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Seasonal dynamics of soil respiration and nitrification in three subtropical plantations in southern China

Weixia Wang [1-2], **Ruimei Cheng** [2-3], **Zuomin Shi** [2-3], **Joachim Ingwersen** [4], **Da Luo** [2], **Shirong Liu** [2]

Numerous studies have documented that soil respiration and nitrogen cycling show a distinct seasonal dependence regulated by environmental factors (*e.g.*, soil temperature and soil water content). The mechanisms controlling the seasonal dependence of these two key ecosystem processes have rarely been linked to both soil microbial community and soil environmental factors. Here, we present results on the seasonal patterns of soil respiration and gross nitrification rates in three subtropical plantations of *Pinus massoniana*, *Castanopsis hystrix* and *Erythrophleum fordii* over a period of 11 months. Turnover rates were measured with the Barometric Process Separation technique (BaPS). We elucidated how soil respiration and gross nitrification are controlled by the soil microbial community and by soil environmental factors. Soil respiration and gross nitrification showed strong seasonal dynamics, although no significant differences were observed among plantations. The turnover rates were the highest during the wet season and the lowest during the dry season. Microbial biomass, total phospholipid fatty acids (PLFAs), fungal PLFAs and bacterial PLFAs peaked during the dry season. Both soil respiration and gross nitrification rates were positively correlated with soil temperature and soil water content. Microbial biomass decreased with increasing turnover rates. Our findings highlight that carbon and nitrogen turnover rates were mostly controlled by soil temperature and soil water content.

Keywords: Soil Respiration, Nitrification, PLFA, Soil Microbial Community, N-fixing Tree Species, Subtropical China

Introduction

Forests are important carbon (C) pools in terrestrial ecosystems and play an important role in the global C and nitrogen (N) cycle. Soil CO_2 efflux (soil respiration) is sensitive to climate, vegetation type and soil properties (Palmroth et al. 2005). Soil temperature and soil water content are recognized as the main factors controlling soil respiration (Janssens et al. 2001), whereas the soil biophysical environment and substrate availability (*e.g.*, aboveground and belowground litter fall, soil organic C) are the main factors controlling heterotrophic respiration (Ryan & Law 2005, Luan et al. 2012).

The N cycle in forests is a complex system with close linkages and interactions between soil, plants and microbes. The natural N supply for plants and microorganisms is derived from the mineralization of organic N compounds (Das et al. 1997). This process occurs in two steps, ammonification and nitrification, which play a key role by making inorganic N compounds available for plants and microbes. The process is influenced by a number of factors such as composition and diversity of the soil microbial community, substrate quality and quantity, and environmental conditions (temperature and water content – Templer et al. 2003, Grenon et al. 2004). These factors are influenced by tree species and plantations. In fact, tree species are known to affect the physicochemical and biological characteristics of soils (Binkley & Giardina 1998, Staelens et al. 2012). Soil microbial biomass (MB), activity, and community structure might thus be tree species dependent (Hackl et al. 2005). Tree species also differ in the quality of leaf litter (*e.g.*, C/N), which directly influences the quality and quantity of organic matter input (Templer et al. 2003, Brüggemann et al. 2005). Moreover, root litter is also species dependent and directly affects root exudation (Burton et al. 2007). Accordingly, microbes receive organic matter of varying quality from different tree species (Templer et al. 2003). This, in turn, may lead to changes in soil microbial communities and MB (Bauhus et al. 1998), which subsequently influence soil N transformations (Patra et al. 2006, Ste-Marie & Houle 2006). Most studies on microbial N cycling have concentrated on determining net nitrification rates (Munson & Timmer 1995, Paavolainen & Smolander 1998, Westbrook et al. 2006) rather than gross rates. Direct comparisons of net and gross nitrification rates, however, reveal that the former can be one order of magnitude lower than the latter. Thus changes in the NO_3^- pool do not necessarily reflect the total turnover from NH_4^+

(1) College of Forestry and Horticulture, Xinjiang Agricultural University, Urumqi 830052 (China); (2) Key Laboratory on Forest Ecology and Environmental Sciences of State Forestry Administration; Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, Beijing 100091 (China); (3) Co-Innovation Center for Sustainable Forestry in Southern China, Nanjing Forestry University, Nanjing 210037 (China); (4) Institute of Soil Science and Land Evaluation, University of Hohenheim, Stuttgart D-70593 (Germany)

@ Shi Zuomin (shizm@caf.ac.cn)

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to NO_3^- (Stark & Hart 1997, Neill et al. 1999, Ingwersen et al. 1999). These findings highlight the importance of measuring gross nitrification rates to understand N transformation in forest ecosystems.

Only few studies have investigated gross nitrification in soil under different tree species/forest types. Brüggemann et al. (2005) studied soil respiration, gross N mineralization and gross nitrification in pure stands of different temperate tree species. Matejek et al. (2010) and Rosenkranz et al. (2010) investigated ammonification and gross nitrification in forest soil layers in southern Germany (temperate climate). Comparable comprehensive studies are missing for subtropical climate regions.

Southern China, which is located mostly in the subtropical region, has 25 million hectares of plantations (Wang et al. 2010a). Plantations are becoming a key component of the world's forest resources and play an important role in the context of sustainable forest management (Wang et al. 2010b). This calls for studies on soil C and N transformation under the main tree species used for afforestation to better understand the C and N cycle of subtropical plantation ecosystems.

Accordingly, the objective of this study was to determine the seasonal dynamics of soil respiration and nitrification in the top soil layer in subtropical plantations and to elucidate the relationships of these two key turnover processes with the composition of the soil microbial community (bacteria *vs.* fungi) and the two environmental factors soil temperature and soil water content.

Materials and methods

Study area

The study was conducted at the Experimental Center of Tropical Forestry, the Chinese Academy of Forestry (22° 06′ N, 106° 46′ E), Pingxiang City, Guangxi Zhuang Autonomous Region, China. Annual rainfall is about 1400 mm and occurs primarily from April to September. The annual mean temperature is 21 °C, the mean monthly minimum is 12.1 °C, and the mean monthly maximum is 26.3 °C. The soil was formed on granite, classified as red soil in Chinese soil classification, equivalent to Oxisol in USDA Soil Taxonomy (Liang & Wen 1992, Wang et al. 2010a, Huang et al. 2014).

We studied three of the most dominant plantations: one conifer plantation (*Pinus massoniana* Lamb.) and two broadleaved plantations (*Castanopsis hystrix* Miq. and *Erythrophleum fordii* Oliv.). *E. fordii* is a N-fixing species. These monoculture plantations were selected based on their similar topography, soil texture, stand age and management history. The three plantations were established after a clear-cut harvest of *P. massoniana* plantation in 1978, at an elevation of 350 m, over areas ranging from 2.2 to 4.8 hectares. Stem density varied from 410 to 415 trees per hectare, the diameter at breast height (DBH) ranged from 22.4 to 26.4 cm. In each plantation, five sampling squared plots (20 × 20m) were randomly selected and delineated.

Soil sampling

Soil was sampled monthly over a period of 11 months (from August 2011 to July 2012; except January, the date of sampling was the same every month, *i.e.*, 15th), covering the entire season, *i.e.*, wet, dry and intermediate conditions. Five intact soil cores were randomly taken from the top soil layer using a soil corer (5.6 cm diameter, 4.1 cm height) at each plot after removing the litter (Kiese et al. 2008, Wang et al. 2010b, Wang et al. 2013). The intact soil cores were analyzed for gross nitrification and soil respiration rates using the BaPS technique (UMS GmbH Inc., Germany – Ingwersen et al. 1999, Breuer et al. 2002, Kiese et al. 2002).

Bulk soil samples for chemical analysis were collected from the top soil layer (0-5 cm) in late February 2012 (dry season) and July 2012 (wet season). A total of six soil cores per plot were randomly collected using a 5.0-cm-diameter stainless steel core and bulked to one composite sample. After collection, samples were immediately delivered to the laboratory for further analysis. In the lab, each composite sample was passed through a sieve (2 mm mesh size), and plant material was manually removed from the sieved soil. The sieved soil was divided into three subsamples. The first subsample was used to determine soil organic carbon (SOC), total nitrogen (TN) and soil pH. The second subsample was kept at 4 °C for analysis of nitrate (NO_3^--N), ammonium (NH_4^+-N), microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN). The third subsample was used for total PLFAs, fungal and bacterial PLFAs determinations, and was stored at -20 °C.

Physicochemical analyses

Soil samples collected for physicochemical analyses were ground to pass through a 0.25 mm sieve. SOC was measured using the potassium dichromate vitriol oxidation method (Liu et al. 1996) and TN concentration was measured after semimicro-Kjeldahl digestion using a flow injection auto-analyzer (FIA®, Lachat Instruments, USA). Soil C/N values were calculated as the ratio of SOC to TN. Soil pH was determined using a 1:2.5 soil/water suspension. Inorganic N (ammonium and nitrate) was extracted with 2 M KCl solution. Ammonium and nitrate in extract were measured using the above flow injection auto-analyzer. Soil MBC and MBN were determined using the fumigation-extraction method (Vance et al. 1987, Tate et al. 1988). Specifically, soil samples from each experimental site were divided into paired subsamples of 20 g. One subsample was immediately extracted with 60 ml 0.5 M K_2SO_4. The second subsample was fumigated with chloroform vapor for 48h in a desiccator followed by 10 vacuum/purge cycles, and then extracted as described above. Soil extractable organic C and TN in the K_2SO_4 extracts before and after the fumigation were quantified using a total C/N analyzer (Multi-N/C 2100®, Analytik Jena AG, Germany). The released C and N were converted to MBC and MBN, respectively, using the conversion factors K_{ec}=0.45 and K_{en}=0.45. Soil temperatures at 5 cm depth (T_5) were determined by a digital thermometer concomitantly with the soil samplings. All results were expressed per unit of oven-dried soil weight.

Phospholipid fatty acid extraction

The soil microbial community was characterized using PLFA analysis as described by Bossio & Scow (1998). Lipids were extracted from 8 g of dry-weight-equivalent fresh soil with a one-phase mixture of chloroform, methanol and phosphate buffer (1:2:0.8). The separated fatty acid methylesters were re-dissolved in 200 µl hexane containing 19:0 as an internal standard and were analyzed using a Hewlett-Packard 6890 Gas Chromatograph equipped with an Ultra 2-methyl polysiloxane column. Concentrations of each PLFA were calculated based on the 19:0 internal standard concentrations. The abundance of individual fatty acids was determined as nmol per g of dry soil and standard nomenclature was used (Tunlid et al. 1989).

Bacteria were considered to be represented by 12 PLFAs (i14:0, i15:0, a15:0, 15:0, i16:0, 16:1ω7c, i17:0, a17:0, 17:0, cy17:0, cy19:0, 18:1ω7c), and gram-positive bacteria were identified by the PLFAs i14:0, i15:0, a15:0, i16:0, i17:0, a17:0, gram-negative bacteria by the PLFAs 16:1ω7c, cy17:0, cy19:0. The fungi were considered to be represented by the PLFAs 18:2ω6.9c and 18:1ω9c (Bååth & Anderson 2003, Högberg et al. 2007). A ratio of the gram-positive bacteria to the gram-negative bacteria PLFAs (G^+/G^-) was used as an indicator of changes in the relative abundance of these two microbial groups; the ratio of 18:2ω6.9c and 18:1ω9c to total bacterial PLFAs was used to estimate the ratio of fungal to bacterial biomass (F/B) in soils (Bardgett & Hobbs 1996). Several other PLFAs such as 16:0, 16:1 2OH, 16:1ω5c, 10Me16:0 and 10Me17:0 were detected and also used to analyze the composition of microbial community.

Determination of gross nitrification and soil respiration

The BaPS technique enables simultaneous determination of gross nitrification and soil respiration (Ingwersen et al. 1999, 2008). Previous studies testing the BaPS method against the ^{15}N pool dilution technique revealed that using the default value of the respiration quotient (RQ) of unity tends to overestimate gross nitrification rates (Müller et al. 2004, Rosenkranz et al. 2006). Müller et al. (2004) thus suggested using the ^{15}N pool dilution technique for determining the RQ value needed in the BaPS

method. For acid forest soils, Rosenkranz et al. (2006) and Matejek et al. (2008) found average RQ values of 0.90 ± 0.01 and 0.89 ± 0.02, respectively. We therefore used a RQ of 0.9 in the present study. The autotrophic-to-heterotrophic nitrification ratio was kept at the default ratio of 3:1 (Ingwersen et al. 1999, 2008).

Gross nitrification and soil respiration rates were determined by incubating intact soil cores (5.6 cm diameter, 4.1 cm height), which were taken from the top soil from each sampling spot. Five replicates per experimental plantation were taken at each sampling date. Immediately after sampling, the undisturbed soil cores were sealed with parafilm and transported to the laboratory, where they were stored in the dark at *in situ* soil temperature as determined by use of Pt100 probes at the field site at 2 pm. Soil samples were incubated in the BaPS incubation chamber for 24h at stable *in situ* soil temperatures. At the end of the incubation, soil water content and bulk density were determined gravimetrically by drying soil samples at 105 °C for 24h. Water-filled pore space (*WFPS*) was calculated using the following formula (Torbert & Wood 1992 – eqn. 1):

$$WFPS = \frac{SWC}{1 - \frac{BD}{PD}}$$

where SWC is the volumetric water content ($cm^3\ cm^{-3}$), BD is the soil bulk density ($g\ cm^{-3}$), and PD denotes the soil particle density, which was assumed to be 2.65 $g\ cm^{-3}$ (Torbert & Wood 1992, Breuer et al. 2002).

Statistical analysis and data evaluation

Statistical analyses to determine significant differences between plantations and sampling dates were performed using SPSS® 16.0 and SigmaPlot® 10.0 (SPSS Inc., Chicago, USA). To test for normal distribution of data we used the normal probability plot. For the analyses of variance we used a one-way analysis of variance (ANOVA) with a least significant differences (LSD) *post hoc* test. Correlations between gross nitrification and soil respiration were also analyzed by bivariate linear regressions.

We used an exponential equation (Luan et al. 2011) to describe the response of the two turnover processes to temperature (eqn. 2):

$$k(T) = a \cdot \exp(bT)$$

where k is the turnover rate of soil respiration or gross nitrification, T is soil temperature measured at 5 cm depth, and a and b are regression coefficients. The temperature sensitivity (Q_{10}) was calculated as (Luan et al. 2011 – eqn. 3):

$$Q_{10} = \exp(10 \cdot b)$$

The effect of *WFPS* on the two turnover processes was evaluated with a simple linear regression (Luan 2010) as follows (eqn. 4):

$$k(WFPS) = cWFPS + d$$

where c and d are the slope and the intercept, respectively.

We incubated the soil samples under *in situ* conditions, *i.e.*, for incubation we used the temperature and the *WFPS* measured at the field site. To disentangle the effect of differing temperature and *WFPS* between the sites from other factors such as vegetation type or soil physicochemical properties, the rates were normalized for each month to the mean temperature and mean *WFPS* used in the incubations (eqn. 5):

$$k^* = k \cdot \exp[b(T - \bar{T})] \frac{c\,\overline{WFPS} + d}{c\,\overline{WFPS} + d}$$

where k is the measured rate, and k^* denotes the normalized rate, T and $\bar{T}$ are the site and mean temperature (N=3), respectively. The same notation was used for *WFPS*.

The composition of the soil microbial community was summarized using principal component analysis (PCA) on the 19 individual PLFAs (nmol g^{-1} dry soil) from the PLFA analysis of soil samples after standardization for equal unit variance. To test for normal distribution of data we used the normal probability plot. Differences in individual soil PLFA among plantations and seasons were tested with one-way analysis of variances (ANOVA).

Results

Soil carbon and nitrogen pools

Soil properties including SOC and TN varied significantly among the plantations (Tab. 1). In particular, the TN content of the top soil in the plantation of the N-fixing species *E. fordii* was substantially higher than in the other two plantations. SOC in the *E. fordii* plantation was significantly higher than that in *P. massoniana*, although it was not significantly different from *C. hystrix*. There were no significant seasonal differences of the topsoil TN content among the plantations, while the SOC difference between dry and wet seasons was significant in the *E. fordii* and the *C. hystrix* plantations.

Soil C to N ratios and nitrate concentrations varied significantly between the N-fixing *vs.* the non-N-fixing plantations ($P < 0.05$). Soil ammonium concentrations were

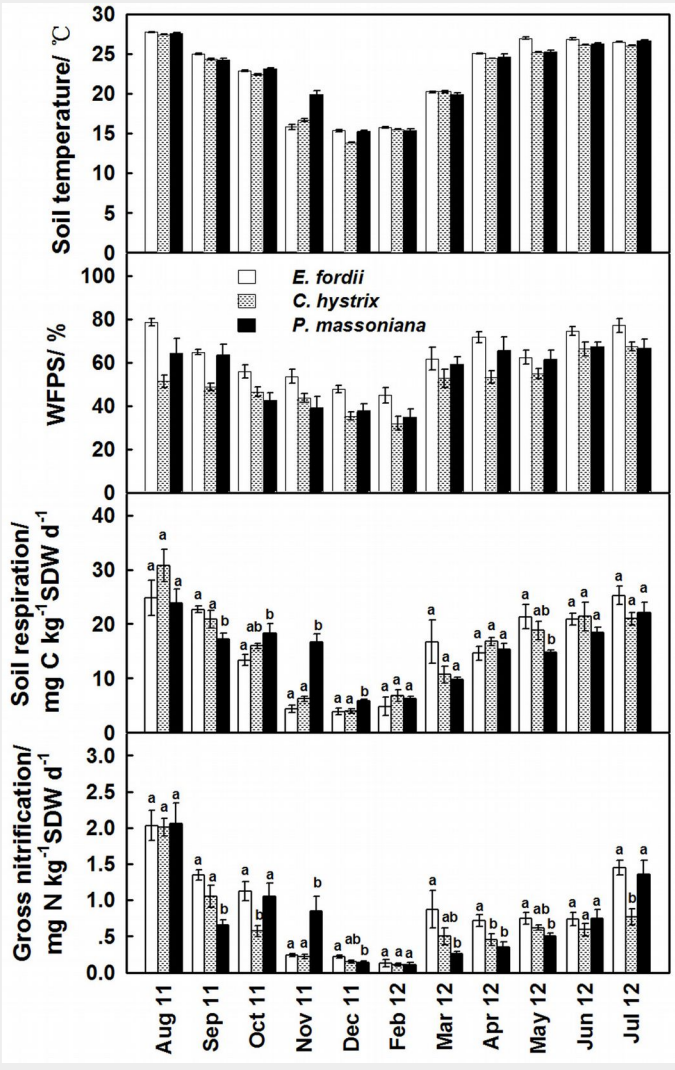

Fig. 1 - Means (± SE) of soil temperature, *WFPS*, soil respiration and gross nitrification in the three plantations at different sampling dates over 2011-2012. A one-way analysis of variance (ANOVA) with a least significant differences (LSD) *post-hoc* test was used. Different letters indicate significant differences ($P<0.05$) among the plantations for a given sampling date. All rates were normalized to the mean temperature and *WFPS* of each month.

Tab. 1 - Soil pH and carbon and nitrogen pools of three subtropical plantations in Southern China. Data are means ± standard error (n=5). A one-way analysis of variance (ANOVA) with a least significant differences (LSD) *post-hoc* test was used. Different letters indicate significant differences (P<0.05) among plantations (lower case letters) or between different seasons (upper case letters).

Variable	Season	*Erythrophleum fordii*	*Castanopsis hystrix*	*Pinus massoniana*
pH	dry	3.93 ± 0.04 Aa	4.26 ± 0.01 Ab	5.18 ± 0.04 Ac
	wet	3.86 ± 0.03 Aa	4.15 ± 0.05 Bb	4.96 ± 0.04 Bc
SOC (g kg^{-1})	dry	35.11 ± 3.93 Aa	32.55 ± 0.36 Aab	26.46 ± 1.29 Ab
	wet	30.25 ± 1.86 Ba	28.58 ± 1.08 Ba	23.94 ± 1.07 Ab
TN (g kg-1)	dry	2.86 ± 0.31 Aa	2.11 ± 0.14 Ab	1.59 ± 0.09 Ab
	wet	2.50 ± 0.13 Aa	2.03 ± 0.20 Ab	1.60 ± 0.04 Ab
C:N ratio	dry	12.28 ± 0.34 Aa	15.63 ± 1.05 Ab	16.69 ± 0.16 Ab
	wet	12.07 ± 0.31 Aa	14.33 ± 0.97 Ab	14.88 ± 0.44 Bb
Nitrate (mg N kg^{-1})	dry	9.73 ± 0.91 Aa	2.07 ± 0.19 Ab	3.07 ± 0.10 Ab
	wet	7.54 ± 0.15 Ba	3.30 ± 0.19 Bb	2.91 ± 0.20 Ab
Ammonium (mg N kg^{-1})	dry	18.26 ± 1.71 Aa	17.26 ± 1.68 Aab	13.38 ± 0.83 Ab
	wet	18.83 ± 0.61 Aa	16.28 ± 1.21 Aa	15.74 ± 1.38 Aa

the highest in the *E. fordii* plantation, where the soil pH values were the lowest.

Soil respiration rates

Soil respiration rates were variable over the two seasons in all the plantations. The minimum respiration rates occurred during the dry season, when soil water content decreased to values below 45.0% *WFPS*. The maximum respiration rates were measured during the wet season when soil water content increased from 50.0% to 78.5% *WFPS* (Fig. 1). Soil respiration rates were not significantly different among the plantations ($P>0.05$). In the dry season, the rates were 3-fold to 5-fold lower than in the wet season (Fig. 1).

In all the three plantations, soil respiration increased with increasing temperature and *WFPS* (Fig. 2). The response to temperature was well described by the exponential function (eqn. 2). The coefficient of determination ranged from 0.76 to 0.86 (Fig. 2a). Based on the regression coefficient b of eqn. 2, Q_{10} values of respiration were 2.87, 3.98 and 2.70 in the *E. fordii*, *C. hystrix* and *P. massoniana* plantations, respectively. Moreover, we found a linear relation between soil respiration and *WFPS* (R^2 = 0.31-0.56, $P < 0.0001$ – Fig. 2b).

Gross nitrification rates

Gross nitrification rates showed a seasonal pattern similar to that of soil respiration (Fig. 1). The highest rates were recorded during the wet season and the lowest rates during the dry season. In the wet season, rates were up to 11-fold higher than in the dry season in the *P. massoniana* plantation (Fig. 1). Over the entire observation

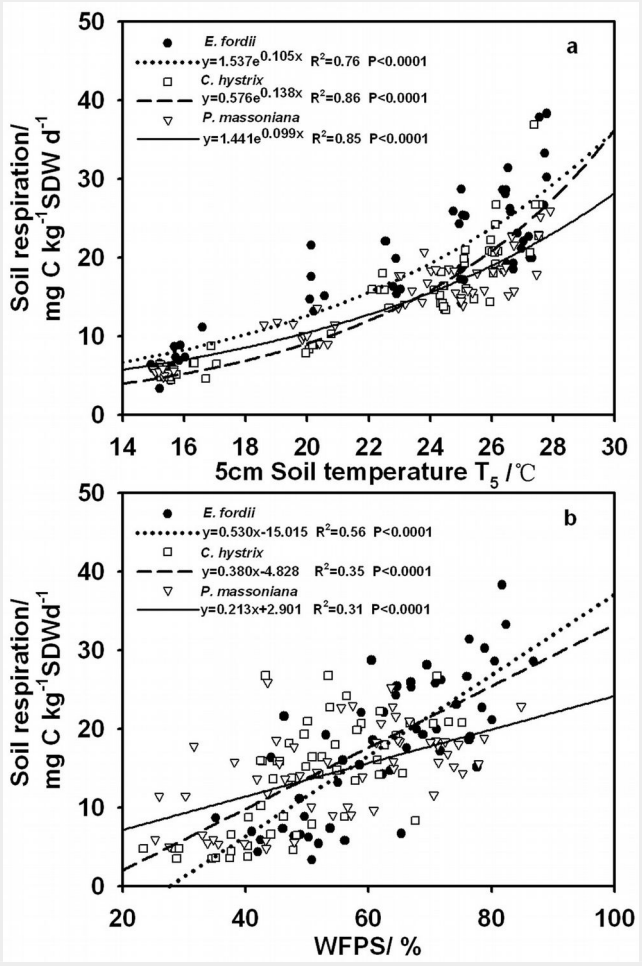

Fig. 2 - Relation between soil respiration rate and (a) soil temperature, or (b) water-filled pore space (*WFPS*) for the three plantations. Soil temperature was measured at 5 cm depth and soil water content was measured at 0-5 cm depth.

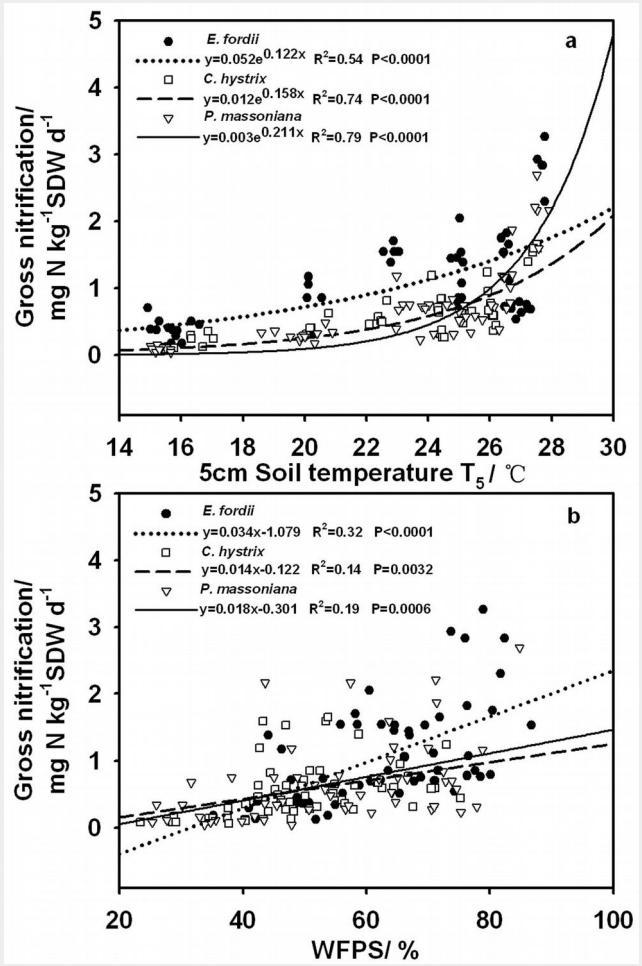

Fig. 3 - Relation between gross nitrification rate and (a) soil temperature, or (b) water-filled pore space (*WFPS*) for the three plantations. Soil temperature was measured at 5 cm depth and soil water content was measured at 0-5 cm depth.

period, mean gross nitrification ranged between 0.11 and 2.06 mg N kg^{-1} SDW d^{-1}. The differences among the plantations were not significant (Fig. 1).

The response of gross nitrification to temperature was well described with the exponential approach (R^2 between 0.54 and 0.79, $P < 0.0001$ – Fig. 3a). The data, however, scattered much more strongly around the fit compared with the soil respiration data. The calculated Q_{10} values were 3.39, 4.85 and 8.25 for *E. fordii, C. hystrix* and *P. massoniana*, respectively. Gross nitrification showed a weak linear relationship to *WFPS* (R^2 = 0.14-0.32, $P < 0.001$ – Fig. 3b).

Significant linear correlations between soil respiration and gross nitrification were found in all three plantations and the strongest correlation was in the *E. fordii* plantation (Fig. 4).

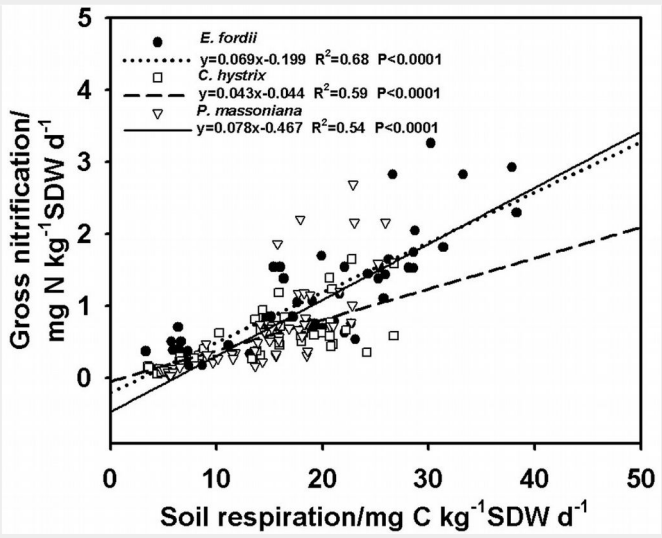

Fig. 4 - Linear correlation between gross nitrification rate and soil respiration rate for the three plantations.

Soil microbial community composition

Total PLFAs did not differ among the plantations, while the abundance of individual PLFAs did (Tab. 2). In the wet season, the abundance of gram-positive bacteria (i15:0, a15:0, i16:0, i17:0, a17:0), gram-negative bacteria (16:1ω7c, cy17:0, cy19:0) and ectomycorrhizal fungi (18:1ω9c) was higher in the *C. hystrix* plantation than in the *E. fordii* plantation ($P < 0.05$). Saprophytic fungi (18:2ω6.9c), arbuscular mycorrhizae fungi (16:1ω5c) and the ratio of $Gram^+$ to $Gram^-$ differed significantly among the three plantations for two seasons; saprophytic fungi (18:2ω6.9c) and arbuscular mycorrhizae fungi (16:1ω5c) were higher in the dry season for all the plantations (Tab. 2).

Principal Components Analysis of the microbial community composition, defined by the 19 PLFAs, showed that the first principal component (PC1) accounted for 65.8% and the second component (PC2) for 20.6% of the total variation in microbial communities (Fig. 5). The *C. hystrix* plantation was clearly separated from the other two on the PC1 axis (Fig. 5). This difference was mainly caused by the relatively higher abundances of Gram-positive bacteria, Gram-negative bacteria, saprophytic fungi and ectomycorrhizal fungi in the *C. hystrix* plantation. The *E. fordii* plantation was clearly separated from the *P. massoniana* plantation on the PC2 axis (Fig. 5) because the *E. fordii* plantation showed lower abundances of ectomycorrhizal fungi, arbuscular mycorrhizae fungi and Gram-negative bacteria (Tab. 2).

Microbial community and its relation to C and N turnover

Soil MB, total PLFAs, fungal PLFAs, bacterial PLFAs, soil respiration and gross nitrification rates were significantly different between the dry and wet season, while the latter two showed a seasonal pattern

Tab. 2 - Abundance of soil indicator lipids in the dry and wet season in the three plantations. Data are means ± standard error (n=5). A one-way analysis of variance (ANOVA) with a least significant differences (LSD) *post-hoc* test was used. Different letters indicate significant differences (P<0.05) among plantations (lower case letters) or between different seasons (upper case letters).

Group	Lipid abundance (nmol g^{-1})	Season	*Erythrophleum fordii*	*Castanopsis hystrix*	*Pinus massoniana*
Overall	Total PLFA	dry	18.46 ± 2.23 Aa	20.89 ± 1.65 Aa	16.19 ± 0.42 Aa
		wet	10.65 ± 0.20 Ba	14.41 ± 0.92 Bb	9.73 ± 0.44 Ba
$Gram^+$	i14:0	dry	0.09 ± 0.02 Aa	0.15 ± 0.02 Ab	0.12 ± 0.02 Aab
		wet	0.10 ± 0.00 Aa	0.13 ± 0.01 Aa	0.12 ± 0.01 Aa
	i15:0	dry	2.16 ± 0.37 Aa	3.32 ± 0.36 Ab	2.27 ± 0.21 Aa
		wet	1.12 ± 0.06 Ba	1.88 ± 0.19 Bb	1.45 ± 0.12 Ba
	a15:0	dry	0.63 ± 0.10 Aa	1.12 ± 0.12 Ab	1.25 ± 0.14 Ab
		wet	0.39 ± 0.01 Ba	0.75 ± 0.06 Bb	0.81 ± 0.07 Bb
	i16:0	dry	1.89 ± 0.35 Aab	1.92 ± 0.11 Aa	1.16 ± 0.05 Ab
		wet	1.19 ± 0.06 Ba	1.51 ± 0.14 Bb	0.72 ± 0.06 Bc
	i17:0	dry	0.59 ± 0.07 Aa	0.71 ± 0.06 Aa	0.63 ± 0.05 Aa
		wet	0.44 ± 0.01 Ba	0.52 ± 0.04 Ba	0.43 ± 0.04 Ba
	a17:0	dry	0.35 ± 0.05 Aa	0.53 ± 0.04 Ab	0.49 ± 0.04 Ab
		wet	0.22 ± 0.00 Ba	0.36 ± 0.03 Bb	0.30 ± 0.03 Bb
$Gram^-$	16:1w7c	dry	0.44 ± 0.10 Aa	0.79 ± 0.09 Ab	0.72 ± 0.08 Aab
		wet	0.22 ± 0.02 Ba	0.42 ± 0.03 Bb	0.38 ± 0.04 Bb
	cy17:0	dry	0.22 ± 0.05 Aa	0.34 ± 0.03 Aac	0.36 ± 0.05 Abc
		wet	0.10 ± 0.01 Ba	0.21 ± 0.01 Bb	0.18 ± 0.02 Bc
	cy19:0	dry	1.37 ± 0.22 Aa	2.04 ± 0.21 Ab	1.60 ± 0.13 Aab
		wet	0.82 ± 0.05 Ba	1.48 ± 0.14 Ab	1.30 ± 0.10 Ab
Saprophytic fungi	18:2w6.9c	dry	0.50 ± 0.08 Aab	0.75 ± 0.04 Aa	0.48 ± 0.01 Ab
		wet	0.30 ± 0.02 Ba	0.42 ± 0.02 Bb	0.20 ± 0.02 Bc
Ectomycorrhizal fungi	18:1ω9c	dry	0.90 ± 0.18 Aa	1.37 ± 0.14 Ab	1.38 ± 0.09 Ab
		wet	0.66 ± 0.05 Aa	1.09 ± 0.08 Ab	0.88 ± 0.08 Ba
Arbuscular mycorrhizal fungi	16:1 w5c	dry	0.32 ± 0.07 Aa	0.50 ± 0.07 Aab	0.66 ± 0.10 Ab
		wet	0.15 ± 0.01 Ba	0.30 ± 0.03 Bb	0.43 ± 0.05 Bc
$Gram^+$ / $Gram^-$	-	dry	2.84 ± 0.07 Aa	2.44 ± 0.09 Ab	2.23 ± 0.05 Ab
		wet	3.07 ± 0.08 Aa	2.45 ± 0.11 Ab	2.06 ± 0.02 Bc

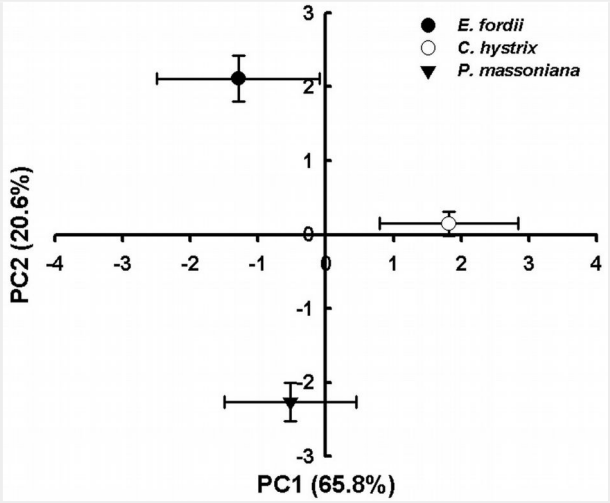

Fig. 5 - Principal component analysis of phospholipid fatty acid (PLFA) structures in the soils of the three plantations.

opposite to that of soil MB, total PLFAs, fungal PLFAs and bacterial PLFAs (Tab. 3). While soil respiration and gross nitrification rates were higher during the wet season, soil MB, total PLFAs, fungal PLFAs and bacterial PLFAs reached their lowest values during the same period.

The highest MBC values were in *C. hystrix*, whereas the highest MBN values were in *E. fordii* for both dry and wet seasons. The *P. massoniana* plantation showed the lowest MBC and MBN contents (Tab. 3). Two PLFAs (18:2ω6.9c and 18:1ω9c) were used as indicators of fungal biomass. Both PLFAs varied among the plantations. The highest fungal PLFAs were recorded in the *C. hystrix* plantation, followed by *P. massoniana* and *E. fordii*. Moreover, the highest amount of bacterial PLFAs was in the *C. hystrix* plantation, and the lowest was in the *P. massoniana* plantation. PLFA-derived F/B ratios did not differ significantly among the plantations (Tab. 3).

Discussion

Soil respiration and gross nitrification in all the three plantations showed a pronounced seasonal pattern with significantly higher rates during the wet *versus* the dry season (Fig. 1 and Tab. 3). These findings are consistent with previous reports on the significant seasonal variation of soil respiration and gross nitrification rates in different geographic regions and different tree species (Brüggemann et al. 2005, Kiese et al. 2008, Zhang et al. 2008, Rosenkranz et al. 2010, Lu et al. 2012).

In all the three plantations, soil respiration rate was significantly related to soil temperature and was well described by an exponential function within the temperature range observed in the field (Fig. 2a). This relation has been often described in the literature (Breuer et al. 2002, Rosenkranz et al. 2010, Miao et al. 2010). Regression analysis showed that the observed variance of soil respiration was largely explained by soil temperature (R^2=0.76-0.86; Fig. 2a). These values correspond very well to data of Luan et al. (2011) in a warm-temperate forest ecosystem (R^2 = 0.83-0.93). Our results also showed that the gross nitrification rate was positively correlated with soil temperature (Fig. 3a). Ingwersen et al. (1999) found the highest gross nitrification at 25 °C, with a Q_{10} value of 4.13 for the temperature range between 15 and 25 °C for coniferous forest in Germany. In the present study, the highest gross nitrification rate was recorded at 27.7 °C, and a Q_{10} value of 5.49 was calculated within the temperature range from 16 to 26 °C. This is somewhat higher than the value obtained by Breuer et al. (2002) for a rainforest ecosystem (Q_{10} = 3.60, temperature range: 14-24 °C) and the values derived from the data set by Ingwersen et al. (1999) for a temperate forest ecosystem. In this context, Q_{10} values derived under field conditions merely indicate the "apparent" temperature sensitivity (Stange & Neue 2009), because other factors such as $WFPS$ or N availability are not constant in time and may superimpose with the temperature response. This may explain the quite high Q_{10} values, which are usually not found in lab incubation experiments.

Soil moisture conditions can markedly impact the microbial processes and ecological interactions involved in nutrient cycling, such as soil C and N turnover rates (Bengtson et al. 2005, Borken & Matzner 2009, Chen et al. 2011, Lu et al. 2012). In this study, both soil respiration and gross nitrification rates were positively correlated with soil $WFPS$ (Fig. 2b and Fig. 3b). Some authors reported that soil water content has significant positive effects on soil respiration rates (Miao et al. 2010, Rosenkranz et al. 2010). In addition, Bengtson et al. (2005) and Chen et al. (2011) found that

Tab. 3 - Microbial, fungal and bacterial biomass along with soil respiration and gross nitrification rates of the top soil in the three plantations. Data are means ± standard error (n=5). A one-way analysis of variance (ANOVA) with a least significant differences (LSD) *post-hoc* test was used. Different letters indicate significant differences (P<0.05) among plantations (lower case letters) or between different seasons (upper case letters). Soil respiration and gross nitrification rates were normalized to the mean temperature and *WFPS*.

Variables	Season	*Erythrophleum fordii*	*Castanopsis hystrix*	*Pinus massoniana*
Microbial biomass C(mg kg^{-1})	dry	412.01 ± 41.98 Aab	516.01 ± 29.62 Aa	368.99 ± 11.07 Ab
	wet	205.44 ± 8.40 Ba	464.61 ± 50.90 Ab	197.36 ± 6.81 Ba
Microbial biomass N (mg kg^{-1})	dry	106.66 ± 8.96 Aa	89.57 ± 9.41 Aac	69.40 ± 7.76 Abc
	wet	58.10 ± 4.69 Ba	55.82 ± 2.59 Ba	53.67 ± 3.79 Aa
Microbial C:N ratio	dry	3.87 ± 0.26 Aa	6.11 ± 0.94 Aa	5.71 ± 0.88 Aa
	wet	3.60 ± 0.24 Aa	8.48 ± 1.11 Ab	3.79 ± 0.37 Aa
Total PLFAs (nmol g^{-1})	dry	18.46 ± 2.23 Aa	20.89 ± 1.64 Aa	16.19 ± 0.42 Aa
	wet	10.65 ± 0.20 Ba	14.42 ± 0.92 Bb	9.73 ± 0.44 Ba
Fungi (nmol g^{-1})	dry	1.41 ± 0.25 Aa	2.12 ± 0.18 Ab	1.86 ± 0.09 Aab
	wet	0.97 ± 0.07 Aa	1.52 ± 0.09 Bb	1.07 ± 0.10 Ba
Bacteria (nmol g^{-1})	dry	12.16 ± 1.43 Aa	14.67 ± 1.17 Aa	11.84 ± 1.05 Aa
	wet	6.48 ± 0.18 Ba	9.59 ± 0.67 Bb	6.29 ± 0.32 Ba
F:B ratio	dry	0.12 ± 0.02 Aa	0.15 ± 0.01 Aa	0.16 ± 0.01 Aa
	wet	0.15 ± 0.01 Aa	0.16 ± 0.01 Aa	0.17 ± 0.02 Aa
Soil respiration(mg C kg^{-1} sdw d^{-1})	dry	4.80 ± 1.67 Aa	6.76 ± 1.11 Aa	6.21 ± 0.46 Aa
	wet	25.26 ± 1.72 Ba	20.96 ± 1.13 Ba	22.04 ± 1.97 Ba
Gross nitrification(mg N kg^{-1} sdw d^{-1})	dry	0.13 ± 0.05 Aa	0.11 ± 0.02 Aa	0.11 ± 0.03 Aa
	wet	1.45 ± 0.10 Ba	0.77 ± 0.11 Bb	1.36 ± 0.19 Ba

both respiration and gross nitrification rates in forest ecosystems increase with increasing moisture under field conditions. Our study demonstrates that those results are applicable under field conditions in subtropical plantations.

Soil C and N turnover are controlled by microbial processes. In general, a warm and humid season is expected to be more favorable for mineralization, whereas the dry season is typically more favorable for immobilization. We found lowest MBC, MBN, total PLFAs, fungal PLFAs and bacterial PLFAs during the wet season, when temperature and soil moisture conditions were favorable for the microbial community (Tab. 3). During the period of the lowest MB, however, we observed the highest soil respiration and gross nitrification rates (Tab. 3). This finding agrees very well with the results of Maithani et al. (1996) and Arunachalam et al. (1998). They found that, in regrowth of a disturbed subtropical humid forest in north-east India, the periods of high mineralization coincided with minimum MB, whereas periods of immobilization corresponded with times of highest MB. In the subtropical forest of Meghalaya, India, Das et al. (1997) also reported highest N-mineralization rates in the rainy season, while MBN was low in the rainy season and high in the dry winter season. As discussed by Maithani et al. (1996) and Barbhuiya et al. (2004), lower MB values during the rainy season, when temperature and soil moisture conditions were favorable for the microbes, indicated a period of rapid mineralization in soil. Sarathchandra et al. (1984) and Singh et al. (1991) reported that the relatively greater nutrient demand by plants during the wet season (the peak vegetative growth period) limited the availability of nutrients to soil microbes and thereby reduced their immobilization in MB. Moreover, when soil dries out during the dry season, substrate supply might become limiting. Then, microbes may experience resource limitation that can slow down biogeochemical processes and force microbes into a dormant state (Stark & Firestone 1995, Schimel et al. 2007). During the dry season, low water content can inhibit microbial activity by lowering intracellular water potential. This causes microbes to acclimate to decreasing water potentials by altering their allocation of resources (Schimel et al. 2007). We therefore expect that microorganisms use most of the available resources to synthesize biomass during the transition between wet and dry season. Chen et al. (2003) also found that a high level of MBC and MBN in late winter in a hoop pine plantation coincided with low temperatures and low microbial activity.

Soil MB and microbial community composition have been shown to affect soil C and N cycling (Boyle et al. 2008, Yin et al. 2012, Lu et al. 2012). Soil in the *E. fordii* plantation had higher concentrations of SOC, TN, inorganic N and MBN than soil in the two other plantations (Tab. 1 and Tab. 3). Moreover, the highest C and N turnover rates coincided with the lowest fungal biomass and highest N availability (Tab. 1 and Tab. 3). This agrees with other studies that found fungal biomass to be negatively correlated with soil fertility and N availability (Grayston & Prescott 2005, Högberg et al. 2007, Boyle et al. 2008). This may be caused by microbial communities affecting C and N processes or, more likely, by N availability affecting the microbial communities (Grayston & Prescott 2005).

Conclusions

The present study revealed no significant differences in soil respiration and gross nitrification among the three plantations, but seasonal variation in the C and N processes was highly significant. The seasonal variation of soil respiration and gross nitrification was mostly controlled by environmental factors such as soil temperature and soil water content. The role of the microbial community in this context was less clear, while respiration and nitrification were related to MBN and fungal biomass. Moreover, MB and total PLFA content were negatively correlated with C and N turnover, showing that these two measures alone are poor indicators for microbial activity in soils that experience environmental stress such as drought.

Abbreviations

The following abbreviations were used throughout the paper:

- BaPS: barometric process separation;
- PLFA: phospholipid fatty acid;
- MB: microbial biomass;
- SOC: soil organic carbon;
- TN: total nitrogen;
- MBC: microbial biomass carbon;
- MBN: microbial biomass nitrogen;
- T_5: soil temperature at 5 cm soil depth;
- F/B: ratio of fungal to bacterial biomass;
- RQ: respiration quotient;
- WFPS: water-filled pore space;
- Q_{10}: temperature sensitivity;
- SDW: soil dry weight.

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