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Litter Decomposition and Nutrient Release in a Tropical Seasonal Rain Forest of Xishuangbanna, Southwest China[1]

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ABSTRACT

We studied litter decomposition and nutrient release in a tropical seasonal rain forest of Xishuangbanna, Southwest China. The monthly decay rates (k) of leaf litter ranged from 0.02 to 0.21/mo, and correlated with rainfall and soil moisture. Annual k values for leaf litter (1.79/yr) averaged 4.2 times of those for coarse wood (2.5–3.5 cm in diameter). The turnover coefficients of forest floor mass (annual litterfall input/mean floor mass) were: 4.11/yr for flowers and fruits, 2.07/yr for leaves, and 1.17/yr for fine wood ($\leq$2 cm in diameter), with resident time decreasing from fine woods (0.85 yr) to leaves (0.48 yr) and to flower and fruits (0.24 yr). Nutrient residence times in the forest floor mass were ranked as: Ca (1.0 yr) > P (0.92 yr) > Mg (0.64 yr) > N (0.36 yr) > K (0.31 yr). Our data suggest that rates of litter decomposition and nutrient release in the seasonal rain forest of Xishuangbanna are slower than those in typical lowland rain forests, but similar to those in tropical semideciduous forests.

Key words: litter decay rates; litter turnover coefficients; nutrient cycling; tropical rain forests.

MUCH OF THE ENERGY ORIGINATING FROM PRIMARY PRODUCTION is released during decomposition (Phillipson *et al.* 1975). During this release, plant nutrients become available for recycling within the ecosystem. Thus, litter decomposition contributes to soil fertility through the regeneration of plant nutrients and the maintenance of soil organic matter. Decomposition and nutrient release processes are particularly important in tropical ecosystems, where soils can be naturally low in fertility and nutrient status (Okeke & Omaliko 1992).

Litter contains a considerable amount of the nutrients necessary for plant growth. In order to release these nutrients, litter must be fragmented and decomposed. Litter breakdown and mineralization are mediated by the decomposer community of soil and forest floor microorganisms and fauna (Wakesman 1952, Swift *et al.* 1979). Decomposition rates are regulated by interactions among the decomposer community, the physiochemical environment, and litter quality (Anderson & Swift 1983). Litter quality refers to intrinsic chemical and structural characteristics that govern the activity of decomposer organisms, which partly determines the rate of organic matter decay (Swift *et al.* 1981). Litter resource quality is determined largely by the species contributing to the forest floor mass. The influence of litter quality on decomposition and mineralization rates in tropical rain forests has seldom been investigated in tropical China, presumably because of the great heterogeneity of tropical forest ecosystems and the consequent difficulty in selecting species to investigate for a meaningful approximation of the decomposition rates for whole forests (Bernhard 1970, Swift *et al.* 1979, Anderson *et al.* 1983, Vitousek 1984, Vitousek *et al.* 1994, Zou *et al.* 1995, Tanner *et al.* 1998, Hobbie & Vitousek 2000, Vitousek & Hobbie 2000, González & Seastedt 2001).

A hierarchical model of decomposition for terrestrial ecosystems, in which climate (more specifically moisture and temperature) normally exert the greatest control on decomposition has been suggested (Songwe *et al.* 1995). Soil characteristics are the second most important controlling factor, followed by litter quality, macroorganisms, and microorganisms. However, in the tropics where climatic and edaphic factors generally favor decomposition, litter quality exerts the greatest control (Songwe *et al.* 1995). Seastedt (1984) and Chapman *et al.* (1988) hypothesized that the mixing of species litter affects decay rates and nutrient dynamics. However, the results of the few studies that have tested this hypothesis have been inconclusive (Taylor *et al.* 1989, Blair *et al.* 1990). In this study, mixed litter from dominant trees in the Xishuangbanna tropical seasonal rain forest was used to investigate litter decay rates. The objectives were: (1) to determine litter decomposition rates of leaves, woods, and

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flowers and fruit, and (2) to investigate rates of litterfall, nutrient input, forest floor mass turnover, and nutrient release in the tropical seasonal rain forest of Xishuangbanna.

METHODS

STUDY SITE.—Xishuangbanna is on the northernmost edge of tropical Asia, where tropical and subtropical flora intermingle. The result is an ecological mosaic of vegetation represented by tropical rain forest and subtropical evergreen broadleaf species. The distribution of these forest plants is not continuous because of the mountainous topography. This study was conducted in the tropical seasonal rain forest as described by Zhu (2006) for two years (from April 1988 to March 1989 and from April 1989 to March 1990).

Research plots were established within an area of 50 × 50 m, at Baka in the Menglun Nature Reserve (21°56′N, 101°11′E, 650 m elev.). The vegetation is a typical seasonal rain forest in Xishuangbanna with forest canopy height of 50 m. Tree density (DBH ≥5 cm) was 796 (trees/ha). The most abundant species were *Pometia tomentosa*, *Amoora tetrapetala*, *Mitrephora wangii*, *Barringtonia macrostachya*, *Knema erratica*, *Knema cinerea*, *Myristica yunnanensis*, *Lasiococca comberi*, *Saprosma ternatum*, and *Baccaurea ramiflora* (Zheng *et al.* 2006).

LITTERFALL AND FOREST FLOOR MASS.—Litterfall was determined using 16 circular traps located within the plot (Proctor *et al.* 1983). These traps were made of plastic gauze bags (0.1 mm mesh, 0.25 m^2) and suspended from galvanized wire frames at a height of about 1 m aboveground. We collected litter samples from litter traps twice a month, on the 15th and the last day of every month to prevent significant decomposition and leaching loss of nutrients. The litter from each trap was air-dried and sorted into leaves, fine wood (≤2 cm in diameter), flowers and fruit, and other materials. Then, each fraction was dried at 70°C, weighed and bulked for chemical analyses. We refer to the sum of leaf, wood, and fruit litter as coarse litterfall.

Forest floor mass was randomly sampled at 15 locations within the plot from a 0.25 m^2 quadrat at each location. The litter was sorted into leaves, fine wood (≤2 cm in diameter), flower and fruit, and other materials. Each fraction was dried, weighed, and bulked for chemical analyses. We refer to leaf, fine wood, and fruit materials as coarse forest floor mass. Forest floor mass was determined at a 3-mo interval during the 2-yr study period.

LITTER DECOMPOSITION EXPERIMENT.—A litterbag technique was used to study leaf litter decomposition rate. Bags were 20 × 20 cm and constructed from nylon with mesh sizes of 1.2 mm. Freshly fallen leaf litter collected from the forest floor was dried at 70°C. Ten grams of mixed leaf samples of mixed species were put into each nylon bag with equal proportions of species composition. On 1 April 1989, a total of 60 litterbags were placed on the forest floor just above the mineral soil, after carefully removing the surface floor mass at ten randomly selected locations within the 50 × 50 m plot. One bag was randomly retrieved at 2-mo intervals from each location. Retrieved samples were sorted to remove soil and arthropods, dried at 70°C, and weighed. The experiment was carried out for 12 mo (six collections). To determine correlations between leaf decomposition rates and changes in monthly temperature and precipitation, we placed ten new litterbags filled with the same leaf litter in the field for each of the 2-mo retrieval periods between April 1989 and March 1990.

Freshly fallen coarse wood (2.5–3.5 cm in diameter) was collected from the forest floor without identifying species. Coarse wood was cut into 25-cm long pieces, dried at 70°C, weighed and labeled. Sixty pieces of coarse wood were placed on the forest floor to determine wood litter mass loss. Ten pieces of coarse wood were randomly retrieved at 2-mo intervals. The study period for the wood decomposition experiment was concurrent with the leaf litterbag experiment.

METEOROLOGICAL OBSERVATION AND SOIL MOISTURE.—Meteorological data were obtained from the Xishuangbanna Research Station of the Tropical Rain Forest Ecosystem, the Chinese Academy of Sciences, at Menglun. Soil moisture was determined by oven drying soil samples at 105°C for 24 h. Soil samples were taken from 0–20 cm depth twice a month during the 2-yr study period.

CHEMICAL ANALYSES.—Each litterfall and forest floor mass sample was ground in a Wiley mill, and subsamples were wet-ashed in concentrated HNO_3-$HClO_4$. The solution was analyzed for P, K, Ca, and Mg contents by inductively coupled plasma atomic emission spectrometry. Nitrogen was determined by Kjeldahl method, and samples were wet-ashed in concentrated H_2SO_4.

STATISTICAL ANALYSES.—For the leaf litter and coarse wood decomposition experiments, the decay constant (k) was calculated following a negative exponential decay model: $W_t = W_0\, e^{-kt}$, where W_0 is the initial dry weight, W_t is the amount remaining (percent of the initial dry weight) at time t, and k is the decay constant (Olson 1963, Anderson *et al.* 1983, Harmon *et al.* 1986, Ezcurra & Becerra 1987). The units of t were month or year in the equation. In this study, the k was calculated on a monthly basis, and the annual decay coefficient is derived from the linear regression $\mathrm{Ln}(X/X_0) = -kt$ with interception set to zero. The time to decompose one-half ($t_{0.5}$) and 95 percent ($t_{0.95}$) of the material are often reported, where $t_{0.5} = 0.693/k$ and $t_{0.95} = 3/k$ (Harmon *et al.* 1986). We also obtained correlation coefficients between the monthly decay constant (k) and variable of rainfall, soil moisture, and air temperature.

The forest floor mass turnover coefficient (K_L) for each litter component was calculated by using the formula $K_L = L/X$, where L is the annual litter input and X is the mean forest floor mass. The value of K_L is an approximation to the proportion of the forest floor mass decomposed in 1 yr (Anderson *et al.* 1983). Resident times of the forest floor mass ($1/K_L$) were calculated by dividing the forest floor mass with annual litterfall. As "other materials" in litterfall could not correspond to that of forest floor mass and vice versa, this component was not included for the calculation of turnover rates or residence times (Proctor *et al.* 1983).

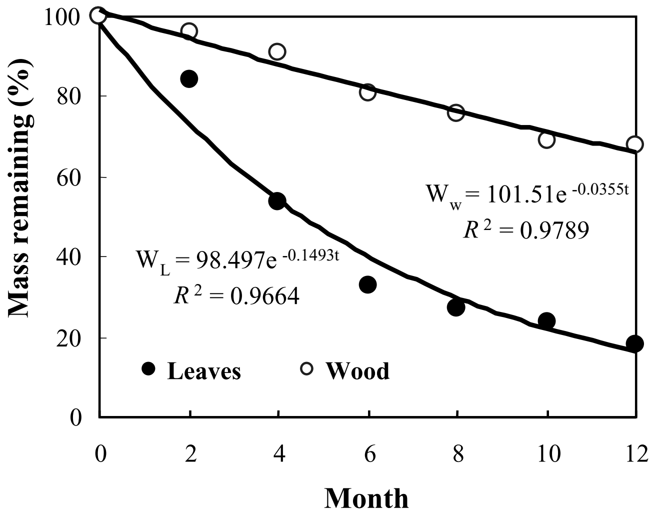

FIGURE 1. Decomposition of leaf and coarse wood materials during a 1-yr study between April 1989 and March 1990 in a tropical seasonal rain forest of Xishuangbanna, Southwest China.

Table 1. *Rainfall, soil moisture, and air temperature as correlated with decay constants of leaf litter during a 1-yr cycle between April 1989 and March 1990 in a seasonal rain forest of Xishuangbanna, Southwest China.*

Period	Decay constant *k* (/mo)	Rainfall (mm)	Soil moisture (w/w %)	Temperature (°C)
April–May	0.086	133.2	14.9	25.5
June–July	0.214	450.6	19.7	25.9
Aug.–Sep.	0.180	335.2	21.9	25.3
Oct.–Nov.	0.119	83.6	18.7	21.7
Dec.–Jan.	0.024	14.7	11.7	16.4
Feb.–March	0.105	113.5	19.5	19.8
R		0.9373*	0.8548**	0.7787

* $0.001 \leq P < 0.01$, ** $0.01 \leq P < 0.05$.
R is correlation coefficient.

RESULTS

LEAF LITTER AND COARSE WOOD DECOMPOSITION.—Weight losses from leaf litter and coarse wood followed a negative exponential pattern (Fig. 1). The leaf litter decayed more quickly than coarse woods. The monthly decomposition constant of leaf litter ($k = 0.15$/mo) was 4.2 times that of coarse wood ($k = 0.036$/mo). The annual decomposition coefficients were 1.79 and 0.43/yr for the leaf litter and coarse wood, respectively. The $t_{0.5}$ values were 4.6 and 19.5 mo and the $t_{0.95}$ values were 20.1 and 84.5 mo, for leaf litter and wood, respectively.

Monthly decay constant (*k*/mo) for leaf litter varied between 0.02 (December and January) and 0.21 (June and July). This constant correlated significantly with the corresponding rainfall and soil moisture over the same period (Table 1). Leaf decomposition constants and air temperature were not significantly correlated. From April 1989 to March 1990, mean annual temperature was 22.4°C. Maximum monthly temperature (27.1°C) occurred in May, and minimum monthly temperature (15.3°C) occurred in December (Fig. 2). The annual rainfall was 1131 mm, which occurred mostly between May and September during the monsoon season. The monthly air relative humidity maintained above 86 percent from June to December, decreased after January, and was the lowest in April.

FLOOR MASS AND TURNOVER.—Litterfall averaged 10.08 Mg/ha/yr for the two years (Table 2). Forest floor mass was variable, and averaged 3.05 Mg/ha for leaves, 1.64 Mg/ha for wood and 0.45 Mg/ha for flower and fruits. The turnover coefficients for wood, leaves, flower and fruits, and fine wood were 1.17, 2.07, and 4.11/yr, respectively. The residence times (yr) of forest floor mass were: fine wood (0.85) > leaves (0.48) > fruits (0.24).

NUTRIENT TURNOVER.—Total annual flux of nutrients in litterfall (kg/ha/yr) followed the pattern Ca > N > Mg > K > P, and was reflected in the quantities of each nutrient in the forest floor mass (Table 3). Calcium had the longest residence time (1.0 yr) followed by P (0.92 yr), Mg (0.64 yr), N (0.36 yr), and K (0.31 yr). Trends in annual nutrient inputs, forest floor mass, and residence times were distinct for the flower and fruit component, illustrating a difference in nutrient concentration. Nutrient input of (kg/ha/yr) in flower and fruit fall were N (12.64) > Ca (8.38) > K (6.14) > Mg (3.98) > P (2.31), contrasting to the order of nutrient input from leaves and wood.

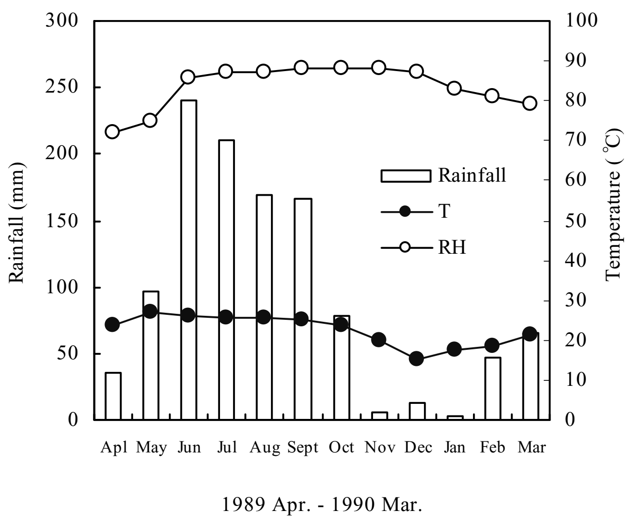

FIGURE 2. Values of temperature (T), relative humidity (RH), and rainfall (RF) of the study site between April 1989 and March 1990 in Xishuangbanna, Southwest China.

Table 2. *Turnover coefficients and residence times of leaf, wood, and fruit materials in litterfall and forest floor mass. Data were collected between April 1988 and March 1990 in a seasonal rain forest of Xishuangbanna, Southwest China.*

Components	Litterfall (*L*, Mg/ha/yr)	Forest floor mass (*X*, Mg/ha/yr)	Turnover coefficient (*L/X*, /yr)	Residence times (*X/L*, yr)
Leaf material	6.31	3.05	2.07	0.48
Wood	1.92	1.64	1.17	0.85
Flower and fruits	1.85	0.45	4.11	0.24
Total	10.08	5.14	1.96	0.51

DISCUSSION

Patterns of forest floor mass accumulation have been observed across a variety of forest ecosystems globally. Ovington (1965) stated that greater forest floor mass accumulation occurs with increasing distance from the equator and tropical forests have less organic matter on the forest floor than temperate forests. In tropical regions, forest floor mass has a wide range of variation, 3.3–10.0 Mg/ha for lowland rain forest, and 5.1–16.5 Mg/ha for montane rain forest (Tanner 1981, Anderson *et al.* 1983). The forest floor mass in Xishuangbanna (5.14 Mg/ha) is within the range of floor mass for lowland rain forest but less than that of the montane rain forest. It is similar to forest floor mass in Ghana (4.9 Mg/ha) and Colombia (5.0 Mg/ha), higher than that in Pasoh Malaysia (3.2 Mg/ha) and Zaire (3.9 Mg/ha), and lower than in Sarawak Malaysia (5.5–7.1 Mg/ha) and Panama (11.2 Mg/ha).

Vogt *et al.* (1986) compared forests worldwide and stated that patterns of forest floor mass accumulation can be distinguished by the evergreenness or deciduousness of forest foliage. Under the same climate conditions, forest floor mass in deciduous forests is generally half of those in evergreen forests. The litter accumulation averaged 22.55 Mg/ha for tropical broadleaf evergreen forests, 8.79 Mg/ha for topical broadleaf deciduous forests, and 2.17 Mg/ha for topical broadleaf semideciduous forests. The forest floor mass in the Xishuangbanna forest was between the topical broadleaf deciduous and broadleaf semideciduous. This is in accordance with the climatic characteristics in Xishuangbanna with mean annual temperature of 21.8°C and rainfall averaging 1493 mm annually over a 40-yr record (Cao *et al.* 2006). Annual temperature and rainfall for typical tropical broadleaf semideciduous and tropical broadleaf deciduous forests were 22.5°C and 1431 mm, and 25°C and 2147 mm, respectively (Vogt *et al.* 1986).

Tanner (1981) and Anderson *et al.* (1983) reported residence times (yr) of forest floor mass in montane and lowland rain forests of 0.7–2.2 and 0.3–1.0, respectively. The residence time of forest floor mass in Xishuangbanna (0.51) is within the range of the lowland rain forests, and is close to Ghana (0.5) and Nigeria (0.45), higher than Pasoh Malaysia and Zaire (both with 0.3), but lower than Sarawak (0.59–0.77) and New Guinea (0.83; Tanner 1981, Anderson *et al.* 1983). Compared with analyses of Vogt *et al.* (1986), the residence time in the Xishuangbanna seasonal rain forest is less than those of tropical broadleaf evergreen (2.4 yr) and tropical

Table 3. *Means ± SE of litter element inputs, element contents, and element residence time (yr) in coarse forest floor mass between April 1988 and March 1990 in a tropical seasonal rain forest of Xishuangbanna, Southwest China.*

Components		Elements (kg/ha/yr)				
		N	P	K	Ca	Mg
Leaves	Litterfall inputs (*L*)	39.81 ± 5.01	6.31 ± 1.05	20.84 ± 2.21	113.6 ± 15.90	25.26 ± 3.51
	Forest floor mass (*X*)	13.12 ± 3.03	4.98 ± 0.83	6.84 ± 1.05	78.98 ± 4.81	14.3 ± 3.06
	Residence times (*X*/*L*)	0.33 ± 0.01	0.79 ± 0.05	0.33 ± 0.01	0.69 ± 0.15	0.57 ± 0.04
Wood (<2 cm)	Litterfall inputs (*L*)	7.30 ± 1.51	1.21 ± 0.09	3.3 ± 0.23	28.2 ± 3.98	4.07 ± 0.81
	Forest floor mass (*X*)	5.31 ± 0.52	2.82 ± 0.21	1.82 ± 0.04	64.65 ± 5.20	5.68 ± 1.51
	Residence times (*X*/*L*)	0.73 ± 0.12	2.33 ± 0.20	0.55 ± 0.03	2.29 ± 0.91	1.48 ± 0.09
Fruits	Litterfall inputs (*L*)	12.64 ± 3.01	2.31 ± 0.30	6.14 ± 1.02	8.38 ± 2.42	3.98 ± 1.02
	Forest floor mass (*X*)	2.91 ± 0.15	1.25 ± 0.02	0.9 ± 0.07	6.78 ± 2.01	1.37 ± 0.09
	Residence times (*X*/*L*)	0.23 ± 0.01	0.54 ± 0.03	0.15 ± 0.01	0.81 ± 0.06	0.33 ± 0.001
Total	Litterfall inputs (*L*)	59.71 ± 5.10	9.83 ± 1.11	30.26 ± 4.30	150.1 ± 15.09	33.1 ± 4.65
	Forest floor mass (*X*)	21.30 ± 3.51	9.05 ± 2.50	9.58 ± 2.10	150.2 ± 14.30	21.2 ± 3.81
	Residence times (*X*/*L*)	0.36 ± 0.01	0.92 ± 0.10	0.31 ± 0.001	1.00 ± 0.01	0.64 ± 0.05

broadleaf deciduous (0.9) forests, but close to tropical broadleaf semideciduous forests (0.4 yr).

Annual decomposition rate (/yr) of leaf litter in Xishuangbanna ($k = 1.79$) is similar to semideciduous monsoon forest ($k = 1.33$) in Hainan Island, China (Lu & Liu 1989). Leaf litter decay constant was determined in three rain forests using fine mesh bags (40 μm) and coarse mesh bags (7–10 mm) in Sarawak: $k = 0.6$–0.84 (in fine mesh) and $k = 0.72$–0.96 (in coarse mesh), which is slower than rain forest in Xishuangbanna. The same trend of litter decomposition rates between our litterbag experiment and forest floor mass turnover coefficients indicated that Xishuangbanna seasonal rain forests have a higher litter decomposition rate than lowland rain forest in Sarawak.

Chemical composition is an intrinsic property of the litter, which determines the turnover rate of organically bound nutrients (Mohan Kumar & Deepu 1992). It is known that the decomposition of litter includes the three stages of leaching, accumulation, and release (Fu Moyui 1988). In the present study, Ca, P, and Mg had long residence times, whereas N and K were released rapidly. The magnitude of nutrient release into the soil system through litter decay is dependent on climate, floristic composition, and soil fauna. Implicitly, forest ecosystems influence nutrient release patterns substantially. Furthermore, each forest community has its own litterfall pattern, which differs in composition, chemical and biochemical characteristics, and nutrient release rates.

Although the rain forest in Xishuangbanna had faster litter decomposition rates, litter elements were released at slower rates than rain forests in Sarawak. The residence times (yr) of four rain forests in Sarawak (Anderson *et al.* 1983) were ranked as: K (0.17–0.29), Mg (0.23–0.43), N (0.36–0.56), P (0.45–0.83), and Ca (0.40–0.71). Xishuangbanna rain forests have longer residence times for K (0.31), Mg (0.64), P (0.92), and Ca (1.0) than those in the Sarawak forests where annual rainfall reaches 5000 mm. The residence time of N in the Xishuangbanna seasonal rain forest is shorter than tropical broadleaf evergreen (2.73), closer to broadleaf semideciduous (0.29). The residence time for P is shorter than tropical broadleaf evergreen (1.62), and deciduous forests (1.3; Vogt *et al.* 1986). These data indicate that the element release pattern in the Xishuangbanna seasonal rain forest is similar to those of broadleaf semideciduous forests.

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