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Coarse woody decay rates vary by physical position in tropical seasonal rainforests of SW China

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ABSTRACT

Decomposition of woody detritus is an important but often ignored process in forest ecosystems. Moisture and temperature regimes are dominant controls over woody decay, contributing to significant variability at local, regional, and global scales. Our focus was on local variability in woody decay rates depending on their physical position. Woody detritus may decay on the forest floor, aboveground, or combination of both, depending on the mortality agent. In this study, we measured decay rates of logs, large branches on the forest floor, and snags over a three-year period. We also collected monthly respiration estimates, and analyzed woody detritus N and P content throughout the study. Logs exhibited the greatest mass loss with a decay-rate constant of $k = 0.606 \pm 0.020$, followed by large branches ($k = 0.316 \pm 0.012$) and snags ($k = 0.268 \pm 0.008$). Heterotrophic respiration was greatest prior to the peak of rainy season, and was greatest for snag material during the first two years of sampling, probably a result of water saturation in ground material. Both N and P were released in all materials, but the rate of P release was much slower in snags. There were large differences of P concentration and C:P among the materials, but their value became similar after three years, indicating P limitation on microbial activities. Our results presented robust evidence for the physical-position-dependence of coarse woody detritus decomposition in the forests.

1. Introduction

Coarse woody detritus (CWD) is a critical component of forested ecosystems where it provides a multitude of ecosystem services. These include structural habitat for multiple vertebrate and invertebrate species (Bull et al., 1997), the primary energy source for saprophyte communities (Nordén et al., 2004), and significant contributions to long-term soil development (Tinker and Knight, 2000; Triska and Cromack, 1980). Input and loss rates of woody detritus also have implications on several ecosystem processes, including nutrient cycling and carbon dynamics (Harmon et al., 1986). Despite having relatively low concentrations of nutrients, woody detritus acts as a long-term nutrient pool with a temporal lag in nutrient release relative to more labile material (Laiho et al., 2004). Woody detritus also contributes significantly to long-term carbon storage as the largest detritus pool in forests, with implications on total carbon stores and ecosystem carbon balance (Freschet et al., 2012).

Carbon fluxes from decaying wood remain one of the largest uncertainties in biogeochemical models (Chambers et al., 2000). Part of this uncertainty can be attributed to the difficulty in quantifying the cause and extent of woody detritus inputs under various environmental conditions or disturbance events (van Mantgem et al., 2011; McDowell et al., 2015). This may be especially difficult since inputs can occur in various physical positions within forests. For example, natural disturbances such as pathogens, insects, wildfires, hurricanes and drought typically produce standing dead trees (snags) with minimal ground contact and increased exposure to solar radiation and drying wind (Harmon, 1982). In contrast, windthrow, ice damage, landslides and logging produce dead stems and branches immediately in contact with the forest floor (Whigham et al., 1991). Most woody detritus research has focused on reducing this uncertainty by quantifying input rates and stocks in various forests under different management and disturbance regimes, but relatively few have estimated decay or flux rates for this

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material which is necessary for quantifying net ecosystem carbon balance with biogeochemical models (Keller et al., 2004; Rice et al., 2004; Palace et al., 2007; Yoneda et al., 1990).

Woody detritus decomposition and nutrient dynamics, as well as factors contributing to variation in these processes, also remain uncertain in many forested ecosystems. Temperature and moisture regimes are regarded as the dominant controlling factors (Harmon et al., 1986; Chambers et al., 2000; Wang et al., 2002). Warm, moist conditions indicative of rainforest environments promote rapid decay (Chapin et al., 2002), while freezing temperatures inhibit decomposer activity by slowing metabolic processes and saturation creates anaerobic environments that suppress decomposition (Progar and Schowalter, 2000). These factors likely contributed to observed variation in woody decay rates by their physical position, where standing or elevated material decayed slower than materials decomposing on the ground in temperate and boreal coniferous forests (Yatskov et al., 2003; Dunn and Bailey, 2012). This trend has also been observed in temperate deciduous forests where the half-life of snags were 11.2 years, compared to 6.3 years for logs (Onega and Eickmeier, 1991). Resource accessibility by wood-degrading fungi has also been found to further influences woody decay rates by their physical position (Boddy, 2001). The magnitude of these observed differences suggests carbon fluxes and nutrient cycling rates may be lagged when woody detritus is inputted as elevated material, contributing to the long-term immobilization of nutrients (Laiho and Prescott, 1999). Additionally, initial concentrations of N and P have been correlated with both litter and woody decay rates (Laiho et al., 2004; Parton et al. 2007). Obtaining estimates for standing and surface decay rates, as well as the influence of variation in nutrient concentrations, are needed to more accurately model these ecosystem processes and to determine whether or not elevated material embodied a different pathway of decay and nutrient cycling than surface material.

In this study, we were interested in characterizing the contribution of woody detritus to carbon fluxes and nutrient cycling in tropical seasonal rainforests of southwest China. Tropical seasonal rainforests have an obvious transition between dry and wet seasons, so we hypothesized that lower water availability during the dry season would result in variation in decay rates of woody detritus depending on their physical position. Additionally, since phosphorus (P) is considered a limiting factor for productivity in tropical forests, we also hypothesized that P or the C:P ratio would be closely correlated with the decay rates of this material. Therefore, we studied decomposition of three types of woody detritus in their original decay position to capture the contribution of these factors (position they were originally input into the system). Heterotrophic respiration rate, mass loss, and nutrient dynamics were measured for three years from 2006 to 2008 for woody material from logs and large branches on the ground, as well as standing snags. This study represents the initial investigation of decay dynamics for woody detritus in this forest type.

2. Method

2.1. Experimental site

This study was conducted at a long-term research site at the Tropical Rainforest Ecosystem Station of the Chinese Academy of Sciences in Xishuangbanna, Yunnan Province, China (21°55′39″N, 101°15′55″E). The climatic conditions of this forest are typical of monsoonal conditions. The 40-year mean annual temperature was 21.7 °C (minimum of 15.9 °C and maximum of 25.7 °C) and a mean annual precipitation was 1539 mm. On average, 87% of precipitation occurs during the rainy season from May to October. Latosol soils are dominant at this research site and have an average pH around 5.

The dominant vegetation type is that of tropical seasonal dry rainforests, which differs from lowland tropical rainforests because of a consistent annual dry season. This vegetation type contains a mixture of evergreen and deciduous trees and deciduous trees do not senesce leaves at the same time so canopy cover remains intact throughout the year. The forest canopy can be divided into three sublayers. The dominant overstory layer ranges from approximately 35–40 m in height and is typically comprised of *Pometia tomentosa*, *Terminnalia myriocarpa,* and *Garuga florobunda var. gamblai*. The mid-canopy layer ranges from 15 to 30 m and typically consists of *Barringtonia macrostachya*, *Chisocheton siamensis*, *Gironniera subaequalis,* and *Beilschmeidia brachythyrsa*. The subordinate layer ranges from 3 to 10 m and is typically comprised of *Millettia laptobotrya*, *Garcinia cowa*, *Drypetes indica*, *Myristica yunnanensis* and *Mezzettiopsis creaghii*.

2.2. Experimental design

We sampled woody material from fallen trees, fallen large branches and snags to test the effects of physical position and nutrient concentrations on decay rates. We obtained each material type with end diameters between 8 and 10 cm during a biomass survey of this tropical seasonal rainforest (Lü et al., 2010) from three 1 ha plots. The materials are a mixture of different tree species in those three plots and represented the major tree species. Only newly formed, lightly decayed materials were selected and brought back to our lab for further processing. These were identified based on physical and visual characteristics that included evidence of insect use, presence of saprotrophic fungi, attached bark and twigs, and friable sapwood or heartwood. The materials were cut into 20 cm segments, weighted freshly, and stored at room temperature before deployment. Five samples of each type of materials were oven dried at 80 °C for 48 h to obtain the water content (% Water of Wet weight). The initial dry mass of all materials was then calculated using their fresh weight and the average water content of the five oven-dried samples.

Five fresh pieces of fallen tree, large branch, and snag material were combined as a sample and deployed at our field site. Fallen tree and large branch material were put in litter bags with 1 mm mesh to exclude wood consuming insects. Snag material was tied together with nylon rope for hanging to simulate standing conditions. A total of 60 replicates were made for each type of material. We utilized a slope adjacent to a CO_2 flux tower so our estimates could be correlated with environmental measurements (i.e., soil temperature, soil moisture, air temperature) and to allow future integration of our findings into net ecosystem carbon balance research and modeling. Five transects perpendicular to the slope, 10 m apart from each other, were stratified from the bottom to top of the slope. The starting location of each transect was randomly located. Twelve litter bags containing log and large branch material were placed on the ground along each transect about 5 m apart in January 2006. Snag material was hung on a tree nearby each litter bag sample 1.5 m above ground.

Our initial estimates for all components of this research were conducted in January 2006 when the woody material was first collected. We visited the field site every three months for sampling, beginning in April 2006, for a period of three years. One bag of each material was randomly selected for sampling from each transect, for a total of five samples during each visit. Each sample was first collected to estimate respiration rate using the dynamic, closed-chamber method. A 22 L plastic bucket was used as the dynamic chamber. The bucket was sealed and two rubber tubes were connected to a Li-cor 820 infra-red CO_2 analyzer (Li-cor, USA). After the CO_2 concentration stabilized, we recorded these concentrations in ppm for 5 min. We then collected the samples for further lab analyses. All dirt, fruiting bodies and other debris were removed from the retrieved samples. All samples were oven-dried at 80 °C for 48 h to obtain the low-weight equilibrium moisture content. Following drying, the weight of each piece within a sample was recorded for estimates of mass loss. Oven dried samples were ground with a Wiley mill and filtered through a #40 mesh sieve. Carbon and N concentrations of all samples were analyzed with a PE-2400 CHN analyzer (Perkin-Elmer, Foster City, USA) and P concentration was determined by persulfate oxidation followed by colorimetric analysis.

2.3. Statistical analyses

We estimated carbon flux from woody detritus for fallen tree, fallen large branch and snag material. CO_2 flux was calculated using the following equation:

$$F = \frac{P \times T_0}{P_0 \times T \times 22.4} \times V \times dc/dt \times 10^6/\mathrm{m}$$

in which F is the CO_2 flux (μmol kg^{-1} s^{-1}); P and T are the air pressure (Pa) and temperature (K) at the time of measurement; P_0 and T_0 are air pressure and temperature in standard condition (273.15 K and 100 kPa, respectively); V is the volume of the chamber, m is the dry mass of the material, *dc/dt* is the slope of CO_2 concentration against time (ppm s^{-1}). We estimated this slope with simple linear regression using R (R Core Team, 2013).

We evaluated the relationship between environmental variables and heterotrophic CO2 flux (R_h) for each year of our sample period. Correlations between CO_2 flux and soil temperature, air temperature, soil moisture and relative humidity were estimated using Pearson's product-moment correlation coefficients (r). Pearson's correlation coefficients were calculated for each year (2006, 2007 and 2008) and all three years combined in R, and each metric was tested for significance at an $\alpha \leqslant 0.05$.

We estimated the annual decay-rate constant for fallen tree, fallen large branch and snag material across our three years sampling period. We assumed a negative exponential model for decomposition of each material type. The model has the following form:

$$Y = e^{-kt}$$

in which Y is the proportion of initial mass remaining, t is the decay time expressed as a year in this study, and k is the decay-rate constant. The decay-rate constant for all material was based on mass loss from the oven-dried samples collected every three months. We used simple linear regression in R to estimate log-transformed mass estimates as a function of time with the slope of the line representing the decay-rate constant.

We obtained estimates of C, N and P from laboratory analyses for all samples collected every three months throughout the study period. All five samples for each type of material were averaged together for all nutrients. We summarized N and P concentrations as both absolute amounts (mg g^{-1}) and percent of initial estimates. We also quantified C:N and C:P ratios across our sampling period and report mean values across all five samples for each type of material.

3. Results

We observed seasonal variation in CO_2 flux for all three woody detritus types. Temperature and moisture estimates were typical of the seasonal rainforests during our three-year study period. Soil and air temperature peaked in July or August concurrent with maximum soil moisture. Relative humidity didn't fluctuate much and remained high throughout the year (Fig. 1). The CO_2 flux for all materials were higher in wet season than dry season across all three years. The highest CO_2 flux for fallen tree and large branch material did not coincide with the peak temperature and moisture conditions, but rather occurred between April and June (Fig. 2). In fact, we observed slight declines in CO_2 flux of fallen tree and branch material by July in 2006 and 2007 when peak moisture and temperatures were observed. CO_2 flux for snag material was statistically correlated with soil temperature, soil moisture and air temperature throughout our sampling period, while respiration rates of fallen tree and branch material was only statistically correlated with these factors in the final year of sampling (Table 1). Precipitation did not correlate well with all the materials in the three years or combined, except for the respiration of snag material during 2008. CO_2 flux for logs and branches increased slightly over the three years, while the respiration of snags declined significantly in 2008. In 2006 and 2007, the respiration rate of snag material during the wet season was higher than that of fallen tree and branch material, but was much lower in 2008.

Decay rates varied by substrate type and decay position (Fig. 3). The decay-rate constant (k) for fallen tree, large branch and snag material were k = 0.606 ± 0.020 yr^{-1}, 0.316 ± 0.012 yr^{-1} and 0.268 ± 0.008 yr^{-1}, respectively ($p < 0.001$ for all three materials). After three years, fallen tree, large branch and snag material lost

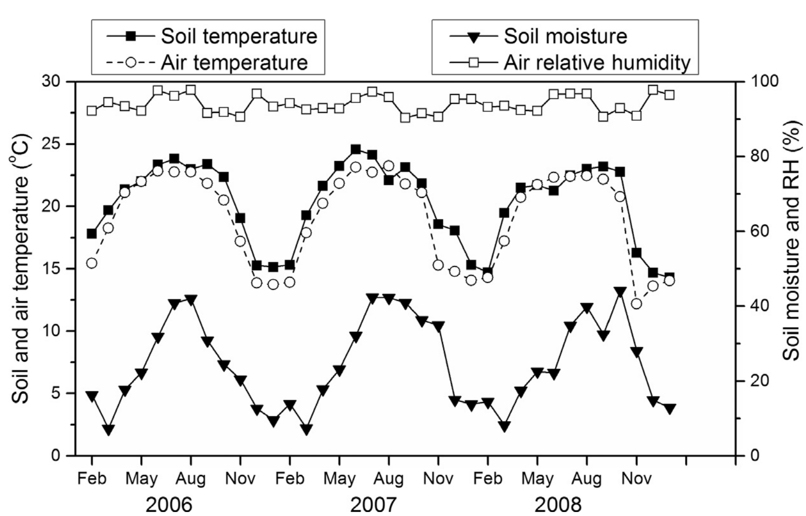

Fig. 1. Environmental factors of the study site between from 2006 to 2008.

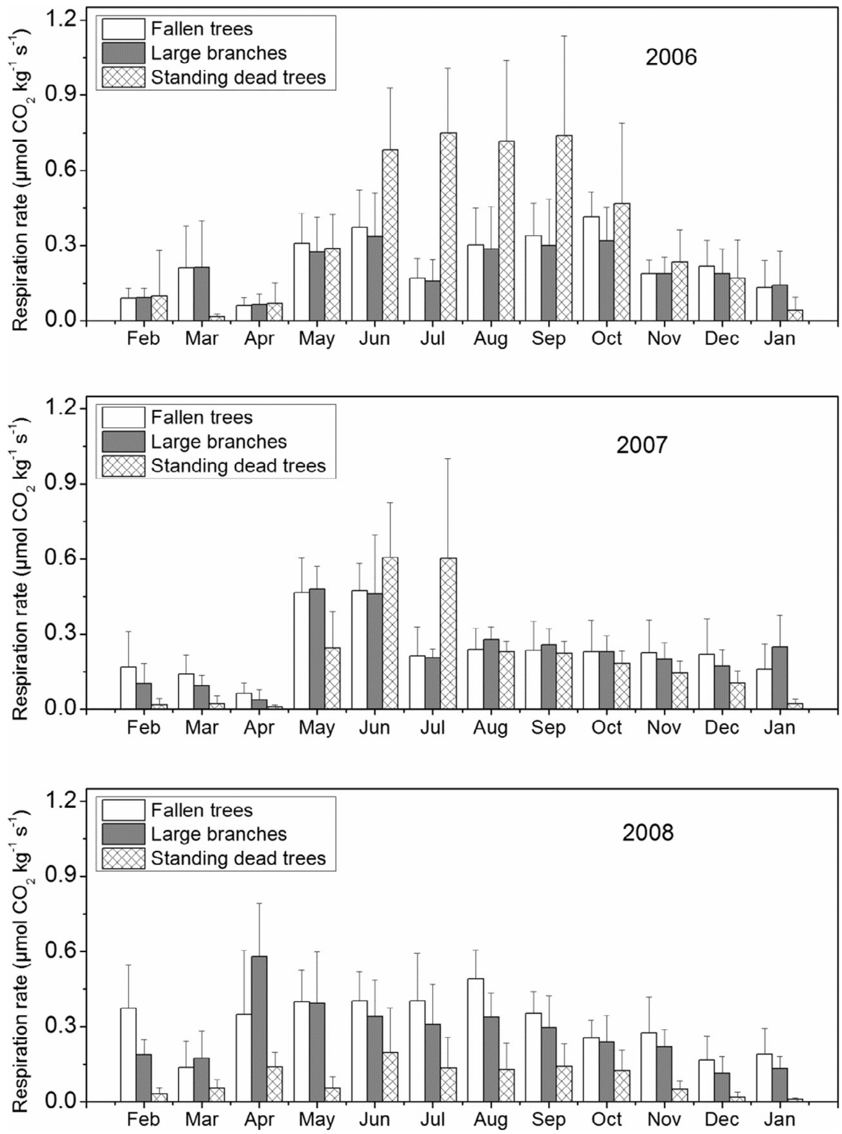

Fig. 2. The respiration rates of fallen trees, large branches and standing dead trees from 2006 to 2008. The error bars are standard deviations.

Table 1
Correlation of respiration rate and environmental factors of three materials.

Year	Materials	Soil T	Air T	Soil M	Precipitation
1st yr	Fallen trees	0.54	0.51	0.45	0.204
	Large branches	0.53	0.52	0.46	0.209
	Standing dead	**0.78**	**0.74**	**0.94**	0.550
2nd yr	Fallen trees	0.52	0.46	0.32	−0.167
	Large branches	0.50	0.49	0.38	0.030
	Standing dead	**0.75**	**0.68**	**0.66**	0.492
3rd yr	Fallen trees	**0.56**	**0.66**	0.51	−0.096
	Large branches	**0.66**	**0.68**	0.23	0.349
	Standing dead	**0.82**	**0.83**	**0.56**	**0.681**
All yrs	Fallen trees	**0.46**	**0.48**	**0.39**	−0.009
	Large branches	**0.52**	**0.53**	**0.33**	0.149
	Standing dead	**0.63**	**0.59**	**0.59**	**0.438**

Values in bold are significant at an $\alpha \leqslant 0.05$.

87%, 68% and 60% of their original mass, respectively. The decay rate of fallen tree material was similar to that of the other two materials during the first six months of sampling, but exhibited an accelerated decay rate thereafter (Fig. 3).

The carbon concentration of all materials did not vary much in the first year, but decreased significantly thereafter (Fig. 4). After three years, the carbon concentration of fallen tree material dropped from an average of 510 mg g^{-1} to 291 mg g^{-1}, or a

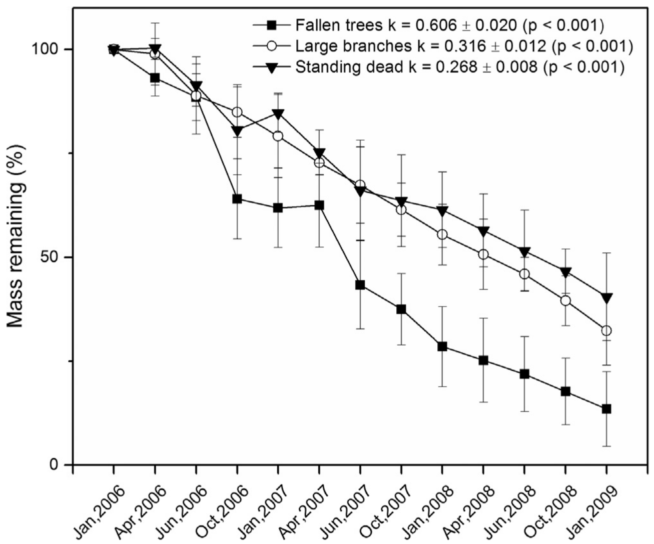

Fig. 3. The change of mass remaining of fallen trees, large branches and standing dead trees from 2006 to 2008.

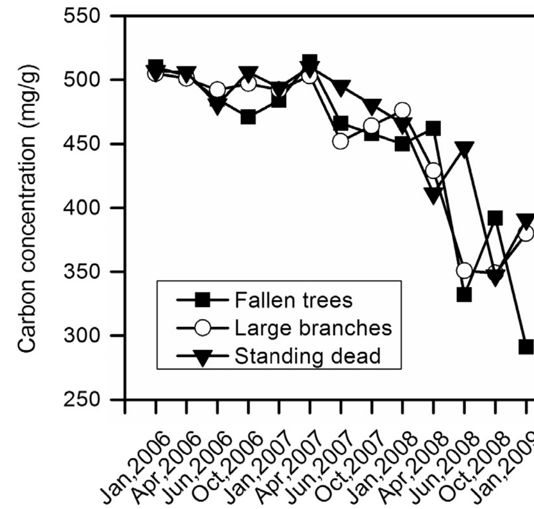

Fig. 4. Change in average carbon concentration of fallen trees, large branches and standing dead trees from 2006 to 2008.

decrease of 42%, while large branches and snags both showed a 23% decline (large branches from 505 mg g^{-1} to 380 mg g^{-1}, snags from 507 mg g^{-1} to 391 mg g^{-1}).

Nitrogen concentrations in the three types of substrates exhibited different temporal trends during our three years sampling period (Fig. 5). The three substrates started with similar average N concentrations of approximately 3 mg g^{-1}. After three years, N concentration in fallen tree material increased by 14.2–3.61 mg g^{-1}, while large branch and snag material increased by 95.5% and 74.6%, to 6.02 mg $g^{-1}$and 5.15 mg g^{-1}, respectively. After accounting for mass loss by weighting N estimates, fallen tree material had 84.6% less N content than initial estimates, while large branch and snag material lost on average 36.8% and 29.4%, respectively.

Phosphorus concentrations also exhibited different temporal trends by substrate type, but in contrast to N the initial average P concentration in large branch material was more than double that in logs or snags. At the end of our three-year sampling period, average P concentration in large branch material decreased by 75.4% to 0.21 mg g^{-1}, while fallen tree and snag material increased 20.2% and 75.4%, to an average of 0.23 and 0.21 mg g^{-1}, respectively. With respect to total P stores, snags remained stable until the end of the second year while logs and branches released P at the very beginning. As a result, snags only lost 29% of their total P stores, but logs and large branches lost 83.8% and 79.2%, respectively. All substrates had similar temporal trends in their C:N ratios, despite the C:N of logs being slightly higher (Fig. 6). In contrast, the C:P ratio of all substrates became more similar across our sampling period despite initial differences.

4. Discussion

Decay position significantly influenced the rate of decomposition for woody detritus in dry tropical rainforests of Xishuangbanna, SW China (Fig. 2). Our estimates were comparable to those observed in other dry tropical rainforests. For example, decay-rate constants for fine woody detritus ranged from 0.151 to 1.019 yr^{-1} (Harmon et al., 1995). Additionally, decay-rate constants for coarse woody detritus in tropical forests of central Amazon ranged from 0.015 to 0.67 yr^{-1} (Chambers et al., 2000). As expected, our estimates for ground and standing decay rates were faster than those observed in temperate deciduous forests (Fasth et al., 2011; Harmon et al., 1995). We did no observe an initial lag phase in our substrates like other studies (e.g., Fasth et al., 2011), which may indicate one does not exist or our selection of already dead material may have already progressed through this stage since we didn't know the exact time of death. A well-replicated, manipulative study removing live trees to create these various substrates would be necessary to determine if a lag phase exists or not.

Temperature is the most commonly used variable to capture woody decomposition in biogeochemical models (Gough et al., 2007). However, in this study, only snag material had a significant correlation with temperature. Our monthly estimates of heterotrophic CO_2 flux (R_h) provide additional insights into the climatic controls on decomposition. A moderate amount of moisture is believed to be critical for the survival of wood-degrading fungi (Carl and Highley, 1999), but excessive water excludes oxygen permeation into the material and effectively suppresses microbial activity (Rayner and Todd, 1980). This effect has been observed in Douglas-fir forests where logs sheltered from rain exhibited higher respiration rate than exposed logs (Progar et al., 2000). Soil respiration has also been shown to decline during periods of high soil moisture in the tropical seasonal rainforest (Sha et al., 2005). Our results suggest that R_h in fallen tree and large branch material were constrained by high moisture conditions during the rainy season. This is supported by the higher levels of R_h on snag material where runoff reduces water concentration in this material. We believe the higher CO_2 flux observed for snag material during the first year of sampling was reflective of ground materials having excessive water content due to heavy rain and poor drainage during the annual rainy season. The initially high CO_2 flux could have been a result of wood endophytes containing potential wood decomposers with a decomposing ability comparable to soil fungi (Parfitt et al., 2010; Song et al., 2016). Once the labile C was consumed, respiration in snag appeared to be limited by water availability and the colonization rate of fungal spores.

Our observed declines in C concentration of three substrates suggests that some newly formed compound with lower carbon content was present. Formation of humic compounds from decomposers, in which C was respired as CO_2 while other elements were left, can form carbon poor complexes. It is worth to note that determination of decay classes was often done by density or observations (Onega and Eickmeier, 1991), C concentration could be a potential indicator of decay stage as shown in this study.

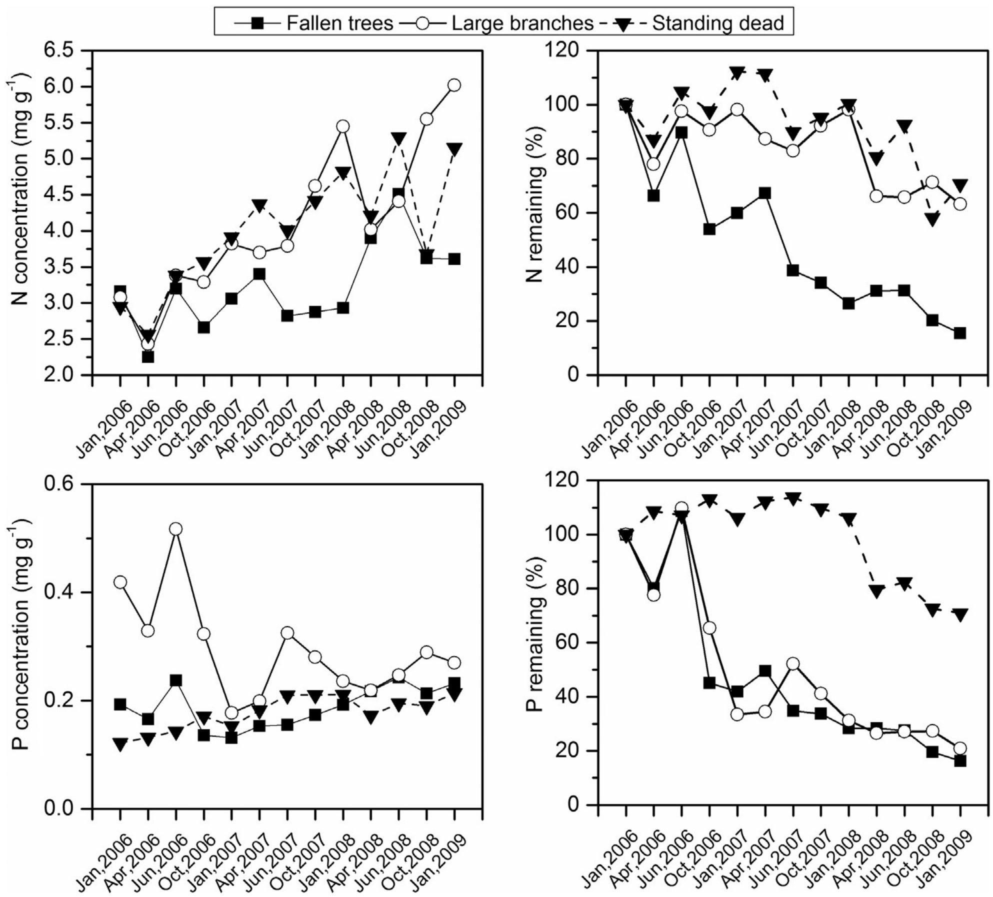

Fig. 5. Dynamics of concentration and total amount of nitrogen and phosphorus of fallen trees, large branches and standing dead trees from 2006 to 2008.

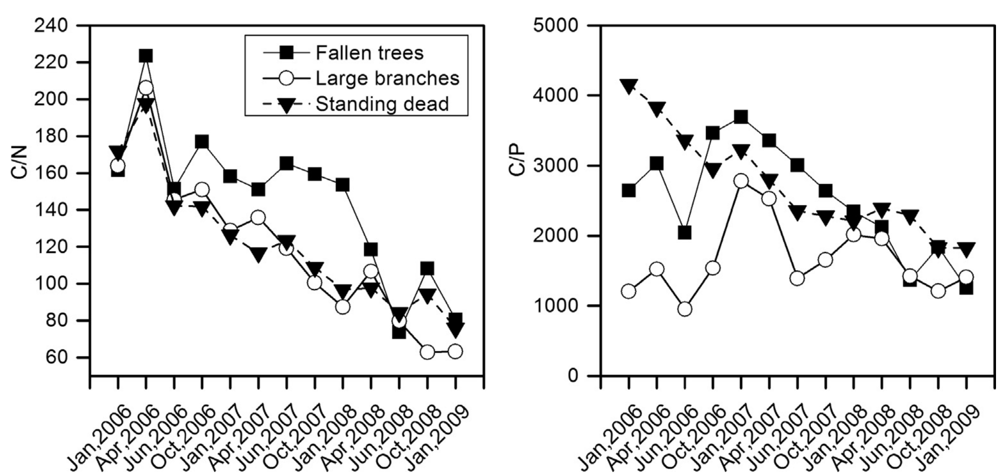

Fig. 6. Change of C:N and C:P of logs, large branches and snags from 2006 to 2008.

Nitrogen concentration has been shown to increase in the initial stages of decomposition, while the relative change of P concentration depends on the initial P concentration in boreal forests (Alban and Pastor, 1993; Laiho and Prescott, 2004). Such dependency and the converging of P concentration was also observed in temperate forests (Laiho and Prescott, 2004). The pattern we observed in this study was probably a result of P limitation in tropical forests, which has been observed by Vitousek (1984) and other studies at this same research site (Xue et al., 2003; Zheng, 2006). Materials originated from different positions differed in their initial P concentration. The concentration of P in standing dead trees, started with lowest level, became similar as the two ground materials after three years of decomposition. The initial P concentration turns out to be a good predictor of P dynamics. Phosphorus can be allocated by cord forming fungi over long distances (Wells and Boddy, 1990), thus the convergence of P concentration and C:P may indicate P limitation and resource relocation by wood-degrading organisms, most of which were white rot fungi in tropical forests (Schilling et al., 2015). The three tree components used in this study also reflect different P dynamics. The convergence of P concentration and C:P ratio indicated an equilibrium between wood-decay community and resource availability. As shown by Laiho et al. (2004), a certain threshold of limiting resource could be a potential indicator of nutrient accumulation or release.

Carbon and nutrient dynamics can be better predicted by incorporating multiple factors into biogeochemical models for tropical seasonal rainforests. Temperature and C:N ratios are commonly used to predict woody decay rates, but our results suggest neither was a good predictor for all substrates we sampled. Even at regional scales, many environmental factors have been shown to be poor predictors of wood decomposition (Bradford et al., 2014). In this study, the decay position, as it relates to water availability, largely determined the rate of decomposition. Many natural disturbances initially create snags so they are a prominent pool of CWD, at least until they fall or break and become logs, so the type of woody detritus should be incorporated as a predictor variable for estimating wood decomposition and C fluxes (Dunn and Bailey, 2015). We have also shown that this can have significant implications on nutrient dynamics for these systems.

5. Conclusion

Mass loss, respiration rate and nutrient dynamics of fallen trees, large branches and standing dead trees were studied in their original decay position in a tropical seasonal rainforest of southwest China. The decay rate of fallen trees was larger than the other two materials. Water availability had a strong influence on the respiration rate of ground materials in rainy season, but the respiration of standing dead trees was not suppressed, at least for the first two years. Decrease of C concentration was observed for all the three materials at the late stage of this study. Phosphorus concentration and C:P showed convergent pattern after three years, indicating P limitation on microbial activities in decomposition.

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