LAGGING EFFECT OF NUTRIENT RELEASE IN TROPICAL SEASONAL FOREST SOILS IN XISHUANGBANNA, SOUTH-WEST CHINA

S Mani[1, 2] & M Cao[1, *]

[1]*Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, 88 Xuefu Road, Kunming 650223, PR China*
[2]*Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India*

**caom@xtbg.ac.cn*

Received April 2015

MANI S & CAO M. 2016. Lagging effect of nutrient release in tropical seasonal forest soils in Xishuangbanna, south-west China. This study assessed how litterfall production and nutrient concentration of leaf litter and soil vary with seasonality of rainfall in primary and secondary tropical forests of south-west China. A total of five 20 m × 20 m plots were established in each of the primary and secondary tropical forests. Leaf litter and top soil were sampled from each plot at monthly intervals for one year. Total annual litterfall production was 6.03 and 8.29 tonnes ha^{-1} year^{-1} in the primary and secondary tropical forests respectively. Total litterfall showed marked peaks at the end of the dry season with smaller peaks at the end of the rainy season. Leaf nutrients (phosphorus, potassium and calcium) were slightly varied between the two sites. Soil nutrients peaked in the middle of the rainy season, i.e. about two months later than the onset of the rainy season, suggesting a lagging effect of nutrient release. Consequently, we postulated that there was nutrient pulse in tropical seasonal forest soils every year, which was driven by alternating dry and rainy seasons in the predominantly monsoon climate areas.

Keywords: Litterfall, leaf nutrients, soil nutrients, seasonal variation, tropical forests

INTRODUCTION

In some monsoonal areas with distinct alternation of dry and rainy seasons, tropical forests maintain a proportion of deciduous tree species (Richards 1996). Generally, the peak of leaf fall during the dry season has been associated with water stress (Proctor et al. 1983, Songwe et al. 1988), photoperiod, evapotranspiration (Meentemeyer et al. 1982) and percentage of deciduous and semideciduous species in forests (Vogt et al. 1985, Bullock & Solis-Magallanes 1990, Morellato 1992). Litterfall showed strong seasonality, with highest deposition in the driest months of the year in low-latitude and low-elevation tropical forests of southern Amazon (Wright & Cornejo 1990, Selva et al. 2007). There was positive relationship during rainy season between rainfall intensity and litterfall rates, whereby intense precipitation coupled with high winds that followed brief dry spells produced high rates of litterfall (Luizao 1989).

One way to test the effects of litter on community dynamics is to test for time-lagged density dependence using models, because the amount of litter at any given time should be correlated with live plant density in the past (Farrer et al. 2010). Incorporating lagged interactions in models suggested new processes that were important for population dynamics such as litter effects and rhizome storage. Time lags due to delay in nutrient release from litter can lead to damped or bound oscillations in plants (Pastor & Walker 2006). Plant species may induce their own population oscillations through life history characteristics, such as litter quality, which affect cycling of nutrients through the ecosystem (Pastor & Walker 2006).

In Xishuangbanna, litterfall peaks in the latter half of the dry season, i.e. from March till April (Tang et al. 2010), indicating seasonal dynamics in litterfall production. Monthly decay rates of leaf litter are correlated with rainfall and soil moisture (Zheng et al. 2006), suggesting a bigger potential contribution from litterfall to the soil nutrient pool during rainy season. Many studies have been conducted on rates of litterfall, decomposition, nutrient input, forest floor mass turnover and nutrient release in the tropical forests of Xishuangbanna (e.g. Shanmughavel et al. 2001a, b, Zheng et al. 2006, Yang & Chen 2009, Tang et al. 2010). However, the relationship between litter production and soil nutrients in terms of seasonal dynamics has not been adequately investigated. Thus, this current study focused on this subject. We hypothesised that although litterfall peaked in the latter half of the dry season, this did not immediately lead to increase in soil nutrients. Drought prevents activities of decomposers, which stop the release of large amount of nutrients from the litter into the soil. The onset of the rainy season at the end of May, however, accelerates the decomposition of litterfall on the forest floor, which, in turn, leads to increase in soil nutrients in the middle of the rainy season, demonstrating a two-month delay in the nutrient release from litter into soil.

MATERIALS AND METHODS

Study site

Xishuangbanna (21° 8'–22° 35' N, 99° 56'–101° 50' E) is located in south-western Yunnan, China, contiguous to Laos in the south and Myanmar in the south-west. The region, though surprisingly far from the equator and at relatively high altitude (550 m above sea level), has rich tropical flora and typical tropical rainforest in the areas below 900 m (Zhu et al. 2006). It experiences monsoon climate and the annual mean temperature is 21.7 °C. The dry season from November till April is further divided into cool–dry (from November till February) and hot–dry (from March till April) periods. Rainy season occurs between May and October and is characterised by high rainfall from the south-west summer monsoon. There are three soil types, namely, laterite soil developed from siliceous rocks (between 600 and 1000 m elevation), lateritic red soil from sandstone substrates (> 1000 m) and limestone hills consisting of soil derived from hard limestone substrate of Permian origin with pH of 6.75 (between 600 and 1800 m).

Plot establishment, sample collection and chemical analysis

The study was conducted from July 2008 till June 2009 in primary and secondary tropical forests in Xishuangbanna. Details about the vegetation are reported in Zhang and Cao (1995) and Cao et al. (1996). A total of five 20 m × 20 m plots were established in each of the two sites. All plots were separated by a distance of 50 m. Leaf litter was collected from five traps measuring 1 m × 1 m (2-mm mesh) in each study plot. All traps were permanently tied using plastic nylon wire at the edges and fixed at 1-m height from above the ground. Litter accumulated over the traps was collected at monthly intervals (once in the middle of every month) for one year. Damaged traps were replaced immediately. Litter collected was brought to the laboratory and separated into three sample layers, namely, recently fallen litter (L_1), leaf fragments including twigs ≤ 1 cm diameter (L_2) and miscellaneous, including flowers and fruits (L_3). All samples were weighed after drying at 80 °C for 24 hours. Only L_1 layer samples were taken for chemical analysis. The traps were emptied monthly to prevent significant decomposition and leaching loss of litter nutrients. Samples were pooled and taken for analysis as plot wise. Five soil samples of 10 cm × 10 cm × 10 cm (top soil) were taken randomly in each plot and pooled for monthly nutrient analysis over a period of 1 year. All soil samples were air dried for 24 hours and roots and stones were removed by hand. Soil samples were sieved (< 2 mm) and subsamples were taken for chemical analysis. Soil pH and moisture were measured monthly using pH and moisture probe meters respectively. Total nitrogen (N), phosphorus (P), potassium (K) and calcium (Ca) were analysed from the collected subsamples. Total N values in litter and soil were determined using C–N analyser while total P, K and Ca, inductively coupled plasma atomic-emission spectrometer.

Data analysis

Litterfall data were combined to report results as litterfall per calendar month. Thus, data for each month represented either 30 or 31 days of litterfall with the exception of February.

Paired *t*-test was performed to test the difference between sites. Leaf and soil chemical contents were analysed within sites and between seasons using one-way ANOVA (without transformation of data) followed by Tukey's HSD test when the differences were significant. Statistical package R (version 2.15, 2012) was used for all analyses.

RESULTS

Environmental factors and litterfall production

Soils are extremely acidic with very low moisture contents in the dry season, suggesting low relative humidity values and high evaporative rates at both sites (Table 1). Soil moisture followed a seasonal pattern and showed significant difference in the dry season (t = -3.803, df = 5, $p < 0.01$) between the sites (Figure 1). Total annual litterfall production was 6.03 and 8.29 tonnes ha^{-1} year^{-1} in the primary and secondary tropical forests respectively (Table 1). Litterfall production in the primary tropical forest was 27.3% lower than that of the secondary tropical forest. Monthly litterfall fractions are shown in Figure 2. The three litterfall fractions (L_1, L_2 and L_3 layers) were higher in the secondary tropical forest than in the primary tropical forest (Table 1, Figure 2). Total litterfall showed marked peaks at the end of the dry season (March–April) with smaller peaks at the end of the rainy season (September–October) in both sites (Figure 2d). The rate of litterfall in July was 3.34 kg month^{-1} in the secondary tropical forest due to greater fall of the L_2 layer (especially twigs) (Figure 2b). Litterfall in L_2 and L_3 layers peaked in the latter part of the dry season (March–April) and beginning of the rainy season (May). The L_1 layer (freshly fallen leaves) showed significant difference between the two sites (Table 1, t = -3.119, df = 11, $p < 0.01$) but no significant difference between seasons. However, L_2 and L_3 layers did not show significant differences between seasons.

Leaf nutrient

There were small variations in leaf nutrient concentrations between the primary and secondary tropical forests (Table 2, Figure 3). At the beginning of the dry season (November–December), leaf nutrients showed increasing trend with the exception of total N and P in the primary tropical forest and decreasing trend at the end of the rainy season (September–October) in the secondary tropical forest (Figure 3). Total K and Ca values decreased at the end of the dry season in March–April but total N and P values were stable in both forests (Figure 3). Total P in the secondary forest showed significant difference throughout the entire year ($F_{(1, 10)} = 8.72$, $p < 0.05$) and also in the dry ($F_{(1, 4)} = 8.63$, $p < 0.05$) and rainy ($F_{(1, 4)} = 7.91$, $p < 0.05$) seasons between the primary and secondary forests. However, total Ca showed significant difference only during the rainy season between these forests ($F_{(1, 4)} = 9.71$, $p < 0.05$).

Soil nutrient

Mean monthly amounts of soil nutrients were stable at the end of the dry season and at the beginning of the rainy season at both sites with the exception of total Ca (Figure 4). Overall, all nutrients were higher in the middle of the rainy season (July–September) in both forests. There were significant differences in total Ca ($F_{(1, 10)} = 10.37$, $p < 0.01$), total P ($F_{(1, 10)} = 14.74$, $p < 0.01$) and total K ($F_{(1, 10)} = 29.68$, $p < 0.001$) between the two sites for the entire year, although total N only showed significant difference between the two sites in the rainy season ($F_{(1, 4)} = 10.89$, $p < 0.05$).

DISCUSSION

Seasonal dynamics of litterfall

Litterfall production values were highest in the latter part of the dry season (March–April) and there was a second minor peak at the end of the rainy season (September–October). Increased litterfall in the dry season may be related to water deficit (Scott et al. (1992). Water stress, which is usually greatest at the end of the dry season, is an important factor leading to leaf fall in the dry season. The proportion of freshly fallen litter (L_1) was lower than leaf fragments including twigs (L_2) in the litterfall at both sites (Table 1). Differences between these two layers could be explained partially by the different characteristics of vegetation, canopy openness and abundance of large trees. Leaf fall (L_1)

Table 1 Mean (± SE) total litterfall production, soil moisture and soil pH at two tropical forest sites in Xishuangbanna, south-west China

Variable	Research site		p-value
	Primary tropical forest	Secondary tropical forest	
Soil moisture (%)			
Dry	16.81 ± 4.60	21.95 ± 4.50	0.01
Rainy	35.76 ± 7.61	37.71 ± 3.66	0.75
Soil pH			
Dry	4.4 ± 0.07	4.2 ± 0.07	0.001
Rainy	4.2 ± 0.06	4.1 ± 0.04	0.05
Litterfall (tonne ha^{-1} $year^{-1}$)			
L_1 layer	0.64 ± 0.19	0.91 ± 0.17	0.01
L_2 layer	3.12 ± 0.45	4.95 ± 0.55	0.07
L_3 layer	2.27 ± 0.38	2.43 ± 0.28	0.11
Total	6.03 ± 0.50	8.29 ± 0.50	
Season (tonne ha^{-1} $year^{-1}$)			
Dry	2.84 ± 0.46	4.70 ± 0.47	0.18
Rainy	3.19 ± 0.39	3.59 ± 0.35	0.06
Total	6.03 ± 0.50	8.29 ± 0.50	

p-value indicates the difference between sites

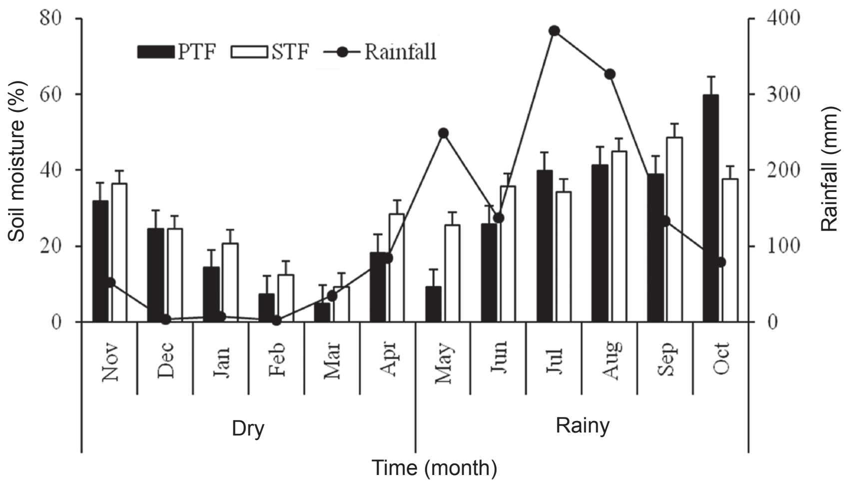

Figure 1 Percentage of soil moisture at the study sites in the primary (PTF) and secondary (STF) tropical forests; bar line = standard error

peaked in February–April (Figure 2a). This corresponded to findings by Scott et al. (1992), Sundarapandian and Swamy (1999), Pandey et al. (2007) and Schessl et al. (2008). Twigs (L_2) and reproductive parts (L_3) accounted for a large proportion of annual litterfall at both study sites (Table 1, Figures 2b and c). Due to the complex structure and canopy architecture in the primary tropical forest, dead branches usually remain on the trees for a long period and may occasionally fall on the forest floor, leading to higher variations in twig litterfall (Tang et al. 2010).

Production of reproductive structures (L_3 layer) showed small amounts of variation between the two sites (Table 1, Figure 2c); this

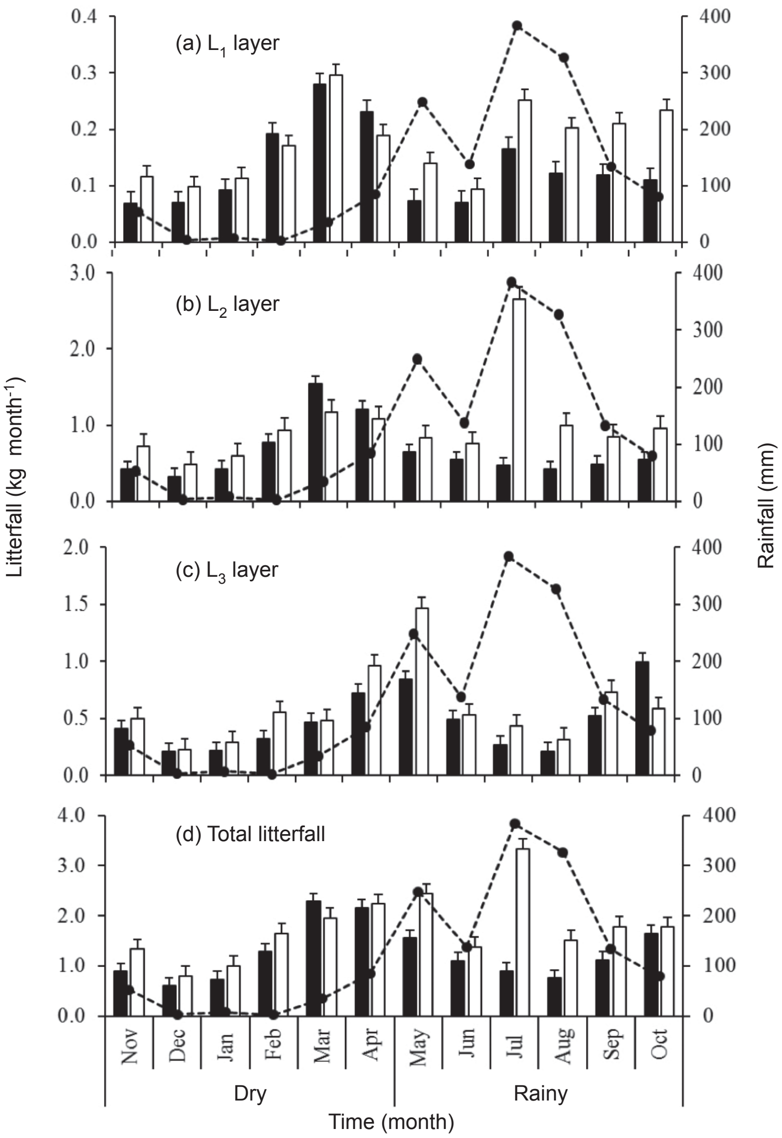

Figure 2 Seasonal variation in litterfall fractions (L_1, L_2 and L_3 layers) of the primary (dark bar) and secondary tropical (blank bar) forests; dotted line = rainfall; bar line = standard error

could be due to similar phenological patterns and the occurrence of common tree species. The high number and density of mature trees in tropical seasonal forests may regularly produce abundant flowers, fruits and seeds in a mast year, resulting in higher variation in reproductive parts (Stocker et al. 1995). Reproductive parts were markedly higher in the latter half of the dry season (March–April) and the early part of the rainy season (May) but produced significant peaks at the end of the rainy season (September–October). The patterns of reproductive litterfall depend on the timing of flowering and fruiting, thus, exhibiting marked seasonality (Mlambo & Nyathi 2008).

Variation in leaf nutrient concentrations

This study demonstrated the strength of using leaf-based nutrients to predict monthly changes in nutrient concentrations in primary and secondary tropical forests. The P of the leaves was lower in the former compared with the latter, although no significant difference between the two sites was observed, indicating that low P availability was likely a common constraint for

Table 2 Mean total leaf and soil nutrient concentrations in the primary and secondary tropical forests

Variable	Primary tropical forest	Secondary tropical forest
Leaf nutrient (g^{-1} kg^{-1})		
N	189.5 (13.7–18.6)	189.8 (14.9–18.2)
P	7.5 (0.5–0.7)	8.2 (0.6–0.8)
K	61.4 (3.7–6.1)	53.5 (2.9–5.9)
Ca	115.0 (7.4–13.2)	105.2 (6.8–9.6)
N:P	25.3:1	23.1:1
Soil nutrient (g^{-1} kg^{-1})		
N	125.7 (9.5–11.2)	157.6 (11.8–15.8)
P	18.4 (1.4–1.6)	24.6 (1.8–2.3)
K	554.6 (43.1–50.4)	716.8 (53.6–62.0)
Ca	13.1 (0.8–1.5)	15.4 (0.9–1.6)
N:P	6.8:1	6.4:1

Range in parenthesis

tropical forest regrowth (Vasconcelos et al. 2008). Total litterfall production and leaf nutrients did not differ significantly in the study sites, which were similar to a litterfall production study in the tropical dry forest of Mexico (Martinez-Yrizar & Sarukhan 1990).

Seasonal dynamics of leaf nutrients

In the study sites, all nutrients gradually decreased (except for K in the secondary forest) in the latter part of the rainy season (Figure 3). Nutrient loss due to leaching may have affected litter nutrient content, especially during wet season, with N being more susceptible to losses than P (Cuevas & Medina 1986). In the primary tropical forest, N and P showed low values in the middle of dry season (February–March), indicating the effect of floristic variation and organic matter turnover. Townsend et al. (2007) observed that even in single, highly P-deficient sites in Amazon Basin, the large range in foliar N and P contents highlights a diversity of physiological strategies in response to P-poor environment, and suggests that the extent of limitation by any given nutrient may vary considerably among individual species within a single site.

Litterfall production peaked in March–April, but leaf nutrient concentrations were very low for total K and Ca (Figure 3). This may reflect retranslocation of essential nutrients during the dry season. The results suggested that the major nutrient values were moderate (except for K in the secondary forest) in the middle of the rainy period (July–August) at both sites. Contents of structural materials (cellular wall) and other compounds such as starch increased at this time due to foliar development that occurred throughout the rainy and early dry seasons (Roca-Perez et al. 2006).

Variation in soil nutrient concentrations

Total K showed greater variation between the sites. Low soil moisture usually means greater availability of K in the dry season (Kuchenbuch et al. 1986). Soil K mobility increased significantly with soil moisture content, suggesting that more K could be released to the plant roots at sufficient soil moisture (Zeng & Brown 2000). The fact that total N and P values were lower in the primary than in the secondary tropical forests could be due to leaching losses. The greatest impact of priming on soil carbon stocks will occur in moderately acidic tropical forest soils of low N availability (Nottingham et al. 2015). On the other hand, tropical ecosystems with low availability of N are normally depleted in ^{15}N (Martinelli et al. 1999).

Seasonal dynamics of soil nutrients

As a result of higher soil moisture and rainfall during the rainy season, soil Ca decreased as the

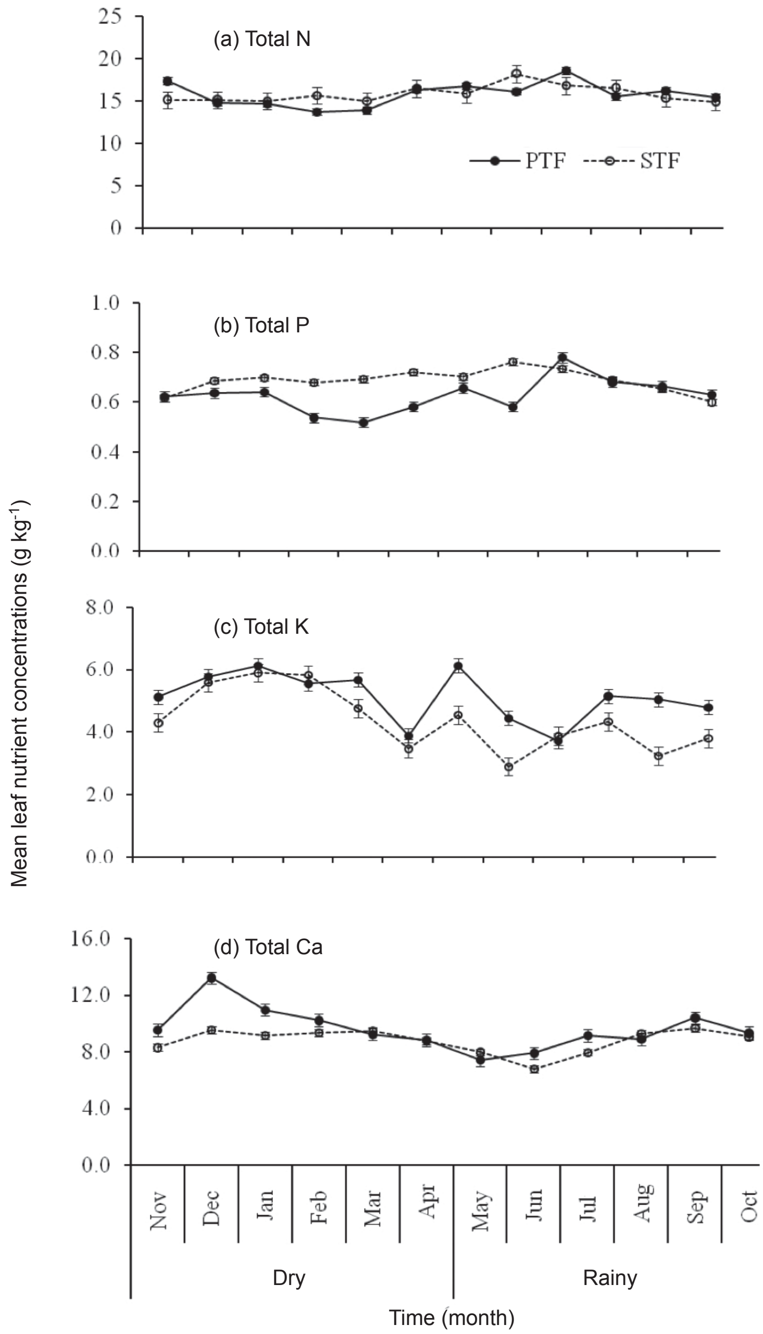

Figure 3 Mean values of seasonal nutrient concentrations (g kg^{-1}) in leaves from L_1 layer of the primary (PTF) and secondary (STF) tropical forests; bar line = standard error

availability of other nutrients increased at the end of the rainy season (September–October), except for N and P in the primary tropical forest (Figure 4). However, lower pH could be one of the reasons for the decrease in Ca. In this study, all major soil nutrients showed highest values in the middle of the rainy season (July–August) except for total N and P in the primary forest. The onset of the rainy season accelerated litter decomposition and nutrient release from litterfall into surface soil. Monthly decay rates of leaf litter in this area are correlated with rainfall and soil moisture (Zheng et al. 2006). The highest decay constant (k value) occurred early in the rainy season, i.e. June and July. Decomposition is slow during dry months and fast during rainy season

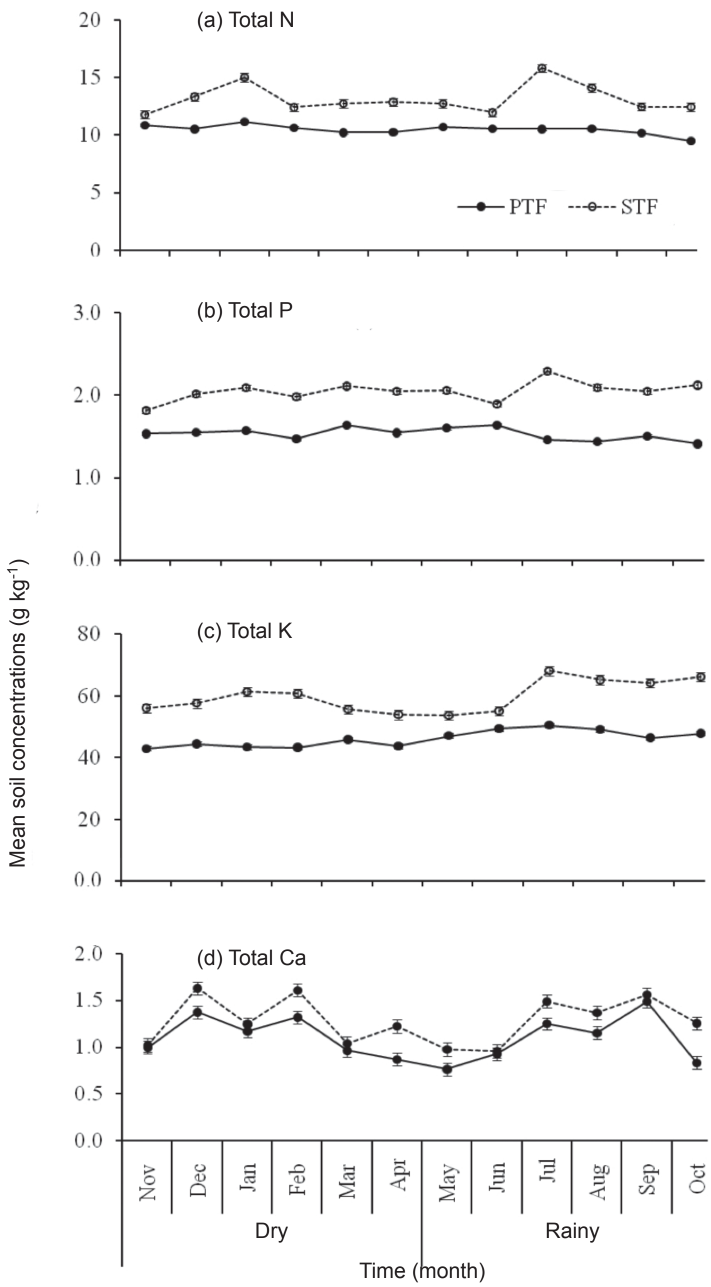

Figure 4 Mean values of seasonal soil nutrient concentrations in the primary (PTF) and secondary (STF) tropical forests; bar line = standard error

(Tang et al. 2010). Therefore, we estimated that lagging time for nutrient release in such forests is about two months later than the onset of the rainy season. Yavitt et al. (2004) also found that the concentrations of N and Ca increased gradually and peaked at the end of the wet season, just prior to the maximum rate of leaf fall before decreasing sharply to the lowest values in the dry season. Thus, there was yearly nutrient pulse cycle in tropical seasonal forest soils which was driven by rainfall.

CONCLUSIONS

Two peaks of litterfall and rainfall were observed in two tropical forests containing deciduous species, although the first peak of litterfall production occurred in March–April (at the end of the dry season). Total P in the primary tropical forest showed low values at the end of the dry season, suggesting the effect of floristic variation and organic matter turnover. The amount of soil nutrients is highest in the middle of the rainy season, indicating that the onset of the rainy season accelerated litter decomposition, and significant nutrient release from litterfall into surface soil took place about two months later. Our findings supported the hypothesis that there would be annual pulse of nutrient release mechanism from litterfall into the soil during rainy season, which led to rapid increase in soil nutrients in the middle of the rainy season in the primary and secondary tropical forests of Xishuangbanna.

ACKNOWLEDGEMENTS

This research was supported by the National Key Basic Research Program of China (2014CB954100) and a grant from the Applied Fundamental Research Foundation of Yunnan Province (2014GA003). The first author thanks the Chinese Academy of Sciences for supporting his post-doctoral research study. We are grateful to D Chen, X Deng and Y Fu for their assistance.

REFERENCES

Bullock SH & Solis-Magallanes A. 1990. Phenology of canopy trees of a tropical deciduous forest in México. *Biotropica* 22: 22–35.

Cao M, Zhang JH, Feng ZL, Deng JW & Deng XB. 1996. Tree species composition of a seasonal rain forest in Xishuangbanna, south-west China. *Tropical Ecology* 37: 183–192.

Cuevas E & Medina E. 1986. Nutrient dynamics within Amazonian forest ecosystems. I. Nutrient flux in fine litter fall and efficiency of nutrient utilization. *Oecologia* 68: 466–472.

Farrer EC, Goldberg DE & King AA. 2010. Time lags and the balance of positive and negative interactions in driving grassland community dynamics. *The American Naturalist* 175: 160–173.

Kuchenbuch R, Claassen N & Jungk A. 1986. Potassium availability in relation to soil moisture. II. Calculations by means of a mathematical simulation model. *Plant and Soil* 95: 233–243.

Luizao FJ. 1989. Litter production and mineral element input to the forest floor in a central Amazonian forest. *GeoJournal* 19.4: 407–417.

Martinelli LA, Piccolo MC, Townsend AR et al. 1999. Nitrogen stable isotopic composition of leaves and soil: tropical versus temperate forests. *Biogeochemistry* 46: 45–65

Martinez-Yrizar A & Sarukhan J. 1990. Litterfall patterns in a tropical deciduous forest in Mexico over a five-year period. *Journal of Tropical Ecology* 6: 433–444.

Meentemeyer V, Box EO & Thompson R. 1982. World patterns and amounts of terrestrial plant litter production. *Bioscience* 32: 125–128.

Mlambo D & Nyathi P. 2008. Litterfall and nutrient return in a semi-arid southern African savanna woodland dominated by *Colophospermum mopane*. *Plant Ecology* 196: 101–110.

Morellato LPC. 1992. Nutrient cycling in two south-east Brazilian forests. I. Litterfall and litter standing crop. *Journal of Tropical Ecology* 8: 205–215.

Nottingham AT, Turner BL, Stott AW & Tanner EVJ. 2015. Nitrogen and phosphorus constrain labile and stable carbon turnover in lowland tropical forest soils. *Soil Biology and Biochemistry* 80: 26–33.

Pandey RR, Sharma G, Tripathi SK & Singh AK. 2007. Litterfall, litter decomposition and nutrient dynamics in a subtropical natural oak forest and managed plantation in northeastern India. *Forest Ecology and Management* 240: 96–104.

Pastor J & Walker RD. 2006. Delays in nutrient cycling and plant population oscillations. *Oikos* 112: 698–705.

Proctor J, Anderson JM, Fogden SCL & Vallack HW. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. II. Litterfall, litter standing crop and preliminary observation on herbivory. *Journal of Ecology* 71: 261–283.

Richards PW. 1996. *The Tropical Rain Forest: An Ecological Study*. Second edition. Cambridge University Press, Cambridge.

Roca-Perez L, Boluda R & Perez-Bermudez P. 2006. Seasonal variation in nutrient status of foxglove leaves. *Journal of Plant Nutrition* 29: 1077–1084.

Schessl M, Da Silvab WL & Gottsbergera G. 2008. Effects of fragmentation on forest structure and litter dynamics in Atlantic rainforest in Pernambuco, Brazil. *Flora* 203: 215–228.

Scott DA, Proctor J & Thompson J. 1992. Ecological studies on a lowland evergreen rain forest on Maraca Island, Roraima, Brazil. II. Litter and nutrient cycling. *Journal of Ecology* 80: 705–717.

Selva EC, Couto EG, Johnson MS & Lehmann J. 2007. Litterfall production and fluvial export in headwater catchments of the southern Amazon. *Journal of Tropical Ecology* 23: 329–335.

Shanmughavel P, Sha LQ, Zheng Z & Cao M. 2001a. Nutrient cycling in a tropical seasonal rain forest of Xishuangbanna, southwest China. Part I. Tree species: nutrient distribution and uptake. *Bioresource Technology* 80: 163-170.

Shanmughavel P, Zheng Z, Sha LQ & Cao M. 2001b. Floristic structure and biomass distribution of a tropical seasonal rain forest in Xishuangbanna, southwest China. *Biomass and Bioenergy* 21: 165–175.

Songwe NC, Fasehun FE & Okali DUU. 1988. Litterfall and productivity in a tropical rain forest, Southern Bakundu Forest Reserve, Cameroon. *Journal of Tropical Ecology* 4: 25–37.

Stocker GC, Thompson WA, Irvine AK, Fitzsimon JD & Thomas PR. 1995. Annual patterns of litterfall in a lowland and tableland rainforest in tropical Australia. *Biotropica* 27: 412–420.

Sundarapandian SM & Swamy PS. 1999. Litter production and leaf-litter decomposition of selected tree species in tropical forests at Kodayar in the Western Ghats, India. *Forest Ecology and Management* 123: 231–244.

Tang JW, Cao M, Zhang JH & Li MH. 2010. Litterfall production, decomposition and nutrient use efficiency varies with tropical forest types in Xishuangbanna, SW China: a 10-year study. *Plant and Soil* 335: 271–288.

Townsend AR, Cleveland CC, Asner GP & Bustamantemm C. 2007. Controls over foliar N:P ratios in tropical rain forests. *Ecology* 88: 107–118.

Vasconcelos SS, Zarin DJ, Araujo MM et al. 2008. Effects of seasonality, litter removal and dry-season irrigation on litterfall quantity and quality in eastern Amazonian forest regrowth, Brazil. *Journal of Tropical Ecology* 24: 27–38.

Vogt KA, Grier CC & Vogt DJ. 1985. Production, turnover and nutrient dynamics of the above- and below-ground detritus of world forests. *Advances in Ecological Research* 15: 303–377.

Wright SJ & Cornejo FH. 1990. Seasonal drought and leaf fall in a tropical forest. *Ecology* 71: 1165–1175.

Yang XD & Chen J. 2009. Plant litter quality influences the contribution of soil fauna to litter decomposition in humid tropical forests, southwestern China. *Soil Biology and Biochemistry* 41: 910–918.

Yavitt JB, Wright SJ & Wieder RK. 2004. Seasonal drought and dry-season irrigation influence leaf-litter nutrients and soil enzymes in a moist, lowland forest in Panama. *Austral Ecology* 29: 177–188.

Zeng Q & Brown PH. 2000. Soil potassium mobility and uptake by corn under differential soil moisture regimes. *Plant and Soil* 221: 121–134.

Zhang JH & Cao M. 1995. Tropical forest vegetation of Xishuangbanna SW China and its secondary changes, with special reference to some problems in local nature conservation. *Biological Conservation* 73: 225–238.

Zheng Z, Shanmugavel P, Sha LQ, Cao M & Warren M. 2006. Litter decomposition and nutrient release in tropical seasonal rainforest of Xishuangbanna, Southwest China. *Biotropica* 38: 342–347.

Zhu H, Cao M & Hu HB. 2006. Geological history, flora, and vegetation of Xishuangbanna, southern Yunnan, China. *Biotropica* 38: 310–317.