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

18   We analyzed the dynamics of soil respiration (R_s) and its relation to environmental factors in

19   a Moso bamboo forest (*Phllostachys heterocycla cv. pubescens*). Annual average R_s was

20   44.07 $tCO_2 \cdot ha^{-1} \cdot a^{-1}$. R_s was significantly correlated with soil temperature ($P < 0.01$), which

21   explained 69.7% of the variation of R_s. Soil moisture was correlated significantly with R_s

22   outside of the winter on a daily scale indicating it affected R_s. A model including both soil

23   temperature and soil moisture explained 93.6% of seasonal variations for R_s. The relationship

24   between R_s and soil temperature during a day showed a clear hysteresis. R_s was in significant

25   and positively ($P < 0.01$) related to gross ecosystem productivity and leaf area index during

26   our study, illustrating the significance of biotic factors as crucial drivers of R_s.

27   **Keywords:** Soil respiration; Moso bamboo forest; environmental determiners; gross ecosystem

28   productivity; leaf area index

Introduction

30   Soils are important sources and sinks in the global carbon budget (*Sheng et al., 2010*). Soil

31   respiration (R_s) presents a major source of CO_2 emissions from terrestrial ecosystem, as the

32   second largest carbon flux between the atmosphere and ecosystems it is surpassed only by

33   gross primary production (*Raich and Schlesinger, 1992*). Soils release approximately 68 ± 4

34   Pg C per year globally, nearly 10 times of the amount of CO_2 released annually by the

35   combustion of fossil fuels (*Raich and Potter ,1995*). Hence, slight variations in R_s may cause

36   profound changes in the atmospheric concentration of CO_2, the accumulation of soil carbon

37   (*Schlesinger & Andrews, 2000*), and subsequently affect global climate.

38   Considering the importance of forest ecosystem in the terrestrial carbon cycle and their

39   response to global climate, numerous studies have been conducted to explore R_s and its

40 dependence on environmental drivers. For instance, the temperature and moisture of soils are

41 two of the major environmental drivers regulating R_s (*Liu et al., 2016*). Additionally,

42 disturbances (as e.g. fire, *Muñoz-Rojas et al., 2016*; *Köster et al., 2014*), harvesting (*Bahn et*

43 *al., 2008*), artificial warming and precipitation changes (*Li et al., 2017a*) or land use changes

44 (*Liu et al., 2011; Willaarts et al., 2016*) can also have large effects on R_s. R_s is a complex

45 biogeochemical process highly related to ecosystem productivity, leaf area index and soil

46 fertility (*Hibbard et al., 2005*). Recently, research has reported R_s to be also influenced by the

47 amount of litter (*Oishi et al., 2013*; *Wu et al., 2017*), vegetation type, latitude (*Mahecha et al.,*

48 *2010*; *Wang et al., 2011*), and composition of the soil microbial community (*Luo et al., 2016*).

49 Furthermore, some biological factors (e.g. leaf area index and ecosystem productivity) are

50 closely related to R_s, suggesting coupling between CO_2 assimilation by the vegetation and

51 emissions from the soil (*Bahn et al., 2008*; *Hibbard et al., 2005*). However, many of the

52 environmental drivers are correlated with each other and it is difficult to distinguish and

53 quantity the contribution of each environmental factor.

54 Bamboo forests are widely distributed in warm temperate, subtropical and tropical zones

55 between 46°N-47°S of the world (*McDowell et al., 2015*). Globally, bamboo forests cover

56 31.5 million ha (*FAO, 2010*). In the context of sustainable development, bamboo plays a

57 significant role in substituting wood as well as in the terrestrial carbon cycle (*Song et al.,*

58 *2011*). Well known as bamboo kingdom, China has 6.16 million ha bamboo forest,

59 accounting for 2.97% of total forest area in China (*SFAPRC, 2015*). Appreciated for its rapid

60 growth and high timber production (*Guan et al., 2017*), Moso bamboo (*Phllostachys*

61 *heterocycla cv. pubescens*) forest is a major vegetation type of subtropical forests in

62 subtropical China (*Song et al., 2013*). Currently, the area covered by Moso bamboo forest

63 increases annually by about 3%, since it provides many benefits (including high income

64 generation and other ecosystem services) to the forest owners.

65 Notably, Moso bamboo has high rates of carbon accumulation, sequestering 4.91 - 5.45 tC ha^{-}

66 ^{1} each year (*Zhou and Jiang, 2004*), showing great potential for alleviating global warming by

67 carbon fixation. Previous studies of Moso bamboo have concentrated on carbon storage,

68 balance and its distribution in the ecosystem (*Li et al., 2013*), as well as on the productivity of

69 bamboo forest (*Cheng et al., 2015*; *Isagi et al., 1997*), variation of soil organic carbon stocks

70 (*Guan et al., 2015*). Previous studies reported a close relationship between R_s and biotic

71 factors in other forest types (*Hibbard et al., 2005*) suggesting a coupling between forest

72 canopy assimilation and carbon emissions from soil. However, comparatively little is known

73 about bamboo forests. Thus, it is imperative to explore the relationship between biotic, abiotic

74 factors and R_s in Moso bamboo forest. Also, it is necessary to explore the driving forces

75 behind soil respiration in the forest.

76 In this study, we used soil respiration measurements from a Moso bamboo stand and

77 combined these with measurements of abiotic as well as biotic factors. Our aims were to

78 explore the temporal dynamics of soil respiration, and to identify the relative importance of

79 biotic and abiotic factors.

80 **Materials and Methods**

81 **Study site**

82 A Moso bamboo stand, with a flux tower observation, was selected as study site at Anji

83 County (30°28′34.5″N, 119°40′25.7″E, and elevation 380 m, Figure S1), located in

84 northwestern of Zhejiang Province, southeast China. As the subtropical monsoon climate,

85   according to Trewartha climate classification, the average annual air temperature and

86   precipitation was 15.6°C and 1413.2 mm, respectively, according to meteorological

87   measurements for 1981-2010 from weather stations of Anji. Effective accumulated

88   temperature above 10°C is 4934.1°C. There are on average hours 2021 h of sunshine

89   annually. Monthly average rainfall and air temperature in the study period were shown in

90   Figure 1. The soil type of this area is yellow red soil (Chinese system of soil classification),

91   equivalent to Hapludult in USDA Soil Taxonomy (*Soil Survey Staff of USDA, 1999*), with a

92   pH ranging from 4.4 to 4.8 and a soil bulk density of 1.5 $g \cdot cm^{-3}$ (*Chen, 2016*).

93   The area of Moso bamboo forest was approximately 1687 hectares and 1km around the flux

94   tower, it accounted for 86.1% (*Xu et al., 2013*) of the area, with stand density of 3235 culms

95   per hectare. The average canopy height and diameter at breast height were 11 m and 9.3 cm,

96   respectively. There was only a sparse understory in the stand. The main management

97   activities were harvesting 6 or 7-year old bamboos, and a proportion of new bamboo shoots

98   each year. No fertilization nor weeding were done in the forest. Further detailed information

99   of the site can be found in Mao et al. (*2017*) . Moso bamboo has a biannual growth pattern.

100   During "off years" (which are the even in our site) few new bamboo shoots are produced,

101   there is leaf senescence of old leaves and vigorous growth of new leaves (*Qiu, 1984*). In "on

102   years" which are uneven years more new bamboo shoots are produced and leaf senescence is

103   limited.

104   **Experimental design and measurement**

105   **Soil CO$_2$ flux measurement**

106   The soil CO$_2$ flux was measured using the LI-8150 (LI-COR Inc., Lincoln, NE, USA)

107   multiplexer automatic soil carbon flux measurement system, from January to December in

108   2013. Four 20 m ×20 m plots were established around the flux tower within the forest. Four

109   sampling polyvinyl chloride (PVC) soil collars (20 cm inside diameter, 10 cm height, and 5

110   cm plugged in the soil from the ground surface) were randomly placed within each plot. All

111   collars remained permanently in place throughout the study period. To reduce the

112   disturbance-induced carbon dioxide emission, the first measurement started 24 h after

113   insertion. Green plants growing inside every soil collar were cut off carefully using scissors.

114   The data and the functioning of the equipment were checked regularly to ensure the

115   experiment stability throughout the year. Soil water content (SWC, $m^3 \cdot m^{-3}$) and soil

116   temperature (T_s, °C) were monitored simultaneously adjacent to each collar at 5 cm depth of

117   the soil, with 2 theta probes (ML2x, Delta-T Inc., UK; Omega Inc., USA) provided with the

118   system. Soil respiration measurements were done at 2-hourly intervals on selected sunny days

119   (about two weeks) in every mid-month of 2013. We defined March through May as spring,

120   June through August as summer, September through November as autumn, January, February

121   and December as winter.

122   **Measurements of environmental variables at the eddy covariance site**

123   Provided with meteorological measurements, T_s and SWC were monitored by soil

124   temperature sensors (109SS, Campbell, USA) and soil moisture sensors (CS616, Campbell,

125   USA), at 5 cm, 50 cm and 100 cm depths, respectively. Air temperature and relative humidity

126   were measured using HMP45C probes (Vaisala, Helsinki, Finland) at seven heights (1 m, 7

127   m, 11 m, 17 m, 23 m, 30 m, 38 m) above the ground. Ground-surface temperature was

128   obtained using a SI-111 infrared temperature sensor (Apogee, USA). All the data were

129   recorded by a data logger (CR1000, Campbell Inc., USA) and saved as 30-min averages.

130   **Biological factors measurement**

131   The biological factors we considered were gross ecosystem productivity (GEP) and leaf area

132   index (LAI). GEP was obtained by eddy co-variance (EC) technique. LAI was measured

133   using digital camera provided with a fish-eye lens then in combination with MODIS LAI

134   following the methods of Li et al. (*2017b*). LAI is reported as the average of three sample

135   points were chosen within the 20 m ×20 m plot on non-rainy days. The LAI data was reported

136   as mean values ±SD (standard deviation). For EC technique, an open-path infrared gas

137   analyzer LI-7500 (Li-Cor Inc., Lincoln, NE, USA), in conjunction with a 3-dimensional sonic

138   anemometer CSAT3 (Campbell Scientific Inc., Logan, UT, USA) was placed at 38 m above

139   the ground. All the raw flux data were sampled at 10 Hz, calculated and recorded by a

140   CR1000 data logger (Campbell Inc., USA) as 30-min average values. Whilst daily carbon

141   fluxes (net ecosystem exchange, NEE, ecosystem respiration, RE and gross ecosystem

142   productivity, GEP) were estimated as described by Xu et al. (*2016*).

143   **Data analysis**
144   We analyzed the soil respiration as a function of soil temperature assuming an exponential
145   Q_{10} type relationship.

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

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

148   Where R_s (μmol·m^{-2}·s^{-1}) is soil respiration, T is soil temperate at 5 cm depth, a and b are

149   parameters, Eq.1 (*van't Hoff, 1884*). Whilst the temperature sensitivity parameter, Q_{10}, was

150   calculated by Eq.2 (*Sheng et al., 2010*; *Song et al., 2013*).

151   One-way analysis of variance (ANOVA) were carried out to test the statistical significance of

152   differences in soil respiration, environmental and biotic factors (Table 2) between seasons.

153   Regression analysis was performed to analyze the relationship between soil respiration, biotic

154   and abiotic variables. All analyses were conducted using the PASW Statistics 18.0 software.

155   **Results**

156   **Seasonal dynamics of environmental and biotic factors in Moso bamboo forest**

157   As can be seen from Figure 1, 2013 was drier and warmer than the long-term average, with

158   average air temperature 1.2 ℃ higher and total precipitation 114.5 mm lower than the long-

159   term average. Especially in July and August, T_a (30.7 and 30.3 ℃) was as much as 7.9 and

160   2.8 ℃ higher than that of the long-term average. Whilst compared to the long-term average,

161   precipitation was 57.2% and 31.5% of the mean, for July and August, respectively. The

162   annual rainfall of 2013 was 1298.7 mm, and most occurred in the period from May to

163   October. Additionally, July was the driest month (Figure 1), showing exceptionally hot and

164   dry conditions (*Yuan et al., 2016*). Figure 2 showed seasonal dynamics of environmental

165   variables and biotic factors during study period. Temperatures at different depths (soil

166   temperature at 5 cm and 50 cm depth, T_{s5}, T_{s50}; air temperature at 1m height, T_a) presented a

167   similar annual pattern (Figure 2A), it increased gradually from January to July, being

168   maximal in July, and then decreased slowly till December. T_{s5} and T_{s50} changed more

169   comparatively smooth and steadily than T_a. Soil water contents (SWC, at 5 cm and 50 cm

170   depths, SWC_5 and SWC_{50}) were obviously affected by rainfall, and decreased greatly in July

171   and August.

172   Seasonal variation of carbon flux (net ecosystem exchange, NEE, ecosystem respiration, RE,

173   gross ecosystem productivity, GEP) showed several peaks during 2013, with lower value in

174   August (0.76 gC·m^{-2} mean daily NEE) (Figure 2C), and maxima in June and September.

175   Besides, NEE was positive on some rainy and cloudy days. Mean daily NEE, RE and GEP

176   was -2.11 gC·m^{-2}·day^{-1}, 5.36 gC·m^{-2}·day^{-1} and 7.48 gC·m^{-2}·day^{-1}, respectively. Due to the

177   impact of drought, GEP decreased significantly in July and August, being 59.9%, 80.0% of

178   the values for 2011 (*Chen et al., 2016*). LAI remained at a lower value (about 3.6) in winter

179   and spring, it increased gradually starting in March, and reached a maximum (5.92) in July.

180   Thereafter, LAI decreased slowly (Figure 2D), exhibiting the typical growth characteristic of

181   Moso bamboo in an "on year".

182   **Diurnal variation of soil CO_2 fluxes and its response to temperature**

183   R_s in our forest presented a similar diurnal cycle throughout the year (Figure 3A). After a

184   daily minimum occurring between 5:00~7:00 o'clock, it increased slowly reaching a

185   maximum value at about 14:00-16:00 o'clock, and then decreased gradually. There were,

186   however, great differences in R_s during the different months. It (the mean instantaneous value

187   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

188     $\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$, and coefficient of variation (*CV*) of 4.5%~23.6%. The maximal measured

189   R_s was in August, with a value of 7.52 $\mu mol \cdot m^{-2} \cdot s^{-1}$ followed by July. Monthly maximum

190   values of R_s ranged from 0.85 to 7.52 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Table 2 showed the correlation

191   coefficients between environmental factors and soil respiration. There was positive significant

192   correlation between diurnal mean values of R_s and soil surface (T_{S5}) and air temperature (T_a)

193   with the correlation with soil surface temperature being larger (Figure 3C and 3D).

194   Furthermore, an exponential relationship was used to estimate R_s based on T_s (Table 1). T_s

195   explained 69.7% variation of R_s at a diurnal scale. Whereas T_{s5} could explain 63.9% of R_s

196   (not shown). Both regression models were statistically significant ($P < 0.01$). We plotted the

197   diurnal variation of R_s against T_s, and T_{s5} (Figure 4). The relationship showed a clear

198   hysteresis. Additionally, there was slight discrepancy in elliptic shape of T_s and T_{s5}. and

199   subtle difference in both could explain the coefficient or determination (R^2) in an exponential

200   relationship of T_s and T_{s5} (Table 1).

Seasonal dynamics of soil CO_2 fluxes and its affecting factors

202   The stand showed a clear seasonal pattern in soil respiration (Figure 3A, 3B), being highest in

203   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

204   (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

205   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 $CO_2 \cdot ha^{-1} \cdot a^{-1}$.

206   Temperatures at different height and depths presented similar seasonal dynamics, being

207   maximum in summer and minimum in winter (Figure 3E). Besides, values Q_{10} were small in

208   summer and large in winter (Table 1).

209   Monthly mean values of LAI, soil temperature and GEP were all significantly related to soil

210   respiration (Table 2 and Figure 5). Maximum Rs was significantly correlated with associated

211   soil temperature (Figure 5E). Within each season, there was a complex relationship between

212   SWC and R_s, with significant ($P < 0.01$) negative correlation in summer ($R= -0.796$, $R_s = -$

213    $19.101*SWC+10.368$, whilst, soil temperature and soil moisture showed significant

214   relationship, $R= -0.939$, $T_s=-0.013*SWC+0.559$, $P < 0.001$), and positive correlation in

215   autumn ($P < 0.01$, $R= 0.552$, $R_s = 47.663*SWC-7.012$) and spring ($P< 0.05$, $R= 0.331$, $R_s =$

216    $36.661*SWC-6.708$), but no correlation ($P > 0.05$) in winter ($R= 0.008$), indicating that SWC

217   played crucial role in R_s at the growing period of Moso bamboo. Whilst R_s was closely related

218   ($P<0.01$) to T_s at all seasons (Figure 3C), with an R of 0.94 in spring, 0.72 in summer, 0.98 in

219   autumn and 0.851 in winter.

220   Moreover, exponential equation model was used to fit the relationship between different

221   temperatures (T_s, T_{s5}, T_{s50} and T_a) and soil respiration (Figure 3C, 3D). The equations of T_{s5}-

222   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),

223   possible because of the relative stability of soil temperature profile measurement in eddy

224   covariance system. Furthermore, due to the complex relationship between SWC and R_s, as

225   well as considering combination of temperature and soil moisture, six models were compared

226   that predict R_s based on soil temperature and soil moistures (Table 3). Based on root mean

227   square (*RMSE*) and R^2, the model (R_s=a+b*exp(c*T_s) +d*T_s*SWC) showed the best result,

228   suggesting T_s and SWC could explain 93.6% temporal variation of R_s in 2013. Compared

229   with a soil temperature (T_s)-soil respiration (R_s) equation (Figure 3C, R^2=0.915), It showed a

230   slight increase R^2(Table 3, R^2=0.936).

231   **Discussion**

232   Our work shows that there are three factors that affect soil respiration in Moso bamboo:

233   temperature, soil humidity and either productivity or LAI. The importance and interactions of

234   the factors will be discussed subsequently. Of the three factors, soil temperature was the

235   dominant driver of soil respiration with an R^2 of over 0.8.

236   Seasonal change of R_s has been investigated in varying ecosystems. Soil temperature and soil

237   water content are commonly to be two major determinants to give rise to seasonal variations

238   in measured R_s (*Davidson et al., 1998*). In this study, soil respiration increased with the rising

239   of soil temperature. Similar results were explored by Shi et al. (*2012*) on a global scale.

240   However, soil temperature explained only 62.7% variation of soil respiration during summer

241   (June, July and August). This was not only due to a lower variation of soil temperature during

242   summer months, but also, as shown in Table 1, the temperature sensitivity of soil respiration

243 was markedly lower in the summer. Indeed, plots of soil respiration against daily temperature

244 patterns show a rather flat relationship for the summer with a strong hysteresis. Similar

245 findings have been reported in Moso bamboo forest of subtropical China by Tang et al. (*2016*)

246 and Song et al. (*2013*). Depth of the soil temperature measurement affected the explanatory

247 power of soil temperature. The explanatory power of the temperature in the humus layer was

248 highest and decreased with the depth of the measurements. This indicates that most of the

249 respiration originates from the humus layer. Zhang et al. (*2016*) made similar observations in

250 winter wheat ecosystems. While Dai et al. (*2004*) found soil respiration of wheat was highly

251 correlated with soil temperature at 10 cm depth.

252 The relationship between soil carbon efflux and soil temperature showed a diurnal hysteresis

253 (Figure 4). This indicates that there is a delayed effect between rapidly varying temperature

254 and diurnal variation of soil respiration, similar to the study of Högberg et al. (*2008*).

255 Furthermore, other research suggested that the length of the delay could vary among different

256 species *(Raich & Schlesinger, 1992)*. Since the depth of the measurements of soil temperature

257 varies between studies, it might be difficult to compare the sensitivity of soil respiration to

258 soil temperature between studies (*Zhang et al., 2016*). Previous research suggested diurnal

259 variation of R_s was out of phase with corresponding T_s at 2 cm depth, resulting in significant

260 hysteresis *(Gaumont-Guay et al., 2006)*. As discussed above, there may be two possible

261 reasons (1) effects of diurnal variations of root respiration supplied by newly produced

262 photosynthetic products (*Bahn et al., 2008*) and (2) diurnal variations of soil water content

263 near the critical value (*Bahn et al., 2008*).

264 The relationship between soil respiration and soil moisture was more complicated in our

265   study. Soil moisture improved marginally our models of soil respiration with a better fit of the

266   models particularly in the dry summer 2013. No significant correlation was found between

267   soil respiration and soil moisture in 2013 (Figure 3F). Similar findings had been reported for

268   Moso bamboo forest in Zhejiang province (*Song et al., 2013*). However, soil moisture had a

269   negative statistically significant ($P < 0.001$, $R= -0.796$, $R_s = -19.101*SWC+10.368$)

270   correlation with soil respiration in summer while correlation in the other seasons was positive.

271   However, previous observation indicated a pronounced correlation between R_s and SWC in

272   subtropical forests *(Sheng et al., 2010; Liu et al., 2011*). The negative correlation of soil

273   respiration and soil moisture in our study was probably caused by a spurious correlation ($R= -$

274   0.939, $P < 0.001$) of soil temperature and soil moisture during summer. When we fitted non-

275   linear models to soil respiration using temperature and soil moisture we got only a small

276   increase in the R^2 when soil moisture was included into the model. This indicates that soil

277   moisture was, even in the dry year of 2013, not an important limitation of soil respiration.

278   The models of soil respiration suggest that the temperature sensitivity of soil respiration

279   declines when soil moisture is decreasing (*Almagro et al., 2009; Jassal et al., 2008; Wang et

280   al., 2006*). Also, Q_{10} varied over the different seasons (Table 1) and we think that this

281   variation is related to differences in soil moisture. This is supported plots of the relationship

282   of soil respiration on temperature within a day. Due to smaller amplitude of soil temperature

283   in deeper layers (*Pavelka et al., 2007*) tend Q_{10} values estimated from deeper soil layers

284   tended to be larger than those of shallower layers. This can partly explain the discrepancy

285   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

286   for forests in China(*Chen et al., 2008*), lower than 4.09 in Moso bamboo forest of central

287   Taiwan (Hsieh et al., 2016), but higher than median of 2.0~2.4 (*Hashimoto, 2005*). Previous

288   observation pointed out that annual Q_{10} value was not only an indicator of the response to soil

289   temperature, but also a comprehensive response to variations of other factors (i.e. SWC, root

290   biomass, root growth, amplitude of R_s, and other seasonal processes, *Yuste et al., 2004*).

291   Another driver of soil respiration is the growth pattern of Moso bamboo which shows a large

292   variation in below ground activities. In the spring, carbon is allocated to the production of

293   new bamboo shoots. After bamboo has completed its main growth period in summer and new

294   leaves are fully-expanded, it accumulates nutrient substance and allocates its main growth to

295   the rhizome. Then in autumn Moso bamboo starts to hatch bamboo shoots for the next year

296   *(Chen et al., 2016)*. In this growing phase, soil moisture was a key factor for soil respiration.

297   Subsequently, the stand got into overwintering stage. Soil moisture became less important in

298   this period. Consequently, the importance of soil moisture for soil respiration varies among

299   seasons and was more important during the time of active growth of Moso bamboo. However,

300   soil temperature rather than soil moisture remained the most important drivers of soil

301   respiration (*Janssens & Pilegaard, 2003*).

302   Another explanation could be that the differences in soil respiration and Q_{10} values are driven

303   by the annual pattern of gross primary production which drives substrate supply to the root

304   and rhizosphere (e.g. *Bahn et al., 2008*). Currently several authors have reported productivity

305   should be considered to improve the prediction of soil respiration (*Bahn et al., 2008*; *Hibbard*

306   *et al., 2005*; *Zhang et al., 2016*). Numerous studies have shown close relations between soil

307   respiration and canopy photosynthesis at different timescales. Högberg et al. (*2008*) reported

308   that soil respiration was largely driven by recent primary production of the vegetation.

309   Monthly soil respiration was significantly related to LAI and GEP in our study (Figure 5A

310   and 5C). The finding agreed with the view of a short-term coupling of photosynthesis and soil

311   respiration. Likewise, Yuste et al. (*2004*) found that seasonal R_s was positively related to LAI.

312   Bahn et al (*2008*) suggested R_s was closely related to LAI across grassland sites. In our study,

313   LAI reflected the productivity of vegetation. There was similar monthly variation pattern of

314   LAI and T_a in our study, which in turn increased the difficulty to detect relationships of R_s in

315   relation to biological variable. Soil respiration is a complex biological process, composed of

316   several processes from both autotrophic and heterotrophic organisms. Besides soil

317   temperature and soil water content, it is known that soil respiration is partly explained by

318   forest type, stand age and altitude in subtropical forests (*Wang et al., 2011*). Additionally,

319   other variables such as management (i.e. fertilization, thinning and harvesting activities, *Gao*

320   *et al., 2014*; *Liu et al., 2011*), litter, soil microbial (*Linn & Doran, 1984*) and physical

321   properties, root biomass and extreme weather (e.g. warming, precipitation events, short-term

322   drought events), all have indirect and direct effects on soil respiration. However, how these

323   influence autotrophic and heterotrophic processes is not well understood and should be a

324   subject of further research.

325   **Conclusions**

326   Soil respiration in the forest exhibited similar daily and seasonal dynamic patterns, with its

327   highest values in summer and lowest values in winter, annual mean soil respiration was 44.1

328    $tCO_2 \cdot ha^{-1} \cdot a^{-1}$. Soil respiration indicated positive significantly correlation with soil temperature

329   ($P < 0.01$), it can explain 69.7% of temporal variation for R_s. No obvious related with soil

330   moisture on daily scale, but significant correlation with soil moisture during seasons except

331   winter, implying soil moisture played a crucial role in different growth phase. The model

332   compound by soil temperature and soil moisture, could explain 93.6% of seasonal variation

333   for R_s. The correspondent relationship between R_s and different soil temperature exhibited an

334   exhibited clear hysteresis. Soil respiration was significantly and positively ($P < 0.01$) in

335   relation to gross ecosystem productivity and LAI during our study, illustrating the

336   significance of biotic factors as crucial driving factors of soil respiration, and importance of

337   future research revealing correspondence mechanism of canopy photosynthesis and soil CO_2

338   flux.

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343   **Additional information and declarations**

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352   **Competing Interests**

353 The authors declare that there are no competing interests.

354 **Author Contributions**

355 Yuli Liu, Guomo Zhou and Huaqiang Du: conception and design; fieldwork; analysis and

356 interpretation; statistical analysis and writing the paper. Frank Berninger, analysis and critical

357 revision of the paper. Fangjie Mao, Xuejian Li and Liang Chen: fieldwork and statistical

358 analysis; Lu Cui, Yangguang Li and Di'en, Zhu: field work; analysis and interpretation.

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511

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.

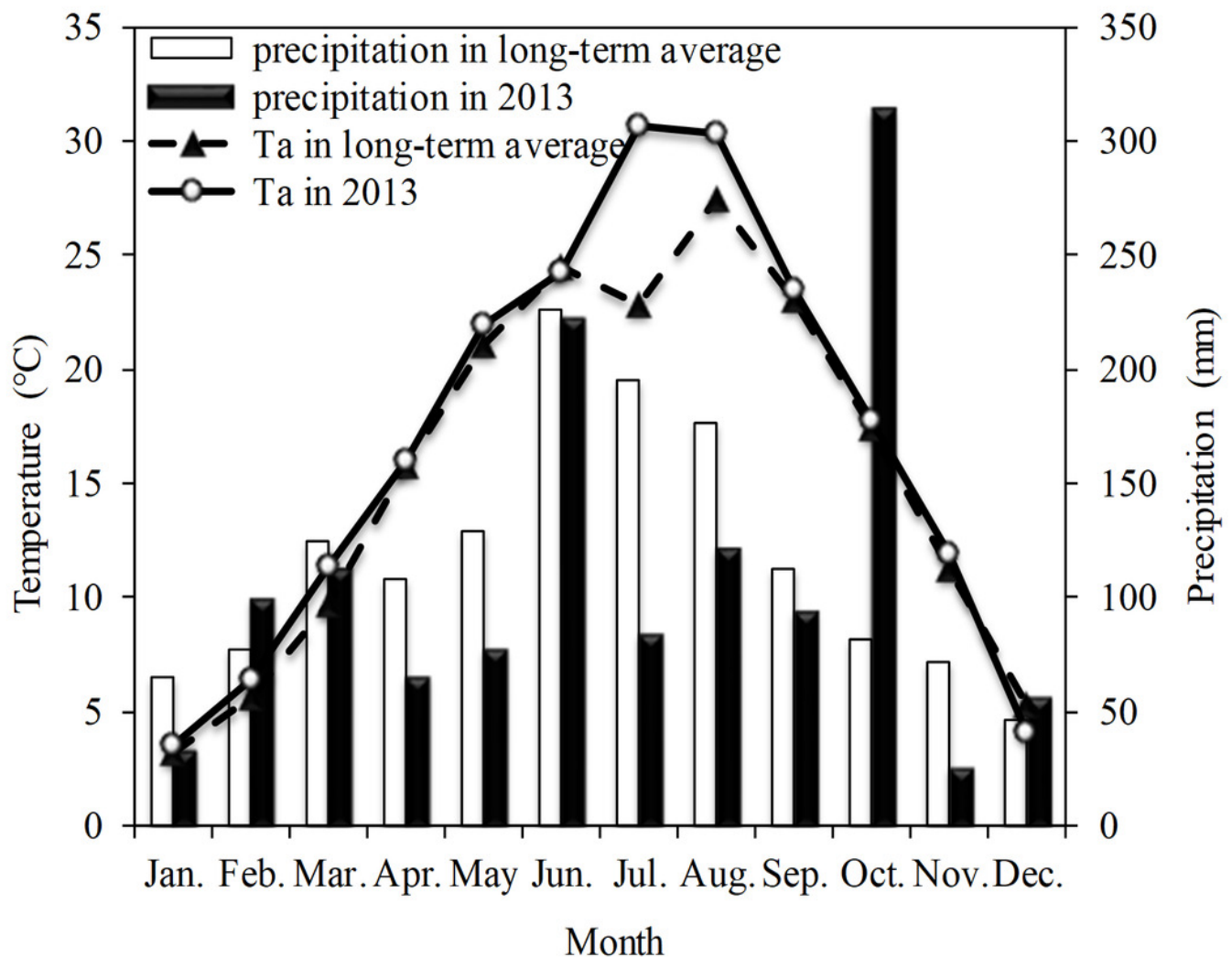



Figure 2

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).

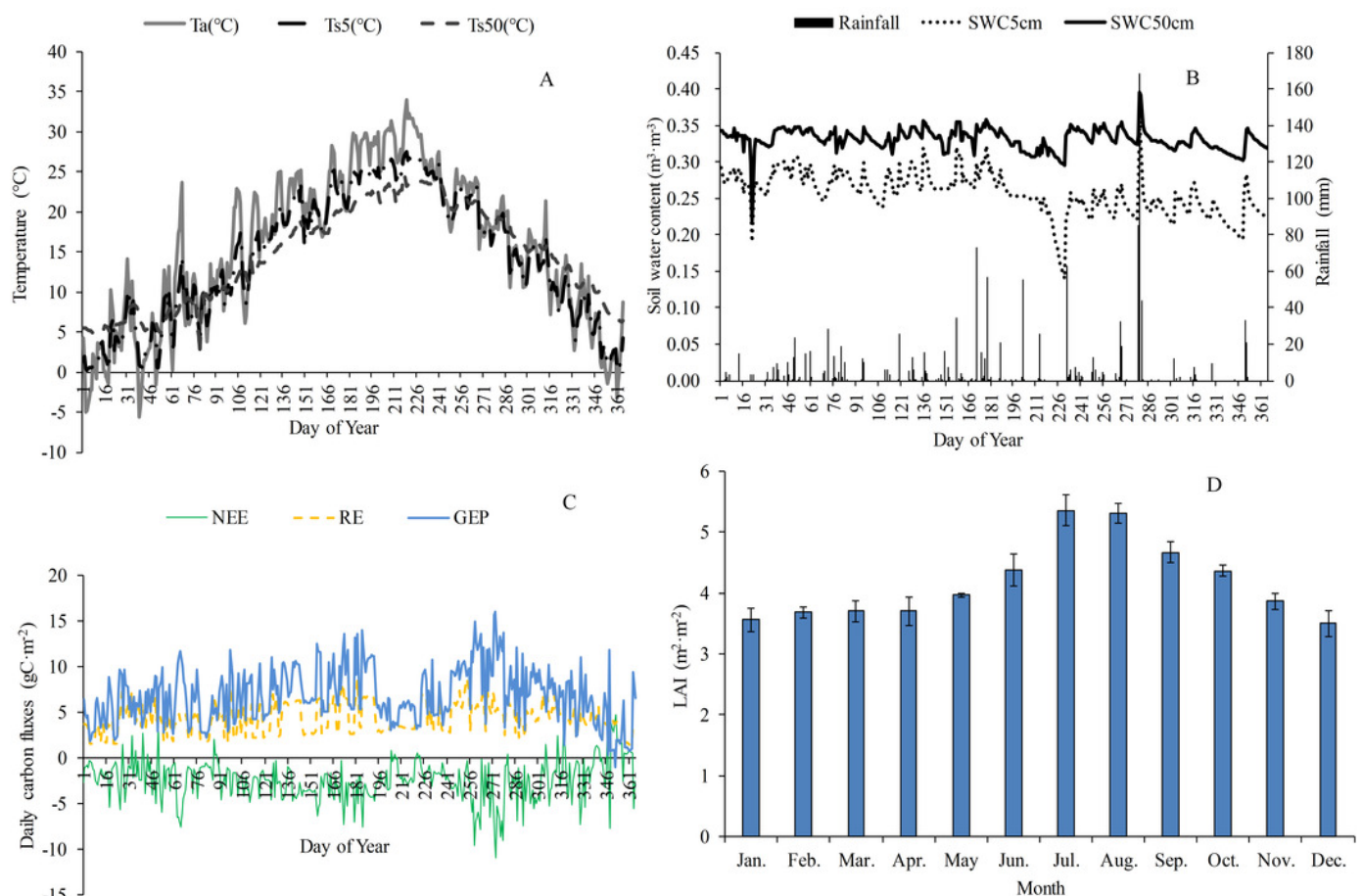



Figure 3

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).

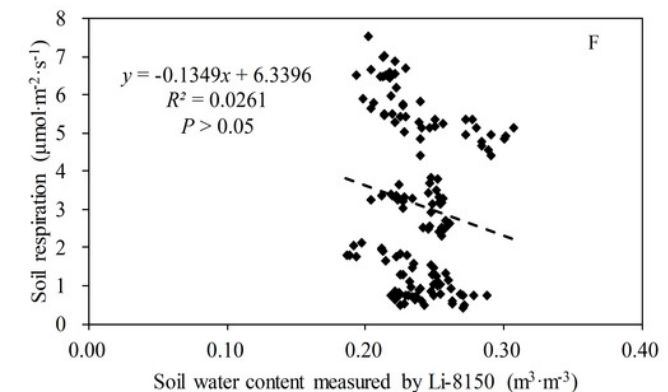
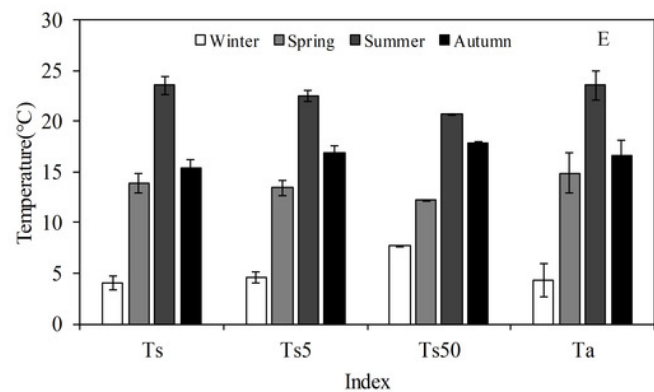
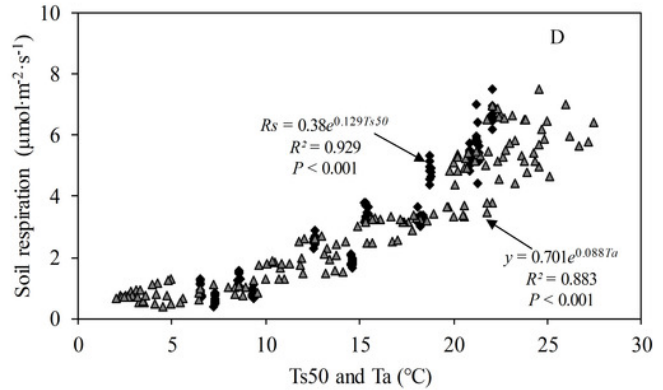
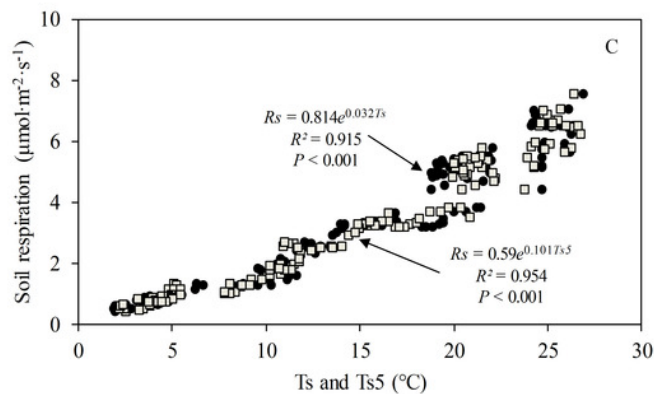
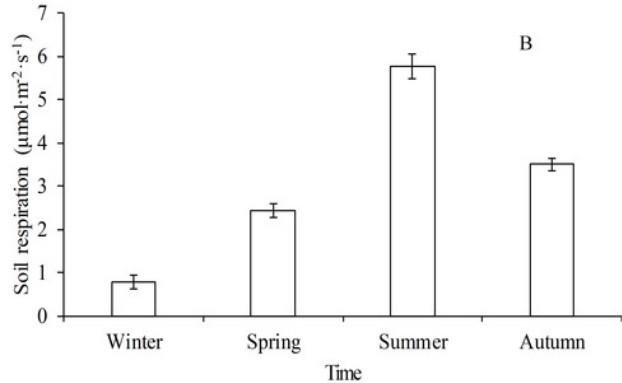
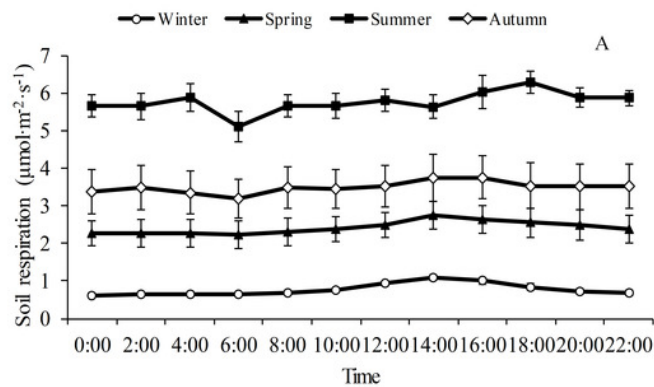



Figure 4

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.

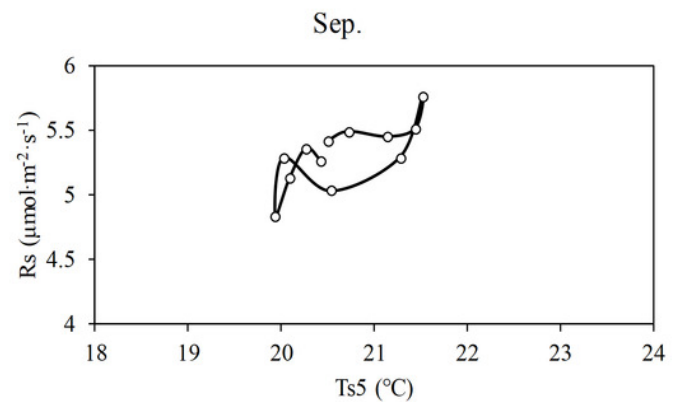
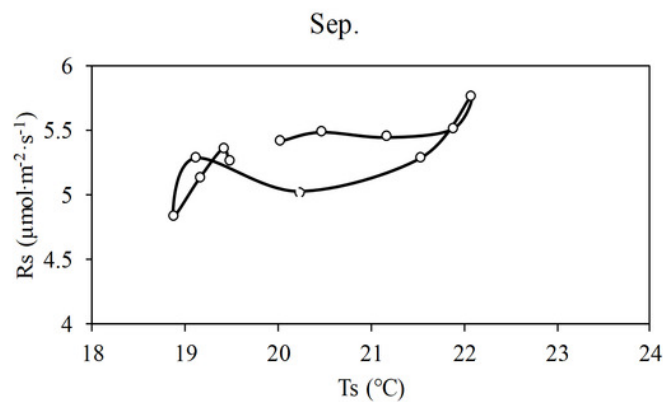
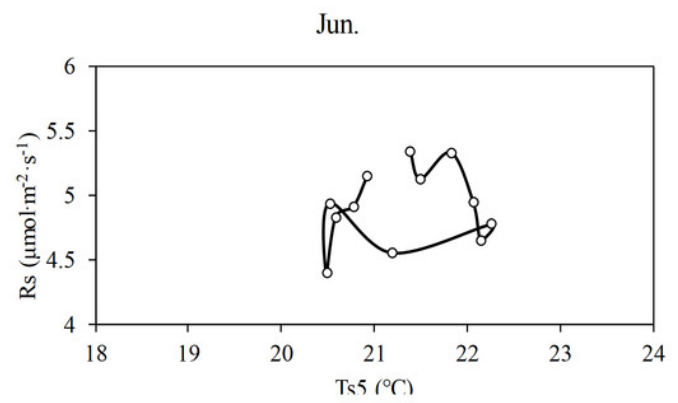
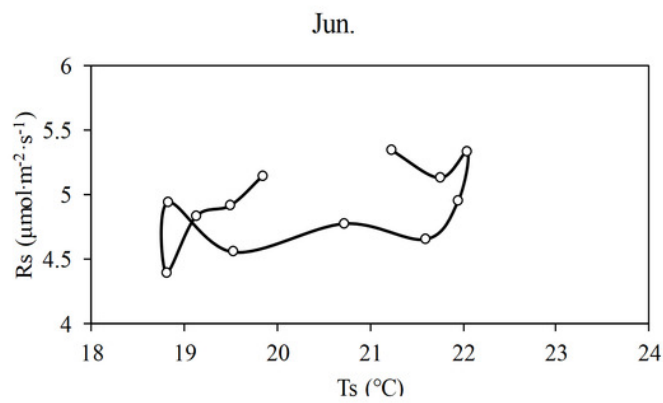
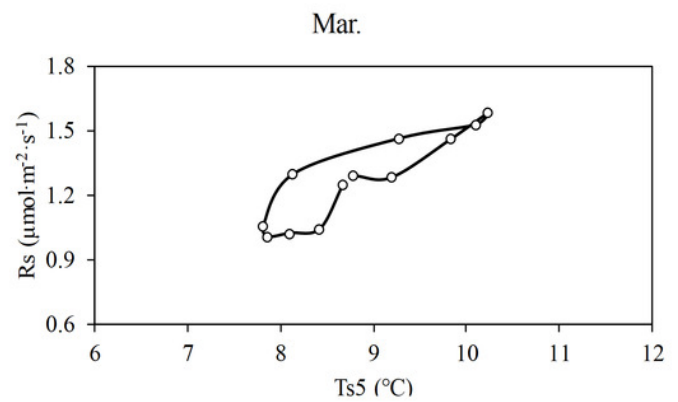
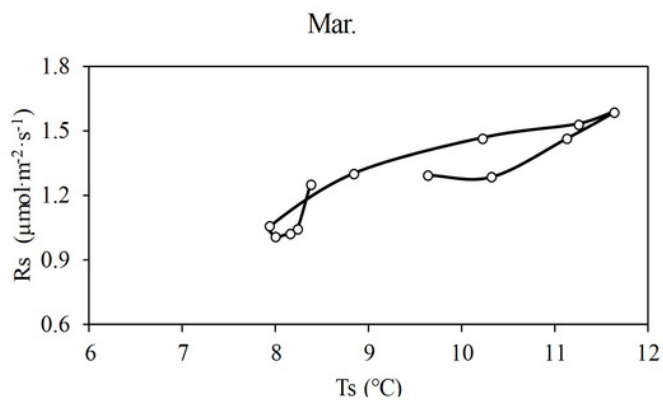
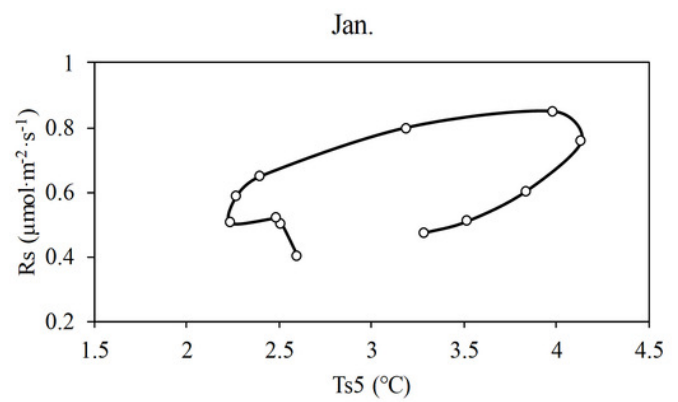
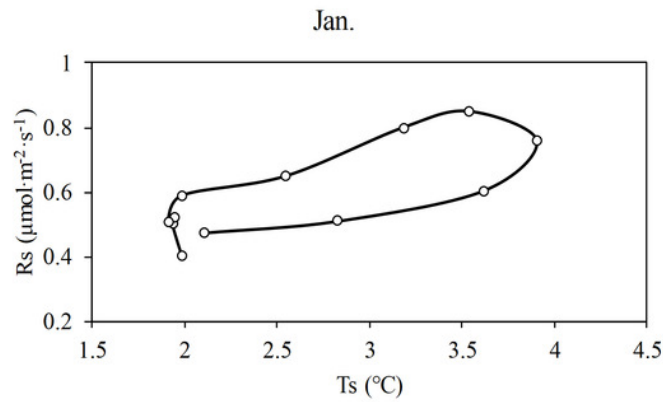
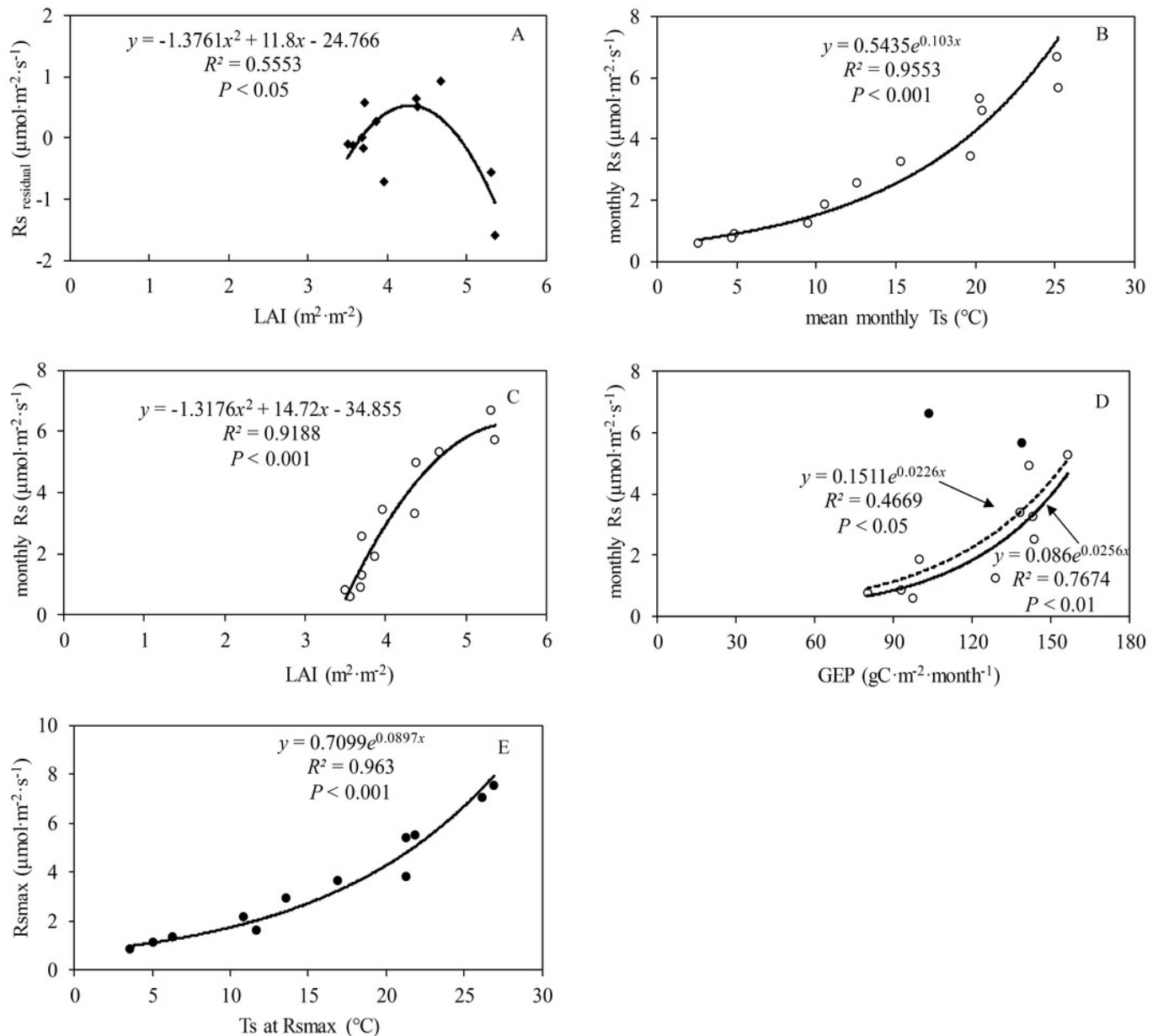



Figure 5

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

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.

2 **Table. 1**. Relationships between mean diurnal soil respiration (R_s) and soil temperature
3 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

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).

1   **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*

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

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.

1   **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

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