.819	2.59	154.39	0.000
Jun.~Aug.	R_s=1.427exp(0.058*T_s)	0.627	1.79	57.08	0.000
Sep.~Nov.	R_s=0.594exp(0.107*T_s)	0.983	2.92	1976.33	0.000

Table 2(on next page)

Correlation coefficients of monthly mean soil CO_2 fluxes and its affecting factors in 2013.

T_s (soil temperature measured by Li-8150 probe), R_h (air relative humidity measured by flux tower at 1m height), GEP (gross ecosystem productivity), other variables shown see Figure 2. Statistical significance with: ** p-values<0.01, * p-values<0.05, besides, due to no significant correlation between soil moisture and other factors, it was not shown in Table 1 (expect GEP in July and August).

Table 2. Correlation coefficients of monthly mean soil CO_2 fluxes and its affecting factors in 2013.

Factors	**R_s**	**Environmental variables**							**GEP**
		T_s	**T_{s5}**	**T_{s50}**	**T_a**	**Rh**	**SWC_5**	**SWC_{50}**	
T_s	0.988^{**}								
T_{s5}	0.968^{**}	0.99^{**}							
T_{s50}	0.966^{**}	0.95^{**}	0.97^{**}						
T_a	0.966^{**}	0.99^{**}	0.99^{**}	0.946^{**}					
Rh	0.21	0.21	0.152	0.133	0.081				
SWC_5	-0.229	-0.135	-0.153	-0.348	0.337	0.438			
SWC_{50}	0.244	0.306	0.296	0.142	0.334	0.688^{*}	0.813^{*}		
GEP	0.841^{**}	0.868^{**}	0.863^{**}	0.752^{*}	0.894^{**}	0.198	0.148	0.555	
LAI	0.937^{**}	0.89^{**}	0.91^{**}	0.914^{**}	0.901^{**}	0.15	-0.275	0.162	0.761^{*}

Note: T_s (soil temperature measured by Li-8150 probe), Rh (air relative humidity measured by flux tower at 1m height), GEP (gross ecosystem productivity), other variables shown see Fig. 2. Statistical significance with: ** p-values $<$ 0.01, * p-values $<$ 0.05, besides, due to no significant correlation between soil moisture and other factors, it was not shown in Table 1 (expect GEP in July and August).

Table 3(on next page)

Relationship between R_s, T_s and SWC. Coefficients of determination (R^2) and root mean square error (*RMSE*) were given

The abbreviation was shown in Figure. 1. *P* value of every model was 0.000.

Table 3. Relationship between R_s, T_s and SWC. Coefficients of determination (R^2) and root mean square error (*RMSE*) were given.

Model	R^2	***a***	***b***	***c***	***d***	***RMSE***
R_s=exp(a+b*T_s) *SWC	0.895	1.07	0.09	-	-	0.663
R_s=(c*SWC+d) *a*exp(b*T_s)	0.918	0.64	0.08	1.13	0.97	0.591
R_s=exp(a+b*T_s+c*SWC+d*T_s*SWC)	0.919	0.22	0.05	-1.97	0.14	0.588
R_s=exp(a+b*T_s+c*SWC+d*SWC^2)	0.922	1.88	0.08	-18	39	0.578
R_s=a+b*T_s+c*SWC+d*T_s*SWC	0.929	-3.74	0.47	13.45	-0.9	0.542
R_s=a+b*exp(c*T_s) +d*T_s*SWC	0.936	-4.73	4.76	0.03	-0.04	0.515

Note: the abbreviation was shown in Figure. 1. P value of every model was 0.000.