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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Moso bamboo has large potential to alleviate global warming through carbon sequestration. Since soil respiration (Rs) is a major source of CO_2 emissions, we analyzed the dynamics of soil respiration (Rs) and its relation to environmental factors in a Moso bamboo (Phllostachys heterocycla cv. pubescens) forest to identify the relative importance of biotic and abiotic drivers of respiration. Annual average Rs was 44.07 t CO_2 ha-1 a-1. Rs correlated significantly with soil temperature ($P < 0.01$), which explained 69.7% of the variation in Rs at a diurnal scale. Soil moisture was correlated significantly with Rs on a daily scale except not during winter, indicating it affected Rs. A model including both soil temperature and soil moisture explained 93.6% of seasonal variations in Rs. The relationship between Rs and soil temperature during a day showed a clear hysteresis. Rs was significantly and positively ($P < 0.01$) related to gross ecosystem productivity and leaf area index, demonstrating the significance of biotic factors as crucial drivers of Rs.

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

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19   **Abstract**

20   Moso bamboo has large potential to alleviate global warming through carbon sequestration. Since

21   soil respiration (R_s) is a major source of CO_2 emissions, we analyzed the dynamics of soil

22   respiration (R_s) and its relation to environmental factors in a Moso bamboo (*Phllostachys*

23   *heterocycla cv. pubescens*) forest to identify the relative importance of biotic and abiotic drivers

24   of respiration. Annual average R_s was 44.07 t CO_2 ha^{-1} a^{-1}. R_s correlated significantly with soil

25   temperature ($P < 0.01$), which explained 69.7% of the variation in R_s at a diurnal scale. Soil

26   moisture was correlated significantly with R_s on a daily scale except not during winter, indicating

27   it affected R_s. A model including both soil temperature and soil moisture explained 93.6% of

28   seasonal variations in R_s. The relationship between R_s and soil temperature during a day showed a

29   clear hysteresis. R_s was significantly and positively ($P < 0.01$) related to gross ecosystem

30   productivity and leaf area index, demonstrating the significance of biotic factors as crucial drivers

31   of R_s.

32   **1. Introduction**

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

34   respiration (R_s) is a major source of CO_2 emissions from terrestrial ecosystem, and as the second

35   largest carbon flux between the atmosphere and ecosystems it is surpassed only by gross primary

36   production (Raich and Potter ,1995). Soils release approximately 75-100 Pg C per year globally

37   (Bond-Lamberty and Thomson, 2010), nearly 10 times of the amount of CO_2 released by the

38   combustion of fossil fuels (Raich and Potter ,1995). Hence, slight shifts in R_s may cause profound

39   changes in the atmospheric concentration of CO_2 and in the accumulation of soil carbon

40   (Schlesinger and Andrews, 2000), thus subsequently affect global climate.

41   Considering the importance of forest ecosystems in the terrestrial carbon cycle and their response

42   to global climate, R_s and its dependence on environmental drivers have been the focus of numerous

43   studies. For instance, soil temperature and moisture of soils are two of the major environmental

44   drivers regulating R_s (Liu et al., 2016). Additionally, disturbances, e.g. fire (Muñoz-Rojas et al.,

45   2016; Köster et al., 2014), harvesting (Bahn et al., 2008), artificial warming and precipitation

46   changes (Li et al., 2017a), or land use changes (Liu et al., 2011; Willaarts et al., 2016) can also

47   have large effects on R_s. R_s is a complex biogeochemical process highly related to ecosystem

48   productivity, leaf area index, and soil fertility (Hibbard et al., 2005), proving coupling between

49   CO_2 assimilation by the vegetation and emissions from the soil (Bahn et al., 2008; Hibbard et al.,

50   2005). R_s is also influenced by the amount of litter (Oishi et al., 2013; Wu et al., 2017), vegetation

51   type (Mahecha et al., 2010; Wang et al., 2011), and composition of the soil microbial community

52   (Luo et al., 2016). However, many of the environmental drivers are correlated with each other,

53   making it difficult to distinguish and quantify the contribution of each environmental factor.

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

55   46°N-47°S (Lu et al., 2014). Globally, bamboo forests cover 31.5 million ha (FAO, 2010). With

56   more than 500 varieties and 39 species, China hosts the largest diversity of bamboo in the world,

57   and the 6.16 million ha bamboo forests account for 2.97% of the total forest area in China

58   (SFAPRC, 2015). Moso bamboo (*Phllostachys heterocycla cv. pubescens*) is appreciated for its

59   rapid growth and high rate of timber production (Guan et al., 2017). Moso bamboo forest is a major

60   forest type of subtropical forests in subtropical China (Song et al., 2013). Currently, the area

61 covered by Moso bamboo forests increases annually by approximately 3%, mostly due to

62 afforestation on wastelands (Chen et al., 2009), but also through conversion conifer and broadleaf

63 forests and farmland (Cui et al., 2011; SFAPRC, 2015). Moso bamboo provides many benefits,

64 including high income generation and other ecosystem services, to the forest owners.

65 Notably, the rate of carbon accumulation by Moso bamboo is high. Moso bamboo sequesters 4.91

66 - 5.45 t C ha^{-1} each year (Zhou and Jiang, 2004), showing great potential for alleviating global

67 warming by carbon fixation. Previous studies on Moso bamboo have concentrated on carbon

68 storage, balance and its distribution in the ecosystem (Li et al., 2013), productivity of bamboo

69 forest (Cheng et al., 2015; Isagi et al., 1997), and the variation in soil organic carbon stocks (Guan

70 et al., 2015). Previous studies reported a close relationship between R_s and biotic factors in other

71 forest types (Hibbard et al., 2005), suggesting a coupling between forest canopy assimilation and

72 carbon emissions from soil. However, comparatively little is known about bamboo forests. Thus,

73 given the ecological importance of Moso bamboo forests at regional scale, there is a need for

74 understanding the relationships between biotic and abiotic factors and R_s in this kind of ecosystem.

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

76 these with measurements of abiotic and biotic factors. Our aims were to explore the temporal

77 dynamics of soil respiration, and to identify the relative importance of the measured environmental

78 factors.

79 **2. Methods**

80 **2.1. Study site**

81 The measurements were done in a Moso bamboo forest with an eddy covariance flux tower in

82   Anji, Zhejiang Province, southeast China (30°28′34.5″N, 119°40′25.7″E) at 380 m elevation. The

83   study area has a typical subtropical monsoon climate with distinct seasons (Li et al., 2018; Peel et

84   al., 2007). The average annual air temperature and precipitation in 1981-2010 was 15.6 °C and

85   1413.2 mm, respectively. Monthly average rainfall and air temperature in the study period are

86   shown in Fig.1. The soil type in this area is yellow red soil (Chinese system of soil classification),

87   equivalent to Hapludult in USDA Soil Taxonomy (Soil Survey Staff of USDA, 1999), pH is from

88   4.4 to 4.8, and soil bulk density is 1.5 g·cm^{-3} (Chen, 2016).

89   The study area (1km around the eddy covariance flux tower) was covered by 86.1% of Moso

90   bamboo forest (Xu et al., 2013). The total area of the forest was 1687 ha. Stand density was 3235

91   culms per hectare, the average canopy height was 11 m with a mean diameter at breast height of

92   9.3 cm. There was only a sparse understory in the study area. The main management activities

93   were harvesting 6 or 7-year old bamboos, and a proportion of new bamboo shoots each year. The

94   forest was not fertilized nor weeded during the study period. Further detailed information of the

95   site is found in Mao et al. (2017). Moso bamboo has a biannual growth pattern. During "off years"

96   (which are the even numbers in our site, i. e. 2012, 2014, 2016) few new bamboo shoots are

97   produced, there is leaf senescence of old leaves, and new leaves grow vigorously (Qiu, 1984). In

98   "on years" which are years with uneven numbers more new bamboo shoots are produced and leaf

99   senescence is limited. In our study site, the study period in 2013 was an "on-year".

100   **2.2. Experimental design and measurement**

101   **2.2.1. Soil CO$_2$ flux measurement**

102   The soil CO$_2$ flux was measured using and automated system consisting of a LI-8100 analyzer and

103   a LI-8100-104 chamber and a multiplexer (LI-8150) (all LI-COR Inc., Lincoln, NE, USA). Soil

104   respiration measurements were done at two hour intervals between 0:00 and 22:00 on selected

105   sunny days for approximately two weeks (usually from day 10 to day 23 of every month) of every

106   month in 2013. The duration of each flux measurement was 2 minutes and the fluxes were

107   calculated by an exponential fit of CO_2 against time by Soil Flux Pro, version. One 40 m × 40 m

108   plot was established around the Flux tower within the forest. Sixteen sampling polyvinyl chloride

109   (PVC) soil collars (20 cm inside diameter, 10 cm height, and 5 cm plugged into the soil) were

110   randomly placed within the plot. All collars remained permanently in place throughout the study

111   period. There were few herbs in the Moso bamboo forest. To reduce the disturbance-induced

112   carbon dioxide emission, the first measurement started at least 24 h after insertion. The areas inside

113   collars were kept free of plants by cutting the plants carefully using scissors about monthly during

114   the year. The data and the performance of the equipment were checked regularly to ensure the

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

116   temperature (T_s, ℃) were monitored adjacent to each collar at 5 cm depth with 2 theta probes

117   inserted vertically (ML2x, Delta-T Inc., UK; Omega Inc., USA) provided with the system. We

118   defined March to May as spring, June to August as summer, September to November as autumn,

119   and January, February and December as winter.

120   **2.2.2. Measurements of environmental variables at the eddy covariance site**

121   T_s and SWC were monitored by soil temperature sensors (109SS, Campbell Inc., USA) and soil

122   moisture sensors (CS616, Campbell Inc., USA), respectively, at 5 cm, 50 cm and 100 cm depths

123   (Ts_5, Ts_{50}, Ts_{100}, SWC5, SWC50, SWC100) close to the eddy covariance tower. Air temperature

124 and relative humidity were measured using HMP45C probes (Vaisala, Helsinki, Finland) at 1 m,

125 7 m, 11 m, 17 m, 23 m, 30 m, and 38 m above the ground. All the data were recorded by a data

126 logger (CR1000, Campbell Inc., USA) and saved as 30-min averages.

127 **2.2.3. Biological factors measurements**

128 Gross ecosystem productivity (GEP) was obtained by eddy covariance (EC) technique. An open-

129 path infrared gas analyzer LI-7500 (Li-Cor Inc., Lincoln, NE, USA), in conjunction with a 3-

130 dimensional sonic anemometer CSAT3 (Campbell Inc., Logan, UT, USA), was placed at 38 m

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

132 CR1000 data logger (Campbell Inc., USA) as 30-min average values. The flux data was processed

133 using the EdiRe software (University of Edinburgh). A double-coordinate rotation was applied and

134 the Webb-Pearman-Leuning correction was conducted to remove the effects of air-density

135 fluctuations. Daily net ecosystem exchange (NEE) was calculated as the daily sum of the measured

136 CO_2 flux and the daily rate of change in CO_2 storage below the height of the EC system. Ecosystem

137 respiration (RE) was calculated for each 30-min by extrapolating the exponential regressions

138 between the night NEE at high-friction velocity and soil temperature at the 5 cm depth and summed

139 into the daily values. Daily gross ecosystem productivity (GEP) was estimated as the difference of

140 daily RE and daily NEE (Song et al., 2017).

141 The flux data were discarded when the following errors were observed (Yan et al., 2013; Yu et al.,

142 2006; Song et al., 2017) (1) the CO_2 flux was beyond the range of -2.0 to 2.0 mg CO_2 m^{-2} s^{-1},

143 CO_2 concentration was < 500 or > 800 mg m^{-3}, and water vapor concentration was outside the

144 range of 0–40 g m^{-3}; (2) abnormal values, i.e. when the absolute value of the difference between

145 a numerical value and a continuous five points was > 2.5 times of its variance; (3) the

146 measurements occurred during precipitation events; (4) the number of valid samples was < 15,000;

147 (5) low friction velocity was low(u^* < 0.2 m s^{-1}). Gaps occurred more frequently at night than

148 during the day. After data filtering, the annual flux data 64 % of the data were retained.

149 Gaps less than 2 h were linearly interpolated, gaps more than 2h were filled with the look-up-table

150 method, which were built up based on the two-adjacent-month periods and two main

151 environmental factors (photosynthetically active radiation and air temperature). For details

152 information, please see the literature by Song et al. (2017).

153 Leaf area index (LAI) was measured at 6:00-10:00 and 15:00-17:50 of sunny, no cumulus days

154 and with good visibility days. Measurements were done monthly using digital camera provided

155 with a fish-eye lens in combination with MODIS LAI following the methods of Li et al. (2017b).

156 LAI was reported as the average of three sample points chosen within the 20 m × 20 m plot on

157 non-rainy days. The LAI data was calculated as mean values ± SD (standard deviation).

158 **2.3. Data analysis**
159 We analyzed the soil respiration as a function of soil temperature assuming an exponential Q_{10}
160 type relationship.

161 $$R_s = ae^{bt} \qquad (1)$$

162 $$Q_{10} = e^{10b} \qquad (2)$$

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

164 parameters, Eq.1 (van't Hoff, 1884).The temperature sensitivity parameter, Q_{10}, was calculated by

165 Eq.2 (Sheng et al., 2010;Song et al., 2013).

166 One-way analysis of variance (ANOVA) and the least significant difference were carried out to

167   test the statistical significance of differences in soil respiration, environmental (Table 1) and biotic

168   factors (Table 2) between seasons. Regression (including nonlinear and linear regression) and

169   correlation analysis was performed to analyze the relationship between soil respiration, biotic and

170   abiotic variables. All analyses were conducted using the PASW software (PASW Statistics 18.0

171   for windows, SPSS Inc., Chicago, IL, USA).

172   **3. Results**

173   **3.1. Seasonal dynamics of environmental and biotic factors in Moso bamboo forest**

174   In 2013, the annual average air temperature was 1.2 ℃ higher and total precipitation 114.5 mm

175   lower than the long-term averages. The 30.7 ℃ in July and 30.3 ℃ in August (Fig. 1) were as much

176   as 7.9 and 2.8 ℃ higher, respectively, than the long-term averages. Precipitation was 57.2% and

177   31.5% of the long-term average in July and August, respectively. The annual rainfall in 2013 was

178   1298.7 mm, and occurred mostly from May to October. Additionally, it decreased by 57.18% in

179   July compared with the corresponding period of long term (Fig. 1), showing exceptionally hot and

180   dry conditions. Temperatures at different soil depths (T_{s5}, T_{s50}) and air temperature at 1m height

181   (T_a) exhibit a similar seasonal pattern (Fig.2A): a gradual increase from January to July, maximum

182   in July, and a slow decrease till December. T_{s5} and T_{s50} changed comparatively more smoothly and

183   steadily than T_a. Soil water content at 5 cm and 50 cm depths (SWC5 and SWC50) were obviously

184   affected by rainfall, and were at the lowest in July and August.

185   Seasonal variation in net ecosystem exchange (NEE), ecosystem respiration (RE) and gross

186   ecosystem productivity (GEP) showed several peaks during 2013. The lowest mean daily NEE

187   was detected in August (0.76 g C m^{-2}) (Fig. 2C), and highest in June and September. Additionally,

188   NEE was positive on some rainy and cloudy days. Mean daily NEE, RE and GEP was -2.11 g C

189   m^{-2} day^{-1}, 5.36 g C m^{-2} day^{-1} and 7.48 g C m^{-2} day^{-1}, respectively. Due to the impact of drought,

190   GEP decreased significantly in July and August, being 59.9% and 80.0%, respectively, of GEP in

191   the corresponding period in 2011 (Chen et al., 2016). LAI remained at approximately 3.6 in winter

192   and spring, increased gradually starting from March, and reached a maximum (5.92) in July (Fig.

193   2D). Thereafter, LAI decreased slowly, exhibiting the typical growth characteristic of Moso

194   bamboo in an "on year" (Chen, 2016).

195   **3.2. Diurnal variation of soil CO_2 fluxes and its response to temperature**

196   Soil respiration (R_s) in our forest presented similar diurnal dynamics across all seasons (Fig. 3A).

197   After a daily minimum occurring between 05:00 to 07:00, it increased slowly reaching the

198   maximum value between 14:00 to 16:00, and then decreased gradually. There were, however, big

199   differences in R_s between months. Monthly maximum values of R_s ranged from 0.75 in January to

200   7.52 µmol m^{-2} s^{-1} in August.

201   Monthly mean values of R_s correlated positively with both soil temperature at 5 cm depth (T_{S5})

202   measured by the EC system and air temperature (T_a) (P < 0.01, not shown), with the correlation

203   with T_{s5} being higher (Fig. 3B, Table 2). An exponential relationship was used to estimate R_s based

204   on T_s (Table 1). T_s explained 69.7% variation of the variation in R_s at a diurnal scale, whereas T_{s5}

205   explained 63.9% (not shown). Both exponential regression models were statistically significant (*P*

206   < 0.01). Plotting the diurnal variation of R_s against T_s, and T_{s5} (Fig.4) showed a clear hysteresis.

207   Additionally, there was slight discrepancy in the elliptic shape of T_s and T_{s5}, and the subtle

208   difference in elliptic shape of both could explain the coefficient or determination (R^2) of

209   exponential regression in the relationship of T_s and T_{s5} (not shown).

3.3. Seasonal dynamics of soil CO$_2$ fluxes and its driving factors

210

211   Soil respiration followed a clear seasonal pattern in soil respiration (Fig. 3A), being highest in

212   summer with 5.77 μmol CO$_2$ m^{-2} s^{-1}, followed by autumn (3.50 μmol CO$_2$ m^{-2} s^{-1}), and spring (2.42

213   μmol CO$_2$ m^{-2} s^{-1}), and lowest in winter (0.76 μmol CO$_2$ m^{-2} s^{-1}). The average annual soil CO$_2$ flux

214   was 3.11 μmol CO$_2$ m^{-2} s^{-1}, equating to an annual R$_s$ of 44.07 t CO$_2$ ha^{-1} a^{-1}. Temperatures at

215   different heights and depths presented similar seasonal dynamics, being highest in summer and

216   lowest in winter (Fig. 3C). Furthermore, Q_{10} values were small in summer and large in winter

217   (Table 1).

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

219   respiration (Table 2 and Fig. 5).

220   Within each seasonal, there was a complex linear relationship between SWC and R$_s$, with

221   significant ($P < 0.01$) negative correlation in summer (R= -0.796, R_s = -19.101*SWC+10.368),

222   positive linear correlational in autumn ($P < 0.01$, R= 0.552, R$_s$ = 47.663*SWC-7.012) and spring

223   (P< 0.05, R= 0.331, R$_s$ = 36.661*SWC-6.708), but no correlation ($P > 0.05$) in winter (R= 0.008),

224   indicating that SWC played crucial role in R$_s$ at the growing period of Moso bamboo. Soil

225   temperature and soil moisture showed significant linear relationship in the summer (R= -0.939,

226   T$_s$=-0.013*SWC+0.559, $P < 0.001$).

227   An exponential equation model was used to fit the relationship between different temperatures (T$_s$,

228   T$_{s5}$) and soil respiration (Fig.3C). The equations of T$_{s5}$-Rs (R^2= 0.954) and T$_{s50}$-R$_s$ (R^2= 0.929)

229   both showed higher R^2 than that of T$_s$-R$_s$ (R^2= 0.915), possible because of the relative stability of

230   soil temperature profile measurement in eddy covariance system. Furthermore, due to the complex

231 relationship between SWC and R_s, as well as considering combination of temperature and soil

232 moisture, six models were compared that predict R_s based on soil temperature and soil moistures

233 (Table 3). Based on *RMSE* and *R^2*, the model (R_s=a + b*exp(c*T_s) +d*T_s*SWC) showed best

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

235 with a soil temperature(T_s)-soil respiration(R_s) equation (Fig.3C, *R^2*= 0.915), It showed a slight

236 increase *R^2* (Table 3, *R^2*= 0.936).

237 **4. Discussion**

238 Our work demonstrates the importance of three factors that affect soil respiration in Moso bamboo:

239 temperature, soil water content and either productivity or LAI. The importance and interactions of

240 the factors will be discussed subsequently.

241 Of the three factors, soil temperature was the dominant driver of soil respiration with an *R^2* of over

242 0.8 (Fig. 3C and 5B). Seasonal change of R_s has been investigated in varying ecosystems. Soil

243 temperature and soil water content are commonly considered to be two major determinants of

244 seasonal variations in measured R_s (Davidson et al., 1998; Davidson et al., 2006a; Davidson et al.,

245 2012; Sihi et al., 2018). In this study, soil respiration increased with the rising of soil temperature.

246 Similar results were explored by Shi et al. (2012) on a global scale. However, soil temperature

247 explained only 62.7% variation of soil respiration during summer (June, July and August). This

248 was not only due to a lower variation of soil temperature during summer months, but also, as

249 shown in Table 1, the temperature sensitivity of soil respiration was markedly lower in the summer,

250 which was likely caused by low SWC values. Additionally, plots of soil respiration against daily

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

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

253 Song et al. (2013). Depth of the soil temperature measurement affected the explanatory power of

254 soil temperature. The explanatory power of the temperature in the organic layer was highest and

255 decreased with the depth of the measurements. This indicates that most of the respiration originates

256 from the organic layer (Davidson et al., 2006b). Zhang et al. (2016) made similar observations in

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

258 correlated with soil temperature at 10 cm depth.

259 The relationship between soil carbon efflux and soil temperature showed a diurnal hysteresis (Fig.

260 4). This indicates that there is a delayed effect of the rapidly varying temperature and diurnal

261 variation of soil respiration, similar to the studies by Högberg et al. (2008), Abramoff et al. (2017)

262 and Savage et al. (2009). One explanation is different diurnal temperature pattern at different

263 depths and delays due to the transport of CO_2 from the sites of respiration to the soil surface (Graf

264 et al., 2008). Furthermore, other research suggested that the length of the delay could vary among

265 different species (Raich and Schlesinger, 1992). The hysteresis could also be an artifact for

266 measuring soil temperature at a different depth than respiration is occurring. However, we tried

267 different depths to measure soil temperature. Since the depth of the measurements of soil

268 temperature varies between studies, it might be difficult to compare the sensitivity of soil

269 respiration to soil temperature between studies (Zhang et al., 2016). Previous research suggested

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

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

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

273   photosynthetic products and (2) diurnal variations of soil water content near the critical value

274   (Bahn et al., 2008; Davidson et al., 2012; Wang et al., 2015; Sihi et al., 2018), while further reasons

275   for this (especially in winter) are needed controlled experiments to explore and demonstrate.

276   The relationship between soil respiration and soil moisture was more complicated in our study.

277   Soil moisture improved marginally our models of soil respiration with a better fit of the models

278   particularly in the dry summer 2013. No significant correlation was found between soil respiration

279   and soil moisture in 2013 (Fig. 3D). Similar findings had been reported for Moso bamboo forest

280   in Zhejiang province (Song et al., 2013). However, soil moisture had a negative statistically

281   significant ($P < 0.001$, $R = -0.796$, $R_s = -19.101*SWC+10.368$) correlation with soil respiration in

282   summer while correlation in the other seasons was positive. Previous observation indicated a

283   pronounced correlation between R_s and SWC in subtropical forests (Sheng et al., 2010; Liu et al.,

284   2011). The negative correlation of soil respiration and soil moisture in our study was probably

285   caused by a spurious correlation of soil temperature and soil moisture during summer ($R = -0.939$,

286    $T_s = -0.013*SWC+0.559$, $P < 0.001$). The cause of a nonexistent or negative linear correlation

287   between SWC and Rs could be that natural variation of SWC covers only a part of response curve

288   (at low to medium SWC, R_s depends positively on it because water is limiting, then there might

289   be a plateau and at high SWC oxygen transport to the soil depth and transport of CO_2 back might

290   be blocked) (Linn and Doran, 1984; Xu et al., 2004). When we fitted non-linear models to soil

291   respiration using temperature and soil moisture we got only a small increase in the R^2 when soil

292   moisture was included into the model. We have also checked the interaction between SWC and

293   temperature (shown in Table 3) and our best model (last row in Table 3) shows that a model which

294   includes interactions was the best. This indicates that soil moisture was, even in the dry year of

295   2013, not an important limitation of soil respiration.

296   The models of soil respiration suggest that the temperature sensitivity of soil respiration declines

297   when soil moisture is decreasing (Almagro et al., 2009; Jassal et al., 2008; Wang et al., 2006), this

298   may be due to the diurnal variation of soil moisture near the criticality value. Also, Q_{10} varied over

299   the different seasons (Table 1). Due to smaller amplitude of soil temperature in deeper layers

300   (Pavelka et al., 2007), Q_{10} values estimated from deeper soil layers tended to be larger than those

301   of shallower layers. This can partly explain the discrepancy between T_a, T_s, and T_{s5}. Q_{10} was about

302   2.80 in our study, within range of 1.33~5.53 estimated for forests in China (Chen et al., 2008),

303   lower than 4.09 in Moso bamboo forest of central Taiwan (Hsieh et al., 2016), but higher than

304   median of 2.0~2.4 (Hashimoto, 2005).

305   Previous observation pointed out that annual Q_{10} value was not only an indicator of the response

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

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

308   Another driver of soil respiration is the phenology of Moso bamboo which shows a large variation

309   in below ground activities. In the spring, carbon is allocated to the production of new bamboo

310   shoots. After bamboo has completed its main growth period in summer and new leaves are fully-

311   expanded, it accumulates nutrient substance and allocates its main growth to the rhizome. Then in

312   autumn Moso bamboo starts to hatch bamboo shoots for the next year (Chen et al., 2016). In this

313   growing phase, soil moisture was a key factor for soil respiration. Subsequently, the stand got into

314   overwintering stage. Soil moisture became less important in this period. Consequently, the

315   importance of soil moisture for soil respiration varies among seasons and was more important

316   during the time of active growth of Moso bamboo. However, soil temperature rather than soil

317   moisture remained the most important drivers of soil respiration (Janssens and Pilegaard, 2003).

318   The explanation for the differences in soil respiration and Q_{10} values are driven by the seasonal

319   pattern of gross primary production which drives substrate supply to the root and rhizosphere

320   (Bahn et al., 2008). Currently several authors have reported productivity should be considered to

321   improve the prediction of soil respiration (Bahn et al., 2008; Hibbard et al., 2005; Vargas et al.,

322   2011; Zhang et al., 2016). Numerous studies have shown close relations between soil respiration

323   and canopy photosynthesis at different timescales. Högberg et al. (2008) reported that soil

324   respiration was largely driven by recent primary production of the vegetation. Monthly soil

325   respiration was significantly related to LAI and GEP in our study (Fig. 5A, 5C and 5D). The

326   finding agreed with the view of a coupling of photosynthesis and soil respiration. Likewise, Yuste

327   et al. (2004) found that seasonal R_s was positively related to LAI. Bahn et al (2008) suggested R_s

328   was closely related to LAI across grassland sites. In our study, LAI was closely related to the

329   productivity of vegetation. There was similar monthly variation pattern of LAI and T_a in our study,

330   which in turn increased the difficulty to detect relationships of R_s in relation to biological variable.

331   Soil respiration is a complex biological process, composed of several processes from both

332   autotrophic and heterotrophic organisms. Besides soil temperature and soil water content, it is

333   known that soil respiration is partly explained by forest type, stand age and altitude in subtropical

334   forests (Wang et al., 2011). Additionally, other variables such as management (i.e. fertilization,

335   thinning and harvesting activities, Gao et al., 2014; Liu et al., 2011), litter, soil microbial (Linn

336   and Doran, 1984) and physical properties, root biomass and extreme weather (e.g. warming,

337   precipitation events, short-term drought events), all have indirect and direct effects on soil

338   respiration. However, how these influence autotrophic and heterotrophic processes is not well

339   understood and should be a subject of further research.

340   **5. Conclusions**

341   Soil respiration (R_s) in the Moso bamboo forest exhibited both daily and seasonal dynamic

342   patterns, with its highest values in summer and lowest values in winter. Soil respiration correlated

343   positively with soil temperature ($P < 0.01$), which explained 69.7% of variation in R_s at a diurnal

344   scale and 91.5% of variation in Rs for the whole year. R_s correlated positively with soil moisture

345   in spring, autumn, and negatively in summer, implying that moisture played a crucial role in

346   different growth phases, but did not correlate significantly on daily scale, this may result from soil

347   carbon substrate supply limiting soil microbial respiration in summer, and enhancing soil

348   respiration in winter given substrate diffusion to the reaction site, which is generally driven by the

349   thickness of the soil water film. The model that included soil temperature and soil moisture

350   explained 93.6% of the seasonal variation in R_s. The relationship between R_s and different soil

351   temperature exhibited a clear hysteresis. Soil respiration correlated positively ($P < 0.01$) with gross

352   ecosystem productivity and LAI in our study, showing the significance of biotic factors in affecting

353   soil respiration, and a need for future research to analyze the relationship between canopy

354   photosynthesis and soil CO_2 flux.

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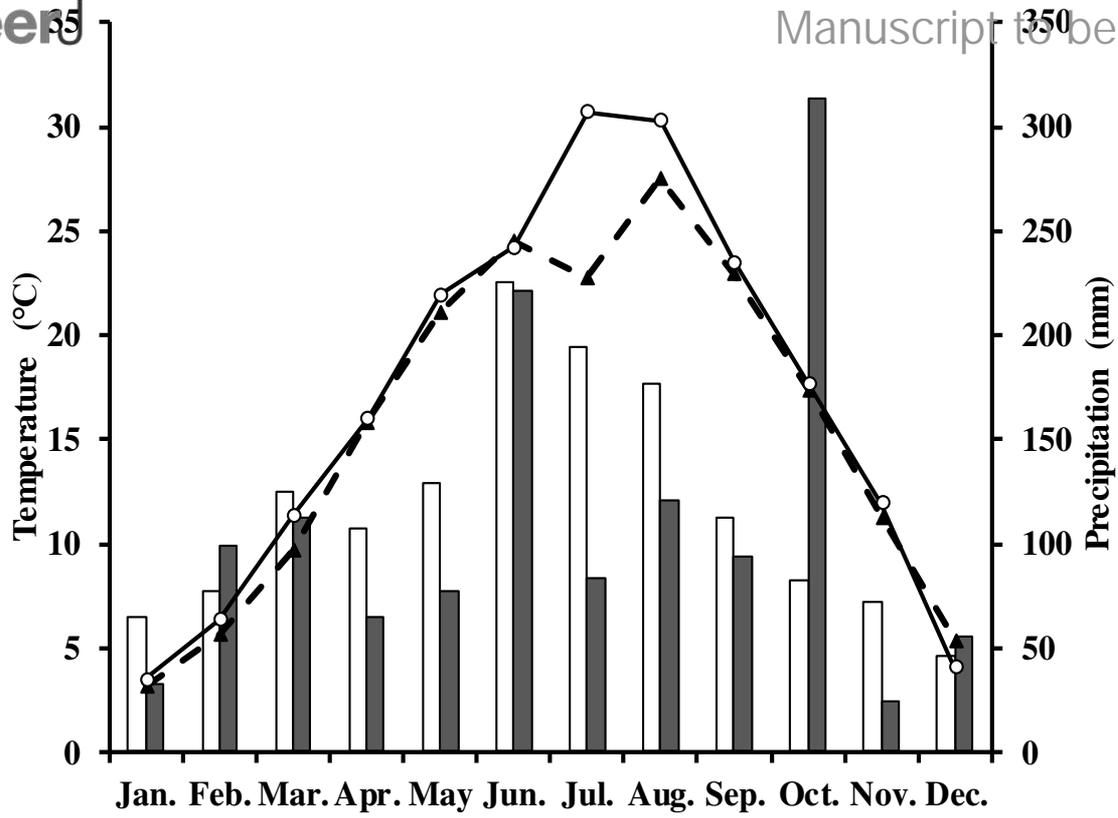
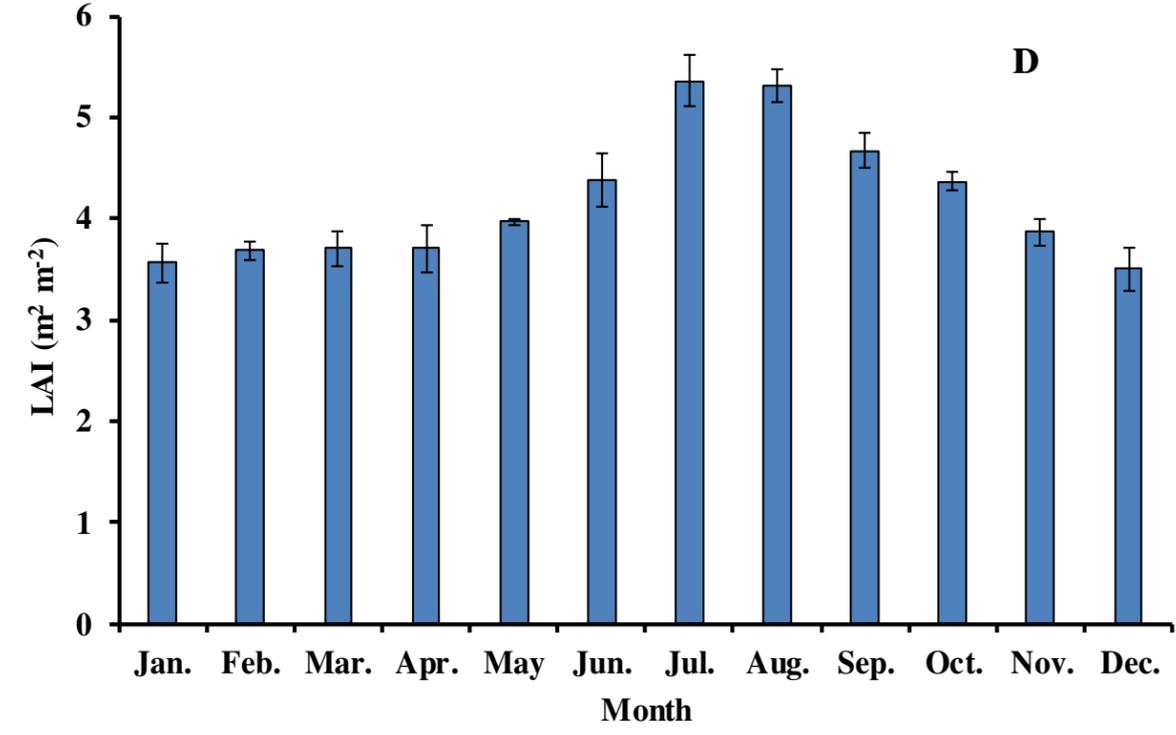
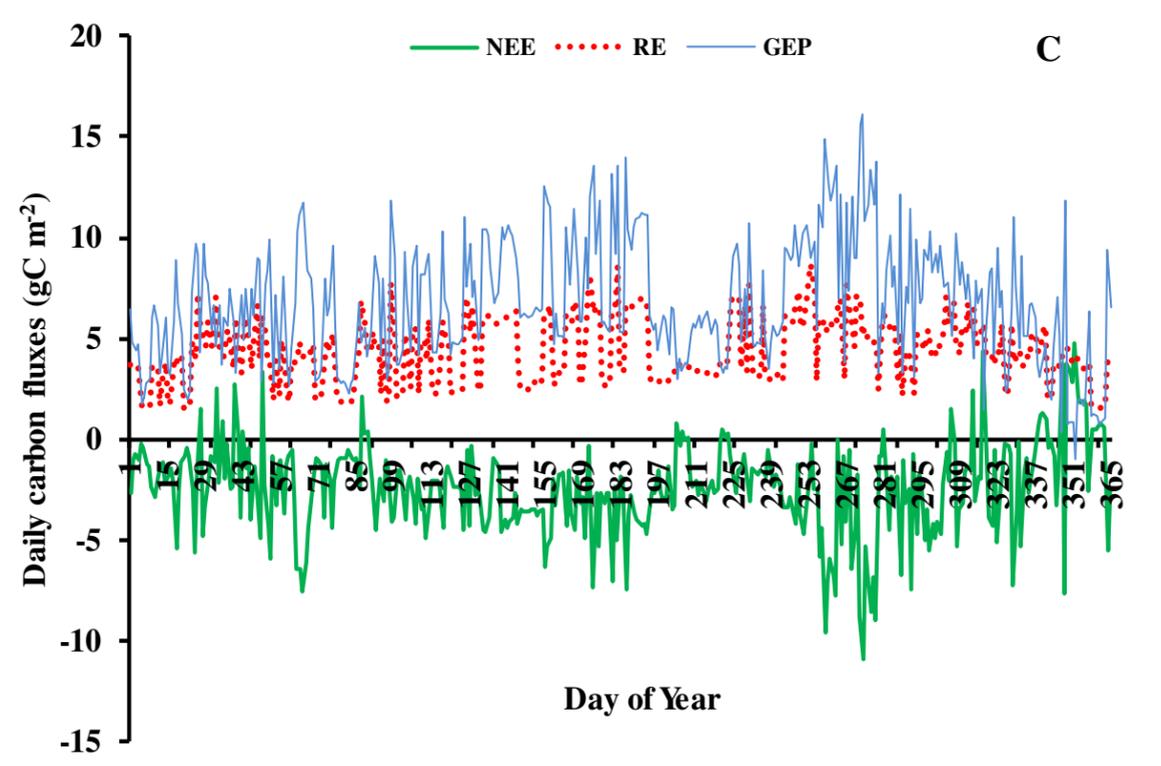
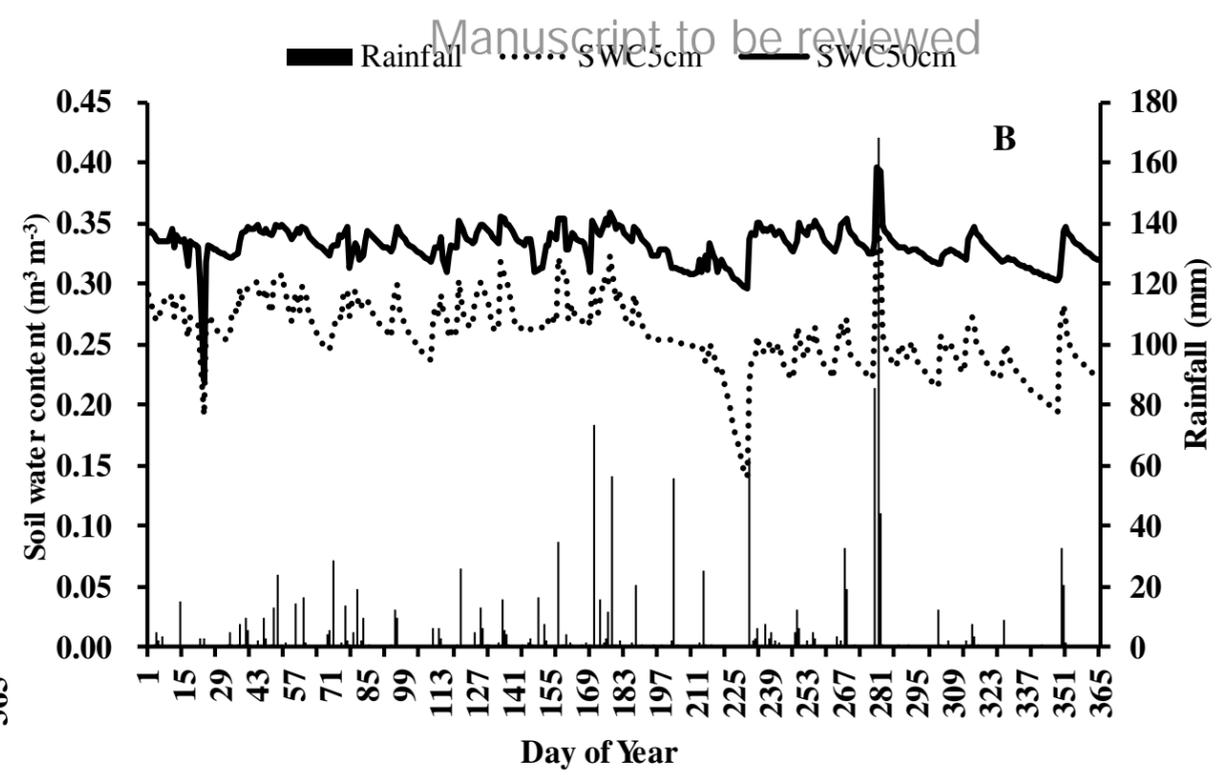
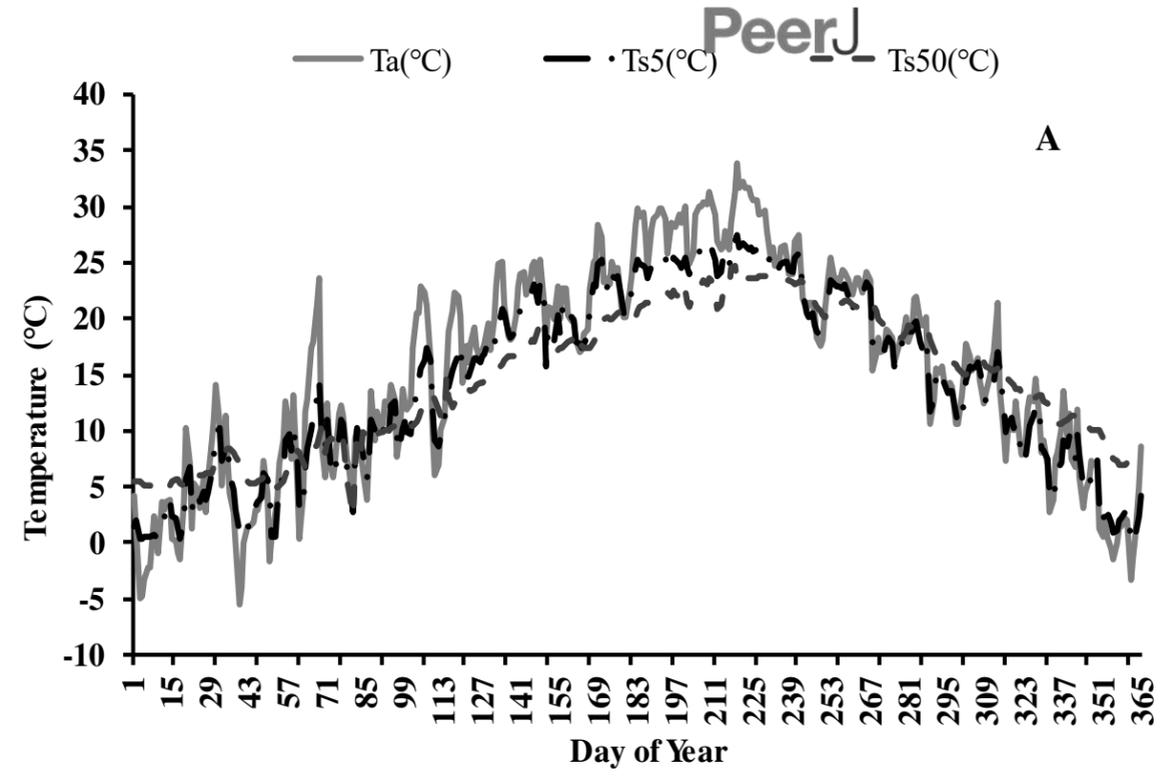
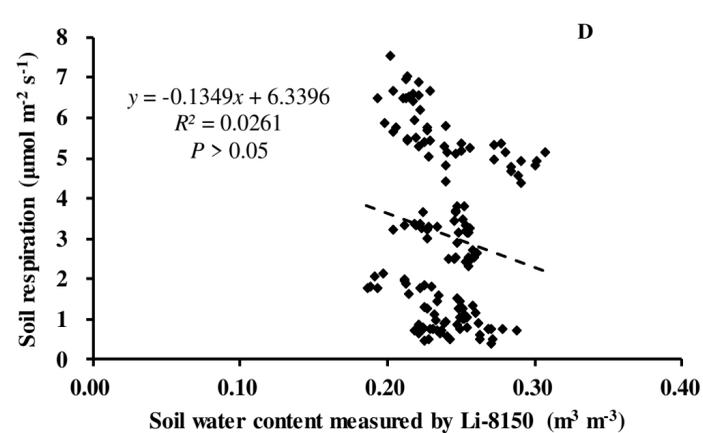
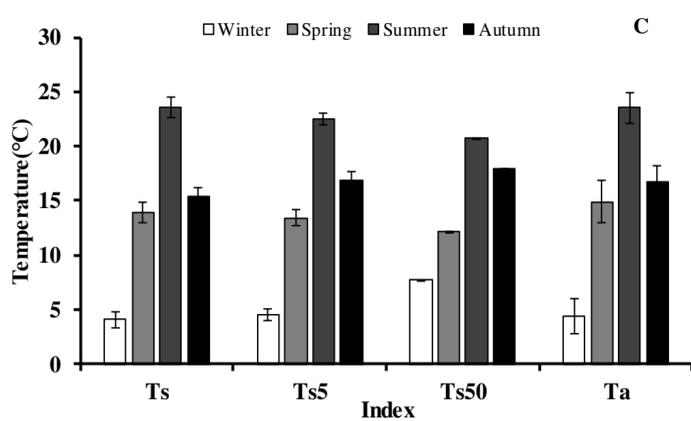
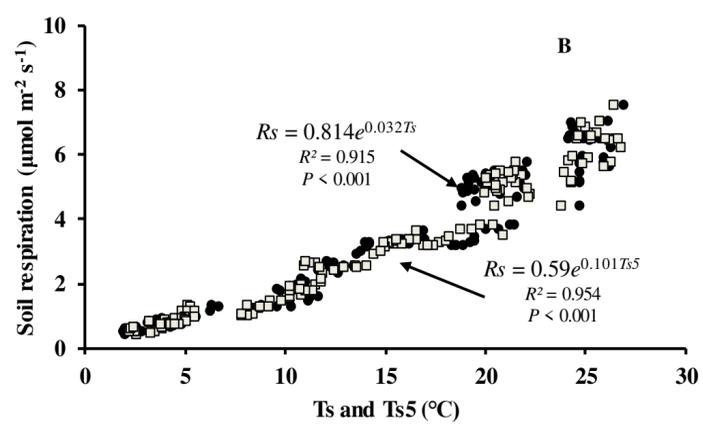
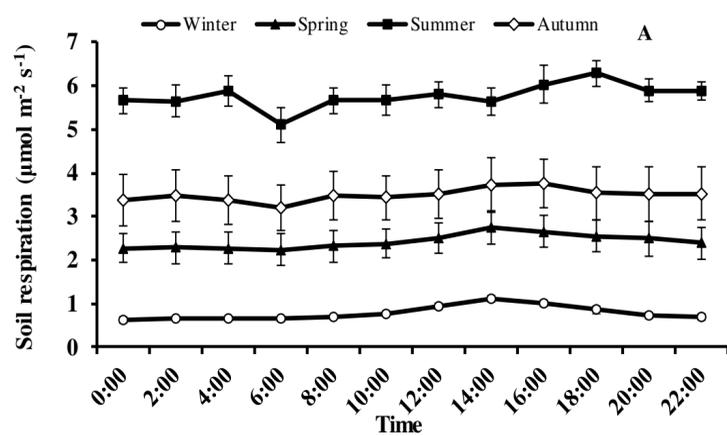
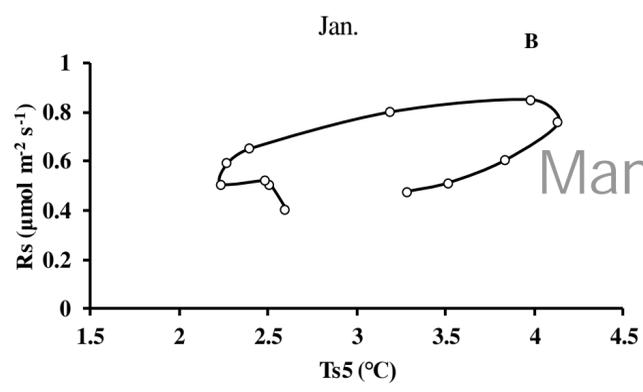
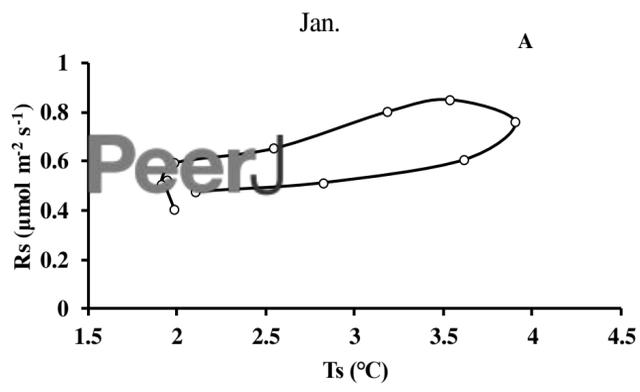
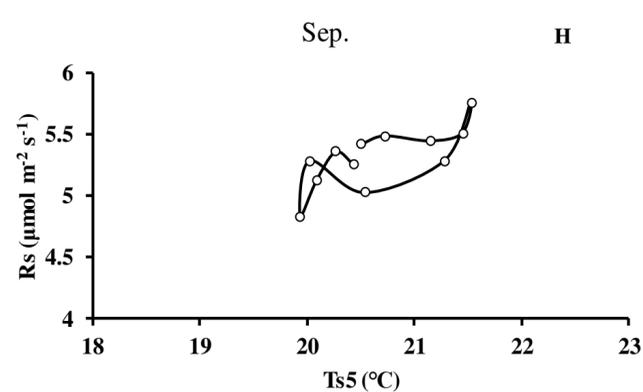
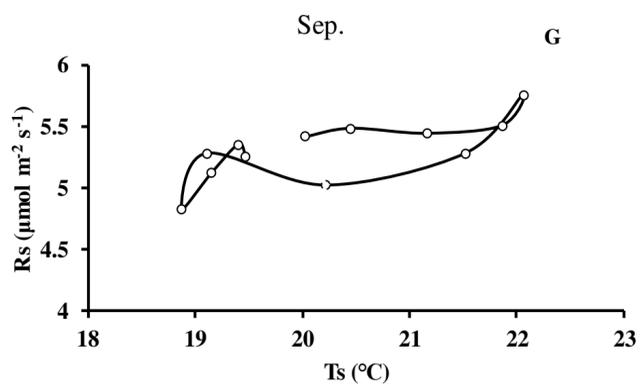
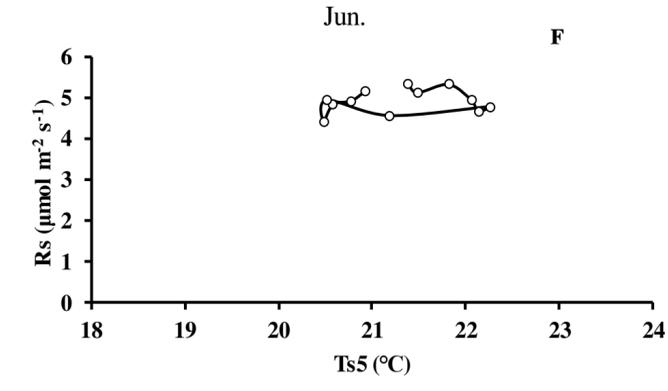
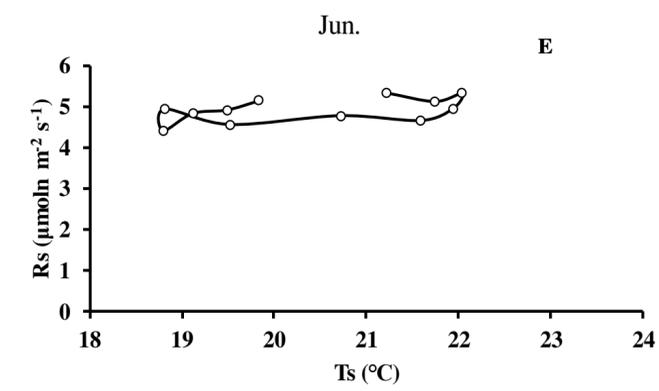
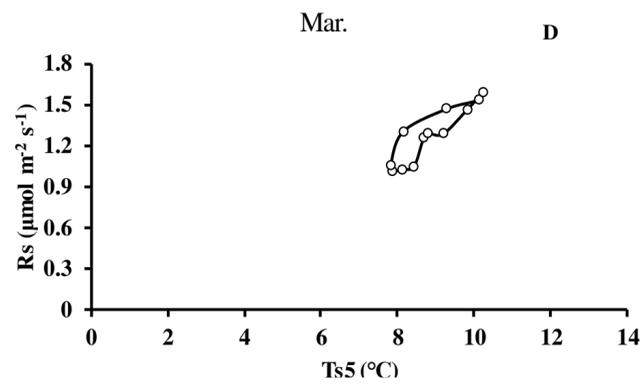
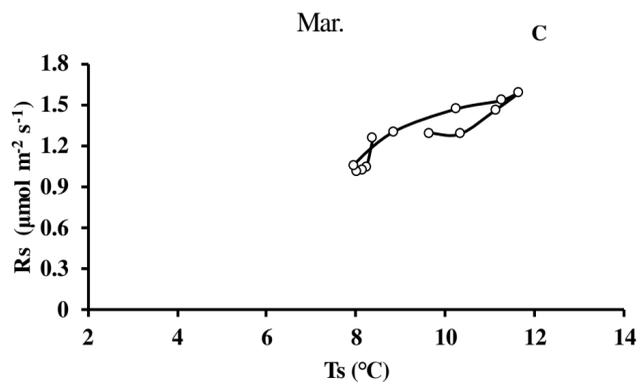
560

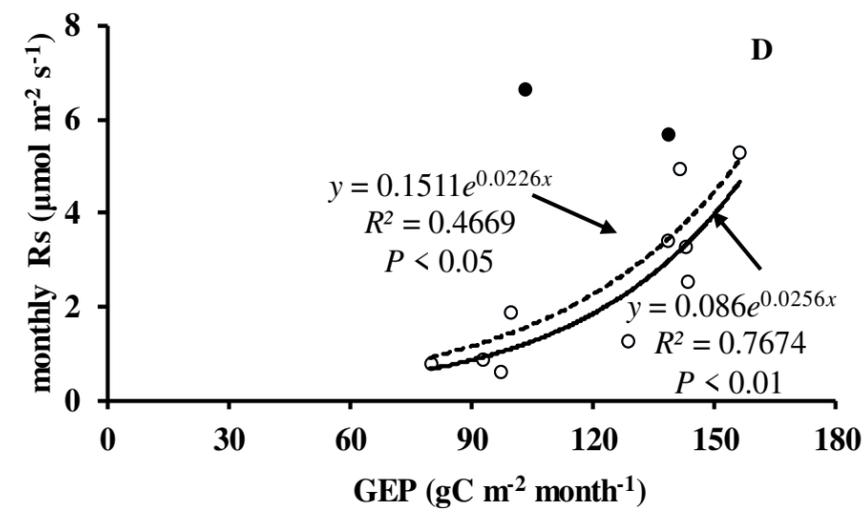
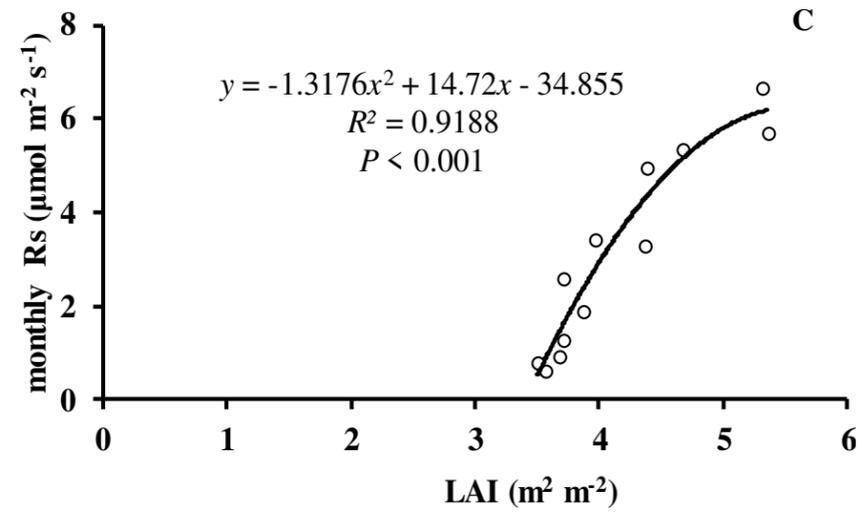
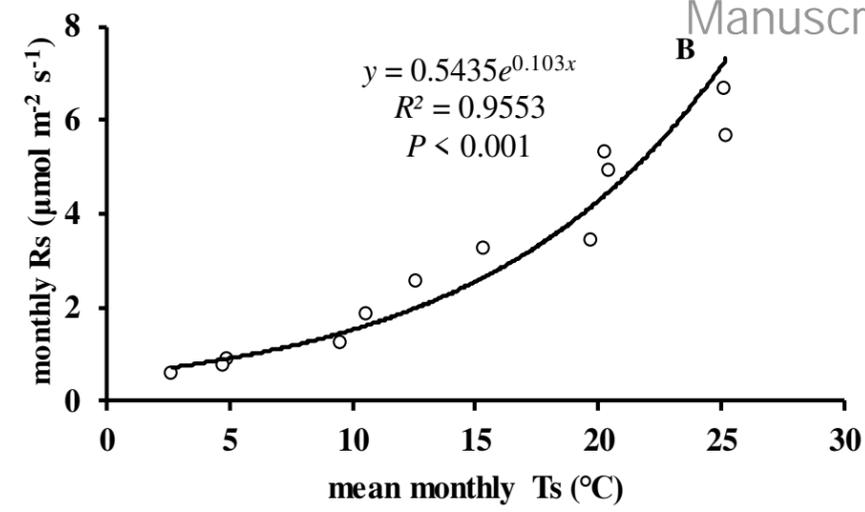
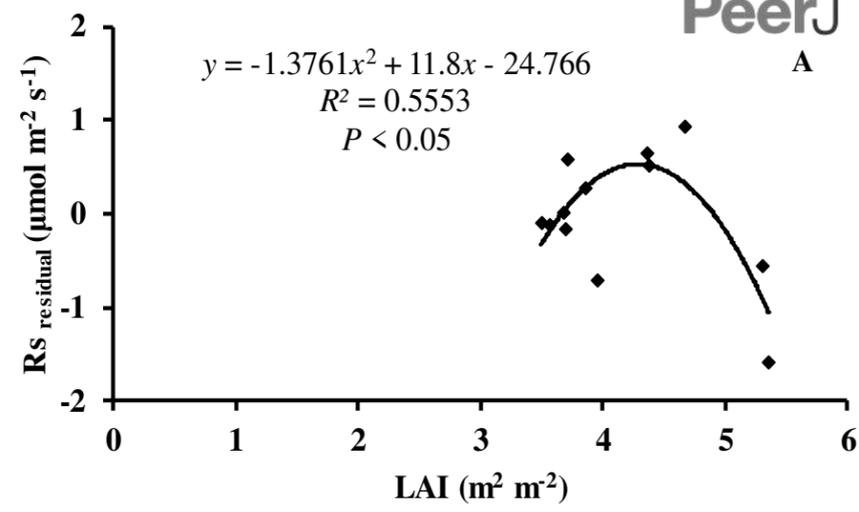
Monthly and long-term average air temperature (T_a) and precipitation at the study site

White circles are monthly air temperature in 2013, black triangles denote long-term average air temperature; grey rectangles are monthly precipitation in 2013, white ones denote long-term average precipitation.

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

(A) daily temperature (°C) of air (Ta) and soil at 5 cm($T_{s5)}$,50cm(T_{s50}) depth, (B) Daily rainfall amount (mm) and soil water content ($m^3 m^{-3}$) at 5 cm depth (SWC_5) and 50 cm depth (SWC_{50}), (C) daily carbon fluxes (NEE, RE, GEP, gC m^{-2}), (D) mean monthly LAI ($m^2 m^{-2}$) during the study period Mean ± SD (n=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, T_s, black circle, T_{s5}, white diamond, n=144), and (C) seasonal variation of different temperatures; (D) relationship between soil water content and soil respiration (n=144) error bars indicate standard deviation of the means (n=12).

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.

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

(A) Residuals of observed minus predicted (calculated by the best model in the last row of Table 3) values of R_s in relation to monthly values of LAI . monthly R_s in relation to (B) mean monthly soil temperature, (C) LAI, and (D) monthly GEP .Black circles denote GEP of July and August, hollow circles are months excluding July and August; Dotted line is relationship including all the months in 2013, whereas solid line is excluding Rs of July and August.

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.

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

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

4   Note: T_s (soil temperature measured by Li-8150 probe), Rh (air relative humidity measured by flux tower at
5   1m height), GEP (gross ecosystem productivity), other variables shown see Fig. 2. Statistical significance
6   with:
7   ** p-values＜0.01, * p-values＜0.05, besides, due to no significant correlation between soil moisture and other
8   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.

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

Model	References	R^2	a	b	c	d	$RMSE$
$R_s=\exp(a+b*T_s) *SWC$	(Gao, 2011)	0.895	1.07	0.09	-	-	0.663
$R_s=(c*SWC+d) *a*\exp(b*T_s)$	(Han et al., 2008)	0.918	0.64	0.08	1.13	0.97	0.591
$R_s=\exp(a+b*T_s+c*SWC+d*T_s*SWC)$	(Li et al., 2000)	0.919	0.22	0.05	-1.97	0.14	0.588
$R_s=\exp(a+b*T_s+c*SWC+d*SWC^2)$	(Tang and Baldocchi, 2005)	0.922	1.88	0.08	-18	39	0.578
$R_s=a+b*T_s+c*SWC+d*T_s*SWC$	(Wang et al., 2003)	0.929	-3.74	0.47	13.45	-0.9	0.542
$R_s=a+b*\exp(c*T_s) +d*T_s*SWC$	(Zhou et al., 2008)	0.936	-4.73	4.76	0.03	-0.04	0.515

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