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REGULAR ARTICLE

Litterfall production, decomposition and nutrient use efficiency varies with tropical forest types in Xishuangbanna, SW China: a 10-year study

Jian-Wei Tang · Min Cao · Jian-Hou Zhang · Mai-He Li

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Abstract Litterfall production, decomposition and nutrient use efficiency in three different tropical forest ecosystems in SW China were studied for 10 years. Annual mean litterfall production in tropical seasonal forest (TSF) (9.47±1.65 Mg ha^{-1}) was similar to that in man-made tropical forest (MTF) (9.23±1.29 Mg ha^{-1}) ($P>0.05$) but both were significantly lower than that in secondary tropical forest (STF) (12.96±1.71 Mg ha^{-1}) ($P<0.05$). The annual variation of litterfall was greater in TSF (17.4%, $P<0.05$) than in MTF (14.0%) or STF (13.2%). The annual mean decomposition rate of litterfall increased followed the order of MTF (2.72)<TSF (3.15)<STF (3.50) ($P<0.05$), which was not correlated with annual precipitation or annual mean temperature, but was rather related to litter quality. The nutrient use efficiency was found to be element-dependent and to vary significantly among the three forest types ($P<0.05$). These results indicate that litterfall production and decomposition rates in different tropical forest systems are related to plant species composition and are influenced strongly by coexisting species and their life stage (age) but less so by the species richness. Constructing multi-species and multistory man-made tropical forest is an effective way to enhance biological productivity and maintain soil nutrients on degraded tropical land.

Keywords Decomposition · Litterfall dynamic · Man-made forest · Nutrient cycling · Nutrient use efficiency · Seasonal rainforest · Secondary tropical forest

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J.-W. Tang
Institute of Botany, Chinese Academy of Sciences,
Beijing 100093, People's Republic of China

J.-W. Tang (✉) · M. Cao · J.-H. Zhang
Tropical Rainforest Ecosystem Station, Xishuangbanna
Tropical Botanical Garden, Chinese Academy of Sciences,
Menglun Township, Mengla County, Yunnan 666303,
People's Republic of China
e-mail: tangjw@xtbg.org.cn

J.-W. Tang
Graduate University of Chinese Academy of Sciences,
Beijing 100049, China

M.-H. Li
Swiss Federal Research Institute WSL,
Zuercherstrasse 111,
8903 Birmensdorf, Switzerland

Introduction

Deforestation across tropical forests during the period from 1990 to 2005 rapidly increased the area of secondary forests and tree plantations (Hansen et al. 2008; FAO 2006). Tropical secondary forests replaced approximately 15% of primary tropical forests during the 1990s (Wright 2005), and the area of tree plantations in the tropics increased rapidly from 17.8 Mha in 1980 to 70 Mha in 2000 (Brown 2000).

Therefore, understanding the ecological characteristics, structure and function of these ecosystems is crucial to restoring degraded tropical lands and managing tropical forest ecosystems in order to meet the demand for natural resources and to further economic development (Lugo 1992; Cuevas and Lugo 1998; Barlow et al. 2007a).

Litter production and decomposition are fundamental ecosystem processes, and play key roles in nutrient cycling, including turnover of carbon and nutrients in terrestrial ecosystems (Melillo et al. 1982; Aber et al. 1991). Litterfall and decomposition processes can serve as an index of primary production and as an indicator of the efficiency of nutrient cycles (Vitousek 1982; Proctor et al. 1983). In tropical forest ecosystems with nutrient-poor soils, litterfall and decomposition processes are particularly important for the nutrient budget (Sundarapandian and Swamy 1999), affecting relationships between biodiversity and ecosystem properties and functions (Swift et al. 1979; Wardle and Lavelle 1997; Hoorens et al. 2003).

Litter production is closely related to species composition, age structure, growth rate and productivity (Facelli and Pickett 1991; Arunachlam et al. 1998; Scherer-Lorenzen et al. 2007). Species composition is the most important factor influencing litter production within a climate zone (Facelli and Pickett 1991; Sundarapandian and Swamy 1999; Paoli and Curran 2007). Numerous studies have reported that litterfall productivity is higher in diverse mixed stands than in monoculture stands (Binkley et al. 1992; Parrotta 1999; Wang et al. 2007; Scherer-Lorenzen et al. 2007). It has also been reported that total litterfall is similar in primary and secondary forests, but lower in plantations (Barlow et al. 2007b; Smith et al. 1998; Brasell et al. 1980). However, the majority of studies related to litterfall in tropical forests have concentrated on mature and pristine forests and only a few papers have focused on secondary tropical forests and plantations (reviewed by Proctor 1984; Vitousek 1984; Lugo 1992; Cuevas and Lugo 1998; Smith et al. 1998; Clark et al. 2001a, b; Barlow et al. 2007b). Our understanding is less complete in disturbed and regenerating habitats in the tropical forests (Barlow et al. 2007b). Furthermore, many of those works were conducted for only brief time periods (<2 years); long-term studies are still rare (Knutson 1997; Liu et al. 2003).

Litter decomposition is also correlated closely with the plant species composition and plant species traits (Hobbie et al. 2006; Scherer-Lorenzen et al. 2007; Vivanco and Austin 2008; Cornwell et al. 2008). Plant species and their community have the potential to influence decomposition process through altering plant species interactions, plant-decomposer interactions, and biotic and abiotic environments such as the microclimate (Hooper et al. 2000; Gartner and Cardon 2004; Hättenschwiler et al. 2005; Vivanco and Austin 2008). Some studies have demonstrated that litter decomposition and decomposers were unaffected by litter species richness (Wardle et al. 2006; Lecerf et al. 2007), and that increasing litter species richness reduced the variability in the litter decomposition system (Keith et al. 2008). However, those decomposition experiments used mesh litterbags containing only small quantities of leaf or litter manipulated from the natural forest litterfall. Little information is currently available on the long-term decomposition rate estimated directly by unconfined litter disappearance on the forest floor.

Ecosystem nutrient use efficiency is an integrative measure of ecosystem functioning (Vitousek 1982, 1984; Hiremath and Ewel 2001) and has been used as an index of nutrient availability and soil fertility (Vitousek 1982). Studies have demonstrated that tree species (life forms) significantly influence ecosystem nutrient use efficiency (Hiremath and Ewel 2001), and the pattern of nutrient use efficiency varies among tropical forest ecosystems (Vitousek 1984; Cuevas and Medina 1986; Lugo 1992; Smith et al. 1998).

To understand the structure, functioning, and ecological processes of tropical forest ecosystems, we initiated a long-term ecological research project under the framework of CERN (Chinese Ecological Research Network), and established permanent plots in different tropical forest types in Xishuangbanna, Yunnan Province, southwestern China, in 1993. Fine litterfall, decomposition rate, mineral-element return, and nutrient use efficiency (NUE) were studied in a tropical seasonal rainforest (TSF), a secondary tropical forest (STF), and a man-made tropical forest (MTF)—the three dominant forest ecosystems (Zhang and Cao 1995) in the region—from 1996 to 2005 (10 years). As the conversion of tropical seasonal rain forest to secondary tropical forest and man-made tropical forest changes tree species composition and characteristics of litterfall, decomposition and nutrient use efficiency, the present study aimed to test the hypotheses that: (1) species-rich stands will produce more litter with less annual variation than species-poor stands; (2) litter-fall decomposition rate is more rapid in species-rich than in species-poor communities; (3) nutrient use efficiency is higher in species-rich than in species-poor communities.

Materials and methods

Study sites

The Xishuangbanna region lies on the northern edge of tropical southeastern Asia, and is famous for its diverse flora and fauna. Due to its unique geographical and climatic features, this area supports a tropical rain forest with a small proportion of deciduous tree species that shed leaves in different seasons (Cao et al. 1996). The forests distributed in wet valleys, lowlands or on low hills with sufficient water supply are defined as tropical seasonal rainforest (Wu et al. 1987). This tropical seasonal rainforest covered 10.9% of the area in 1976 but only 3.6% by 2003 (Li et al. 2007). A total of 139,576 ha tropical seasonal rain forest was lost during that period (Li et al. 2007), the coverage of rubber plantations expanded from 1.1% of the area by 1976 to 11.3% by 2003 (Li et al. 2007), and about 26% of the land area was covered by secondary forests (Liu et al. 1990).

The study area has a seasonal climate influenced by the southwestern monsoon with a rainy season from May to October, and a dry season from November to April. The forest plots studied are close to the Xishuangbanna Tropical Rainforest Ecosystem Station (XTRES, 21°54′N, 101°16′E, 560 ma.s.l.) in Menglun, Mengla county, Xishuangbanna, southwestern China. Data collected at XTRES from 1980 to 2005 yield the following climatic characteristics for the study sites: annual mean temperature 21.6°C; mean temperature of the coldest (January) and the hottest month (May) 16.4°C and 25.9°C, respectively; the absolute minimum temperature 2.0°C (recorded in 1974 and 1999); mean annual precipitation 1,476.4 mm (of which ~85% falls during the rainy season between May and October); average annual relative humidity 86%. The majority of the yearly total 173 foggy days occur during the cool and dry season (November–April), which partially compensates for the scarcity of rainfall.

The soils in the forests studied belong to yellow latosol soil developed from purple sandstone (Cao et al. 1996). The soil of STF and MTF is less stony but deeper than in TSF. Other site characteristics are summarized in Table 1, based on data collected from the permanent plots in each forest type (Cao et al. 1996; Zhu 1998).

The canopy of TSF is 25–30 m in height and was divided into top (I; >20 m in height), middle (II; 13–20 m), and bottom (III; 5–13 m) tree layers. Tree species composition in these different layers was described in detail by Cao et al. (1996). The shrub layer, 1–3 m in height, is composed mainly of young trees and shrub species including *Randia acuminatissima*, Pittosporopsis kerrii, *Chesalia curviflora*, *Lasianthus fordii*, *Mycetia gracilis*, *Neonauclea griffithii*, *Saprosma ternatum*, *Goniothalamus cheliensis* and *Aporusa yunnanensis*. The sparse herb layer has only a few of species including *Pratia nummularia*, *Stachyphrynium sinensis*, *Piper sarmentosum*, *Elatostema macintyrei* and some pteridophytes including *Selaginella delicatula*, *Angiopteris latemarginata*, *Lygodium japonicum*, *Pteris finotii*, *Allantodia maxima* and *Tectaria gemifera*.

The secondary tropical forest (~150 ha) regenerated naturally on abandoned land after slash and burn cultivation in 1968. The stand at the beginning of this study in 1996 was in the early building phase (Watt 1947) with a stand age of 28 years. The canopy height was 15 m and the vertical structure of the forest could be divided into tree, shrub and herbaceous layers. The tree layer was dominated by *Syzygium oblatum*, *Millettia leptobotrya*, *Phoebe lanceolata*, *Castanopsis indica* and *Garcinia cowa*. The shrub layer, 1–3 m in height, was dominated by *Prismatomeria tetrandra*, *Psychotria henryi*, *Goniothalamus griffithi*, *Chassalia curviflora*, and by saplings and seedlings of the overstory tree species. The herb species were sparse, and only *Digitaria sanguinalis* and *Aglaonema pierreanum* occur occasionally.

The man-made forest (~7.5 ha) was established in 1960. The rubber tree (*Hevea brasiliensis*) occupied the first tree layer (18–20 m in height) accompanied by a few individuals of *Baccaurea ramiflora* and *Raovolfia vomitoria*. *H. brasiliensis*, *B. ramiflora* and *R. vomitoria* formed the second tree layer (7–12 m in height). *Homalomena occulta* occurred sparsely in the herbaceous layer.

Table 1 Characteristics of the study sites in Xishuangbanna, SW China. *TSF* Tropical seasonal rainforest, *STF* secondary tropical forest, *MTF* man-made tropical forest

Forest type	TSF	STF	MTF
Plot size (ha)	1.0	0.25	0.25
Slope	15°–20°	15°	3°
Aspect	Northwesterly	Northwesterly	Northwesterly
Altitude (m above sea level)	730	560	560
Species number of trees (DBH≥2.0 cm)	295	63	39
Mean age of the stand (years)	250–300	28	36
Tree density (DBH≥2.0 cm)	2,591	750	320
Mean canopy height (m)	18.6±5.6	12.0±3.4	20.0±2.2
Mean canopy coverage (%)	85.0±8.4	90.0±5.3	75.0±6.5
Leaf area index	5.73	7.41	7.06
Basal area ($m^2 ha^{-1}$)	31.15	16.01	38.49
Biomass of tree layer (t ha^{-1})	352.6	100.9	362.5
Soil characteristics (0–20 cm)			
Organic matter (%)	3.35±0.48	4.01±0.32	4.54±0.21
Total nitrogen (%)	0.21±0.016	0.24±0.014	0.16±0.011
Total phosphorus (%)	0.028±0.002	0.028±0.002	0.061±0.004
Total potassium (%)	0.53±0.016	0.73±0.018	1.27±0.053
Bulk density (g cm^{-3})	1.22±0.15	1.04±0.11	1.23±0.13
pH	5.18±0.11	4.47±0.14	4.51±0.16

Plant nomenclature follows Li et al. (1996).

Fine litterfall

Round litterfall traps (nylon gauze with 1.0 mm mesh, 0.25 m^2 surface area) with wire on the mouth were suspended at a height of 1.0 m from the ground with three bamboo stakes. Forty litterfall traps in TSF and 20 traps in each of STF and MTF were placed. From January 1996 to December 2005 (10 years), litterfall was collected monthly during the dry season (November–April) and every 2 weeks during the rainy season (May–October) from all traps. Fine litterfall was sorted into four categories: leaves, twigs (≤2.5 cm in diameter), reproductive parts (flowers, fruits, and seeds) and miscellaneous. Twigs were oven-dried at 105°C and other components at 75°C to constant weight and weighed, and the mean monthly litter mass (kg ha^{-1}) of each plot was calculated.

Standing crop of litter

Litter standing crop on the floor was collected from 20 (for TSF) and 10 (for STF and MTF) cylinders (50.3 cm in diameter) every 3 months from 29 March to 30 December during1996–2005 (10 years). The cylinder was pressed into the ground to collect all the litter within it, including twigs ≤2.5 cm in diameter. Each collected location was marked with a small bamboo stake to avoid repeated collections. According to Scott et al. (1992), organic matter with ≥2 mm in diameter is defined as litter and <2 mm as soil organic matter. The litter was separated into leaves, twigs (≤2.5 cm in diameter), reproductive parts (flowers and fruits) and miscellaneous. Others could not be distinguished from the soil organic matter and was not recorded. All components were oven-dried at 75°C and weighed separately.

Chemical analysis

Mineral-element contents in fine litterfall (1999, 2002 and 2005 samples only) for each sampling date at each site were analyzed. Samples for analysis were ground, homogenized and passed through a 0.2 mm sieve. Contents of potassium (K), calcium (Ca), and magnesium (Mg) were determined using Atomic Absorption Spectrophotometry (Model-932, GBC Scientific Equipment, Melbourne, Australia). Contents of nitrogen (N) and phosphorus (P) were analyzed according to the micro-Kjeldahl method. Organic carbon was determined using the wet digestion method with $K_2Cr_2O_7$ (Institute of Soil, Academia Sinica 1978). All chemical analyses were carried out in triplicate on the same sub-sample, and mean values were calculated.

Data processing and statistical analysis

Mean values were calculated for each category and each sampling date at each site. Mineral-nutrient content was calculated by mean concentration (g kg^{-1}) of each mineral-element multiplied by the mean mass of each litterfall components. The ratios of C to N or P were calculated by C concentration in litterfall divided by N or P concentration. The nutrient content (kg ha^{-1}) of each litterfall component per month and/or per year was estimated by mean concentrations (g kg^{-1}) of each mineral-element in each litterfall components multiplied by the mean mass of the litterfall component (Mg ha^{-1}) per month and/or per year for each site.

Turnover rate (k) was calculated for each litterfall component, using $k=A/F$, where A is the annual fine litterfall input to the forest floor and F is the mean litter standing crop (Scott et al. 1992). This approach assumes that the secondary forest and man-made forest floors were at steady state.

Nutrient use efficiency (NUE) is defined as the ratio of the dry matter to the nutrient content of litterfall, according to Vitousek's (1982, 1984) definition.

A normality test and Levene's test to check the equality of variances were carried out on datasets prior to statistical analyses to verify normal distributions and homogeneity of the variances. We used repeated-measures analyses of variance (RM ANOVAs) to analyze the differences in litterfall, standing crop among the three forest types through time. One-way ANOVAs were used to compare the differences in annual total fine litterfall, mineral-element concentrations and mineral elements fluxes from litterfall, and in NUE at each given date among the three forest ecosystems. The correlation between litterfall pattern, litterfall decomposition rate with climatic factors was examined by Pearson's bivariate correlations. All statistical analyses were performed at $\alpha=0.05$ with SPSS 13.0 (SPSS Chicago, IL).

Results

Fine litterfall production

The annual mean mass of fine litterfall was significantly greater in STF (12.96±1.71 Mg ha^{-1} $year^{-1}$), followed by that in TSF (9.47±1.65 Mg ha^{-1} $year^{-1}$) and MTF (9.23±1.29 Mg ha^{-1} $year^{-1}$) ($P<0.05$) (Table 2). No statistical difference ($P>0.05$) in the annual total litterfall between TSF and MTF was detected (Fig. 1, Table 2). The results of repeated measure ANOVA showed that, across the three forest types, the total litterfall and its components did not vary significantly over the 10-year period (Table 3). The maximum values of the total litterfall occurred in 1997 (TSF), 2000 (STF), and 1998 (MTF), and the minimum values in 2005 (TSF), 2004 (STF), and 2002 (MTF), respectively (Fig. 1).

Repeated measures ANOVA indicated that all litterfall components varied among the three forest types (Tables 2, 3; Fig. 1). Leaves dominated annual litterfall production. The mean leaf fraction in fine litterfall averaged for the 10 years followed the order of STF (61.1±6.7%) > MTF (57.6±8.4%) > TSF (55.8±7.6%) (Table 2). Among the three forest types, the components of fine litterfall showed different composition patterns in order of leaves > miscellaneous > twigs > reproductive parts in TSF, leaves > twigs > miscellaneous > reproductive parts in STF, and leaves > reproductive parts > twigs > miscellaneous in MTF (Table 2). Except for leaf litter, other components of litterfall were significantly affected by time. However, there were no interaction effects of forest types and time for any components of litterfall (Table 3).

The annual variation of litter production during the 10-year period was different among the three forest sites (Table 2). The highest variability of annual litterfall was found in TSF (17.4%, $P<0.05$), followed by MTF (14.0%, $P<0.01$), and STF (13.2%, $P<0.01$) (Table 2). Correspondingly, the ratio of maximum to minimum litter production over the 10-year period showed the same order of TSF (1.76) > MTF (1.56) > STF (1.52). The annual variation of litterfall components varied among forest types (Table 2). The greatest coefficient of variation for leaves (21.2%), twigs (54.7%), reproductive parts (60.5%), and miscellaneous (66.2%) was found in MTF, TSF, TSF, and MTF, respectively (Table 2). The STF

Table 2 Annual mean litterfall, standing crop and its components (mean values ± SD, Mg ha^{-1} year^{-1}) averaged over the 10-year research period (1996–2005) in three tropical forests in Xishuangbanna, SW China. Different letters indicate statistically significant ($P<0.05$) differences within each category among the three forests. *Max* Maximum annual litterfall, *Min* Minimum annual litterfall

	Leaves	Twigs	Reproductive parts	Miscellaneous	Total
Litterfall					
Tropical seasonal rainforest (TSF)					
Mean	5.19±0.45 b	1.28±0.70 b	1.20±0.7 b	1.80±0.72 a	9.47±1.65 b
Fraction (%)	55. 8±7.6 b	13.1±5.3 b	12.3±6.14 b	18.8±6.1 a	100
Coefficients of variation (%)	8.6	54.7	60.5	39.9	17.4
Ratio (Max/Min)	1.37	5.49	5.55	3.69	1.76
Secondary tropical forest (STF)					
Mean	7.88±1.03 a	2.87±1.05 a	0.78±0.42 c	1.43±0.54 b	12.96±1.71 a
Fraction (%)	61.1±6.7 b	21.8±5.9 a	6.2±3.7 c	10.9±3.55 b	100.0
Coefficients of variation (%)	13.1	36.7	53.9	38.1	13.2
Ratio (Max/Min)	1.47	3.19	7.10	3.13	1.52
Man-made tropical forest (MTF)					
Mean	5.33±1.128 b	1.15±0.51 b	1.97±0.99 a	0.78±0.51 c	9.23±1.29 b
Fraction (%)	57.6±8.4 b	12.4±4.7 b	21.6 ± 11.3 a	8.5±5.9 b	100.0
Coefficients of variation (%)	21.2	43.9	50.4	66.2	14.0
Ratio (Max/Min)	2.19	4.71	9.98	6.41	1.56
Standing crop					
Tropical seasonal rainforest (TSF)	1.75±0.34 a	0.91±0.77 a	0.27±0.11 b	0.34±0.16 a	3.25±0.91 a
STF	1.58±0.52 a	1.03±0.38 a	0.15±0.10 b	0.38±0.25 a	3.15±1.00 a
MTF	1.78±0.64 a	0.78±0.41 a	0.72±0.27 a	0.28±0.24 a	3.54±0.80 a

showed an intermediate variability of litterfall components (Table 2). The coefficient of variation of annual total litterfall and litterfall components showed no correlation with measured climatic variables for the three tropical forest systems (Table 4).

Seasonal variations of fine litterfall

The total fine litterfall showed a marked seasonal variation during the 10-year period (Fig. 1). Most of the litter fell between January and April, with only a small fraction between July and October for each forest type. Each forest type had two yearly litterfall peaks (Fig. 1). The higher peak occurred during the cool and dry season (January–February) for MTF, whereas the higher peak occurred during the hot and dry season (March–May) for TSF and STF (Fig. 1). The minor peak occurred also in the middle-late rain season (August–October) for all three forest types (Fig. 1). The leaf litter showed similar seasonal patterns to the total fine literfall (Fig. 1). The twigs litter occurred mainly during the late dry season (March–May) to the beginning of rainy season (May–June; Fig. 1). The amount of twigs litter in STF was much higher than that in the other two forest types (both the absolute and fractional values; Table 2). The reproductive parts peaked between September and November (Fig. 1). The reproductive parts in MTF showed 1.5- to 2.5-fold higher values (both absolute and relative values) than those in the other two forests. This reflected the fact that the rubber tree (*H. brasiliensis*) produced a large amount of flowers and seeds every year.

Litter standing crop and decomposition quotient (k_L)

The amount of the annual mean standing crop on the forest floor and its components did not differ among the three forest types, except for a significant difference in the reproductive parts ($P<0.05$; Fig. 2, Table 2). The results of repeated measures ANOVA showed that the reproductive parts were not affected

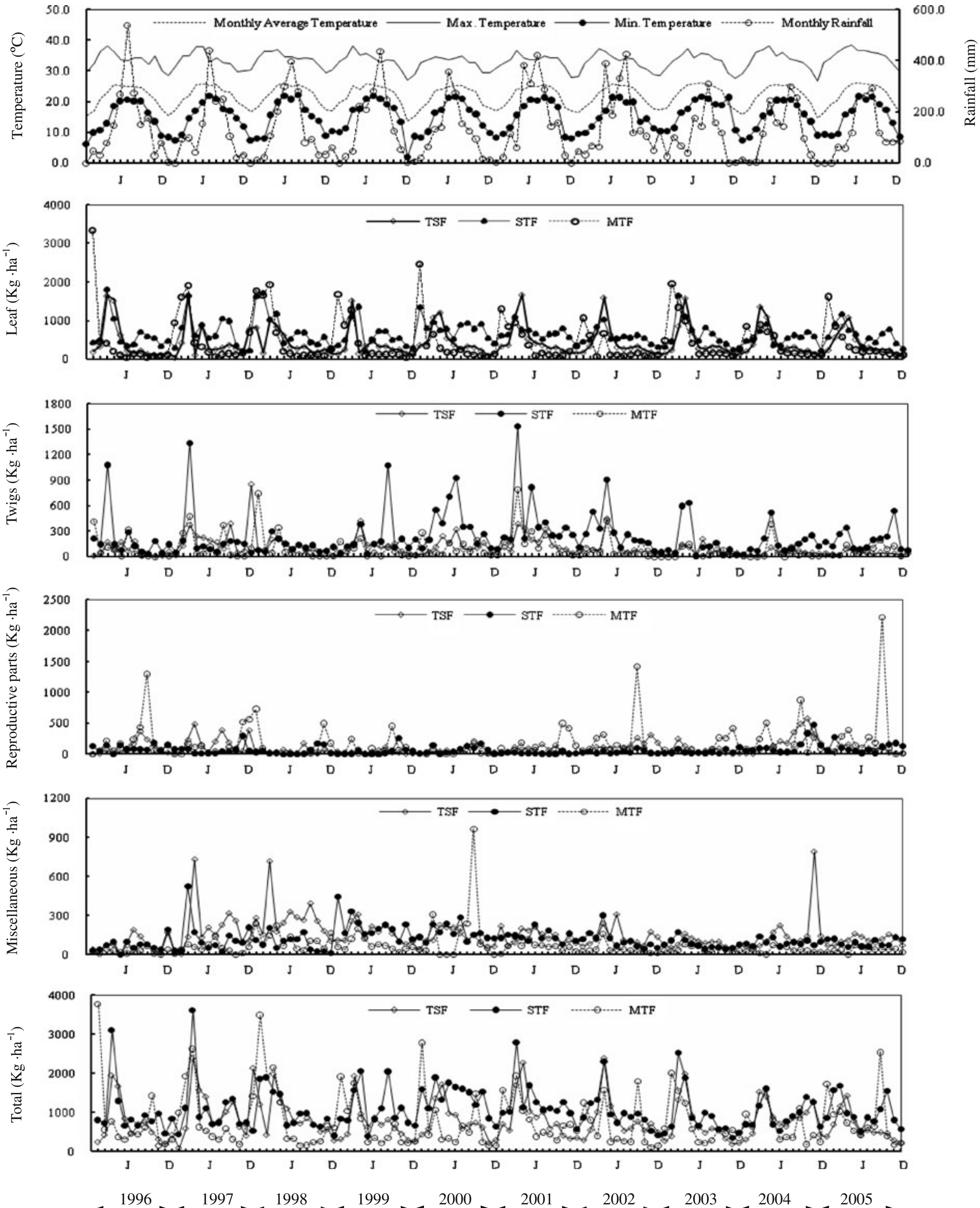

Fig. 1 Climatic variables and temporal (1996–2005) distribution of litterfall and its components in three tropical forests in Xishuangbanna, SW China. *TSF* Tropical seasonal rainforest, *STF* secondary tropical forest, *MTF* man-made tropical forest

Table 3 Results of repeated measures ANOVA showing the F values and levels of significance for litterfall and its components and standing crop over the 10-year research period (1996–2005) in three tropical forests

	Leaves	Twigs	Reproductive parts	Miscellaneous	Total
Litterfall					
Forest types (F)	3.43*	7.79**	3.55*	3.63*	3.56*
Time (T)	1.47 ns	4.26**	3.26*	12.74***	1.71 ns
F × T	0.57 ns	1.07 ns	1.23 ns	0.39 ns	0.89 ns
Standing crop					
Forest types (F)	0.14 ns	0.64 ns	7.10**	1.63 ns	0.18 ns
Time (T)	11.76***	10.07**	1.75 ns	12.74***	9.65**
F × T	0.90 ns	1.50 ns	0.82 ns	0.39 ns	1.80 ns

*P<0.05; **P<0.01; ***P<0.001; ns>0.05

by time, while time had significant effect on other parts. There were no interaction effects of forest types and time on any components of litter standing crop (Table 3). Litter standing crop in the three forest types showed similar seasonal variation (Figs. 2 and 3). The total litter standing crop was higher in the period from the late dry and hot season to the early rainy season (Figs. 2, 3), coinciding with the period of maximum litterfall (Fig. 1). The components of the litter standing crop showed similar seasonal patterns to the total litter standing crop (Tables 2, 3). These results reflected the seasonal variation in decomposition rate which is slow during the dry months and fast during the wet season (Figs. 2, 3)

The annual mean decomposition quotient (k_L) of the total fine litter in STF (3.50±1.48) was significantly higher than that in TSF (3.15±1.13) and MTF (2.72±0.66; P<0.05; Table 5). Similarly, the turnover rate of litterfall components in STF was also significantly higher than that in TSF and MTF (Table 5; P<0.05).

The k_L of the total fine litter in each forest type was not significantly correlated with either with annual precipitation nor the annual mean temperature (P>0.05; Fig. 4). Instead, the annual total decomposition was closely correlated with the annual total fine litter input for each forest type (P<0.01 each, Fig. 5).

Table 4 Pearson's correlation coefficient (r) between coefficients of variation of monthly mean climatic variables and monthly mean litterfall components measured in three tropical forest systems from 1996 to 2005, in Xishuangbanna, SW China

	Monthly mean temperature	Monthly mean precipitation	Monthly maximum temperature	Monthly minimum temperature
TSF				
Leaf	0.15	0.05	0.45	−0.19
Twig	−0.29	0.02	0.37	−0.49
Reproductive parts	−0.13	0.17	0.17	−0.26
Miscellaneous	0.35	0.63	0.56	−0.08
Total litterfall	−0.49	−0.32	−0.02	−0.41
STF				
Leaf	−0.18	0.28	0.21	0.02
Twig	−0.07	0.18	0.41	−0.27
Reproductive parts	0.47	0.47	0.38	0.54
Miscellaneous	−0.44	0.59	0.16	−0.14
Total litterfall	−0.32	0.22	0.35	−0.31
MTF				
Leaf	−0.41	0.07	−0.45	−0.03
Twig	0.11	0.37	0.38	−0.02
Reproductive parts	−0.35	−0.11	−0.59	0.17
Miscellaneous	−0.14	0.05	−0.23	−0.19
Total litterfall	−0.50	0.19	−0.45	0.04

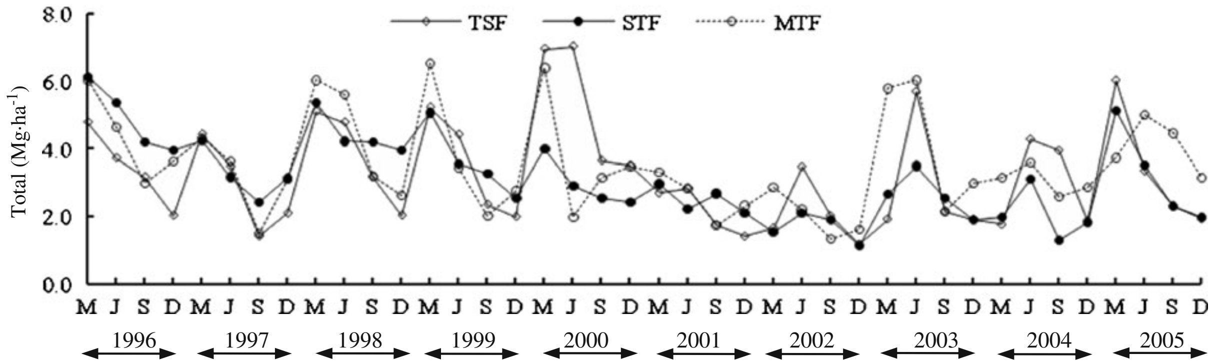

Fig. 2 Seasonal dynamics of total litterfall standing crop on the floor from 1996 to 2005 in three tropical forests in Xishuangbanna, SW China. *TSF* Tropical seasonal rainforest, *STF* secondary tropical forest, *MTF* man-made tropical forest

Fig. 3 Seasonal variations in mean standing crop of litterfall on the forest floor in three tropical forest ecosystems measured from 1996 to 2005, in Xishuangbanna, SW China. Different letters indicate statistically significant ($P<0.05$) differences within each category among sampling dates. *TSF* Tropical seasonal rainforest, *STF* secondary tropical forest, *MTF* man-made tropical forest

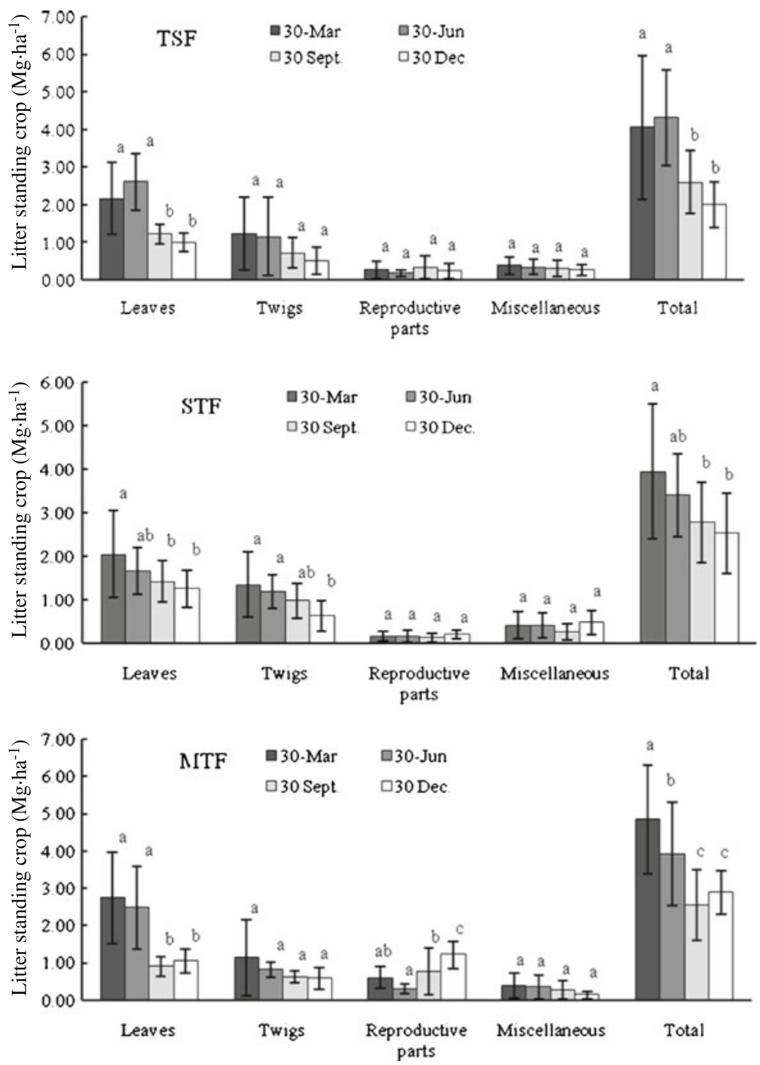

Table 5 Annual mean turnover rate (mean values ± SD) of litterfall over the 10-year research period (1996–2005) in three tropical forest systems in Xishuangbanna, SW China. Different letters indicate statistically significant ($P<0.05$) differences within each category among the three forests

	Leaves	Twigs (<2.5 cm in diameter)	Reproductive parts	Miscellaneous	Total
TSF	3.10±0.85 b	1.85±1.37 b	4.89±2.70 a	6.15±2.53 a	3.15±1.13 b
STF	3.63±2.58 a	3.11±1.47 a	5.11±3.53 a	5.56±3.78 a	3.50±1.48 a
MTF	3.28±1.20 b	1.63±0.72 b	3.10±1.73 b	4.85±3.83 a	2.72±0.0.66 c

Mineral-element concentrations and C-N-P relationships

The mean mineral-element concentrations of fine litterfall varied with forest types (Table 6). The STF litterfall contained higher C, N, and Mg than MTF and TSF litterfall (Table 6). The highest P and K concentrations were in MTF litterfall, while the highest Ca concentration was in TSF litterfall (Table 6).

The ratios of C/N, C/P, and N/P in fine litterfall differed significantly among the three forest types ($P<0.05$; Table 6). Significantly lower C/N ratios were observed in STF, and the highest ratios of C/P and N/P were in STF, followed by TSF and MTF (Table 6).

Mineral-element fluxes in litterfall

The total amount of mineral element return in STF was significantly greater than that in TSF or MTF; $P<0.05$; Fig. 6, Table 7). The annual average total mineral element return in STF was 2,458.5 kg ha^{-1} year^{-1}

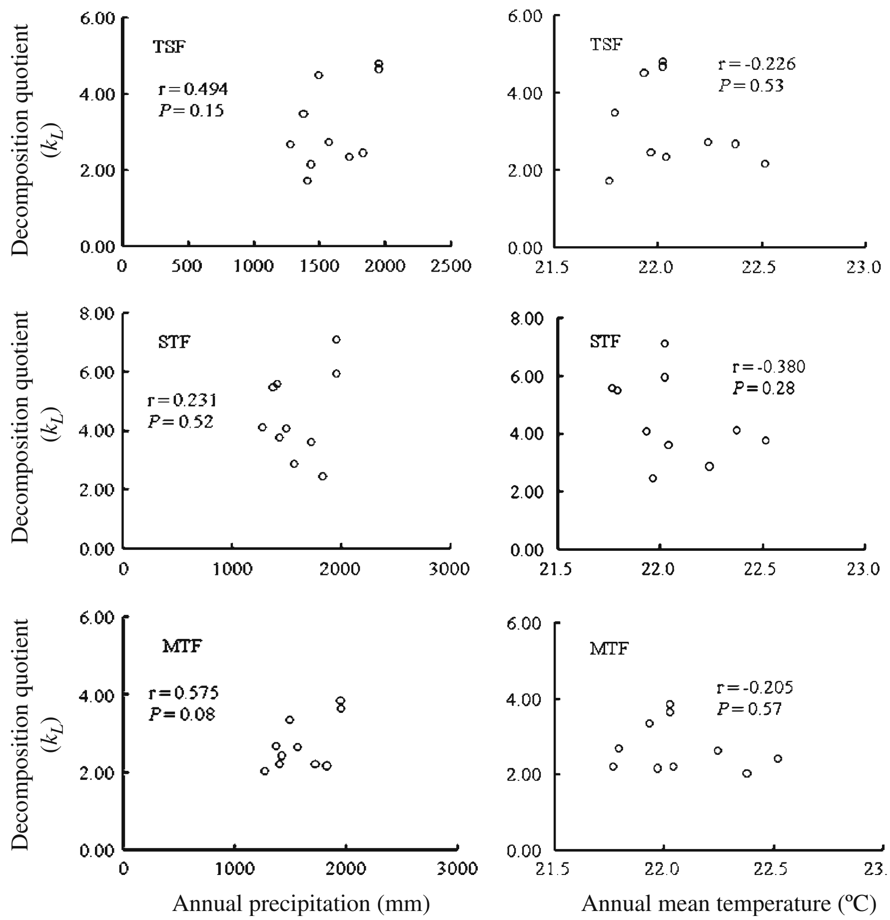

Fig. 4 The correlation between fine litterfall decomposition quotient value (k_L) and annual precipitation and annual mean temperature in three tropical forests from 1996 to 2005, in Xishuangbanna, SW China. *TSF* Tropical seasonal rainforest, *STF* secondary tropical forest, *MTF* man-made tropical forest

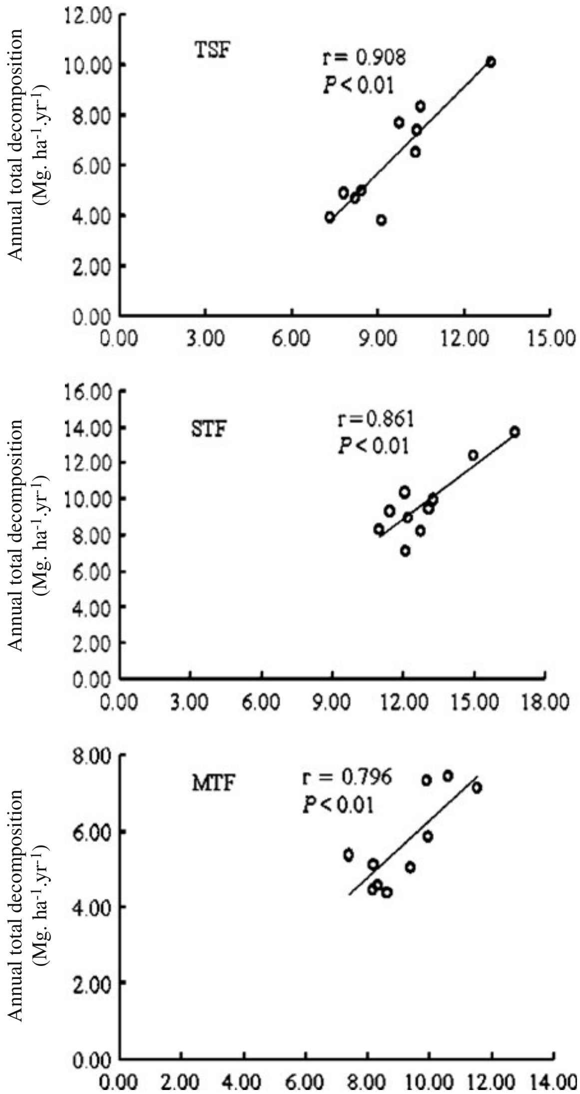

Fig. 5 The correlation between annual total fine litterfall and annual decomposition in three tropical forests from 1996 to 2005 in Xishuangbanna, SW China. *TSF* Tropical seasonal rainforest, *STF* secondary tropical forest, *MTF* man-made tropical forest

(+56.5%) higher than in TSF and 2,225.7 kg ha^{-1} year^{-1} (+48.5%) higher than in MTF. Correspondingly, the amount of each mineral element return in STF was greater than that in TSF and MTF, except for Ca return among the three forest types (Table 7). Neither the total amount nor each mineral element return was different between TSF and MTF (Table 6). The mineral elements showed decreasing fluxes of C > Ca > N > K > Mg > P in TSF, and C > N > Ca > K > Mg > P in STF and MTF (Table 7).

The percentage contribution of litterfall components to the annual fluxes of mineral elements varied among the three forest types (Fig. 7). Generally, leaves contributed >50% (Fig. 5). In TSF, 53.5% of the total mineral elements returned to the forest floor was contributed by leaf litter, followed by miscellaneous (21.1%), twigs (13.1%), and reproductive parts (12.3%). In STF, 61.5% of the total nutrient mass was provided by leaf litter, followed by twigs (22.0%), miscellaneous (11.1%), and reproductive parts (5.4%). In MTF, the highest mineral element return was contributed also by leaf litter (58.4%), but followed by reproductive parts (19.5%), twigs (13.0%), and miscellaneous (9.0%). These element return patterns did not differ from the fraction orders of fine litterfall components for each forest type (Table 2).

Nutrient use efficiency

The NUE varied significantly for different elements among the three forest types ($P<0.05$; Table 8). In each forest type, the highest NUE was found for P, followed by Mg and K (Table 8). The NUE showed a descending order of P > Mg > K > N > Ca in TSF, and P > Mg > K > Ca > N in STF and MTF (Table 8). STF had the lowest NUE of N and the highest NUE of P and Ca, whereas K was most effectively used in TSF, followed by STF and MTF. The use efficiency of Mg was significantly lower in STF than in TSF and MTF.

Discussion

Litter production and dynamics

The results of the total fine litterfall produced in STF (12.96±1.71 Mg ha^{-1} year^{-1}), TSF (9.47± 1.65 Mg ha^{-1} year^{-1}), and MTF (9.23± 1.29 Mg ha^{-1} year^{-1}) (Table 2) do not fully support our hypothesis 1 of greater litterfall in a species-rich than in a species-poor stand. TSF is the most species-rich stand with the most complex structure and the highest tree density, while MTF is the species-poorest stand with simpler structure (Table 1). On the other hand, our results also do not support the conclusions of Brown and Lugo (1982) and Stohlgren (1988).

Table 6 Mean mineral-element concentrations (mean values ± SD, g kg^{-1}) and ratios of C/N, C/P, and N/P for litterfall in three tropical forest systems in Xishuangbanna, SW China. Different letters indicate statistically significant (P<0.05) differences within each category among the three forests

	C	N	P	K	Ca	Mg	C/N	C/P	N/P
TSF	468.15±17.09 b	16.60±1.59 b	1.05±0.013 b	4.77±0.87 b	17.45±1.54 a	2.32±0.21 b	28.64±32.17 a	459.17±57.05 a	16.17±1.76 b
STF	503.34±11.05 a	22.30±1.59 a	1.07±0.10 b	5.71±0.99 ab	10.85±1.08 c	2.90±0.21 a	22.67±0.71 b	492.41±57.06 a	21.68±2.43 a
MTF	492.03±11.99 a	17.05±2.25 b	1.39±0.29 a	6.61±1.50 a	14.33±1.69 b	1.82±0.30 c	29.94±4.87 a	388.86±99.83 b	12.87±1.74 c

Brown and Lugo (1982) that there is a significant positive relationship between stand biomass and litter production. Stohlgren (1988) suggested that the annual litterfall can be predicted by a function derived from the individual tree basal area and live crown ratio. However, neither the biomass order nor the basal area order of the tree layer (MTF ≥ TSF > STF; Table 1) coincided with the fine litterfall order of STF > TSF > MTF (Table 2). Similarly, previous studies also failed to establish cause-effect relationships between such stand parameters and litterfall production in temperate forests (e.g. Bray and Gorham 1964) and tropical forests (Kumar and Deepu 1992; Sundarapandian and Swamy 1999). Our present results, in line with the work of Bray and Gorham (1964), appear to indicate that litter production in closed-canopy forests is somewhat correlated with tree density but independent of stand age and wood production. However, the species composition seems to be important for litter production within the same climate range (Facelli and Pickett 1991).

In line with our findings, it has been demonstrated that tropical secondary forests and plantations, being fast-growing and highly productive ecosystems, usually produce higher litterfall (Lugo 1992), many studies reported that litterfall production in young tropical secondary forests was similar to that in tropical primary forest in eastern Guatemala (Ewel 1976) and in north-east Brazilian Amazon (Barlow et al. 2007b). Similarly, litterfall production in plantations was not significantly different from that in primary rain forests in the eastern Brazilian Amazon (Smith et al 1998) and in Australia (Brasell et al. 1980). Such findings suggest that constructing mixed plantation and naturally regenerated forests on abandoned and degraded land in the study region could be effective for restoring ecosystem processes such as litter production (Barlow et al. 2007a).

A global comparison showed that litterfall production in tropical forests varied from region to region, indicating that litterfall production is affected by many biotic and abiotic factors across regions. Our litterfall data obtained in TSF and in MTF is similar to those recorded in tropical broadleaf deciduous forests (9.438 Mg ha^{-1}) and tropical broadleaf evergreen forests (9.369 Mg ha^{-1}; Vogt et al. 1986), but lower than those in equatorial Congo (Zaire) (Laudelout and Meyer 1954), in the alluvial rain

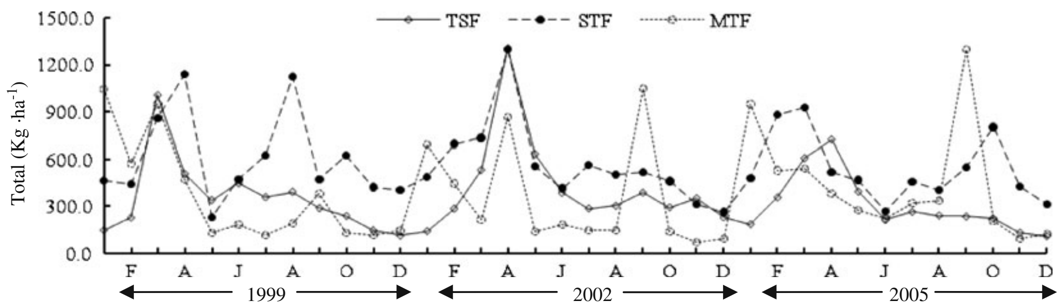

Fig. 6 Monthly total mineral-element return (kg ha^{-1} year^{-1}) from fine litterfall in three tropical forests in 1999, 2002 and 2005 in Xishuangbanna, SW China. *TSF* Tropical seasonal rainforest, *STF* secondary tropical forest, *MTF* man-made tropical forest

forest, and in the forest over limestone sites in Sarawak (Proctor et al. 1983), in a Bornean rain forest (Burghouts et al. 1998) and in Panama tropical forest (Wieder and Wright 1995). The STF litterfall is only lower than that in the *Macrolobium* forest in equatorial Congo (Zaire) (Laudelout and Meyer 1954). The litterfall data in present study lies in the upper range of the litterfall previously recorded for tropical forests (Brown and Lugo 1982; Vitousek 1984; Proctor 1984).

Annual variation of litter production

The greatest annual variation of litter production was observed in the richest forest in terms of species TSF, followed by MTF and STF (Table 2, see also Table 1) which was also not consistent with our hypothesis 1 that species-rich stands will produce more litter with less annual variation than species-poor stands. The higher annual variation of litterfall production in TSF was mainly from twigs and reproductive parts (Table 2). The TSF is a climax rainforest ecosystem with greater variations in canopy architecture and tree species. Due to its complex structure and canopy architecture, dead branches usually remain on trees for a long period, which may occasionally fall on the forest floor (Facelli and Pickett 1991; Maass et al. 2002) leading to higher variations in twig litterfall. The number and density of mature trees in TSF may regularly produce an abundant flowers, fruits, and seeds in a masting year (Stocker et al. 1995) resulting in a higher variation in reproductive parts.

The species-poor MTF was dominated by two deciduous species *H. brasiliensis* and *R. vomitoria*. *H. brasiliensis* sheds leaves in January and *R. vomitoria* does so between January and March. Similarly, STF was in the successional stage with many deciduous tree species such as *Dolichandrone stipulate*, *Aporusa yunnanensis*, *Alchornea tiliaefolia*, *Cratoxylon cochinchinensis*, *Dolichandrone stipulate* and *Styrax tonkinensis*, which accounted for about 30% of the total stems. These deciduous individuals yearly produced a large amount of litter during the dry and hot season (March–April). Compared to the complex structure and canopy architecture in TSF with older trees, on the other hand, relatively young trees with simple community structure in STF and MTF (Table 1) may have less twig litter remaining in the canopy for a long time. Therefore, more litter production but less annual variation occurred in STF and MTF.

Table 7 Annual mean mineral-element return (mean values ± SD, kg ha^{-1} year^{-1}) from fine litterfall in three tropical forests in Xishuangbanna, SW China. Different letters indicate statistically significant ($P<0.05$) differences within each category among the three forests

	C	N	P	K	Ca	Mg	Total
TSF	4002.3±655.7 b	135.9±18.6 b	8.4±0.9 b	40.4±5.4 b	145.8±27.9 a	19.6±2.3 b	4352.3±698.5 b
STF	6277.3±368.9 a	277.2±15.0 a	13.0±1.1 a	70.7±4.6 a	136.3±8.5 a	36.2±1.1 a	6810.8±387.1 a
MTF	4234.6±501.5 b	144.1±20.8 b	11.9±3.0 ab	56.9±11.5 ab	122.4±26.8 a	15.2±2.7 b	4585.1±564.5 b

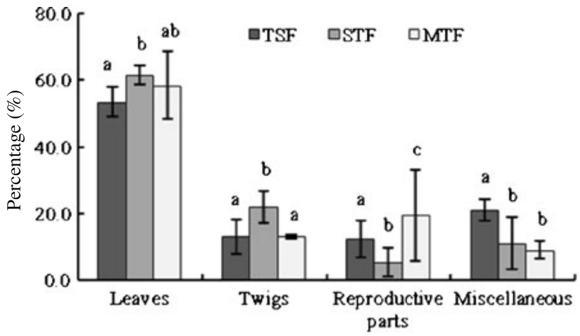

Fig. 7 The percentage of annual mean mineral element returns among litterfall components in three tropical forests from 1996 to 2005, in Xishuangbanna, SW China. Different letters indicate statistically significant ($P<0.05$) differences within each category among forest types. *TSF* Tropical seasonal rainforest, *STF* secondary tropical forest, *MTF* man-made tropical forest

Based on these analyses, we suggest that published litterfall data (production, annual variation, composition) may imply an age effect (Table 1) associated with successional stage, species composition, community structure, and canopy architecture. In addition, occasional natural and man-made disturbances can also contribute to elevated litterfall production and annual variations.

Litter seasonality

Around 50–80% of the total litterfall occurred during the dry season (November–April), showing a marked seasonality of litterfall (Fig. 1). Whitmore (1975) pointed out that the seasonality of litterfall is often related to a period of water stress. The litter accumulation was particularly high with a major peak during the dry season (November–April) and a minor peak in the middle of the rainy season (May–October; Fig. 1), which is in agreement with previous studies (e.g., John 1973; Cuevas and Medina 1986; Sundarapandian and Swamy 1999; Pandey et al. 2007). These findings demonstrate that the seasonality of litterfall not only coincides with the rhythm of leaf senescence and abscission of the forest tree species, it also largely follows the annual cycle of environmental parameters such as temperature and moisture at a regional scale (Sundarapandian and Swamy 1999).

Fine litter turnover and decomposition (k_L)

The turnover rates of litterfall in TSF and MTF were similar (k_L=3.15 in TSF vs.2.72 in MTF, $P>0.05$) but significantly lower than that in STF (k_L=3.50, $P<0.05$; Table 5). This result does not support our hypothesis that litterfall decomposition rate is more rapid in species-rich (i.e., TSF) than in species-poor (i.e., MTF) communities (see Introduction). The amount or rate of decomposition was closely correlated with annual total fine litter input (Fig. 5) but not with annual precipitation and annual mean temperature (Fig. 4). The decomposition rates (STF > TSF > MTF) were reverse with the C-N ratios (STF < TSF < MTF) but consistent with the C-P or N-P ratios (STF > TSF > MTF) in the three forests (Tables 5, 6). These results indicated that the litter decomposition rate is determined mainly by its resources quality but less affected by tree species richness within the same climate zone. Similarly, previous studies found that litter decomposition rates are controlled primarily by litter quality at a regional scale with similar climatic conditions (Swift et al. 1979; Güsewell and Verhoeven 2006). Lower C-N ratio and higher N-P ratio of litterfall can accelerate decomposition (Swift et al. 1979; Güsewell and Verhoeven 2006). Another aspect is that the micro-environmental conditions such as temperature, moisture, and microorganisms in the upper soil could play an important role in determining the litter decomposition processes (Berg and McClaugherty 2003).

The turnover rate of 3.15 in TSF is similar to the results obtained from Dipterocarp forests in Pasoh, Malaya (3.3; Ogawa 1978; Yoda 1978), and in Zaire

Table 8 Annual mean nutrient use efficiency (mean values ± SD) in three tropical forests in Xishuangbanna, SW China. Different letters indicate statistically significant ($P<0.05$) differences within each category among the three forests

	N	P	K	Ca	Mg
TSF	61.1±2.5a	979.2±48.8b	228.6±36.4a	59.7±7.1c	439.0±30.6b
STF	45.0±0.9b	1214.4±425.6a	187.6±6.9b	94.1±2.2a	352.1±21.7c
MTF	60.8±1.4a	786.3±141.6c	168.5±24.1b	74.1±9.7b	574.7±29.2a

(3.2; Laudelout and Meyer 1954), but higher than the values found in the tropical lowland moist forests in Nigeria (2.2) and Ghana (2.0; Anderson and Swift 1983), in Brazil (2.02–2.22; Scott et al. 1992, 1994), in Australia (1.3–2.2; Spain 1984), and in Panama (1.53–2.41; Wieder and Wright 1995). The turnover time of litter mass in the present study (0.32–0.39 years) is close to the tropical broadleaf semi-deciduous forests (0.37 years), but much lower than that of tropical broadleaf deciduous forests (0.94 years), tropical broadleaf evergreen forests (2.41 years; Vogt et al. 1986), and the range (0.57–0.88 years) suggested by Brown and Lugo (1982). The decomposition rates obtained in our study (2.72–3.50) are relatively high, which may have resulted from an underestimate of litterfall production from the litterfall traps (Clark et al. 2001a), but there were within the upper range of decomposition rates previously recorded for tropical rainforests (1.0–3.3; Anderson and Swift 1983)

Nutrient return and nutrient use efficiency

Annual quantities of carbon and nutrients returned to the forest floor followed a descending order of STF > MTF > TSF (Table 7). The greater quantity of carbon and nutrients returned in STF coincided with the higher litter mass (Table 2) and higher nutrient concentrations in that litter (Table 6). The concentrations of nutrients found in the present study were higher than most values previously recorded and was in the upper range reported for other tropical forests (Proctor 1984; Vitousek 1984). Differences in nutrient return among the three forest types studied (Table 7) may be mainly caused by differences in species composition of the forest stands, and the quantity and quality of litter (Vitousek and Sanford 1986; Herbohn and Congdon 1998).

One of our hypotheses (hypothesis 3, see Introduction) was that NUE would be positively correlated with tree species richness. Our data does not support that hypothesis. The NUE was found to be element-dependent and to vary significantly among the three forest types (Table 8). This indicated that NUE in a forest stand is associated closely with the assemblage of co-existing species in a community but not with the number of species. Our results are consistent with the results of Hiremath and Ewel (2001), who stated that the species or life forms comprising an ecosystem exert considerable influence on ecosystem NUE. Ecosystem NUE depends mainly on the identity of the species making up the system, but not on a greater diversity of species per se (Hiremath and Ewel 2001).

STF had higher P, Ca and Mg but lower N use efficiency than TSF and MTF. However, MTF had lower N, P, K but higher Mg use efficiency than TSF (Table 8). STF had lower N use efficiency which may be caused by N-fixing species (leguminous species) accounting for >30% of the total individuals in that forest. Higher N returned from litterfall of N-fixing species has been reported (Vitousek 1984). Lower N, P and K use efficiency in MTF may be caused by N, P and K fertilizer applied to this plantation.

The NUE of N, P, and Ca in the present study are within the lower range previously reported for tropical forests (Vitousek 1984), which may reflect a slower circulation of nutrients in Xishuangbanna tropical forests. The lower annual precipitation and lower temperature here may limit primary production compared to tropical forests closer to the equator.

Conclusion

The three studied Xishuangbanna tropical forests showed obvious differences in ecological characteristics such as plant species composition, community structure and biomass. Litterfall production, nutrient return and decomposition rates of litterfall and NUE varied with forest types. However, litterfall production, nutrient return and decomposition rate of litterfall in these tropical forests were not significantly correlated with tree species richness or tree density or stand biomass. Instead, they seemed to be related strongly to species composition. Litterfall production and monthly/annual variations did not coincide with monthly/annual variation of climatic variables, but appeared to be dependent upon stand age associated with canopy architecture and life stage of trees. The annual mean decomposition rates of the total fine litter in each forest type was not significantly correlated with the annual precipitation and annual mean temperature, but determined mainly by its resource quality. The present study suggests that litterfall production and decomposition process are influenced strongly by the specific assemblage of coexisting species and their life stage (age) but less affected by species richness. Our findings indicate that establishing multi-species and multistory man-made tropical forest can be an effective way to enhance biological productivity and maintain soil nutrients on degraded tropical land.

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