

# Environmental controls and the influence of tree species on temporal variation in soil respiration in subtropical China

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## Abstract

**Background and aims** The knowledge of individual tree species impacts on soil respiration based on rigorous experimental designs is limited, but is crucial to help guide selection of species for reforestation and carbon (C) management purposes.

**Methods** We assessed monthly soil respiration and its components, litterfall input, fine root production and mortality under 19-year-old native coniferous *Cunninghamia lanceolata* and broadleaved *Mytilaria laosensis* plantations in sub-tropical China.

**Results** Total soil respiration from October 2011 to March 2013 was significantly lower under the *C. lanceolata* than the *M. laosensis* plantation. The difference in respiration rates derived from fine roots and the litter layer explained much of the variation of total soil respiration between the two tree species. We used an exponential equation and base temperature (10 °C) to normalize soil respiration rate and its components ( $R_{10}$ ) and determined the correlation between  $R_{10}$  and soil moisture. Although soil moisture had a positive relationship with  $R_{10}$  derived from roots or litter under both *C. lanceolata* and *M. laosensis* forests, these positive correlations were masked by negative relationships between soil moisture and  $R_{10}$  derived from root-free

soil, which resulted in a neutral correlation between total  $R_{10}$  and soil moisture under *C. lanceolata* forests. Monthly litterfall input was associated with variation in concurrent total soil respiration rate under the *M. laosensis* plantation and respiration rate lagging 3 months behind under the *C. lanceolata* plantation, which may suggest that litterfall input from *M. laosensis* can more rapidly produce C substrates for microbial respiration than litterfall from *C. lanceolata*. **Conclusions** This study highlighted that tree species-induced variation in the quality and quantity of fine roots and litterfall can impact not only the soil respiration rate but also the seasonal variation model of forest soil respiration.

**Keywords** *Cunninghamia lanceolata* · Fine root production · Litter production · Litter respiration · *Mytilaria laosensis* · Root respiration

## Introduction

Soil respiration is a major process controlling carbon (C) loss from terrestrial ecosystems. On a global scale, it was estimated that soil respiration produced about 80 Pg C year<sup>-1</sup>, accounting for 60–90 % of total respiration in global terrestrial ecosystems (Schimel et al. 2001). Soil respiration in forest ecosystems is the sum of autotrophic respiration produced by living roots and their associated rhizosphere microflora (i.e. mycorrhizae and rhizosphere bacteria) and heterotrophic respiration generated by microbial decomposition

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of soil organic matter. Factors such as fine roots and their turnover rates (Tang et al. 2009), plant productivity (Högberg et al. 2001) and stand structure (Katayama et al. 2009) contribute to spatial and temporal variation of soil autotrophic respiration. On the other hand, soil temperature is regarded as the most important factor controlling the spatial and temporal variation of soil heterotrophic respiration while soil moisture is secondary, its regulation over soil heterotrophic respiration being greatest under extreme moisture conditions (Bonal et al. 2008; Kosugi et al. 2007).

Temporal patterns of soil respiration have been simulated by using the continuous records of soil temperature and moisture (Davidson et al. 1998; Xu and Qi 2001). The temperature effect is nearly always expressed as an exponential function, although there has been some debate on the issue of which exponential formulation is best (Kirschbaum 2000). The effect of soil water content, in contrast, has been described by many equations, including linear, logarithmic, quadratic, and parabolic functions which suggest that the mechanisms behind the impact of soil moisture on soil respiration are more complex. Furthermore, the correlations of soil respiration with soil moisture have been reported to be positive (Pang et al. 2013), negative (Olajuyigbe et al. 2012), or neutral (Sheng et al. 2010). In laboratory incubations of root-free soil samples, where the effects of temperature and spatial heterogeneity are controlled, a log-linear relationship between soil moisture and CO<sub>2</sub> production was found where soil moisture was below field capacity (Orchard and Cook 1983). This result suggested that very low soil moisture can inhibit heterotrophic respiration in soils. Linn and Doran (1984) explained this phenomenon mechanistically for microbial respiration as limitation of soluble organic-C substrates in water films in very dry soils. However, at high volumetric soil moisture (e.g. >19 %) (Xu and Qi 2001), a negative correlation between soil respiration and soil moisture was often observed because of limitation of O<sub>2</sub> diffusion through pore spaces in very wet soils, which affects microbial activity. On the other hand, the increased soil moisture may affect fine root biomass, production and mortality (Pregitzer et al. 1993), which might lead to variation in root-derived respiration. A positive correlation between fine root growth and soil moisture has been reported in many tropical forests (Green et al. 2005; Katterer et al. 1995).

The soils in humid subtropical forests of China seldom experience prolonged drought owing to the plentiful rainfall. Previous studies in these ecosystems have shown that total soil respiration is primarily affected by soil temperature, the correlation of total soil respiration with soil moisture availability being relatively poor (Sheng et al. 2010; Tian et al. 2011). However, as noted above, the impact of soil moisture on soil respiration is complex, so the first objective of this study was to gain a better understanding of the impacts of soil moisture on microbial respiration and root respiration in humid subtropical forests. We hypothesized that high soil moisture availability would increase fine root growth and root and rhizosphere derived respiration, but would decrease soil microbial autotrophic respiration.

Effects of individual tree species on both soil autotrophic and heterotrophic respiration are difficult to predict owing to strong interactions between abiotic (e.g. soil moisture, temperature, and texture) and biotic (e.g. quality and quantity of organic matter input) factors (Binkley and Giardina 1998). Previous studies measuring field soil respiration among different tree species within similar climates are rare (Berger et al. 2010; Nsabimana et al. 2009), and few studies have addressed tree species effects on soil respiration and its temporal variation in well-designed and replicated experimental plots where the effects of confounding management history and site-related factors can be minimized (Vesterdal et al. 2012).

Broadleaf and Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook.) forests are important forest types in southern China. Plantations of *C. lanceolata* alone cover 9.11 million hectares and account for more than 18 and 5 % of all forest plantations in China and the world, respectively (Huang et al. 2013a; Mo et al. 2008). Growth of *C. lanceolata* in replanted forests is, however, significantly reduced compared with its previous rotation and this problem occurs in many regions (Mo et al. 2008). As a result, plantings of native broadleaved tree species at *C. lanceolata* sites are currently encouraged to provide environmental benefits of enhanced biodiversity and improved concentration of soil organic matter (Xu 2011; Yu 2002). Broadleaf trees usually provide a higher quantity and better quality of litterfall and produce more fine roots than coniferous *C. lanceolata* (Laganière et al. 2010; Yang et al. 2004). Our second hypothesis was that a land use transition from *C. lanceolata* to a broadleaf species, *Mytilaria laosensis* Hamamelidaceae plantation would increase

soil respiration because of higher quantity of litterfall and greater fine root biomass under the *M. laosensis* plantation. Plantings of *C. lanceolata* and *M. laosensis* in adjoining replicated plots in 1993, after harvest of *C. lanceolata*, provided a unique opportunity to examine the impacts of tree species on micro-environmental condition, litterfall, fine root properties and soil respiration. Specifically, the objectives of this study also included: (1) determination of relationships between soil moisture and soil respiration; (2) determination of soil respiration and its components under *C. lanceolata* and *M. laosensis*, and (3) examination of the influence of tree species on the quality and quantity of litterfall and the production and mortality of fine roots.

## Materials and methods

### Site description and experimental design

The experimental site is located at Xiayang forest farm (26°48'N, 117°58'E), northwest Fujian Province, South Eastern China. The site has a deep red soil classified as a sandy clay loam Ferric Acrisol according to the FAO/UNESCO classification. The upper (0–5 cm) soil layer under the two plantations had similar pH and bulk density, but total C and N and C:N were all higher under *M. laosensis* than *C. lanceolata* (Table 1). The experimental site has a short and mild winter (with occasional frost) in January and February, and long, hot and humid summers between June and October. Spring and autumn are warm transitional periods. Annual precipitation is concentrated in spring and summer. Autumn and winter are comparatively drier, but not arid. Annual rainfall and average temperature in 2011 were 1,669 mm and 19.3°C, respectively.

In October 1992, a second rotation 29 year old plantation of *C. lanceolata* with an area of 5 ha was harvested using chainsaws. The understory vegetation was slashed and all surface organic matter was burnt on the

site. In April 1993, eight 20 m×30 m plots were established on hill slopes (230–278 m elevation) at the harvesting site. Two species were then planted in the eight plots as pure forest plantations with four plots of *C. lanceolata* seedlings and four plots of *M. laosensis* seedlings. The trees were spaced at 2 m×2 m to make up 150 trees per plot (2,500 stems ha<sup>-1</sup>). The plots were separated by more than 10 buffer tree rows. In 2010, the mean tree height was 15.4 m in *M. laosensis* plots and 13.8 m in *C. lanceolata* plots. The mean basal area was 30.4 and 31.9 m<sup>2</sup> ha<sup>-1</sup> in *M. laosensis* and *C. lanceolata* plots, respectively. The *M. laosensis* forest had greater leaf area index than *C. lanceolata* forest and supported less understory plants. The total leaf area index and understory biomass measured in August 2011 was 1.63 m<sup>2</sup> m<sup>-2</sup> and 2.2 Mg ha<sup>-1</sup>, respectively in *M. laosensis* forest and 1.37 m<sup>2</sup> m<sup>-2</sup> and 9.2 Mg ha<sup>-1</sup>, respectively in *C. lanceolata* forest.

To examine the different components of soil respiration, two sub-plots (each measuring 2 m×2 m and about 3 m apart) were randomly established in July 2011 within each plot. The sub-plots were randomly subject to two treatments: (1) no litter, the litter layer on the soil surface was carefully removed within the subplot with minimum disturbance of surface soil. To prevent the input of fresh fallen litter, a litter trap (200 cm×200 cm) with a 1-mm mesh nylon netting bag was placed 80 cm above the sub-plot. The materials in the litter trap were cleared every 2 weeks; (2) no roots, on the outside edges of the subplots, we dug trenches of 60 cm depth, below which few roots existed (data not shown). Trenches were lined with a double-layer of 0.1 mm nylon mesh, and refilled and packed carefully with the excavated soil. After that, we carefully removed all aboveground vegetation with minimal soil disturbances, and kept the trenched plots free of live vegetation throughout the study. The trenching of the 'no roots' plots was conducted in April 2011, 12 months before the measurement of soil respiration. Previous studies indicated that any increase in soil respiration

**Table 1** Soil chemical and physical properties in the 0–5 cm soil layer under 19-year-old *M. laosensis* and *C. lanceolata* plantations

Tree species	pH	Bulk density (g cm <sup>-3</sup> )	Soil C (g kg <sup>-1</sup> )	Soil N (g kg <sup>-1</sup> )	C:N ratio
<i>M. laosensis</i>	4.3 (0.2)a	0.94 (0.14)a	39.5 (2.1)a	2.2 (0.13)a	17.9 (0.42)a
<i>C. lanceolata</i>	4.6 (0.3)a	0.96 (0.26)a	30.2 (2.9)b	1.9 (0.15)b	16.2 (1.08)b

For a given parameter, means followed by different letters differ significantly ( $P < 0.05$  by *t*-test)

Data are means of four replicates with standard deviations in parentheses

due to decomposition of fine roots killed by the trenching was largely completed within 1 year of trenching (Yang et al. 2007).

### Soil respiration and microclimate

In each 20 m × 30 m plot, six polyvinyl chloride (PVC) collars (5 cm high and 20 cm inner diameter) were randomly inserted into the soil for soil respiration measurement which began in October 2011 and lasted for 18 months. The insertion depth varied from 0.5 to 2.5 cm to ensure the collars were gas-tight and to minimize disturbance of the shallow fine roots. All collars were kept in the same locations throughout the whole study period. The average CO<sub>2</sub> efflux measured in the 20 m × 30 m plots was the total soil respiration. For each 2 m × 2 m subplot, three PVC collars were installed for soil CO<sub>2</sub> flux sampling which began in April 2012 and lasted for 12 months. Field measurements were usually conducted towards the end of each month. Instantaneous respiration rate was measured using three automated soil CO<sub>2</sub> flux systems (Li-8100, Li-Cor Inc., Lincoln, NE, USA) equipped with the 20 cm survey chamber (Model 8100–103). Before sampling, green plants growing inside the collar were carefully cut and removed. At the time of sampling, headspace air was circulated by a pump from the chamber to the analyzer unit with an air flow rate at 1.7 L min<sup>-1</sup>. The CO<sub>2</sub> concentration in the chamber was measured by an absolute, nondispersive, infrared gas analyzer and logged every second for 2–5 min depending on the respiration rates. The CO<sub>2</sub> flux was calculated by the exponential regression of the CO<sub>2</sub> concentration over time. The measurement data during the first 15 s were discarded from the regression to avoid any artifact by closing the chamber. The sampling time was restricted to between 09:00 and 12:00 h and sampling was restricted to rainless mornings (Sheng et al. 2010). In order to validate whether the CO<sub>2</sub> flux during the sampling time was representative of that during the whole day, the CO<sub>2</sub> flux in six selected plots were sampled for 24 h at 2-h intervals in January and July 2012, with six PVC collars at each plot. At the time of soil respiration sampling, soil temperature at 10 cm depth was measured using a hand-held long-stem thermometer (Model SK-250WP, Sato Keiryoki Mfg. Co. Ltd, Tokyo, Japan) placed adjacent to each collar, and soil moisture at 0–12 cm depth was recorded using a time domain reflectometry (TDR) unit (Model TDR300, Spectrum

Technologies Inc., Plainfield, IL, USA) with two 12-cm-long rods vertically inserted into the ground near each collar. A micrometeorological weather station 5 km away provided the daily air temperature and precipitation during the sampling period. The litter and root-derived soil respiration rates were calculated by the following formula: (1) Litter-derived respiration = total soil respiration - respiration in no litter subplots; (2) Root-derived respiration = total soil respiration - respiration in no root subplots; and (3) Respiration derived from root-free soil = total soil respiration - root-derived respiration - litter-derived respiration.

### Litter production and fine root dynamics

Litterfall was measured monthly from five 0.5 m<sup>2</sup> litter traps, systematically positioned within each plot. The trap comprised an open bag of 1 mm mesh window screen material raised 80 cm above the ground on a PVC frame. The litter was collected, oven dried to constant mass at 60°C and weighed. Litter quality was assessed by C/N and Lignin/N ratios. The C and N concentrations of litter were determined using an Elementar Vario EL III CN analyzer with ground samples. Klason lignin content was measured as dry weight of solids after hydrolysis with 72 % (w/w) H<sub>2</sub>SO<sub>4</sub> (Kirk and Obst 1988).

Fine roots were harvested from soil cores taken once in March 2012 to estimate the fine root biomass under the two forest plantations. Five cores (5 cm in diameter) per plot were sampled to the depth of 40 cm and live and dead roots ≤ 2 mm diameter were carefully washed free of soil. The fine roots were oven-dried at 65 °C and weighed. To determine the fine root production and mortality, a total of 5 minirhizotron tubes (80 cm long 5 cm internal diameter) were installed in July 2010 in each plot. The tubes were installed at an angle of 45° with the soil surface to a depth of 50 cm. We started collecting data from March 2012 and continued collection for 12 months. We measured root length density monthly at 4 cm depth intervals along the center surface of the minirhizotron tube as well as at a 90° angle to the left and right of center. Images were collected using a Bartz Technology digital camera (McCormack et al. 2010), and digital images were stored on a laptop computer during field collection. Total root length density was measured by digitizing all roots using RooTracker software (McCormack et al. 2012). Root production for

each sampling interval was determined by summing the length of all new roots while root mortality was measured by summing the length of the roots that had disappeared from the image (Verburg et al. 2013).

#### Data analysis

In the analysis of soil respiration and its components as well as environmental and plant parameters under each species, monthly measurements were interpreted as repeated measurements of the same experimental unit. Therefore the statistical analysis needed to accommodate the possible autocorrelation between measurements in different months within the same plot. Effects of tree species on soil respiration, and its components as well as environmental and plant parameters were consequently analyzed by one-way repeated measures ANOVA. Pearson correlation coefficients were calculated to test the relationships between monthly average soil respiration and litter quantity, fine root properties, soil temperature and moisture.

Soil temperature data recorded during the field respiration measurements were used to model the relationship between soil temperature and soil respiration (Eq. (1)) and develop stand-specific soil respiration models.

$$R_s = \alpha \times e^{\beta \times T} \quad (1)$$

where  $R_s$  is the measured soil respiration rate ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ),  $T$  is soil temperature ( $^{\circ}\text{C}$ ) at the depth of 10 cm.

Soil respiration for each measurement date was then normalized to 10  $^{\circ}\text{C}$  using Eq. (2), where  $R_{10}$  is the soil respiration base rate (normalized to 10  $^{\circ}\text{C}$ ) (Campbell and Law 2005; Gaumont-Guay et al. 2006).

$$R_s = R_{10} \times Q_{10}^{(T-10)/10} \quad (2)$$

Note that  $Q_{10} = e^{10\beta}$ , and  $\beta$  is the exponential coefficient fit in Eq. (1). A linear function was used to quantify the dependence of  $R_{10}$  on soil moisture using Eq. (3) (Zhou et al. 2007).

$$R_{10} = m \times M + n \quad (3)$$

where  $M$  is volumetric soil moisture ( $\text{cm}^3 \text{ cm}^{-3}$ ) at 0–12 cm depth and  $m$ ,  $n$  are constants fitted by the least-square technique.

## Results

Total soil respiration and respiration derived from litter and roots under different tree species

Total soil respiration from October 2011 to March 2013 under the *C. lanceolata* and *M. laosensis* plantations followed significant seasonal patterns ( $P=0.01$ ) (Fig. 1). Under the *C. lanceolata* plantation, total soil respiration reached the maximum rate ( $3.66 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) in July 2012 and the minimum ( $0.92 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) in February 2012, whereas the *M. laosensis* plantation had the highest total soil respiration rate in September 2012 and the lowest rate in January 2012. Repeated measure ANOVA showed that total soil respiration rate was significantly ( $P=0.01$ ) lower under the *C. lanceolata* than the *M. laosensis* plantations. Mean total soil respiration rates were 2.03 and 2.70  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  under the *C. lanceolata* and *M. laosensis* plantations, respectively.

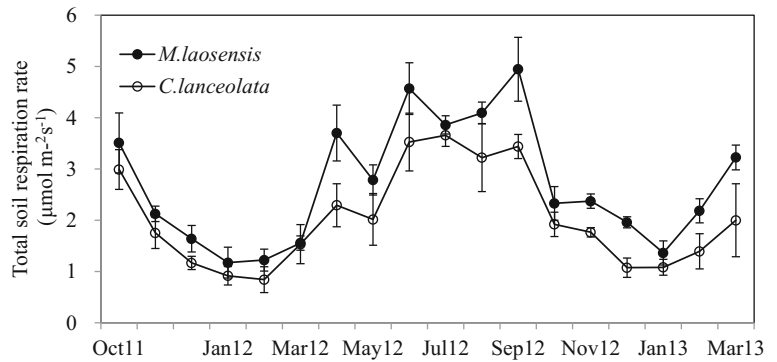
Respiration derived from roots and litter under the *C. lanceolata* and *M. laosensis* plantations from April 2012 to March 2013 showed distinct variations among months ( $P=0.03$ ) (Fig. 2). Mean respiration rates derived from roots were 0.44 and 0.64  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  under the *C. lanceolata* and *M. laosensis* plantations, respectively. Mean respiration rates derived from the litter layer were 0.29 and 0.51  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  under the *C. lanceolata* and *M. laosensis* plantations, respectively. Repeated measure ANOVA showed that the differences in respiration rates derived from roots or litter between the two species were significant at  $P=0.03$  and 0.04, respectively.

Average respiration rates derived from root-free soils under the *C. lanceolata* and *M. laosensis* plantations from April 2012 to March 2013 were 1.49 and 1.68  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  under the *C. lanceolata* and *M. laosensis* plantations, respectively. Repeated measures ANOVA showed that there was no significant differences in respiration rates derived from root-free soils between the two species ( $P=0.11$ ).

Environmental and plant parameters under different tree species

Soil temperature at 10 cm depth ( $T_{10}$ ) ranged from 7.4  $^{\circ}\text{C}$  in January 2012 to 25.8  $^{\circ}\text{C}$  in August 2012 in the two forests (Fig. 3). Soil moisture varied between 0.16 and 0.30  $\text{cm}^3 \text{ H}_2\text{O cm}^{-3}$  soil.  $T_{10}$  was not

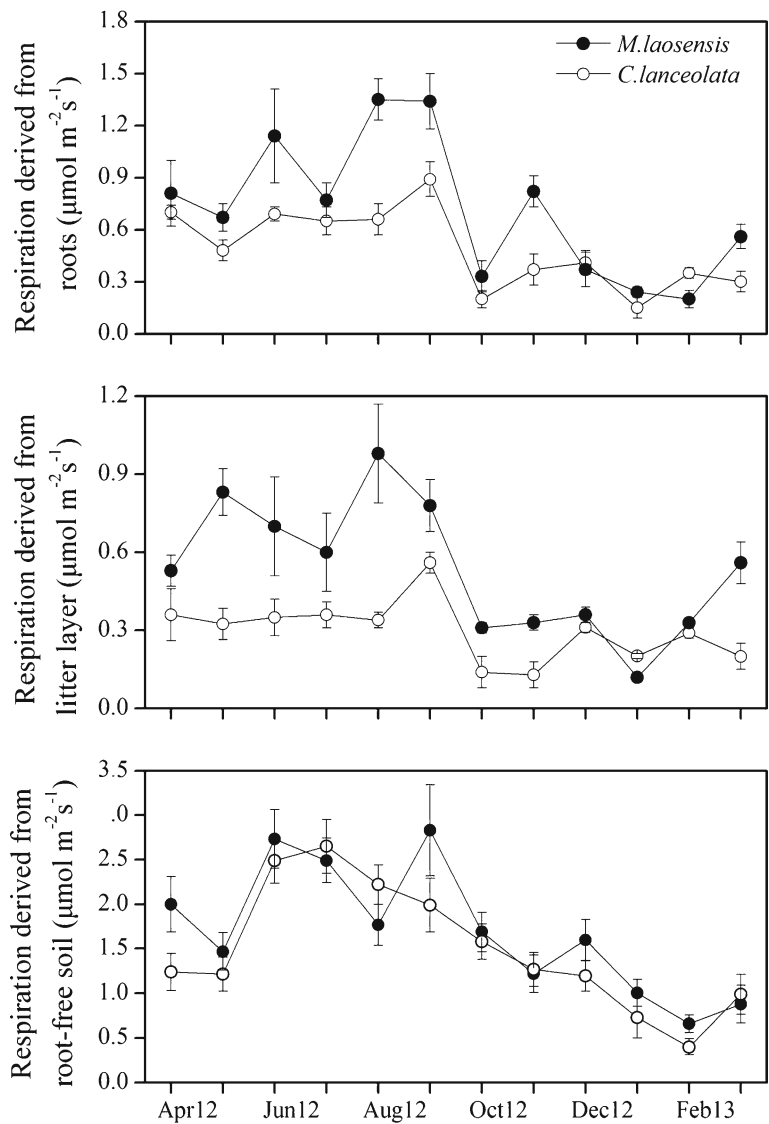
**Fig. 1** Monthly measured soil respiration rates between October 2011 and March 2013 under the *C. lanceolata* and *M. laosensis* plantations at Xiayang forest farm in Fujian province, China. Error bars represent standard errors

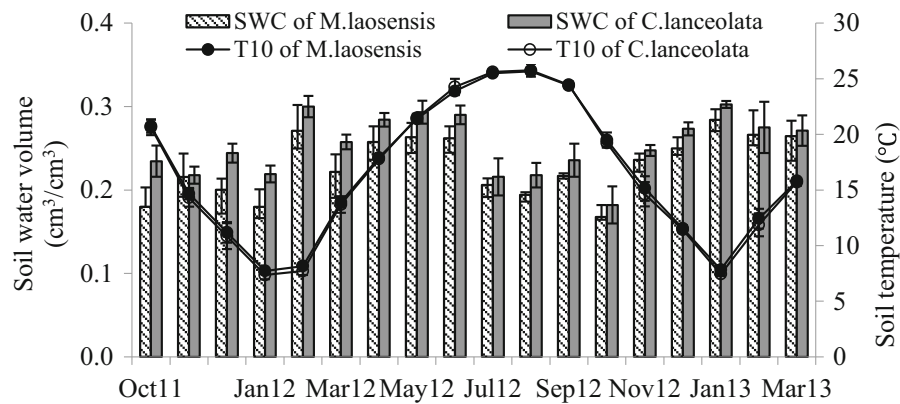


significantly ( $P=0.15$ ) different between the two species, whereas soil moisture was significantly ( $P=0.04$ )

lower under the *M. laosensis* than under the *C. lanceolata* plantation.

**Fig. 2** Monthly measured respiration rates derived from litter layer, roots or root-free soils under the *C. lanceolata* and *M. laosensis* plantations from April 2012 to March 2013 at Xiayang forest farm in Fujian province, China. Error bars represent standard errors





**Fig. 3** Monthly means of soil temperature ( $T_{10}$ ) at 10 cm depth and mean soil volumetric water content (VWC) in the 0–12 cm layer under *C. lanceolata* and *M. laosensis* plantations from

October 2011 to March 2013 at Xiayang forest farm in Fujian province, China. Error bars represent standard errors

Under the *C. lanceolata* and *M. laosensis* plantations, the amount of litterfall showed strong seasonal patterns ( $P=0.01$ ) (Fig. 4). The litterfall under the *M. laosensis* plantation peaked in March, whereas under the *C. lanceolata* plantation, the peaks of litterfall varied in different years. In 2012, annual litterfall biomass was  $5.0 \text{ Mg ha}^{-1}$  under the *C. lanceolata* plantation, significantly ( $P=0.01$ ) less than that under the *M. laosensis* plantation ( $9.8 \text{ Mg ha}^{-1}$ ). The lignin content and lignin:N in the *C. lanceolata* litter were on average 36.5 % and 37.4, respectively, higher than those in the *M. laosensis* litter (the lignin content of 28.6 % and lignin:N of 15.3).

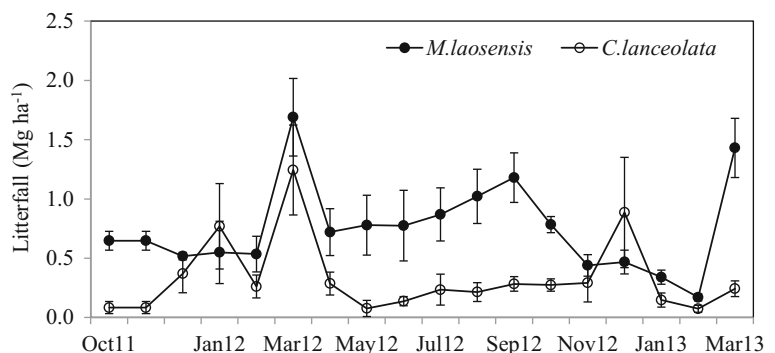
As measured in March 2012, fine root biomass ( $\leq 2 \text{ mm}$  in diameter) in the 0–40 cm soil layer was  $8.2 \pm 1.5 \text{ Mg ha}^{-1}$  under the *M. laosensis* plantation which was significantly ( $P=0.04$ ) greater than that under the *C. lanceolata* plantation ( $6.0 \pm 0.8 \text{ Mg ha}^{-1}$ ). Between March 2012 and March 2013, the average length density of fine roots in the 0–40 cm soil layer was  $46.9 \text{ m m}^{-2}$  under the *M. laosensis*

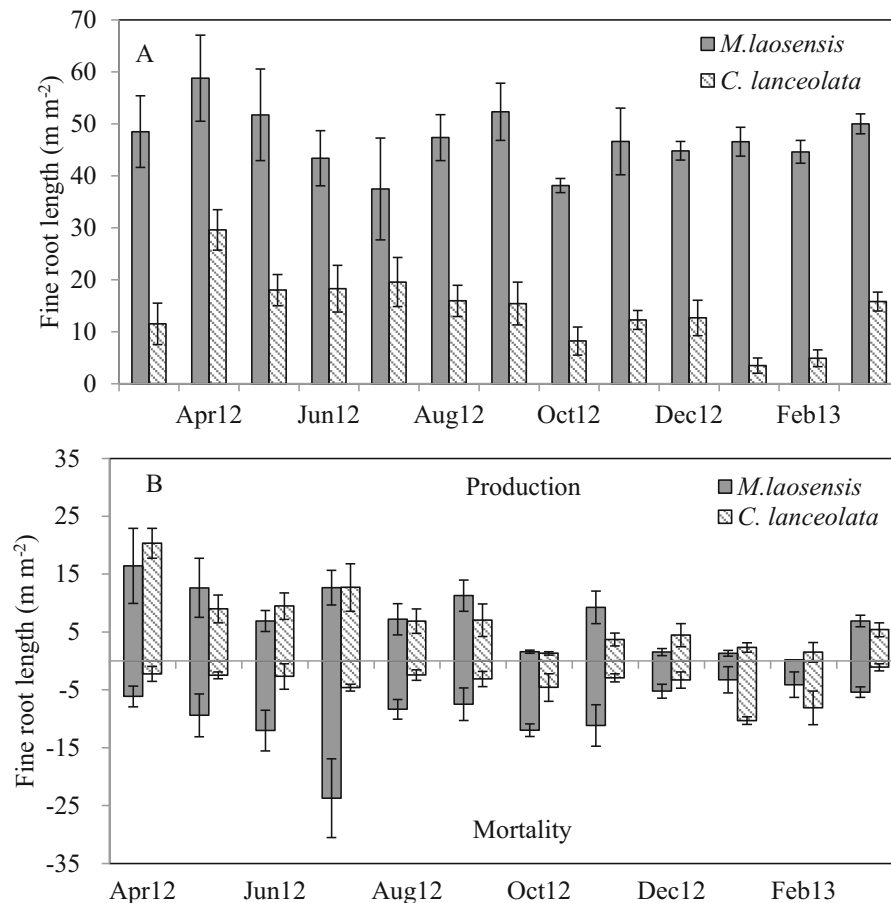
plantation which was significantly ( $P=0.01$ ) greater than that under the *C. lanceolata* plantation ( $14.3 \text{ m m}^{-2}$ ) (Fig. 5a). Fine root production occurred throughout the year under both plantations. Peak monthly root production occurred in April under both *C. lanceolata* and *M. laosensis* forests. The fine root mortality peaked in July under the *M. laosensis* plantation, but the peak of fine root mortality happened in January under the *C. lanceolata* plantation (Fig. 5b).

#### Correlations between environmental and plant variables

Seasonal variation of litterfall was not correlated with either monthly mean air temperature or monthly rainfall. Fine root production was significantly correlated with soil temperature, soil moisture and monthly rainfall under both forests. Under the *M. laosensis* plantation, fine root mortality was significantly related to soil temperature. Fine root mortality was related to

**Fig. 4** Monthly variations of litterfall biomass under *C. lanceolata* and *M. laosensis* plantations from October 2011 to March 2013 at Xiayang forest farm in Fujian province, China. Error bars represent standard errors





**Fig. 5** Fine root length (a) and monthly production and mortality of fine roots (b) under the *C. lanceolata* and *M. laosensis* plantations from April 2012 to February 2013 at Xiayang forest farm in Fujian province, China. Error bars represent standard errors

soil temperature and monthly rainfall under the *C. lanceolata* plantation (Table 2).

The contribution of biophysical and plant variables to temporal variation of soil respiration

Total soil respiration exhibited a positive exponential correlation with  $T_{10}$  under the two tree species. The relationship between total soil respiration and  $T_{10}$  showed a better fit for *C. lanceolata* ( $R^2=0.78$ ,  $P=0.01$ ) than for *M. laosensis* ( $R^2=0.72$ ,  $P=0.01$ ). Under the *M. laosensis* plantation, soil moisture was positively correlated ( $P=0.04$ ) with seasonal  $R_{10}$ . However, the relationship explained only 12 % of the variation in  $R_{10}$ . The correlation between  $R_{10}$  and soil moisture was not significant under the *C. lanceolata* plantation (Fig. 6).

Under the *M. laosensis* plantation we found monthly mean total soil respiration was significantly and positively correlated with monthly litterfall biomass and fine root production. Monthly total soil respiration under the *C. lanceolata* plantation was also significantly correlated with monthly fine root production, but in contrast to *M. laosensis* was not correlated with monthly litter fall data collected concurrently (Table 2). Monthly litterfall input under the *C. lanceolata* plantation was related to respiration fluxes lagging 3 months behind ( $R=0.63$ ,  $P=0.05$ ,  $n=12$ ).

Soil respiration derived from root, litter layer or root-free soil was positively and significantly correlated with  $T_{10}$  under both forests (Table 3). Seasonal  $R_{10}$  derived from roots was positively and significantly related to soil moisture, which explained 23 and 19 % of the variation in  $R_{10}$  derived from roots under the

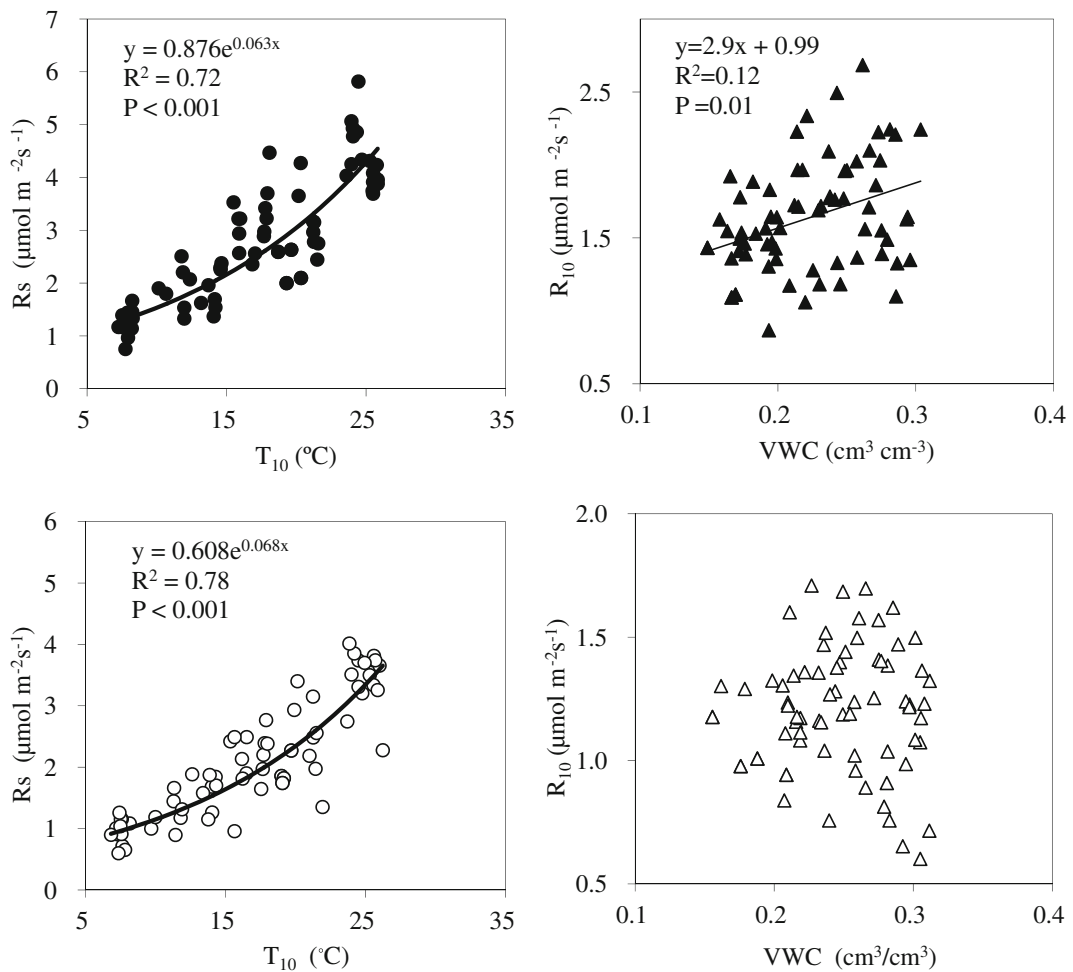


**Table 2** Pearson correlation coefficients between monthly mean soil respiration ( $R_s$ ), soil temperature ( $T_{10}$ ), monthly rainfall, soil moisture (VWC), litterfall biomass, fine root production and fine root mortality under the *M. laosensis* and *C. lanceolata* plantations ( $n=12$ )

Tree species	Parameters	Litterfall	Fine root production	Fine root mortality
<i>M. laosensis</i>	$T_{10}$	$R=0.09; P=0.98$	$R=0.66; P=0.03$	$R=0.60; P=0.04$
	Rainfall	$R=0.21; P=0.48$	$R=0.61; P=0.04$	$R=0.16; P=0.61$
	VWC	$R=0.26; P=0.31$	$R=0.58; P=0.05$	$R=0.42; P=0.18$
	Total $R_s$	$R=0.60; P=0.04$	$R=0.78; P=0.02$	$R=0.31; P=0.28$
<i>C. lanceolata</i>	$T_{10}$	$R=0.17; P=0.60$	$R=0.59; P=0.05$	$R=0.64; P=0.03$
	Rainfall	$R=0.31; P=0.28$	$R=0.57; P=0.05$	$R=0.62; P=0.03$
	VWC	$R=0.16; P=0.61$	$R=0.56; P=0.05$	$R=0.53; P=0.08$
	Total $R_s$	$R=0.28; P=0.21$	$R=0.59; P=0.05$	$R=0.27; P=0.45$

*M. laosensis* and *C. lanceolata* plantations, respectively.  $R_{10}$  derived from root-free soil was negatively correlated

with soil moisture, but the correlation was only significant under *C. lanceolata*.



**Fig. 6** The relationship between total soil respiration and soil temperature ( $T_{10}$ ) at a soil depth of 10 cm and soil moisture (VWC) in the 0–12 cm layer between October 2011 and March

2013 under the *M. laosensis* (closed circles and triangles,  $n=72$ ) and *C. lanceolata* (open circles and triangles,  $n=72$ ) plantations

**Table 3** Coefficients of determination for exponential or linear regressions between components of soil respiration ( $R_s$ ) and soil temperature ( $T_{10}$ ) or moisture (VWC) under *M. laosensis* and *C. lanceolata* plantations ( $n=48$ )

Tree species	Components	$R_s$ vs $T_{10}$	$R_{10}$ vs VWC
<i>M. laosensis</i>	Root-free soil	$R=0.81$ ; $P=0.01$	$R=-0.28$ ; $P=0.19$
	Root	$R=0.69$ ; $P=0.01$	$R=0.48$ ; $P=0.02$
	Litter layer	$R=0.55$ ; $P=0.02$	$R=0.40$ ; $P=0.05$
<i>C. lanceolata</i>	Root-free soil	$R=0.84$ ; $P=0.01$	$R=-0.69$ ; $P=0.01$
	Root	$R=0.61$ ; $P=0.01$	$R=0.43$ ; $P=0.03$
	Litter layer	$R=0.57$ ; $P=0.02$	$R=0.39$ ; $P=0.05$

## Discussion

Effect of tree species on soil respiration, its components and microclimatic conditions

Few studies have been conducted regarding soil respiration under different tree species in the subtropics, especially in woodland with same management history and climate. In order to understand the mechanisms behind ecosystem C alteration due to tree species transition from monoculture *C. lanceolata* to broadleaved plantation, we carried out soil respiration measurements in adjoining replicated plots under *C. lanceolata* and *M. laosensis* plantations. In this study, annual mean soil respiration rates under *C. lanceolata* forest were comparable to rates measured by Sheng *et al.* (2010) in the same province, but higher than those reported by Wang *et al.* (2013) and Tian *et al.* (2011) in Hunan Province where the annual mean temperature and annual rainfall are 17.1°C and 1,422 mm, respectively. For example, Tian *et al.* (2011) reported an annual mean soil respiration rate of 1.21  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in a 13 year-old *C. lanceolata* forest. In another measurement under a 16 year-old *C. lanceolata* forest located in Hunan province, Wang *et al.* (2013) reported an annual mean soil respiration rate of 1.16  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ .

Based on 18 months of measurements, the results of this study support the hypothesis that a land use transition from *C. lanceolata* to a native broadleaf *M. laosensis* plantation would increase soil respiration. Similar to our finding, Sheng *et al.* (2010) reported lower soil respiration in a pure *C. lanceolata* stand than in a broadleaf mixed species stand. Both studies support the suggestion in the review by Raich and Tufekciogul (2000) that broadleaved forest has higher soil respiration than coniferous forest. There are many different sources of  $\text{CO}_2$  efflux from soil, including plant root respiration and microbial decomposition of SOM and plant residues. The responses of different soil respiration components

to tree species transition determine the direction of total soil respiration response. In this study, the difference in respiration derived from roots and the litter layer between the two tree species explained much of the variation in total soil respiration. The results from this study and others (Brechet *et al.* 2009; Valverde-Barrantes 2007) highlight the roles of root production and litterfall in explaining the effects of tree species on soil respiration.

The data we collected in this study showed that the litter layer and plant roots almost equally contributed to the greater soil respiration under the *M. laosensis* plantation than under the *C. lanceolata* plantation. However, it is unclear whether the quantity or quality of litter contributed to the effects of tree species on soil respiration in this study. Tewary *et al.* (1982) found that soil respiration rates beneath coniferous trees were lower than those beneath broad-leaved trees in a mixed forest in northern India, and that these microhabitat differences correlated with higher N and lower lignin contents in the oak litter. Therefore, the production and decomposition rates of litterfall and fine roots as well as the quality of litterfall may have contributed to the difference observed between broad-leaved and coniferous forest respiration rates.

It should be noted that respiration derived from roots in this study included autotrophic respiration from roots, mycorrhizal fungi and rhizosphere organisms. It was estimated that mycorrhizal fungi contributed up to 60 % of the autotrophic respiration in a *Pinus contorta* forest (Heinemeyer *et al.* 2007). Our previous study showed that tree species transition from *C. lanceolata* to *M. laosensis* significantly increased the content of soil arbuscular mycorrhizal and ectomycorrhizal fungi as indicated by phospholipid fatty acid analysis. Therefore, the increase in autotrophic respiration associated with change in tree species from conifer to broadleaf may have resulted from a change in the mycorrhizal fungi community.

Substrate availability is one of the most important factors controlling soil respiration. Soil respiration is

dependent on the replenishment of available substrates from the bulk organic C pool (Wang et al. 2003). Although there were greater contents of soil organic C and light fraction soil organic C in the *M. laosensis* soil (Huang et al. 2013b), the difference in respiration derived from root-free soil was not significant between the two forests. The present study therefore suggests that substrate availability may not be a limiting factor for soil respiration in these forests.

In addition to the quantity and quality of litter and roots produced by forests, observed differences in total soil respiration among tree species have been attributed directly to plant-mediated effects on soil microclimate. For example, Vesterdal et al. (2012) assessed total soil respiration under six tree species in a common garden experiment in Denmark and found Norway spruce (*Picea abies* Pseudo-Maxwellii) had distinctly lower soil moisture compared with other tree species. The lower respiration rate under Norway spruce was attributed to the lower soil moisture under this species. In our study, we evaluated the tree species effect on soil temperature and moisture and found no difference in temperature between the two species. In other words, the lower total soil respiration rate under the *C. lanceolata* plantation cannot be explained by soil temperature alone. In contrast to the lack of species effect on soil temperature, the *C. lanceolata* plantation had significantly higher soil moisture than the *M. laosensis* plantation. We determined the relationships between  $R_{10}$  and soil moisture and found either positive or no relationships in the two forests. This result suggests that the lower soil moisture under the *M. laosensis* plantation may not have contributed to the greater total soil respiration rate under this species than under *C. lanceolata*.

#### Temporal variation of soil respiration, microclimatic conditions and tree species effects

The observed temporal pattern of variation in total soil respiration and its components under both *M. laosensis* and *C. lanceolata* plantations was mainly attributed to the variation of soil temperature. This is in agreement with most studies in ecosystems with significant temperature fluctuation, particularly in the absence of soil water stress (Andersen et al. 2005). The temporal variation of soil temperature might coincide with the seasonal patterns of soil nutrient availability and photosynthetic active radiation which may also contribute to the seasonal pattern of variation of soil respiration (Liu et al. 2006).

The impact of soil moisture on the temporal pattern of variation in soil respiration is much more complicated and frequently masked by the temperature effect (Gaumont-Guay et al. 2006). Therefore normalized soil respiration rate by soil temperature using an exponential equation and base temperature (e.g. 10 °C) ( $R_{10}$ ) are often used to analyze the relationship between soil moisture and soil respiration. However, the relationship has been found to be variable, depending not only on the soil and vegetation type (Vincent et al. 2006), but also on climate zone (Davidson et al. 1998). In this study, we found a significantly positive relationship between soil moisture and  $R_{10}$  under *M. laosensis* but no significant relationship under the *C. lanceolata*, which suggested a tree species effect on the relationship between soil moisture and  $R_{10}$ . Total  $R_{10}$  is a sum flux derived from several components and response of any single component to variation in soil moisture can be masked by opposite changes in another. Although correlation between soil moisture and  $R_{10}$  derived from root-free soil was statistically significant only under the *C. lanceolata* plantation, we found that the correlation under both forests was negative. This result agrees with other studies (Davidson et al. 1998; Xu and Qi 2001) which suggested that soil respiration and soil moisture were negatively correlated at high volumetric soil moisture content (>19 %). Under the *C. lanceolata* plantation, the mean soil moisture was 26.6 % in 2012 and higher than that (24.9 %) under *M. laosensis*, which may lead to a more negative correlation between soil moisture and  $R_{10}$  derived from root-free soils. Too much water can inhibit microbial activity,  $CO_2$  production and emission (Curiel Yuste et al. 2007; Drewitt et al. 2002). In contrast to  $R_{10}$  derived from root-free soils,  $R_{10}$  derived from roots and the litter layer increased significantly with increased soil moisture under both forests. The increase in  $R_{10}$  derived from roots due to increased soil moisture may coincide with a flush in fine root production as we found a significant correlation between soil respiration and fine root production as well as a significant correlation between fine root production and soil moisture. In addition, the increase in  $R_{10}$  derived from roots can also be explained by the energy requirements of living cells of fine roots with high respiration for maintenance and nutrient uptake under higher soil moisture environment (Makita et al. 2012).

In the current study, monthly variation in total soil respiration was significantly associated with variation in concurrent monthly litterfall input under the *M. laosensis* plantation, but not significantly correlated

with concurrent monthly litterfall input under the *C. lanceolata* plantation. Several studies in subtropical mixed forests have suggested a potentially delayed effect of litterfall on soil respiration (Mo et al. 2008; Yan et al. 2006). Indeed, the correlation between monthly soil respiration rate and litterfall input under the *C. lanceolata* plantation was found to be significant when litterfall data were compared with respiration fluxes lagging 3 months behind. The more rapid response of soil respiration to litterfall input under the *M. laosensis* plantation in comparison to the *C. lanceolata* plantation might be due to a higher proportion of litterfall with lower C:N and lignin:N ratios under *M. laosensis* (Huang et al. 2013b). Litterfall input from *M. laosensis* can more rapidly produce C substrates for microbial respiration than litterfall from *C. lanceolata* (Wan et al. 2013). This study therefore highlights that species-induced variation in litterfall quality and quantity can impact not only the total soil respiration but also the seasonal pattern of variation in soil respiration.

We investigated C loss via soil respiration in response to tree species transition in subtropical forests which accounts for 8 % of the global forest net ecosystem productivity (Yu et al. 2014). The lack of difference in respiration rate derived from root-free mineral soils under the two species implied that the increases of aboveground and belowground litterfall input to soil due to tree species change did not result in a priming effect. Therefore, the enhanced forest productivity through tree species transition could increase soil C storage as shown at this site.

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