Science of the Total Environment 758 (2021) 143619

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Litterfall biomass and nutrient cycling in karst and nearby non-karst forests in tropical China: A 10-year comparison

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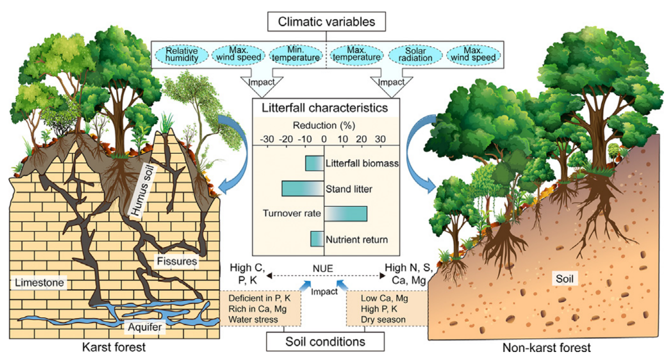
HIGHLIGHTS

- A 10-year comparative study was conducted to estimate litterfall characteristics.
- Litterfall biomass, stand litter and nutrient return had clear temporal variations.
- NKF had significantly higher litterfall biomass, turnover rate and nutrient return.
- KF had significantly higher C, P and K but lower N, S, Ca and Mg use efficiency.
- KF tends to develop a nutrient cycling mechanism well-adapted to karst habitats.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 14 September 2020
Received in revised form 8 November 2020
Accepted 8 November 2020
Available online 12 November 2020

Editor: Elena Paoletti

Keywords:
Litterfall biomass
Turnover rate
Karst forest
Nutrient cycling
Climatic variable

ABSTRACT

Litterfall helps maintaining primary production and nutrient cycling in forest ecosystems. However, few studies have investigated long-term characteristics of litterfall in tropical karst and non-karst forests co-occurring in the same region. A 10-year comparative study was conducted to estimate the biomass, litter accumulation, turnover rate, nutrient return and nutrient use efficiency associated with litterfall in a karst forest (KF) and a nearby non-karst forest (NKF) in northern tropical China. Significant spatial-temporal variation was observed in monthly and annual litterfall biomass in the two forests. Annual mean litterfall biomass in KF (9.75 Mg ha^{-1} $year^{-1}$) was obviously lower than that in NKF (10.49 Mg ha^{-1} $year^{-1}$). The litterfall biomass in NKF was significantly correlated with maximum air temperature, wind speed and total solar radiation, whereas that in KF was significantly correlated with relative humidity, wind speed and low temperature. Average stand litter in KF (2.92 Mg ha^{-1} $year^{-1}$) was significantly higher than that in NKF (2.38 Mg ha^{-1} $year^{-1}$). Stand litter mostly occurred during the cool and dry season, which coincided with litterfall input and exhibited bimodal pattern. Turnover rate was 1.3 time higher in NKF than in KF, suggesting that litter decomposed slowly in karst habitats. Distinct temporal dynamic and significant differences were observed in chemical composition of litterfall between KF and NKF. Total amounts of C, P, K and total nutrients returned to the topsoil in KF were significantly lower than those in NKF. The KF exhibited relatively high P and K use efficiency because of their low availability in karst soils. Compared with the non-karst habitat, the tropical karst habitats are more likely to develop a plant community with certain nutrient concentrations of litterfall and with a nutrient cycling mechanism that is well-adapted to harsh and heterogeneous condition.

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https://doi.org/10.1016/j.scitotenv.2020.143619
0048-9697/

1. Introduction

In global forest ecosystems, a large amount of organic debris generates and returns to the mineral soil in the form of litterfall (Qin et al., 2019; Shen et al., 2019). Litterfall biomass, litter accumulation and involved nutrient return are essential processes for functioning nutrient cycling (Muqaddas and Lewis, 2020; Zhou et al., 2016; Berg and McClaugherty, 2014; Barlow et al., 2007), water and soil conservation (Dunkerley, 2015; Sayer, 2006), energy transfer (Kavvadias et al., 2001), soil fertility (Pandey et al., 2007) and other ecosystem services. Several studies have demonstrated that nutrient recirculation from litter decomposition makes up more than 90% of the nitrogen (N) and phosphorus (P), 88% of the potassium (K) and 60%–90% of the total nutrients required by plant growth in many terrestrial ecosystems (Campos et al., 2016; Chapin III et al., 2002). Therefore, understanding the nutrient fluxes, decomposition processes and temporal variations of forest litterfall at various ecosystems is important for ecological restoration and forestry practice (Shen et al., 2019; Wei et al., 2012; Wang et al., 2008).

Litterfall biomass and associated nutrient deposition within forest ecosystems show high spatial-temporal heterogeneity (Zhu et al., 2019; Tang et al., 2010), and they are affected by species composition (Jasińska et al., 2020; Staelens et al., 2011), forest type (Tang et al., 2010; Kavvadias et al., 2001), anthropogenic disturbance (Blanco et al., 2008), topography features (Qin et al., 2019), climatic conditions (e.g. wind, rainfall, temperature and soil moisture) and soil nutrient availability (Kitayama et al., 2020; Kotowska et al., 2016; Watanabe et al., 2013). For example, Guo et al. (2017) suggested that the annual litterfall in a northern tropical karst forest is lower than that in non-karst rain forests in southern China. Parsons et al. (2014) noted that litterfall patterns closely coincide with plant species richness across tropical rain forests in northern Australia. Studies on seasonally dry tropical forests demonstrated that litterfall peaks generally occur during the early dry season to avoid drought damage to the canopy (Kotowska et al., 2016; Chave et al., 2010; Tang et al., 2010). In addition, litter quality (e.g. mineral-element concentrations and its ratios) greatly affects the litter decomposition rate (Wardle et al., 2002) and contributes to spatial variability in nutrient return and soil nutrients (Paudel et al., 2015). However, the information on litterfall characteristics in some heterogeneous natural forests, such as diverse tropical karst ecosystems, is not fully understood (Guo et al., 2019).

Karst landscapes account for approximately 15% of the global continental area and inhabit about 25% of the world's population (Hartmann et al., 2014). Karst habitats cover extensive humid tropical and subtropical regions in southwestern China (Wang et al., 2019). These habitats are rich in biodiversity and conserve numerous endemic species (Zhu et al., 2003). Karst is also an extremely fragile and heterogeneous ecosystem that is easily degraded and damaged by anthropogenic activities, such as agricultural expansion and limestone quarrying, and many karst species are facing the extinction risk (Clements et al., 2006). In general, karst habitats are characterised by scarce vegetation (Wang et al., 2004), widespread rock outcrops (Liu et al., 2019), shallow and poorly developed soil layer (Zhu et al., 2017b), P-deficient, calcium (Ca)- and magnesium (Mg)-rich soil conditions (Clements et al., 2006; Niinemets and Kull, 2005) and low water and nutrient holding capacity (Zhao et al., 2017). Karst-suitable plants exhibit adaptability to drought by developing typical leaf functional traits (Fu et al., 2019) and hydraulic properties (Zhu et al., 2017a). Therefore, the study on karst vegetation provides crucial information for the ecological rehabilitation of fragile karst lands.

In Xishuangbanna, southern Yunnan of China, seasonal karst forest (KF) and tropical rain forest (non-karst forest, NKF) co-exist in the same region (Fu et al., 2019; Zhu et al., 2006). Chen et al. (2015) noted that KF suffers greater water stress than NKF during the pronounced dry season (November–April). A period of water stress usually affects the seasonality of forest litterfall (de Queiroz et al., 2019; Whitmore, 1975). The unique geological features and heterogeneous habitats may influence litter characteristics and thus regulate the functions and services of the fragile karst ecosystem. Although KF represents one of the world's most remarkable types of karst forest, few studies have investigated its litterfall pattern and associated biogeochemical cycling in comparison with those of NKF in a long-term experiment. The specific objectives of this study are to (1) investigate the temporal variations of litterfall biomass, stand litter and nutrient returns in a KF and a NKF; (2) examine the differences in litterfall quality, litter decomposition, and nutrient use efficiency between the KF and NKF habitats; and (3) assess the effects of environmental factors on litterfall biomass and whether or not these effects differ between the two habitats. We hypothesized that the NKF had higher litterfall biomass, litter accumulation, turnover rate, nutrient return, and nutrient use efficiency associated with plant litter compared with the KF.

2. Materials and methods

2.1. Study site

The study site is located in the Xishuangbanna Tropical Botanical Garden in the Xishuangbanna Prefecture of Yunnan Province, Southwest China (21°56′N, 101°16′E; Fig. 1). The average altitude of the study site is 625 m above sea level, and the slopes range from 10° to 20° (Table 1). Local climate is dominated by a contrasting seasonal climate, with a distinct wet season from May to October and a dry season from November to February (Fig. 2). Historical climate data from a nearby weather station show that the annual mean precipitation is 1328 mm during the study period (2009–2018) (Fig. 2). More than 80% of precipitation occurs in the wet season, with the rest occurring in the dry season. The annual mean air temperature is 22.6 °C, with monthly mean maximum and minimum air temperature of 30.3 °C and 17.9 °C, respectively. The monthly mean maximum wind speed in the study region is 9.94 m s^{-1} (Fig. 2). The monthly means of total solar radiation ranges from 421.62 MJ m^{-2} to 493.36 MJ m^{-2}. The soil of the study site is classified as a Ferralic Cambisol (Zhu et al., 2019).

Field observations were performed in the KF and the nearby NKF. The KF and the NKF are permanent plots for long-term ecological research and are governed by the Xishuangbanna Station for Tropical Rainforest Ecosystem, Chinese Academy of Sciences. The KF is a seasonal tropical moist forest forms on the limestone hills and mountains (outcrops) of the northern tropical region under the influence of cyclical dry and wet climate (Zhu et al., 2006). According to the species-area curve theory, we established the area of the KF (lower species diversity compared with the NKF) as 0.25 ha (Tang et al., 2011). The KF has a clear vertical community structure: a tree layer dominated by *Cleistanthus sumatranus*, *Celtis philippensis* var. *wightii*, *Beilschmiedia brachythyrsa*, and *Lagerstroemia tomentosa*; a shrub layer dominated by *Lasiococca comberi* var. *pseudoverticillata* and *Celtis wighetii*, which are most evergreens; and an herb layer consists of *Pseuderanthemum latifolium* and many seedlings of tree species (Tang et al., 2011). The average canopy height of the KF is 18.96 m, and the trees density (diameter at breast height > 1 cm) is approximately 7124 ha^{-1} (Table 1). The NKF is a seasonal tropical rain forest and mainly occurs in wet valleys and on lower hills below 900–1000 m elevation (Zhu et al., 2006). The area of the NKF is 1 ha, and it is a climatic climax community formed by the natural succession of primary forest. A 1.5-m wide stream flows through this study site. The NKF consists of a majority of evergreen tree species and a small proportion of deciduous species that shed leaves in different time. The community structure is clear and can be divided into three strata vertically: upper tree stratum dominated by *Pometia pinnata*, *Barringtonia fusicarpa*, *Terminalia myriocarpa* and *Gironniera subaequalis*; middle shrub stratum containing *Saprosma temata*, *Ardisia thyrsiflora*, *Pittosporopsis kerrii* and *Drypetes indica*; and lower herb stratum dominated by *Selaginella delicatula*, *Tectaria subtriphylla*, *Pilea bracteosa* and *Elatostema parvum*. The canopy height and trees density of the NKF

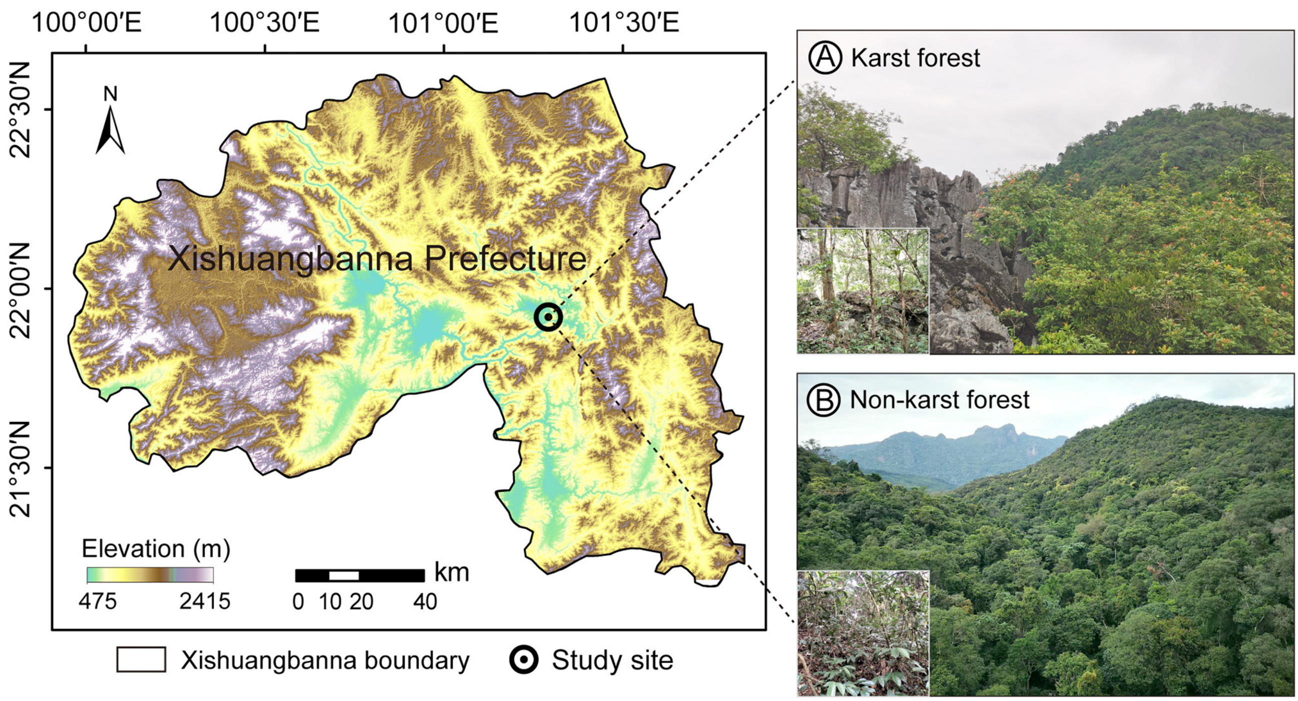

Fig. 1. Geographical location of the study area in Xishuangbanna Prefecture, Southwest China.

are approximately 29.81 m and 4929 ha^{-1}, respectively. The NKF suffers low level of human disturbance due to its central location at the Xishuangbanna Nature Reserve. Compared with the NKF, the KF has higher soil pH, organic matter content and mineral nutrients (i.e. N, P, Ca and Mg). Detailed information about the two study sites is provided in Table 1.

2.2. Experimental design and sampling

Quadrate litterfall trap (0.2 m^2 surface area) consists of nylon gauze (1.0 mm mesh), and an iron wire was randomly installed under the canopy. The trap was fixed using four PVC tubes inserted into the soil 10 cm, and the bottom of the trap was suspended at 20 cm above the ground. A total of 20 litterfall traps were set in the KF and 40 traps in the NKF. Plant litters in the traps were collected monthly in each site during January 2009 and December 2018 (10 years). Litterfall samples were brought back to the laboratory and then sorted into four fractions: (a) leaf, (b) twig (< 2.0 cm in diameter) and bark, (c) reproductive litter (i.e. seeds, flowers and fruits) and (d) miscellaneous (unidentified plant matters). Each fraction of litterfall was oven-dried at 65 °C to a constant weight and then weighed using an electronic balance. Monthly and annual mean litterfall biomass per unit area (Mg ha^{-1}) for each site was calculated.

Litter mass on the ground (stand litter) was investigated every 3 months from 2009 to 2018 (four times every year). The metal hoop (with a diameter 58 cm) was tossed into the certain subplot, and all litters within it were collected manually. Five to ten litter samples were collected for each study site and each sampling date. Once the sampling was complete, the location was marked to avoid sampling at the same place. Litter samples were separated into four categories as mentioned above. All the separated stand litters were weighed after oven drying at 65 °C for 48 h to a constant weight.

Table 1
Specific characteristics of the study forests in Xishuangbanna, Southwest China (Sun et al., 2010). The available phosphate content in soil was determined by Mo-Sb colorimetric method after the extraction of HCl-NH_4F solution. The available K content was determined by CH_3COONH_4-extraction-ICP method. Data are expressed as mean ± SE ($n = 6$). The "–" between numbers indicated the variation range of indicators investigated in study forests.

Forest type	Karst forest	Non-karst forest
Plot area (ha)	0.25	1.00
Altitude (m)	700	550
Slope (°)	15–20	10–18
Number of species	75	400
Canopy height (m)	18.96 ± 1.73	29.81 ± 2.96
Canopy cover (%)	78.40 ± 9.92	90.84 ± 1.69
Leaf area index (m^2 m^{-2})	3.54 ± 0.36	4.48 ± 0.28
Crown width (m)	6.79 ± 0.21	8.63 ± 0.92
Trees density (DBH > 1 cm, ha^{-1})	7124	4929
Soil pH (1:2.5)	6.62 ± 0.27	4.51 ± 0.20
Soil organic matter (g kg^{-1})	19.47 ± 3.49	12.34 ± 3.32
Total nitrogen (g kg^{-1})	1.80 ± 0.25	1.71 ± 0.36
Available phosphate (mg kg^{-1})	0.67 ± 0.07	3.98 ± 0.10
Available potassium (mg kg^{-1})	95.88 ± 3.09	109.17 ± 18.28
Sulphur (g kg^{-1})	0.023 ± 0.00	0.020 ± 0.00
Calcium (%)	0.56 ± 0.08	0.09 ± 0.01
Magnesium (%)	0.67 ± 0.15	0.31 ± 0.10
Bulk density (g cm^{-3})	1.32 ± 0.02	1.46 ± 0.04

2.3. Chemical analysis

Monthly litterfall were mixed into three to five samples for chemical analysis. Oven-dried samples were ground using a mortar and then sieved through a sifter with a 0.2 mm mesh. Total organic carbon (TOC) was determined by an acid digestion method (H_2SO_4-$K_2Cr_2O_7$) and spectrophotometric procedure. Total N was analysed with the micro-Kjeldahl method after the H_2SO_4 digestion. The P, K, sulphur (S), Ca and Mg concentrations were determined using inductively coupled plasma atomic-emission spectrometry (iCAP7400, Thermo Fisher Scientific, USA) after the HNO_3-$HClO_4$ digestion.

2.4. Statistical analysis

Average litterfall biomass, stand litter and nutrient concentrations were calculated at each site and on each sampling time. Monthly nutrient amount returned to the soil was expressed as the monthly mean dry

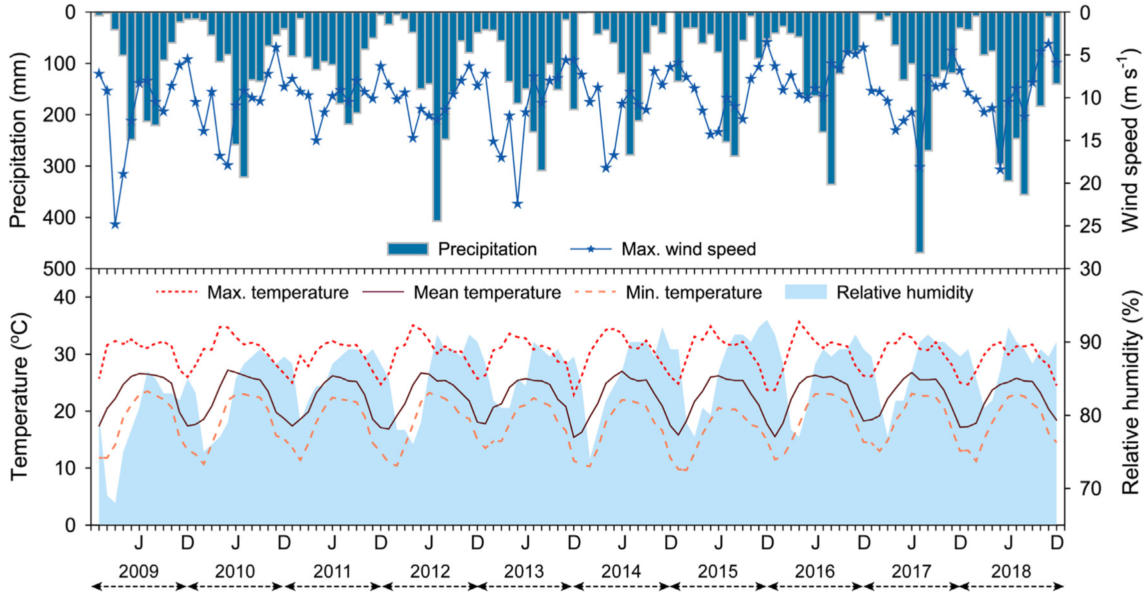

Fig. 2. Monthly precipitation, maximum (max.) wind speed, monthly mean, maximum and minimum (min.) air temperatures over the study period (2009–2018). Historical weather data are provided by the Xishuangbanna Station for Tropical Rainforest Ecosystem nearby the study site.

weight of litterfall biomass multiplied by the mean nutrient concentration. Annual nutrient return was calculated by summing the monthly nutrient return.

According to Scott et al. (1992), turnover rate (K_L) can estimate the proportion of litter layer decomposed within one year. This approach assumes that the karst forest and non-karst forest were at steady state. K_L is calculated using following equation:

$$K_L = AL/SL, \tag{1}$$

where AL is the annual litterfall biomass (Mg ha^{-1} year^{-1}) and SL is the annual mean stand litter biomass (Mg ha^{-1} year^{-1}) on the forest floor. SL is calculated as average value of stand litter biomass that experienced four collections every year. The inverse of $1/K_L$ (unit: year) is the mean residence time (Smith et al., 1998).

Nutrient use efficiency (NUE) is defined as the ratio of litterfall biomass to the annual litterfall nutrient return and is calculated based on the formula below (Vitousek, 1982):

$$NUE = AL/NR, \tag{2}$$

$$NR = \sum_{i=1}^{n=12} C_i \times M_i, \tag{3}$$

where AL is the annual litterfall biomass (Mg ha^{-1} year^{-1}), NR is the annual nutrient return of litterfall (kg ha^{-1} year^{-1}), i represents the sampling month, C represents the mean nutrient concentration (g kg^{-1}) of litterfall samples in each month, and M_i represents the litterfall biomass (kg ha^{-1}) in each month.

The Shapiro–Wilk test and Levene's test were used to check the normality and homogeneity of variances of experimental datasets. A square-root or log transformation of data was conducted if the assumptions were not satisfied. One-ANOVA was used to estimate the differences in litterfall biomass, stand litter, turnover rate, mineral-element concentrations, nutrient return and NUE between the KF and the NKF. Pearson correlation analysis was used to assess the relationships

Table 2
Annual mean litterfall biomass (Mg ha^{-1} year^{-1}) and its components in the two forests from 2009 to 2018. Data are expressed as mean ± SE (n = 10). Different letters within each component denote significant differences ($P < 0.05$) between the two forests. Summary of repeated-measures ANOVA shows the F values and levels of significance. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, and *ns* $P > 0.05$.

Forest	Component				
	Leaf	Twig & bark	Reproductive	Miscellaneous	Total
Karst forest (KF)					
Mean	6.16 ± 0.19 a	1.44 ± 0.13 a	0.45 ± 0.13 b	1.70 ± 0.08 a	9.75 ± 0.31 a
Proportion (%)	63.4 ± 1.7 a	14.6 ± 1.1 a	4.5 ± 1.1 b	17.5 ± 0.6 a	100.0
Coefficients of variation (%)	10.0	29.6	88.4	12.3	10.1
Max./Min.	1.36	2.33	20.64	1.59	1.38
Non-karst forest (NKF)					
Mean	6.19 ± 0.16 a	1.18 ± 0.09 a	1.33 ± 0.18 a	1.79 ± 0.10 a	10.49 ± 0.42 a
Proportion (%)	59.4 ± 1.4 a	11.2 ± 0.7 b	12.4 ± 1.3 a	17.0 ± 0.4 a	100.0
Coefficients of variation (%)	8.0	25.3	43.4	17.3	12.8
Max./Min.	1.37	2.16	4.11	1.83	1.62
Summary of ANOVA					
Forest type	1.79 *ns*	4.36*	59.57***	1.95 *ns*	0.26 *ns*
Year	2.25*	2.43*	4.06***	5.48***	2.25*
Forest type × Year	2.21*	1.02 *ns*	3.56***	0.82 *ns*	1.93*

between litterfall biomass and the climatic variables. All data processing and analysis were performed at $\alpha = 0.05$ with IBM SPSS Statistics for Windows version 25 (SPSS Inc., Chicago, IL).

3. Results

3.1. Litterfall biomass and its temporal dynamics

The annual mean total litterfall biomass in the KF (9.75 Mg ha^{-1} year^{-1}) was slightly lower than that in the NKF (10.49 Mg ha^{-1} year^{-1}) (Table 2). The maximum values of total litterfall biomass in the KF and the NKF were recorded in 2012 and 2016, and the minimum values in 2017 and 2011, respectively (Fig. 3). No significant differences ($P > 0.05$) in the production of annual mean leaf litter, twig & bark and miscellaneous were detected between the KF and the NKF. The annual production of reproductive litter in the NKF (1.33 Mg ha^{-1} year^{-1}) was significantly higher than that in the KF (0.45 Mg ha^{-1} year^{-1}).

Averaged for the 10-year research period, leaf litter dominated the annual litterfall biomass and followed the order of KF (63.4%) > NKF (59.4%) (Table 2). The litterfall components exhibited different composition patterns in the order of leaf > miscellaneous > twig & bark > reproductive litter for KF and leaf > miscellaneous > reproductive litter > twig & bark for NKF. Repeated-measures ANOVA showed that the total litterfall and its components significantly varied with time (i.e. year) in the two forests. Moreover, time and forest type exerted interactive effects on the production of leaf litter, reproductive litter and total litterfall.

The litterfall biomass during the 10-year period showed different annual variations between KF and NKF (Table 2; Fig. 3). The NKF had higher variability (12.8%) of annual litterfall than the KF (10.1%). Except for miscellaneous litter, other components in the KF exhibited higher variability than those in the NKF. Correspondingly, the maximum/minimum ratios also showed the similar variation patterns of the litterfall components between the KF and the NKF. The coefficient of variation of the litterfall components in the two forests followed the order of reproductive > twig & bark > miscellaneous > total litterfall > leaf. Most of the litterfall (> 50%) occurred between November and April (dry season), with the rest occurring between May and October (rainy season) (Fig. 4; Fig. 3). In general, two yearly litterfall peaks were found for each forest type. The higher peak was observed in February for the KF and April for the NKF, whereas the minor peak was observed in November for the KF and August for the NKF, respectively. Leaf litter had similar monthly distribution patterns to the total litterfall. The twig & bark mainly fell in the late dry season (April) and the early rainy season (May). The peak of reproductive litter occurred in June for the KF and September for the NKF, respectively. No marked seasonal pattern was found in the miscellaneous litter, but it mainly fell between April and October.

Various climatic parameters had different effects on the litterfall biomass in the two forest systems (Fig. S1). The litterfall biomass positively correlated with maximum air temperature, maximum wind speed, total solar radiation and photosynthetically active radiation in the KF and the NKF. A stronger and significant negative correlation was found between litterfall biomass and mean relative humidity and minimum relative humidity in the KF than in the NKF (Fig. S1). The monthly precipitation, mean temperature and minimum temperature had negative impacts on litterfall biomass in the KF, whereas they had positive impacts on litterfall biomass in the NKF. In addition, the similar correlations

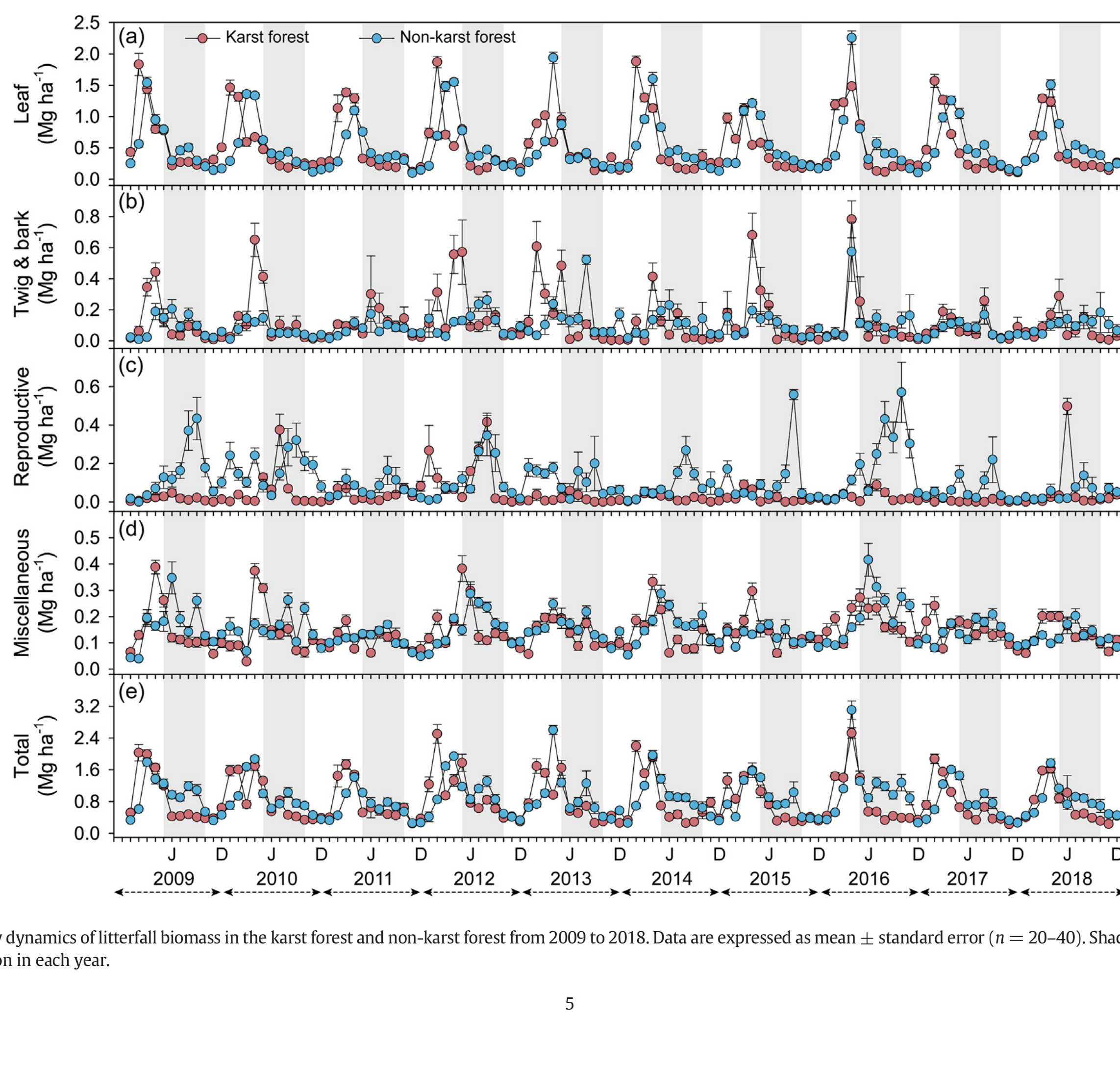

Fig. 3. Monthly dynamics of litterfall biomass in the karst forest and non-karst forest from 2009 to 2018. Data are expressed as mean ± standard error ($n = 20$–40). Shaded area indicates the rainy season in each year.

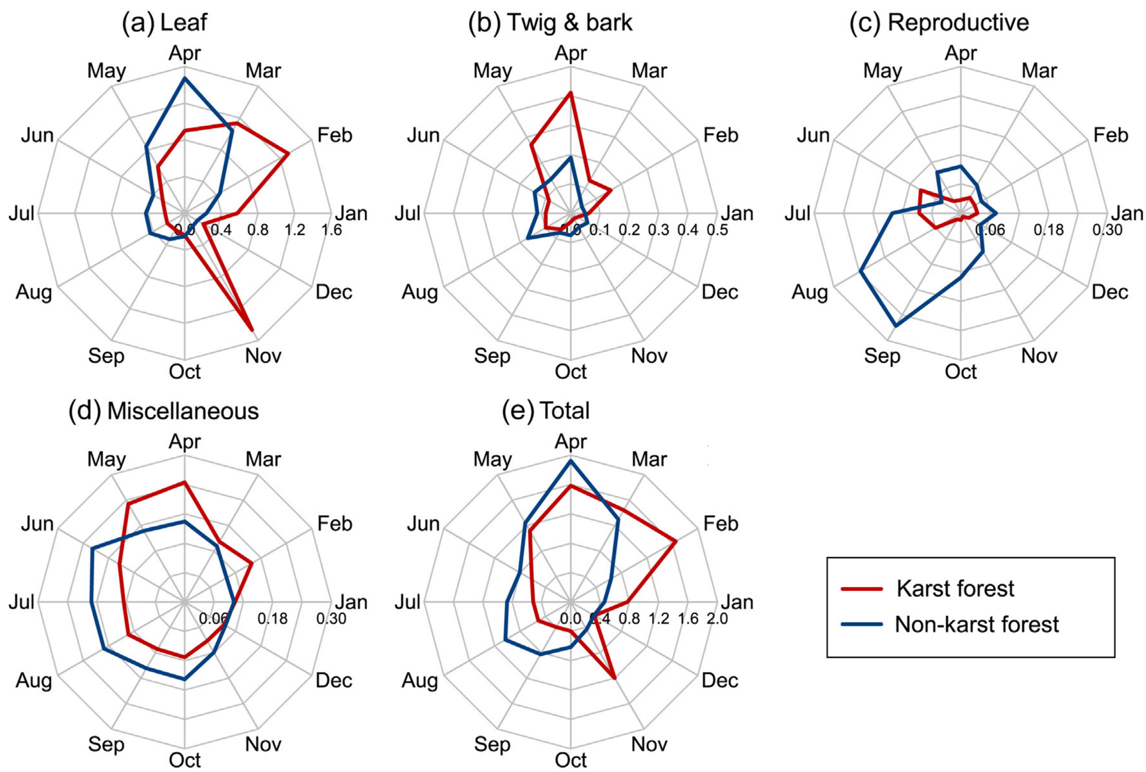

Fig. 4. Mean monthly distribution of litterfall biomass for each litter component in karst and non-karst forests over the 10-year study period.

between the climatic factors and litterfall biomass were obtained by comparing the Fig. 2 and Fig. 3.

3.2. Stand litter and turnover rate (K_L)

The annual mean stand litter on the forest floor was significantly higher in the KF (2.92 Mg ha^{-1}) than in the NKF (2.38 Mg ha^{-1}) (Table 3). Except for the reproductive litter, the other components were evidently lower in the NKF than in the KF. The leaf litter of the two forest systems constituted the highest proportion (ranged from 63.9% to 72.8%), followed by twig & bark (15.2%–26.9%), miscellaneous (7.2%–8.1%) and reproductive litter (1.1%–5.1%). Repeated-measures ANOVA indicated that the total stand litter and its components were significantly affected by time and forest type. Except for leaf and reproductive litter, time and forest type exerted significant interaction effects on the other components of stand litter.

The KF and the NKF showed similar seasonal pattern of stand litter (Fig. 5; Fig. S2). The leaf litter and total stand litter were relatively high from the late dry season to the early rainy season, which coincided with the annual litterfall biomass. Other components of stand litter showed no significant seasonal variation among different months, except for the reproductive litter in KF. In specific, the variability of annual stand litter and its components (but excluding leaf) was higher in the KF than in the NKF (Table 3). In terms of litter composition, the variability of stand litter in the two forests followed the order of reproductive > twig & bark > miscellaneous > total stand litter > leaf.

Table 3
Annual mean stand litter (Mg ha^{-1} year^{-1}) and its components in the two forests from 2009 to 2018. Data are expressed as mean ± SE (n = 10). Different letters within each component denote significant differences ($P < 0.05$) between the two forests. Summary of repeated-measures ANOVA shows the F values and levels of significance. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, and *ns* $P > 0.05$.

Forest	Component				
	Leaf	Twig & bark	Reproductive	Miscellaneous	Total
Karst forest (KF)					
Mean	1.81 ± 0.09 a	0.83 ± 0.14 a	0.04 ± 0.01 b	0.24 ± 0.03 a	2.92 ± 0.21 a
Proportion (%)	63.9 ± 3.7 a	26.9 ± 3.6 a	1.1 ± 0.2 b	8.1 ± 0.9 a	100.0
Coefficients of variation (%)	14.9	52.1	77.7	42.6	22.3
Max./Min.	1.60	7.85	8.31	6.47	2.13
Non-karst forest (NKF)					
Mean	1.71 ± 0.08 a	0.37 ± 0.06 b	0.13 ± 0.03 a	0.17 ± 0.02 a	2.38 ± 0.15 b
Proportion (%)	72.8 ± 2.8 a	15.2 ± 2.0 b	5.1 ± 1.1 a	7.2 ± 0.8 a	100.0
Coefficients of variation (%)	15.2	48.1	76.4	38.0	19.6
Max./Min.	1.57	8.78	13.52	4.79	1.93
Summary of ANOVA					
Forest type	1.72 *ns*	121.63***	16.66***	30.94***	33.02***
Year	3.74***	19.89***	2.16*	15.70***	11.09***
Forest type × Year	1.60 *ns*	5.56***	1.73 *ns*	3.84***	3.60***

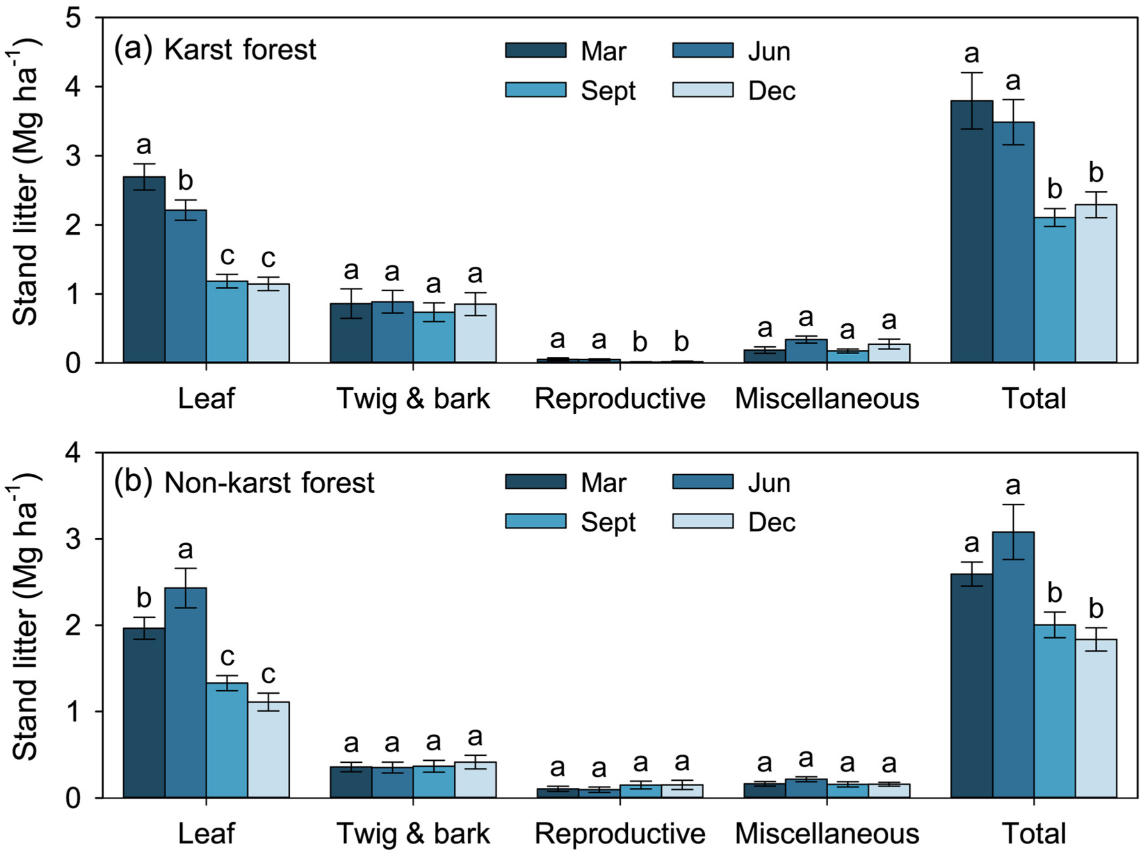

Fig. 5. Seasonal variability of stand litter fractions in the two forests. Data are expressed as mean ± SE ($n = 10$). Different lowercase letters above the bars indicated significant differences ($P < 0.05$) within each fraction among sampling dates.

The annual mean turnover rate (K_L) in the KF (3.52) was significantly lower than that in the NKF (4.53, $P < 0.05$, Fig. 6). The K_L of any litterfall components was evidently higher in the NKF than in the KF, although no significant difference was detected between them. For each forest system, the K_L values varied with litterfall components and showed the order of leaf > reproductive > miscellaneous > twig & bark.

3.3. Nutrient fluxes and nutrient use efficiency (NUE)

Mineral-element concentrations and C/N, C/P and N/P ratios of litterfall varied with time and forest types (Fig. S3). On average, the concentrations of C, K and C/N in KF litterfall were significantly lower than those in NKF litterfall (Table 4). The KF litterfall contained higher N, S, Ca, Mg, C/P and N/P than the NKF litterfall. The temporal variation of mineral-element return from the litterfall was similar to that of the total litterfall biomass (Fig. 7; Fig. 3). Most of the nutrient return mainly occurred between February and May with a small proportion occurring between June and October. The total nutrient return in the KF (4877.19 kg ha^{-1} year^{-1}) was significantly lower than that in NKF (5409.01 kg ha^{-1} year^{-1}) (Table 4). Compared with the KF, the NKF had significantly higher C, P and K returns but lower S and Ca returns in litterfall. The mineral-element returns showed a descending order

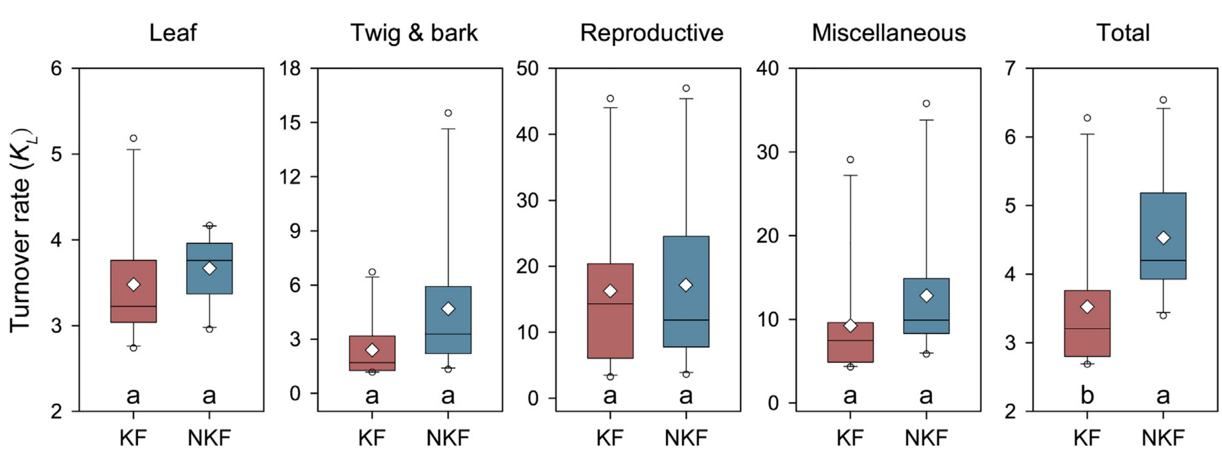

Fig. 6. Box-plots of the turnover rate (K_L) for litter components in karst forest (KF) and non-karst forest (NKF). Different lowercase letters above x-axis indicate significant differences ($P < 0.05$) between the two forests. The upper and lower edges of boxes indicated 75th and 25th percentiles. The upper and lower short lines extend from the boxes edges indicated 1.5 fold the interquartile range. The lines and rhombic markers within the box indicated median and mean value (n = 10), respectively.

Table 4
Annual mean mineral-element concentrations (g kg^{-1}), nutrient return (kg ha^{-1} year^{-1}) and nutrient use efficiency of litterfall in the karst forest (KF) and the non-karst forest (NKF). Stand errors are given in parentheses (n = 10–12). Different lowercase letters within a row indicate significant differences ($P < 0.05$) between the two forests. The "–" in the table indicated the null values.

Forest type	C	N	P	K	S	Ca	Mg	C/N	C/P	N/P	Total
Mineral-element concentration											
KF	442.65 (6.28) b	18.12 (0.99) a	0.97 (0.06) a	2.92 (0.17) b	1.97 (0.11) a	23.75 (1.24) a	2.81 (0.15) a	27.21 (1.72) b	614.39 (56.77) a	20.95 (0.64) a	–
NKF	473.80 (1.70) a	16.21 (0.35) a	1.09 (0.03) a	5.18 (0.25) a	1.60 (0.04) b	14.35 (0.80) b	2.37 (0.04) b	32.70 (1.00) a	545.51 (23.70) a	16.37 (0.28) b	–
Nutrient return											
KF	4379.14 (140.42) b	167.43 (5.38) a	9.13 (0.28) b	29.93 (0.84) b	19.18 (0.53) a	246.00 (8.05) a	26.38 (0.82) a	–	–	–	4877.19 (156.18) b
NKF	4980.87 (201.63) a	167.40 (6.77) a	11.12 (0.43) a	53.14 (1.98) a	16.43 (0.65) b	155.36 (6.35) b	24.70 (0.98) a	–	–	–	5409.01 (218.77) a
Nutrient use efficiency											
KF	2.23 (0.01) a	58.25 (0.20) b	1067.14 (4.23) a	325.53 (2.14) a	508.02 (4.75) b	39.65 (0.09) b	369.63 (2.16) b	–	–	–	–
NKF	2.11 (0.01) b	62.66 (0.09) a	943.02 (1.85) b	197.25 (0.93) b	638.55 (1.08) a	67.53 (0.18) a	424.70 (0.38) a	–	–	–	–

of C > Ca > N > K > Mg > S > P in the KF, and C > N > Ca > K > Mg > S > P in the NKF.

The NUE significantly differed among the elements and forest types ($P < 0.05$; Table 4). In general, the NUE followed the decreasing order of P > S > Mg > K > N > Ca > C in KF and P > S > Mg > K > Ca > N > C in NKF. The KF had significantly lower N, S, Ca and Mg use efficiency, but had higher C, P and K use efficiency, compared with the NKF.

4. Discussion

4.1. Litterfall biomass and its seasonality

Litterfall biomass generally exhibits seasonal variability and varies with forest types (Staelens et al., 2011). The litterfall in the present study was collected from two stands (KF and NKF), and the experiment was conducted for 10 years (2009–2018). On average, the observed litterfall biomass (10.1 Mg ha^{-1} year^{-1}) was within the upper range of the reported values (0.4–15.3 Mg ha^{-1} year^{-1}) for tropical forests (Table 2; Vitousek, 1984), and it was higher than the mean value (7.9 Mg ha^{-1} year^{-1}) in the world's forests (Shen et al., 2019). The litterfall biomass obtained in the KF (9.8 Mg ha^{-1} year^{-1}) was much higher than those in a northern tropical karst seasonal forest (0.7–-7.1 Mg ha^{-1} year^{-1}; Guo et al., 2019) and in subtropical karst forests (1.8–4.5 Mg ha^{-1} year^{-1}; Yu et al., 2011; Zeng et al., 2011) in SW China but lower than that in a tropical limestone forest of Malaysia (12.0 Mg ha^{-1} year^{-1}; Proctor et al., 1983). These differences in the litterfall input of karst forests could be attributed to the fact that litterfall biomass decreases as latitude increases on a global scale (Shen et al., 2019). In particular, despite experiencing parallel climatic conditions from the same region, the NKF showed greater total litterfall than the KF (Table 2). This result could be partly explained by the higher species richness in NKF (Table 1). The litterfall amount in karst forest

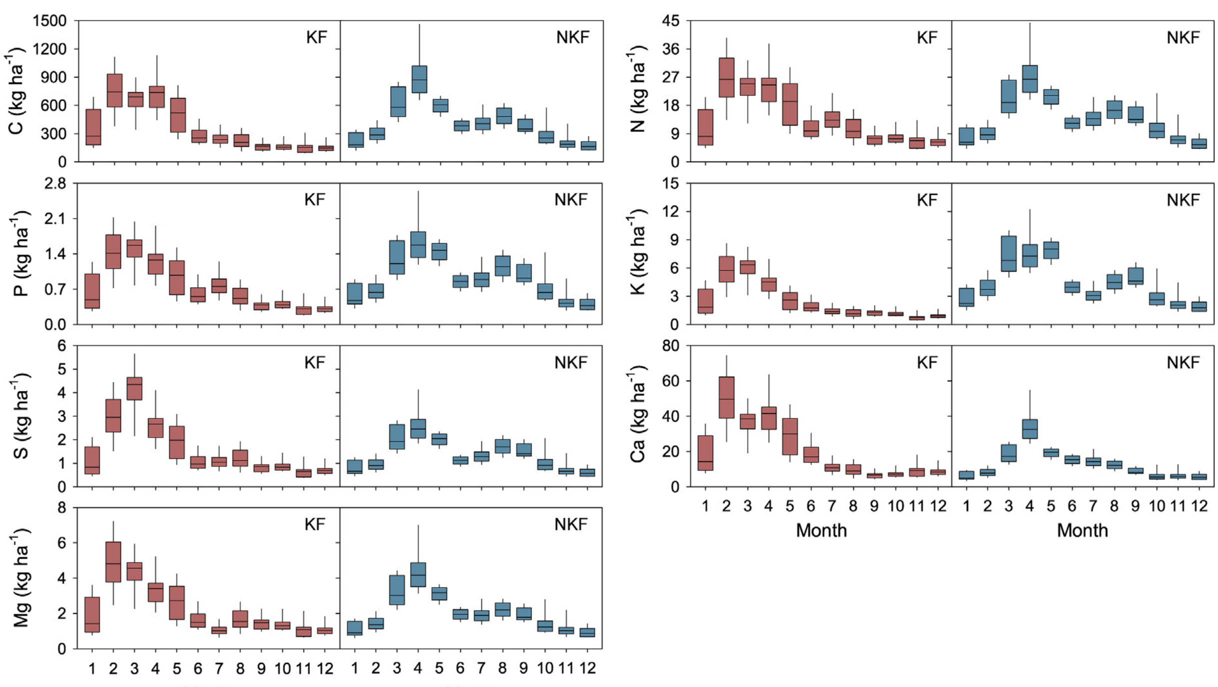

Fig. 7. Monthly nutrient return of litterfall in karst forest (KF) and non-karst forest (NKF) in Xishuangbanna, SW China. The upper and lower edges of boxes indicated 75th and 25th percentiles. The upper and lower short lines extend from the boxes edges indicated 1.5 fold the interquartile range. The lines within the box indicated median value.

ecosystems is also limited by harsh stand characteristics, such as thin soil layer, water stress, natural disturbance, and thus slow tree growth and short life (Guo et al., 2017).

The proportion of litterfall components is greatly influenced by different biotic and abiotic factors among forest types (Zhu et al., 2019). Similar to many other forest ecosystems, leaf litter made up the largest proportion (approximately 60%; Table 2) of the annual total litterfall in the KF and the NKF. The second largest proportion of litterfall was the miscellaneous part for the two forests. The main reason for this phenomenon is the acceleration of litter decomposition resulting from the relatively high temperature and rainfall in the study site (Ren et al., 1999). In addition, the rodent and bird activities in the forest may produce a small number of faeces and plant debris, thus increasing the fractions of miscellaneous litter.

Seasonal patterns of litterfall are greatly affected by environmental variables and forest types, and exhibit unimodal, bimodal, and irregular models (Zhang et al., 2014). On the basis of long-term monitoring, the variation of total litterfall biomass in the study forests exhibited bimodal patterns (i.e. two litterfall peaks) in each year (Fig. 3), which is consistent with previous studies (Guo et al., 2017; Tang et al., 2010; Pandey et al., 2007; Ren et al., 1999). The monthly variability of litterfall biomass was higher in the KF than in the NKF, and the leaf litter dominated the temporal dynamics of annual litterfall. Previous studies demonstrated that leaf abscission in many seasonally dry tropical forests is an ecological and physiological mechanism of adaptability to drought (Zhu et al., 2019; Kotowska et al., 2016; Chave et al., 2010; Whitmore, 1975). In the present study, the large litterfall peaks of the two forests occurred in the dry season because of the water stress (Fig. 3). Moreover, a significantly positive correlation was found between litterfall biomass and total solar radiation (Fig. S1). This is probably due to the fact that strong solar radiation by sunny weather increases drought stress, and thus inducing the defoliation of trees in the study forests. In the KF, the small litterfall peak was observed in November when the monthly mean air temperature began to drop to 20 °C (Fig. 2). This result indicates that low temperature exerts a positive effect on the litter production in the KF. However, the small litterfall peak in the NKF was found in August. This result was mainly due to the contribution of the reproductive component during the rainy season (Fig. 3). In addition, the heavy wind in the rainy season may blow off the dead organic matter detained in the canopy layer, thereby increasing additional litterfall.

4.2. Stand litter and litter turnover

Stand litter (litter accumulation) is a common feature of diverse forest ecosystems, from boreal coniferous forest to tropical rain forests (Dunkerley, 2015). In the present study, the annual mean stand litter was 2.65 Mg ha^{-1} year^{-1}, which was slightly higher than that of a seasonal dry tropical forest (2.05 Mg ha^{-1} year^{-1}) in northeast Brazil (de Queiroz et al., 2019). The seasonal variation pattern of stand litter showed high accumulation in the dry season but low in the rainy season (Fig. 5; Fig. S2), coinciding with that observed in litterfall biomass (Fig. 3). In specific, the stand litter in the KF was significantly higher than that in the NKF (Table 3). This finding indicates that decomposition of the litterfall was slower in the harsh karst habitat than in the non-karst habitat within the same climate area. This conclusion was also supported by the low turnover rate (K_L) of litterfall in the KF (Fig. 6).

The amount of accumulated litter on the ground greatly depends on the litter production, K_L and litter quality. The K_L of litter in this study varied from 2.68 to 6.54, with a mean value of 4.03 (Fig. 6), which was higher than those of a lowland rain forest (2.01; Scott et al., 1992) and a primary forest (0.74; Smith et al., 1998) in Brazil. The mean residence time ($1/K_L$) of litter was 0.25 years in the present study. This value was much lower than the range (0.50–3.03 years) reported in many tropical forests worldwide (de Queiroz et al., 2019; Tang et al., 2010; Vogt et al., 1986). In addition, the litterfall in the KF had high quality (e.g. low C/N ratio, high N content and N/P ratio) that make decomposition more readily (Table 4; Wardle et al., 2002). However, the longer residence time (0.28 years) of litterfall in the KF suggested that it had slower decomposition than the litterfall in the NKF (0.22 years). These results indicated that the decomposition rate in the karst forest may not be greatly affected by litter quality but by other factors. Notably, the low water availability in karst habitats is likely to restrict local microbial activity, thus inhibiting litter decomposition (Yan et al., 2020; Guo et al., 2019).

4.3. Litter chemistry, nutrient return and nutrient use efficiency

Plants absorb mineral nutrients mainly from the soil and element concentrations of plant tissues are therefore affected by soil chemical status (Bai et al., 2019). In the present study, the variation pattern of nutrient concentrations in the KF and the NKF litterfall followed the trend of that in soil (Table 1; Table 4), suggesting that soil nutrients are an important driver of litterfall chemical attributes. P availability generally limits the tree growth because of high leaching loss in tropical forest soils (Baribault et al., 2012; Vitousek, 1984). The litterfall in the KF had lower P concentration than the litterfall in the NKF. This discrepancy may be due to the high P reutilisation in karst plants (Table 4). The K concentration of the KF litterfall was significantly lower than that of the NKF litterfall. This result is consistent with the findings of Cao et al. (2014) that most of the tropical karst plants are deficient in K. The KF litterfall was richer in Ca and Mg than the NKF litterfall, which would help improve the ability of stress resistance, disease resistance and wound healing of karst plants (Cao et al., 2014; Hirschi, 2004). In terms of temporal dynamics of element concentrations, the KF litterfall showed higher C to adapt to water stress in the dry season, and had higher N and P to promote growth metabolism in the rainy season (Fig. S3). These results indicate that the biogeochemical conditions may select plant species with certain litterfall nutrient concentrations that are well-adapted to tropical karst environment.

In general, the monthly dynamics of C and nutrient returns coincides with litter production, and they show a bimodal pattern (Fig. 7). High litter production and high element concentration bring great amounts of nutrients returned to the forest floor (Table 4). The total nutrient return in the NKF was 1.1 times higher than that in the KF, implying that NKF could maintain soil fertility and forest productivity better. In addition, the total nutrient returns in the NKF (5409.0 kg ha^{-1} year^{-1}) were higher than those of tropical seasonal rain forests within the same region (4352.3–5107.3 kg ha^{-1} year^{-1}; Zhu et al., 2019; Tang et al., 2010). This discrepancy could be explained by the more litterfall and addition of S return in the present study.

The NUE was element- and site-dependent across various forest types (Kotowska et al., 2016; Smith et al., 1998; Vitousek, 1984). In the present study, the use efficiency of all mineral elements showed significant differences between the KF and the NKF (Table 4). Significantly higher C use efficiency in the KF suggested that the KF had higher turnover of organic matter than the NKF. This corresponds well to the findings of Zhao et al. (2020). The KF showed more efficient P and K circulations to avoid nutrient loss through litterfall compared with the NKF. Considering the low available P and K contents in the KF soil (Table 1), this result suggested that the KF suffered the limitation of P and K. The litterfall in the KF had higher N, S, Ca and Mg concentrations than that in the NKF. However, the use efficiencies of these nutrients were significantly lower than those in the NKF. This result might be related to the definition of NUE (i.e. the NUE is equal to the inverse of nutrient concentration in the litterfall; Vitousek, 1982). A higher nutrient concentration in litter might lead to a lower NUE. Another possible reason for this result might be that these nutrient contents were rich in local soil and thus reduced their use efficiencies (Zhou et al., 2016). These findings indicated that the plants in the KF had not utilised the excessive N, S, Ca and Mg for growth probably because of limitation of other elements.

5. Conclusions

A 10-year comparative study was performed to investigate the litterfall biomass, litter accumulation, decomposition process and associated nutrient return and NUE for two typical forest types (e.g. KF and NKF) in seasonally dry tropics. The KF showed significantly higher stand litter but lower annual mean litterfall biomass, turnover rate and nutrient return than the NKF. The temporal dynamics of stand litter and nutrient return coincided with the litterfall trend and showed a bimodal pattern. The maximum air temperature, solar radiation and maximum wind speed had positive effects on the litterfall biomass for the two forests. The low temperature and low relative humidity during the cool and dry season greatly promoted the litterfall inputs in the KF. The litter decomposition in the KF was slightly affected by litter quality but seemed regulated by other factors, such as water scarcity of karst habitats. The KF exhibited relatively high P and K use efficiency because of their low availability in karst soils. Therefore, special attention should be paid to the supplement of P and K during the ecological restoration of degraded karst vegetation in tropical area. From the long-term evolutionary process, the karst habitats tended to develop plant communities with certain chemical composition of litterfall and with a nutrient cycling mechanism that is well-adapted to the high harshness and heterogeneity.

CRediT authorship contribution statement

Xiai Zhu: Conceptualization, Methodology, Writing - original draft. **Xin Zou:** Formal analysis, Writing - review & editing. **Enfu Lu:** Formal analysis, Software. **Yun Deng:** Methodology, Investigation. **Yan Luo:** Investigation. **Hui Chen:** Methodology, Validation. **Wenjie Liu:** Conceptualization, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors deeply appreciate three anonymous reviewers for their constructive comments. We also thank the Central Laboratory of Xishuangbanna Tropical Botanical Garden for their help in chemical determination, and the Xishuangbanna Station for Tropical Rainforest Ecosystem Studies for providing the dataset in the present study. This study was supported by the National Natural Science Foundation of China (31570622 and 31700560), the Yunnan Fundamental Research Projects (2018FB043) and the CAS 135-Program (No. 2017XTBG-F01).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.143619.

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