

A comparison of soil respiration, carbon balance and root carbon use efficiency in two managed Moso bamboo forests in subtropical China

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Abstract. Moso bamboo forest (*Phyllostachys heterocyclus* [Carr.] Mitford cv. Pubescens) is an important forest type in subtropical China and comprises an important pool in the global carbon cycle. Understanding the effects of the stand management, such as understory removal, on soil respiration (RS) will help to provide a more accurate estimation of carbon cycling and predict future climate change. The study aimed to compare RS and net ecosystem production (NEP) in two Moso bamboo forests managed by the application of herbicide (AH) and conventional hand-weeded (HW) treatment, and further examine their root carbon use efficiency (RCUE). Trenching and litter removal were used to partition the source components of RS and one-year field measurement was conducted. Maximum-minimum approach was used to estimate fine root production. NEP was determined by the balance between NPP of vegetation and heterotrophic respiration (RH) of soil. RCUE was calculated using an indirect method. In both stands, soil temperature and soil moisture at 5 cm depth were the main driving forces to the seasonality of RS. Annual RS was 31.6 t CO₂ ha⁻¹ for the stand AH and 33.9 t CO₂ ha⁻¹ for the stand HW, while net ecosystem production (NEP) were 21.9 and 21.1 t CO₂ ha⁻¹, respectively, indicating that the both Moso bamboo stands acted as carbon sinks in the scenarios of current climate change. The RCUE was 30.6% for the stand AH, which was significantly lower than that for the stand HW (58.8%). This result indicates that different stand management practices can alter RCUE and the assumed constant universal carbon use efficiency (CUE) of 50% is not appropriate in Moso bamboo forests. This study highlight the importance of partition the source components of RS and accurate estimation of RCUE in modelling carbon cycling in Moso bamboo forests.

Keywords soil respiration, carbon cycling, net ecosystem production, carbon use efficiency, Moso bamboo forests

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Introduction

Soil respiration (RS), a primary CO₂ exchange process between soil and atmosphere, is the second largest carbon (C) flux in global C cycling after gross primary productivity (Raich & Schlesinger 1992). Approximately 83% of the gross primary productivity of terrestrial ecosystems return back to atmosphere due to ecosystem respiration, and 30% to 80% comes from RS (Davidson & Janssens 2006, Davidson et al. 2000, Law et al. 2002). C release from RS is estimated to be 98 Pg C per year in 2008 (1 Pg C=10¹⁵ g C) (Bond-Lamberty & Thomson 2010). This amount is more than 10 times of that from fossil fuel combustion (IPCC 2007). Therefore, a minor change in RS could significantly affect the atmospheric CO₂ concentrations and an understanding of the belowground C process is becoming increasingly important to estimate global C budget (Wu et al. 2014b).

RS consists of rhizospheric respiration (respiration from roots, mycorrhizae and microbial respiration in the rhizosphere) and heterotrophic respiration (respiration by microbial organisms and soil fauna) (Bond-Lamberty et al. 2004, Wang & Yang 2007). Soil temperature, moisture and substrate quality are important environmental factors driving the changes of RS (Subke & Bahn 2010, Wang et al. 2010).

However, the rhizospheric respiration and heterotrophic respiration responded differently to environmental conditions (Giardina & Ryan 2000, Högberg et al. 2001), and are driven by different mechanisms (Wang & Yang 2007). For example, photosynthesis and fine root biomass have been recognized as important drivers of rhizospheric respiration (Kuzyakov

& Gavrichkova 2010). Therefore, partitioning RS is an essential step to understand global carbon cycling (Hanson et al. 2000, Wang & Yang 2007).

Carbon use efficiency (CUE), defined as the ratio of net primary production and gross primary production (Chambers et al. 2004), can be applied to assess not only the capacity of forests to transfer C from the atmosphere to the terrestrial biomass, but also to determine the impact of respiration on productivity in forests (Chambers et al. 2004, Manzoni et al. 2012). CUE is a very helpful ecological parameter to determine whether the terrestrial ecosystem is a C source or sink (Zhu 2013). In many landscape-scale carbon cycling models, the constant CUE is widely assumed (DeLucia et al. 2007). However, the constant value is doubtful to the universal uses (Ryan et al. 1997, Tan et al. 2010, Zhu 2013). For example, the CUE is 34% in a primary tropical seasonal rain forest (Tan et al. 2010) and 27% for a young jack pine forest (Ryan et al. 1997).

Moreover, CUE also differs in aboveground, belowground and organs (Zhu 2013). Generally, CUE of aboveground is higher than that of belowground (Zhu 2013), and stem wood CUE is higher than leaf and root CUE (RCUE) (Chambers et al. 2004, Tan et al. 2010). As one of the most important part in forest ecosystem, RCUE is less intensively studies due to the direct measurement of CUE and labour intensity. Based on a meta-analysis of worldwide mature forests, Chen et al. (2011) found RCUE ranges from 0.10 to 0.87. However, to our knowledge, a study on RCUE in bamboo forests has not been observed.

As a special forest type in Southern China, bamboo forest is well-known for fast biomass accumulation (Du et al. 2010). The area of

bamboo forests has increased from 3.05 million hectares in 1973 to 6.2 million hectares in 2013, 70% of which is Moso bamboo forest (*Phyllostachys heterocyclus* [Carr.] Mitford *cv. Pubescens*) (State Forestry Administration 2014). The C stock in bamboo forests contributes 11% of the total C stock of China's forest ecosystems (Chen et al. 2009). Therefore, bamboo forests play a critical role in regional, national, even in global C cycle (Tu et al. 2013). In recent decades, Moso bamboo has expanded fast driven by good price and sustainable forest development policies (Wang et al. 2008). To have good timber output, regular management, such as understory removal, tillage and fertilization has been widely applied (Liu et al. 2011). Effects of understory removal on RS in Chinese chestnut plantations (Zhang et al. 2013), *Eucalyptus* plantations (Wu et al. 2011), and mixed *Magnoliaceae glanica*, *Liquidambar formosana* and *Tsoongiodendron odorum* plantations (Wang et al. 2011b) have been observed. It is expected that understory removal affects RS and RCUE due to the changes in soil environment and root biomass (Wang et al. 2011b). However, RS and RCUE in Moso bamboo forests managed under understory removal treatment have been not observed. Therefore, this study aimed to: (1) describe the seasonality of RS and compared the effects of two understory removal practices on RS dynamics; (2) qualify the relationships between RS and its source components and soil temperature and moisture; (3) estimate annual RS and ecosystem carbon balance; (4) compare the effects of two understory removal practices on RCUE and test whether the constant RCUE value of 50% is available to Moso bamboo forests.

Materials and methods

Study area

The study area is located in a Forest Farm in

Xianning city (29°02' to 30°19' N, 113°32' to 114°58' E), Hubei province, China. It has a typical subtropical monsoon climate with a forest cover of 52.3%. The annual precipitation is 1496.2 mm with 72% occurring in spring and summer (Liu et al. 2012). The mean annual temperature is 17.1 °C (Liu et al. 2012). The lowest temperature was -15.4 °C in January while the highest temperature was 41.4 °C in July. There are 245~258 frost-free days annually.

The pure Moso bamboo forests were established since the 1960s, currently these expanded to an area of about 400 hectares. Many understory, including *Castanopsis tessellate*, *Castanea seguinii*, *Castanopsis tibetana*, *Rhus chinensis*, *Liriodendron chinense*, *Loropetalum Chinense*, *Smilax glabra* and some grasses, were found under the canopy. To improve bamboo production and reduce the competitions between bamboo and understory, understory removals are widely used.

Experimental design

Two Moso bamboo stands with similar site conditions (soil, stand structure) managed by the application of herbicides (AH) and conventional hand-weeded (HW), which were the typical management practices of local area, were selected. The application of herbicides, consisting a solution of Nonda and Jialijia with 5% concentration, was conducted in every July in sunny days since 2000. Traditional hand-weeded was conducted twice a year in every May and September using billhook since 2000. In order to compare the two managements, the traditional hand-weeded was considered as a control. Therefore, the differences of RS between the two stands were considered as a result of different managements. However, it is recognized that such pseudo-replication is the limitation of such studies in forests. In March 2011, three 20 m × 20 m plots were established for each stand. There was a 10 m buffer zone between the two adjacent plots.

In each plot, four polyvinyl chloride collars (PVC, 20 cm inside diameter, 12 cm in height) were inserted into the intact soil 5 m away from the plot centre along a diagonal transect at a depth of 3 cm (Li et al. 2010b). The soil CO₂ flux in the intact soil was the total RS. Similarly, soil CO₂ flux with no litter (RNL) was measured on another four PVC collars installed on the litter-free soil, which were 50 cm away from PVC collars on the intact soil. The difference of soil CO₂ flux between the intact and litter-free soil was litter respiration (RL).

To partition RR, an 80 cm × 80 cm subplot was trenched to a depth of 80 cm in the plot centre in March 2011. Vegetation and litter in the subplots were removed carefully to minimize soil disturbance, and the subplots were kept free of live vegetation and litter throughout the study period. Since most of the bamboo roots were distributed within 40 cm of the surface (Tang et al. 2012), trenching to 80 cm was sufficient to achieve the objectives of this research. Four 0.5 cm thick polyethylene boards were inserted into the trenches vertically to prevent root ingrowth after trenching. Subsequently, two PVC collars were installed.

All PVC collars remained unchanged during the whole study period. The soil CO₂ flux from these trenched subplots was the sum of the soil organic matter derived CO₂ (RM) and root decomposition (R_{trench}) because the dead roots were decomposed by soil microbes and animals and turned into humus. Therefore, dead root decomposition rate should be excluded.

Root decomposition rate (v) was calculated (Lee et al. 2003):

$$v = 0.64k \quad (1)$$

where v is the decomposition rate of dead roots ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), k is the relative decomposition rate constant obtained by the exponential decay function. k is 0.6063 for fine root (<2 mm) and 0.52 for coarse root (>2 mm) for bamboo forests (Fan et al. 2009b, Silver & Miya 2001).

The CO₂ flux due to the decomposition of residual roots of each size class R_d ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) at given time was calculated as follows:

$$R_d = B_r \cdot (a \cdot e^{-v(t-1)} - a \cdot e^{-v \cdot t}) \quad (2)$$

$$R_D = \sum R_d \quad (3)$$

where B_r is the root biomass for each size class (g m^{-2}), t is the decomposition time (a^{-1}). R_D is the total root decomposition rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$); a is the intercept for dead root decomposition rate, which is 104.01 for bamboo forests (Fan et al. 2009b). The root sampling was described in details in the following section. Hence, RM and RR can be calculated:

$$RM = R_{trench} - R_D \quad (4)$$

$$RR = RNL - RM = RNL - (R_{trench} - R_D) \quad (5)$$

Root sampling and root NPP calculation

Roots within 0-40 cm were collected by sequential soil cores (8 cm in diameter) in the middle of each month from April 2011 to March 2012, because most of the bamboo roots were distributed above 40 cm due to its special biological characteristics (Tang et al. 2012). Five soil cores were randomly selected in each plot. Roots with diameter < 2 mm were treated as fine roots, while roots with diameter > 2 mm were treated as coarse roots (Fan et al. 2009b, Tang et al. 2012). A total of 720 soil sequential cores were collected. The roots were washed free of soil manually in the flowing water. In the lab, root samples were dried to constant weight at 65 °C and weighted to 0.01g. The carbon concentration of root were determined by determined using the $\text{K}_2\text{Cr}_2\text{O}_7\text{-H}_2\text{SO}_4$ wet oxidation method (Zhang et al. 1999). The fine root NPP was estimate by maximum-minimum approach (Brunner et al. 2013, McClaugherty et al. 1982):

$$NPP_{fr} = B_{max} - B_{min} \quad (6)$$

where NPP_{fr} is the fine root net primary production (g m^{-2}), B_{max} and B_{min} are the maximum and minimum fine root biomass (g m^{-2}).

Because 95% of biomass increment results from 1 “du” bamboos in Moso bamboo forests (Tang et al. 2015), and no diameter and height increment in 2, 3 and 4 “du” bamboos (Fu 2000), the coarse root production of 2, 3 and 4 “du” bamboo was ignored. Therefore, coarse root production of 1 “du” bamboos was estimated as the difference between new established belowground biomass and fine root NPP. The new established belowground biomass was estimated using the ratio of root/shoot of 0.2 (China Green Foundation 2008). Therefore, bamboo NPP was the sum of aboveground and belowground NPP.

RS, soil temperature (ST) and soil moisture (SM) measurements

One-year field measurement of RS was conducted using a Li-Cor-8100 (Li-Cor Inc., Lincoln, NE., USA) automated soil CO_2 flux system starting from April 2011. Wang et al. (2011a) proposed that RS rates between 9:00 a.m. and 12:00 a.m. represent the diurnal average in Moso bamboo forests, therefore, we measured RS during that time period. ST and SM near the collars at a depth of 5 cm were measured using the ST and SM sensors of the Li-Cor-8100 while measuring CO_2 flux over the entire study period.

Carbon stock in vegetation layer

In May 2011, the diameter at breast height (DBH, 1.3 m) of all bamboos in the inventory plots were measured nearest to 0.1 cm with a diameter tape. At the same time, the age of each bamboo were recorded based on upon visual examination on the culm colour, eye-

lash on cycle of culm sheath, powder under cycle of culm sheath and sheath in culm base (Zhang et al. 2014). The age was expressed by “du”, which shows the growth habit in “on-year” and “off-year” bamboo stands. One “du” corresponds to 1–2 years, whereas 2–4 “du” represent 3–4, 5–6 and 7–8 years, respectively (Fu 2000). The aboveground biomass of individual bamboo stems was estimated using equation (1) (Zhou et al. 2010). For simplicity, 0.5 was used as carbon concentration to convert biomass to carbon (Zhou & Jiang 2004).

$$AGB = 747.784 \times DBH^{2.771} \times [(0.148 \times A) / (0.028 + A)]^{5.555} + 3.772 \quad (7)$$

where AGB is the aboveground biomass; A is the age (du) (Fu 2000, Zhou et al. 2010), DBH is the diameter at breast height (1.3 m), expressed by cm.

Understory was harvested by uprooting in three $1 \text{ m} \times 1 \text{ m}$ subplots in each plot in July when the understory biomass peaked. The samples were washed in floating water in the lab then. Three $1 \text{ m} \times 1 \text{ m}$ collectors set in a similar equilateral triangle shape were used to collect monthly litterfall in each plot. All samples were dried to constant weight at 65°C . The annual biomass of understory is equal to annually formed biomass because the understory is newly formed every year.

Net ecosystem production (NEP)

The annual CO_2 flux of RS and source components are calculated as follows (eq. 8):

$$R_{annual} = \sum_{i=1}^{12} R_i \times 10^{-6} \times 3600 \times 24 \times 30(29/31) \times 10^{-6}$$

where R_{annual} is the annual CO_2 flux of RS and its components ($\text{t CO}_2 \text{ ha}^{-1} \text{ a}^{-1}$); R_i is the mean monthly respiration rates of RS and its components ($\mu\text{mol m}^{-2} \text{ s}^{-1}$); the first 10^{-6} is the unit conversion of 1 μmol to 1 mol while the second 10^{-6} is the unit conversion from 1g CO_2 to 1 t CO_2 ; 1 day = 3600×24 s; 30 (29/31) are the

days of each month.

In forest ecosystems, NEP is determined by the balance between NPP of vegetation and heterotrophic respiration (RH) of soil (Lee et al. 2003, Luo & Zhou 2006):

$$NEP = NPP - R_h \quad (9)$$

Because total R_s is the sum of autotrophic (RR) and RH, therefore, in our study, based on a year scale, NEP was calculated (Luo & Zhou 2006):

$$NEP = NPP - (RS_{annual} - RR_{annual}) \quad (10)$$

where NPP is the net primary production ($\text{CO}_2 \text{ ha}^{-1} \text{ a}^{-1}$), which was obtained as the sum of annual C from biomass, litterfall and vegetation; RR_{annual} and RS_{annual} are the annual CO_2 flux ($\text{t CO}_2 \text{ ha}^{-1} \text{ a}^{-1}$) of RR and RS, respectively.

Root carbon use efficiency

Carbon use efficiency is an important parameter for comparing carbon cycle variability among ecosystems (Ryan et al. 1997). Root is an important part in forest ecosystem and less intensive studied. In this study, RCUE was calculated using an indirect method (Chen et al. 2008a, Raich & Nadelhoffer 1989):

$$RCUE = 1 - RR_{annual}/TBCA \quad (11)$$

$$TBCA = RS_{annual} - LF + \Delta C_b \quad (12)$$

where TBCA is the total belowground carbon allocation based on a year scale, LF is the annual litterfall, ΔC_b is the changes of belowground carbon pools (including litter layer, mineral layer, root layer). ΔC_b is assumed to be zero in the stable forest (Raich & Nadelhoffer 1989). Because the Moso bamboo forest remain dynamic balance all the time, ΔC_b is considered too small that it was ignored in the Moso bamboo forests (Zhou & Jiang 2004). Therefore, RCUE can be expressed:

$$RCUE = 1 - RR_{annual}/(RS_{annual} - LF) \quad (13)$$

Data analysis

Data analysis was processed in R 3.1.2 (R Core Team 2014). First, respiration rates, ST and SM from four collars (two collars for RM) were averaged for each plot, and the average rates represented each plot. Two-way factorial ANOVA analysis was processed to exam the effects of month, understory removal and their interactions on ST, SM and respiration rates at the level of 0.05. Regression analysis was used to model the relationship between respiration rates and soil temperature and moisture. Exponential models were used to describe the relationships between RS and ST while linearly models were used to describe the relationship between RS and SM (Liu et al. 2011, Wu et al. 2014b):

$$RS = a \times e^{b \times ST} \quad (14)$$

$$RS = a \times SM + b \quad (15)$$

where RS is the measured soil CO_2 rates or its component respiration rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), ST ($^{\circ}\text{C}$) and SM (%) are the measured soil temperature and moisture at 5 cm depth, respectively, and a and b are fitted coefficients.

Temperature sensitivity (Q_{10}), which is related to the increase in the RS rate at 10°C intervals in temperature, was calculated from RS_{ST+10}/RS_{ST} . Although Q_{10} can well describe the temperature sensitivity of RS, it is a result of many processes, such as the changes of carbohydrates, root biomass, root activity, soil nutrient availability and litter biomass (Lee & Jose 2003, Pregitzer et al. 2000, Ryan et al. 1996, Yan et al. 2006), but the high correlations between RS and ST and SM mask these direct effects on R_s (Kuz'yakov & Gavrichkova 2010). As a result, Wu et al. (2014a) applied a two-factor regression (including ST and SM) to calculate Q_{10} , while most of the studies use soil temperature only (Liu et al. 2011, Yuste

et al. 2003). In this study, despite there was a strong relationship between RS and SM (see result part) like many other studies (Liu et al. 2011, Wang et al. 2011b), to make the Q_{10} comparable to most of the studies, ST was only used to calculate Q_{10} as following (Yuste et al. 2003):

$$Q_{10} = a \times e^{b \times (ST+10)} / a \times e^{b \times ST} = e^{10b} \quad (16)$$

where b is taken from formula (14). For each treatment, the Q_{10} was calculated based on monthly RS and ST in each plot.

Results

During the study period, regardless of the management, ST, SM, RS, RR, RL and RM varied greatly with the seasons (Fig. 1, 2, Table 1). RS in the stand AH ranged from 0.60 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in February to 4.24 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in June with an annual average of 2.27 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, while RS in the stand HW changed from 0.76 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in February to 4.42 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in June with an annual average of 2.44 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Fig. 2 a). There was no significant difference in total RS rates between the stand AH and HW ($p = 0.18$, Table 1).

RR in the stand AH and HW peaked in July and August, respectively, and bottomed in February (Fig. 2 b). The annual mean rate was 0.78 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the stand AH and 0.73 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the stand HW, and they were not significantly different ($p =$

0.219, Table 1). Similarly, the highest rates of RL occurred in June for the stand AH and August for the stand HW, while the lowest rates were found in February for both stands (Fig. 2 c). No significant difference was observed in the annual average rates between the two stand (0.52 and 0.53 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively, $p = 0.909$).

There was a similar changing pattern in RM between the two stands (Fig. 2 d). The maximum rate was found in June while the minimum rate occurred in February for both stands. RM of the stand AH was always higher than that of the stand HW. Annually, on average, RM was 0.88 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the stand AH, and it was lower than that for the stand HW (1.18 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $p = 0.001$).

RS, RR, RL and RM were exponentially related to the ST at 5 cm depth for both stands (Fig. 3). ST could explain 29% to 89% variations in the respiration rates (Table 2). Q_{10} values of RS, RR, RL and RM were 1.82, 1.29, 1.91 and 2.21 for the stand AH, respectively, and 1.77, 1.89, 1.39 and 2.19 for the stand HW. RS, RR, RL and RM were linearly related to SM at 5 cm depth (Fig. 3), and SM could explain 31% to 85% of these seasonal variations (Table 2).

Annual CO_2 flux of RS, RR, RL and RM were 31.6, 12.1, 7.2 and 12.3 $\text{t CO}_2 \text{ ha}^{-1}$ for the stand AH, respectively, compared to 33.9, 10.1, 7.3 and 16.5 $\text{t CO}_2 \text{ ha}^{-1}$ for the stand HW (Table 3).

Annual CO_2 flux of RM for the stand AH was significantly lower than that of the stand HW ($p = 0.003$), while there were no significant

Table 1 Two-way factorial ANOVA analysis of the effects of month, understory removal and their interactions on ST, SM and respiration rates

Time/treatment effects	ST	SM	RS	RR	RL	RM
Month	<0.001	<0.001	<0.001	<0.001	0.007	<0.001
Understory removal	0.002	0.36	0.18	0.219	0.909	<0.001
Month \times understory removal	<0.001	<0.001	0.362	0.511	0.561	0.001

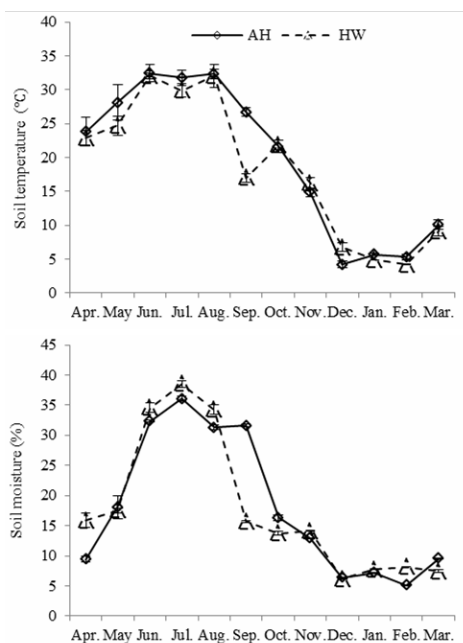


Figure 1 Seasonal changes in soil temperature (°C) and soil moisture (%) at 5 cm depth. The bars mean the standard error (n = 3). AH and HW represent the application of herbicides and hand-weeded stands

difference in RS, RR and RL (all $p > 0.05$). In the stand AH, RR, RL and RM contributed 38%, 23% and 39% to total RS, respectively, while RR, RL and RM contributed 30%, 21% and 49% to RS in the stand HW. They were not statistically different (all $p > 0.05$).

Litter represented an import carbon pool of 14.1 t CO₂ ha⁻¹ for stand AH (Table 3), which was significantly higher than that of stand HW (9.0 t CO₂ ha⁻¹, $p < 0.001$). In contrast, bamboo NPP and RCUE of stand AH was significantly lower than that of the stand HW ($p = 0.013$ and 0.021). NEP of the two stands was similar (21.9 and 21.3 t CO₂ ha⁻¹, respectively).

Discussion

Effects of understory removal on RS

Understory removal represent an important management practice in the Moso bamboo forests. Understory removed by hand-weeded and herbicide application was widely used due to easy-to-operate. In this study, the effects of

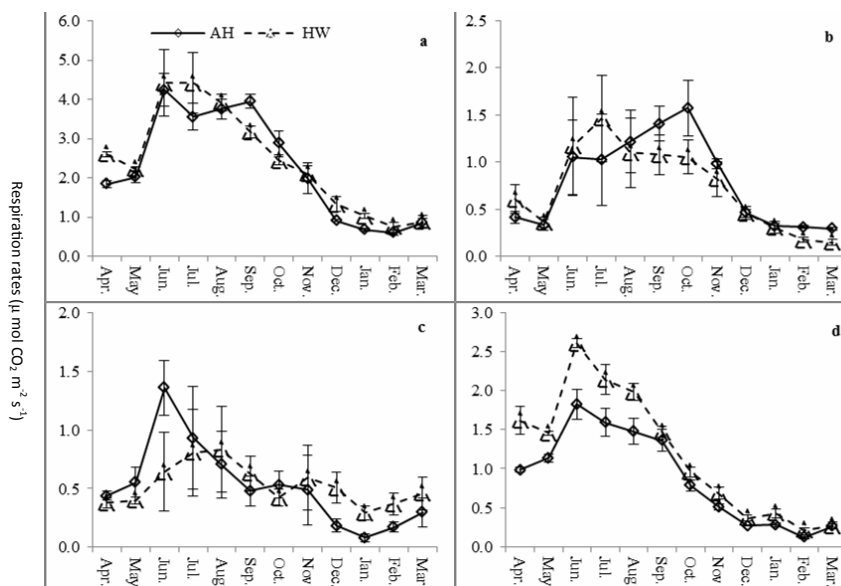


Figure 2 Seasonal changes of total soil respiration (a), root respiration (b), litter respiration (c) and soil organic matter derived respiration (d) (μmol CO₂ m⁻² s⁻¹). The bars mean the standard error (n = 3). AH and HW represent the application of herbicides and hand-weeded stands.

Table 2 The coefficients (a) of the relationships between soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and soil temperature ($^{\circ}\text{C}$), soil moisture (%)

Variables	Stands	Components	a	p	b	p	R ²	Q ₁₀
Soil temperature	I	RS	0.564	<0.001	0.060	<0.001	0.82	1.82
		RR	0.384	<0.001	0.025	<0.001	0.29	1.29
		RL	0.100	<0.001	0.065	<0.001	0.59	1.91
	II	RM	0.140	<0.001	0.079	<0.001	0.89	2.21
		RS	0.719	<0.001	0.057	<0.001	0.81	1.77
		RR	0.203	<0.001	0.052	<0.001	0.37	1.68
Soil moisture	I	RL	0.271	<0.001	0.033	<0.001	0.36	1.39
		RM	0.206	<0.001	0.078	<0.001	0.85	2.19
		RS	0.110	<0.001	0.292	0.110	0.84	
	II	RR	0.043	<0.001	0.144	0.368	0.50	
		RL	0.024	<0.001	0.062	0.590	0.39	
		RM	0.046	<0.001	-0.023	0.767	0.85	
II	RS	0.108	<0.001	0.520	0.022	0.76		
	RR	0.032	<0.001	0.161	0.352	0.31		
	RL	0.019	<0.001	0.230	0.007	0.45		
		RM	0.020	<0.001	0.063	0.846	0.82	

Note. AH and HW represent the application of herbicides and hand-weeded stands. RS, RR, RL and RM represent total soil respiration, root respiration, litter respiration and soil organic matter derived respiration, respectively.

Table 3 The carbon flux components and net ecosystem primary production ($\text{t CO}_2 \text{ ha}^{-1}$)

Stand	RS	RR	RL	RM	litter	Understory	NPP	NEP	RCUE
AH	31.6±1.7 ^a	12.1±0.7 ^a	7.2±1.2 ^a	12.3±0.3 ^a	14.1±0.5 ^b	0.9±0.1 ^a	26.4±0.1 ^a	21.9±2.0 ^a	30.6±6.3 ^a
HW	33.9±2.0 ^a	10.1±0.7 ^a	7.3±1.5 ^a	16.5±0.5 ^b	9.0±0.2 ^a	3.0±0.4 ^b	33.2±3.5 ^b	21.3±4.8 ^a	58.8±4.9 ^b

Note. AH and HW represent the application of herbicides and hand-weeded stands. RS, RR, RL and RM represent total soil respiration, root respiration, litter respiration and soil organic matter derived respiration, respectively. BNPP is bamboo net primary production, NEP is net ecosystem production and RCUE is the root carbon use efficiency.

hand-weeded and herbicide application were compared. Between the two stands, there was no significant difference in total RS, RR and RL, however, RM differed significantly ($p = 0.001$). This may be due to the application of herbicide in the AH stand. RM mainly comes from soil organic matter decomposed by soil microbes and fauna (Li et al. 2006, Subke et al. 2006). Although there was no direct evidence about the effects of the application of herbicide on microbial biomass in this study, previous studies suggested that herbicide lowered the microbial biomass carbon and had a long-lasting negative effect on soil microbial biomass, which directly led a decrease in respiration rates (Perucci et al. 2000).

Annual CO_2 from RS were 31.6 $\text{t CO}_2 \text{ ha}^{-1} \text{ a}^{-1}$ for stand AH and 33.9 $\text{t CO}_2 \text{ ha}^{-1} \text{ a}^{-1}$ for the stand HW, which were close to the soil CO_2 flux in Moso bamboo forests in Hunan Province, China (Table 4) (Fan et al. 2009a), *Cunninghamia lanceolata* forests in subtropical China (Wu et al. 2014b) and the aspen forest in boreal area (Gaumont-Guay et al. 2009).

The value was higher than the reported CO_2 flux in the *Pleioblastus amarus* bamboo (Tu et al. 2013), *Eucalyptus* forests in North Australia (Chen et al. 2003) and *Quercus* forests (Lee et al. 2010). On the other hand, the values was lower than that of Moso bamboo forest in Zhejiang and Fujian Province (Song et al. 2013, Wang et al. 2011a), natural and planted

Castanopsis kawakamii forests in subtropical China (Yang et al. 2007) and black forest (Gaumont-Guay et al. 2009). These great variations in RS flux mainly resulted from (1) forest types and stand structure because these variables strongly influence C allocation patterns (Wang et al. 2001); (2) belowground metabolism because RS was always correlated to fine root and root production (Coleman et al. 2000, Pregitzer et al. 1998); (3) allocation of new plant photosynthesis to roots (Högberg et al. 2001); (4) leaf area and primary productivity (Högberg et al. 2001, Rey et al. 2002); (5) climate conditions (Raich & Schlesinger 1992, Wang et al. 2010).

Contribution of source components of RS to total RS

Previous studies has demonstrated that the contribution of RR to total RS varies significantly from 10% to 90% (Hanson et al. 2000) due to the variability to methodological issues, forest types, soil conditions, stand age, forest structure and forest management (Hanson et al. 2000, Li et al. 2008, Rey et al. 2002). Hanson et al. (2000) further pointed out that RR contributed 30%-80% to total RS with a world average of 46% in forest ecosystems. Similarly, Chen et al. (2008b) estimated the contribution of RR to total RS amounted from 10% to 65% with an average of 35% in Chinese forest ecosystems. In this study, RR contributed 30% and 38% to total RS, which lied in the ranged for these reported values and was highly comparable to the average of China's forests. In addition, the contribution of each component to total RS was not statistically significant between the two stands, indicating that compared to traditional hand-weeded, application of herbicides did not change these contributions.

Trenching is a widely used approach due to its easy-to-operation and low cost that allows a partitioning of RS to explore the components of soil CO₂ efflux (Hanson et al. 2000). However, there are some well-known problems associated with the trenching approach, such

as the decomposition of remaining dead roots and the increase of SM in the trenched plots (Hanson et al. 2000, Wang & Yang 2007). To overcome these problems, Ewel et al. (1987) addressed these problems by measuring RS four month after the trenching and sampled the fine roots in the trenched subplots. Similarly, some scientists recommended that the starting measurement of soil CO₂ flux was not conducted until the flux in the trenched subplots remained stable, which always took 2-9 months (Hanson et al. 2000, Wang & Yang 2007, Yan et al. 2015). Therefore, to reduce the bias, the respiration due to root decomposition in the trenched plots should be removed. In this study, although soil CO₂ flux was measured one month after the trenching, to minimize the effects of residual roots, equation (1) – (5) were used to exclude the CO₂ flux from the decomposition of dead roots.

Influence of environmental factors on RS

ST and SM are two of the most important environmental factors driving the seasonal and diurnal changes of RS (Davidson et al. 1998, Tang et al. 2015, Wang et al. 2010), and RS is highly sensitive to ST (Davidson & Janssens 2006, Wang et al. 2011a). This study confirmed these conclusions that ST and SM were the main driving forces of the seasonality of source components of RS and total RS (Fig. 3 and 4). This study is still consistent with the results from Liu et al. (2011) and Tang et al. (2015), who observed a strong relationship between RS and ST, RS and SM in the Moso bamboo forests in the subtropical China. However, the degree of correlation (R²) between components of RS and ST and SM varied.

Similar results were found in other studies in Moso bamboo forests that ST could explain 86% variations of seasonal changes of RS, while ST could only explain 46% and 51% to variation of RR and RL (Tang et al. 2015). SM could explain 78% variation of seasonal changes of RS and 55% and 41% variation of RR and RL (Tang et al. 2015). This discrepan-

Table 4 Annual CO₂ flux (t CO₂ ha⁻¹ a⁻¹), ratio of RR/RS, net ecosystem production (NEP, t CO₂ ha⁻¹ a⁻¹), Q₁₀ of RS in different forest ecosystems

Forest type	Study area	Method	Annual CO ₂ flux	RR/RS (%)	NEP	Q ₁₀ of RS	Reference
Moso bamboo forest	SC	T	31.6	38.3	21.90	1.82	This study
Moso bamboo forest	SC	T	33.9	29.8	21.30	1.77	This study
Moso bamboo forest	SC	T	33.9	28.3	-	-	Fan et al. (2009a)
Moso bamboo forest	SC	-	52.9	-	-	2.18	Song et al. (2013)
Intensively managed Moso bamboo forest	SC	-	56.8	-	-	2.46	Liu et al. (2011)
Conventionally managed Moso bamboo forest	SC	-	41.2	-	-	3.24	Liu et al. (2011)
Moso bamboo forest	SC	-	49.9	-	-	2.08	Wang et al. (2011a)
<i>Pleioblastus amarus</i> bamboo	SC	T	15.7	49.1	-	2.87	Tu et al. (2013)
<i>Cunninghamia lanceolata</i>	SC	T	16.7	33.0	-	2.08	Tian et al. (2011)
<i>Pinus massoniana</i>	SC	T	62.0	44.5	-	2.38	Han et al. (2011)
<i>Quercus</i>	NT	TG		53.0	-	2.95	Högberg et al. (2009)
<i>Castanopsis carlesii</i>	SC	T	45.1	35.1	-	2.41	Wu et al. (2014b)
<i>Cunninghamia lanceolata</i>	SC	T	33.2	37.6	-	2.12	Wu et al. (2014b)
<i>Setaria italica</i>	SC	T	-	67.3	5.16	-	Li et al. (2010a)
Natural <i>Castanopsis kawakamii</i>	SC	T	41.2	47.6	15.20	-	Yang et al. (2007)
Planted <i>Castanopsis kawakamii</i>	SC	T	48.6	42.5	27.60	-	Yang et al. (2007)
<i>Cunninghamia lanceolata</i>	SC	T	23.8	40.2	13.50	-	Yang et al. (2007)
<i>Eucalyptus tetrodonta</i> , <i>Eucalyptus miniata</i>	NA	-	20.9	-	13.90	-	Chen et al. (2003)
<i>Abies holophylla</i>	CT	T	28.6	34.0	4.30		Lee et al. (2010)
<i>Quercus</i>	CT	T	22.3	31.0	3.60		Lee et al. (2010)
Aspen forest	BF	EC	30.3	-	3.80	3.20	Gaumont-Guay et al. (2009)
Black forest	BF	EC	20.8	-	2.90	2.50	Gaumont-Guay et al. (2009)

Note. Abbreviations: SC - Subtropical China, NT - Northern temperate deciduous forest, NA - North Australia, CT - cool-temperate forest, BF - Boreal forest, T - Trenching, TG - Tree-girdling, EC - eddy-covariance technique.

cy may result from different response mechanisms of source components of RS to ST and SM. For instance, temperature can affect photosynthetic C supply for photosynthesis, thereby affecting the carbon use for RR (Kaspar & Bland 1992, Tang et al. 2005). ST and SM affect RM by decomposition and oxidation of soil organic matter, the movement of air in soil, activity and abundance of microorganisms (Davidson & Janssens 2006, Luo & Zhou 2006). However, it should be aware that besides ST and SM, other biotic factors, such as carbohydrates, root biomass, root activity, soil nutrient availability and litter biomass, had significant effects on RS (Lee & Jose 2003, Pregitzer et al. 2000, Ryan et al. 1996, Yan et

al. 2006), but the high correlations between RS and ST and SM mask these direct effects on RS (Kuzyakov & Gavrichkova 2010).

Q₁₀ has been widely used to describe the temperature dependence of RS, which is calculated from a series of measured RS values over a time period while soil temperature changes (Ma et al. 2014, Rey et al. 2002).

Based on a meta-analysis of the global soil respiration rates, recent studies show that Q₁₀ value varies from 1.1 to 6.7, depending on the measured ST of different depths (Bahn et al. 2010, Chen et al. 2008b, Song et al. 2014). In this study, Q₁₀ ranged from 1.29 to 2.21 (Table 2), which lies in the lower range of China's forests (1.33-5.53) and were lower the average

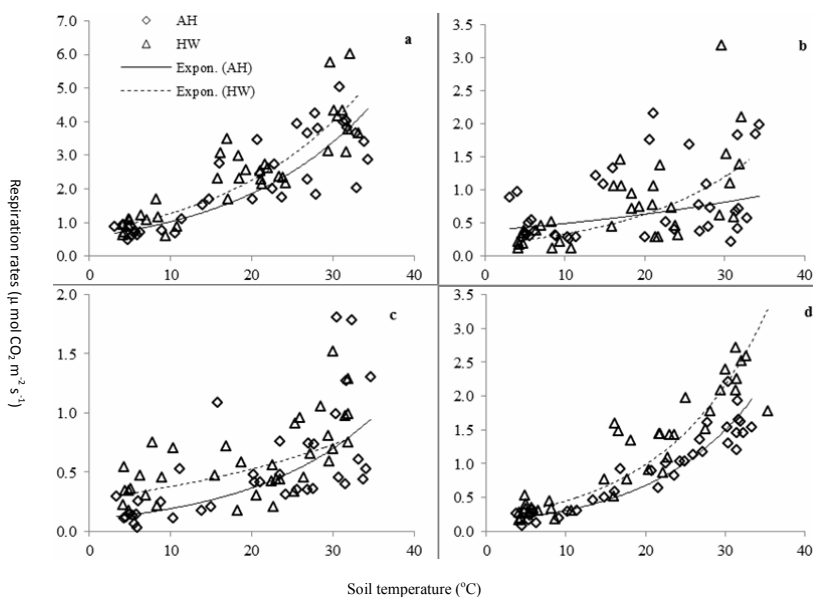


Figure 3 The relationship between total soil respiration (a), root respiration (b), litter respiration (c) and soil organic matter derived respiration (d) and soil temperature. AH and HW represent the application of herbicides and hand-weeded stands. The coefficients are shown in Table 2.

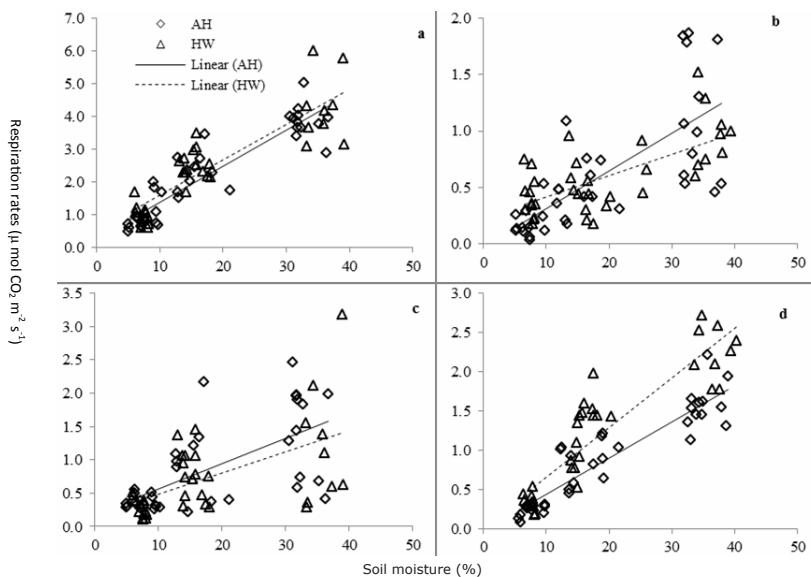


Figure 4 The relationship between total soil respiration (a), root respiration (b), litter respiration (c) and soil organic matter derived respiration (d) and soil moisture. AH and HW represent the application of herbicides and hand-weeded stands. The coefficients are shown in Table 2.

(2.65) (Chen et al. 2008b), suggesting that soil CO₂ flux in Moso bamboo forests is less sensitive to ST changes and exerts less soil CO₂ to future climate change compared other forest types in China. Q_{10} of this study was compared to Moso bamboo forests in Wangmulin natural reserve (2.08, Wang et al. 2011a), and the average Q_{10} of bamboo forests in China (2.1, Song et al. 2014).

In both stands, Q_{10} of RM was highest compared to other components and total RS. This highlights the importance of RM in regulating Q_{10} of RS, which is consistent with other studies in subtropical forests (Li et al. 2011, Luan et al. 2011), as well as Moso bamboo forests (Tang et al. 2015). However, disagreements among the studies still remain. Boone et al. (1998) estimated Q_{10} value was 2.5 for heterotrophic respiration and 4.6 for RR in a temperate forest. On the other hand, Luan et al. (2011) found a Q_{10} value of 3.93 for heterotrophic respiration, which was significantly higher than that of RR (2.78). While Yan et al. (2015) found no difference in Q_{10} values between heterotrophic respiration (2.13) and RR (1.90). However, the variability of Q_{10} of different components of RS will affect the accumulative soil CO₂ flux across the stands. Thus, partitioning of RS and their Q_{10} values should be required in ecosystem carbon cycling models of future climate change (Luan et al. 2011).

Net ecosystem production

NEP of the terrestrial ecosystems is a key process when managing the C cycle (Harmon et al. 2004). NEP of the stand AH and HW were 21.9 and 21.1 t CO₂ ha⁻¹, respectively, indicating that the both Moso bamboo stands were C sinks in current climate change. The results were higher than *Eucalyptus tetradonta* (Chen et al. 2003), *Abies holophyll*, *Quercus* (Lee et al. 2010), Aspen forest and Black forest (Gaumont-Guay et al. 2009), but lower than the planted *Castanopsis kawakamii* (Table 4) (Yang et al. 2007). These great differences may

result from tree species and their biological characteristics, soil conditions, and different method applications (Malhi et al. 1999, Xiao et al. 2010). For instance, the estimation of NEP from component process approach generate greater error compared to the eddy-covariance flux measurement (Malhi et al. 1999). However, in this study, soil CO₂ measurement was conducted in one-month interval, but this is somehow limited due to the significant changes of environmental factors. This can be overcome by increasing the measurement intervals (e.g. bio-weekly or weekly). It also calls for the installation of continuous measurement technique with a high time resolution (e.g. 1 h) in the field. Because of the special biological characteristics of Moso bamboo forests, long-term measurements including at least “on-year” and “off-year” are recommended, which could improve our understanding of role of Moso bamboo forests in global carbon cycling. Root carbon use efficiency

Carbon use efficiency is an important ecological variable to describe the capacity of forest to transfer the carbon from atmosphere to biomass (Chambers et al. 2004), which includes important parameters to compare carbon cycle variability among ecosystems (Ryan et al. 1997). Compared to the aboveground carbon allocation and CUE, the allocation of belowground carbon and RCUE is one of the most important but least well quantified carbon flux in terrestrial ecosystems (Tan et al. 2010). In most of the carbon budget models, the RCUE is assumed to be 50% (Giardina et al. 2003, Law et al. 1999) although some researches propose that the NPP decrease with the increase of age while the ecosystem respiration increase with the age, which could lead to the decrease of total forest carbon use efficiency (Ryan et al. 1997). However, how the RCUE changes with the stand development is still unclear. In our study, RCUE was 30.6% for the stand AH, which was comparable to the young jack pine forest 27% (Ryan et al. 1997), while these values were lower than that

of the stand HW (58.8%). These results indicated that the constant RCUE (50%) in Moso bamboo forest was not available and different management practices could affect RCUE. Zhu (2013) attributed these differences to the variations in ecosystems, forest types, species and ontogeny of plant development. However, the differences in RCUE among different forest ecosystems might be partly attributed to different methods.

For example, CUE estimated from the biometrical approach was 42% while CUE estimated from meteorological approach was 54% in a northern hardwood forest over five-year measurement (Curtis et al. 2005). Therefore, the selection of appropriate approach to measure RCUE could improve the estimate accuracy.

Conclusions

One-year field measurements of RS and its source components were conducted in two managed Moso bamboo forests. In both stands, RS and source components shown significantly seasonal changes, and ST and SM were the main driving forces to the seasonal changes.

Compared to conventional hand-weeded, the application of herbicide had no significant effects on total RS, RR and RL, but significantly decreased RM. Q_{10} values was highest for RM.

However, studies on the temperature sensitivity of each component of RS are limited, and no general agreement has been achieved.

Both stands act as carbon sinks in current climate change. RCUE varied significantly among the two stands, suggesting RCUE could be altered by different stand management practices. The constant CUE value of 50% was not appropriate in Moso bamboo forests. However, this study was conducted in “on-year” Moso bamboo stand, due to special biological characteristics of Moso bamboo forests, long-term measurements including “on-year” and “off-year” are recommended to improve our understanding its role in global carbon cycling.

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