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ORIGINAL PAPER

Litterfall and nutrient return in moist evergreen broad-leaved primary forest and mixed subtropical secondary deciduous broad-leaved forest in China

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Abstract Litterfall plays an important role in carbon and nutrient cycling of a forest ecosystem which is generally affected by climate, vegetation, forest type and age. The majority of the subtropical forests of China are occurring in nutrient poor environment, and thus there is a need to understand the role of litterfall on the recycling of C and nutrients in these forests for their proper management. We measured litter production, and carbon and nutrient return in an evergreen broad-leaved primary forest (Mt. Ailao, SW China) and a deciduous broad-leaved secondary forest (Mt. Damei, East China). The annual litterfall productions were 1124 and 490 g m^{-2} at the primary evergreen forest and secondary deciduous forest, respectively. Carbon return in primary evergreen forest was approximately three times greater than that in secondary deciduous forest. Litter N concentrations in the secondary deciduous forest were higher than that of the primary evergreen forest and consequently, the use efficiency of N of the secondary deciduous forest was lower than the primary evergreen forest. This reflects a stronger nutrient conservation mechanism in the primary evergreen forest than in the secondary forest.

Keywords Forests · Litterfall · Nutrient · Litterfall nutrient fluxes · Nutrient use efficiency

Introduction

Litterfall plays an important role in forest nutrient cycling and is fundamental for understanding long-term functioning and appropriate management of forest ecosystems. Litter production and its chemical composition are important features of the forest ecosystem that regulates the pattern of organic matter deposition and nutrient cycling in forest and modified ecosystems (Facelli and Pickett 1991; Tripathi and Singh 1992, 1995, Singh et al. 1999; Pandey et al. 2007). In natural forest ecosystems, litterfall dynamics have shown high dependence on ecological factors, such as forest type, species composition, tree density, soil, light, forest age structures, altitude, latitude, and season (Hansen et al. 2009; Gonzalez-Rodriguez et al. 2013; Lu and Liu 2012; Watanabe et al. 2013). Anthropogenic and physical disturbance on forests (e.g., as grazing, deforestation, fire, wind and hurricanes) have reported to induce pulses of litterfall (Blanco et al. 2008, 2012). Actual evapotranspiration accounted for more than half of the variability in litterfall amounts for boreal forest, and rainfall and temperature could explain up to half of the variability (Berg and Meentemeyer 2001; Tang et al. 2010). Studies have indicated significant role of climate change on litterfall at global scale, but further regional

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studies would be needed to provide base line data for establishing more robust models to document changes in litterfall in relation to environment by using regional empirical data.

The spatiotemporal variability of litterfall strongly depends on forest stand species (Binkley 1996) and nutritional condition during the growing season (Diaz-Maroto and Vila-Lameiro 2005). A previous study has confirmed that the nutrient of twigs and leaves can be from soil via roots and from the atmosphere through stomata (Staaf and Berg 1981). For different forest stand species, seasonal fluctuations of N concentrations in green litterfall, with the maximum values in fresh leaves and the minimum values in old ones, have been reported in the literatures (Martínez-Alonso et al. 2007; Hansen et al. 2009; Fife et al. 2008). Litterfall nutrient concentrations have also been related to other factors, such as soil nutrient availability, climatic and growth conditions (Binkley 1996; Augusto et al. 2000). Forest soil supplies nutrients and water, and is also a medium for roots stretch and physical support for plant growth. However, nutrient release through the decomposition of litterfall is fundamental to the ecological equilibrium maintenance of mature forest ecosystems. Concurrently, at a regional scale, litterfall chemistry affects the decomposition rate and nutrient cycling of litterfall (Liu et al. 2002). It is important to understand the intricacies of variations in litterfall production between years and nutrient dynamics in natural forests (Sundarapandian and Swamy 1999).

China is a large land area country with relatively low forest coverage rate, although slight increase in forest coverage rate was obtained in recent years (State Forestry Administration 2010). Historically, subtropical forests were wide-spreaded in the center and south of China. Due to the massive deforestation in the 1950s, most of the subtropical primary forest in eastern and southeastern China disappeared and only small portion was reserved in southwestern China (Wu 1995). Number of secondary forests have been developed in eastern and southern China after 1960s with a view to sustainable development (Zhou et al. 2015), which has improved the soil fertility levels. In China most of the soil in subtropical secondary forest is highly weathered, leached and poor nutrient (Li et al. 2015; Wei et al. 2012). However, proper management of these forests is needed to understand the role of litterfall on the recycling of C and nutrients. The information on this aspect is highly on the litterfall and nutrient recycle in these forests in China.

In this study, continuous measurements of litterfall and nutrients in a primary evergreen forest (Mt. Ailao, SW China) and a secondary deciduous forest (Mt. Damei, East China) were taken. The objectives of present work were to (1) evaluate the effects of forest type and tree species on the litterfall pattern and nutrient return, (2) demonstrate the temporal variation of litterfall pattern and nutrient in relation to species and meteorological variables, and (3) assess the litterfall nutrient use efficiency (LNUE) at different forest type. This study can provide critical information on the management of primary evergreen and secondary deciduous forest ecosystem in China.

Materials and methods

Sites description

Litterfall was collected at Mt. Ailao (a primary evergreen forest in Yunnan province, SW China) and Mt. Damei (a secondary deciduous forest in Zhejiang province, East China) (Fig. 1). Basic information of the sampling sites, including altitude, forest type, soil type, annual precipitation and air temperature, are given in Table 1.

In the primary forest, primary lithocarpus forest (PLF) covers nearly 85 % of the forest area (Young et al. 1992) and the dominant tree species were *Manglietia insignis*, *Lithocarpus chintungensis*, *Vaccinium duclouxii* (Level) Hand-Mazz., *Castanopsis wattii* and *Lithocarpus xylocarpus* based on an investigation conducted in 2011 by Ailaoshan Station for Subtropical Forest Ecosystem Research. In the secondary forest, *Forsythia suspensa*, *Rhamnus utilis* and *Quercus dentate* were the dominant tree species and were mixed together.

Sample collection

Litterfall trap (1 m × 1 m) were placed to collect litterfall samples. Litterfall samples were collected monthly in each sampling site which had two traps. For the primary forest, the sampling period was from June 2011 to November 2014. Five sampling sites, representing five typical dominant species, including *Manglietia insignis, Lithocarpus chintungensis, Vaccinium duclouxii, Castanopsis wattii,* and *Lithocarpus xylocarpu*, were selected and the litter traps were placed under the dominant tree species. According to a general survey conducted by Research Station of Ailao Mountain Forest Ecosystems in 2011, the five species are dominated and typical, which covers 90 % of surface area in the study region of the primary forest. Although the traps was placed under the single species of several trees, litterfall in the corresponding traps cannot be the only species because of other species leaves falling into the traps and each species were not separated. For the secondary forest, four random locations were selected where *Forsythia suspensa, Rhamnus utilis* and *Quercus dentate* were mixed together. No sample was collected from January to March in 2013 due to little litterfall

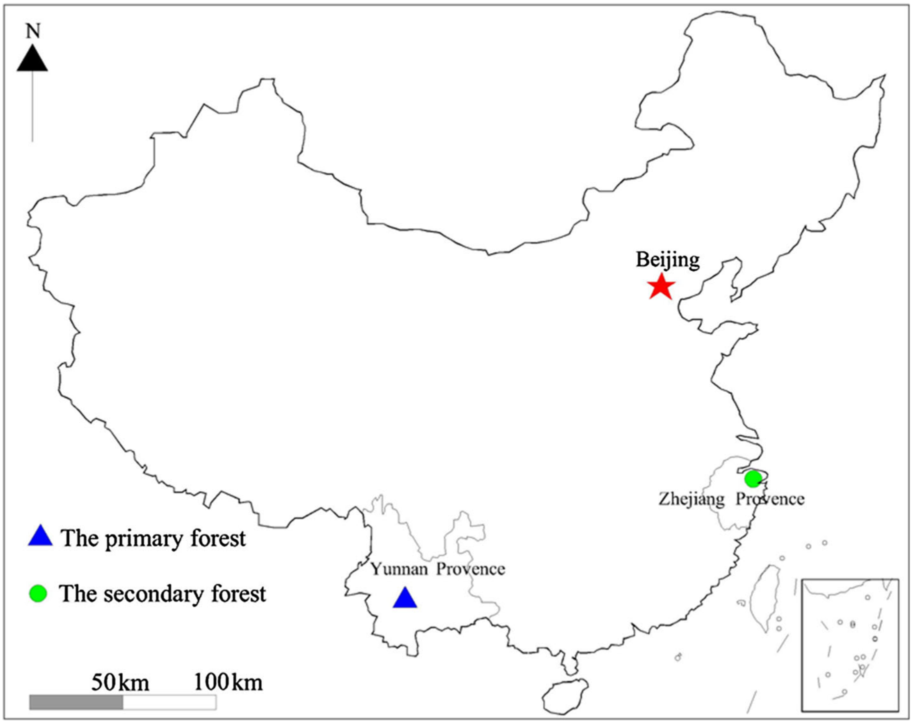

Fig. 1 Locations of the study sites

Table 1 Basic information of two research forests

Studied area	Mt. Ailao	Mt. Damei
Specific sampling site	Xujiaba (24°32′N, 101°01′E)	Hengxi (29°40′N, 121°37′E)
altitude	2650 m a.s.l.	550 m a.s.l.
Forest type	Primary evergreen forest	Secondary deciduous broad-leaved forests
Soil type	Loam	Loam
	Ferric Luvisols in FAO-Unesco	Ferric Luvisols in FAO-Unesco
Annual precipitation	1947 mm	1500 mm
Air temperature	11.3 °C	15.0 °C

produced in the growing season. Thus, a total of 10 and 8 traps were set in the primary forest and the secondary forest, respectively. After collection, all samples were air-dried and grounded into a fine powder in a pre-cleaned blender (Table 2).

Chemical analysis

C and N in litterfall were determined by a PE2400-II Element Analyzer (Perkin-Elmer, USA). As for Ca, K and Mg, samples were analyzed by ICP-OES (Vista MPX,

Table 2 Litterfall amount (g m^{-2} $year^{-1}$) in the primary forest from June 2011 to November 2014 and the secondary forest from April 2012 to March 2013

Tree species in the primary forest				
Manglietia insignis	*Lithocarpus chintungensis*	*Vaccinium duclouxii*	*Castanopsis wattii*	*Lithocarpus xylocarpus*
1731 ± 75	1179 ± 54	1322 ± 63	1177 ± 68	872 ± 42
Sampling site in the secondary forest				
R1	R2	R3	R4	
390	600	570	350	

USA) after digestion with mixed acid (HNO_3:$HClO_4$, 4:1 in volume).

Certified reference materials, including Bean (GBW10021) and sulfanilamide (C17000000), were employed for quality assurance. The precision were 3.0 % for Ca, 3.6 % for K, 3.3 % for Mg, 0.8 % for C and 0.3 % for N. The recoveries were 92–100 % for Ca, 93–109 % for K, 92–101 % for Mg, 99–101 % for C and 99–100 % for N, respectively. The average relative standard deviation was less than 5 %.

Data analysis

The annual litterfall flux calculation in the primary forest was following formula (1):

$$M_{\mathrm{AL}} = \sum_{i}^{n=5} \sum_{j}^{n=12} p_i \times m_{ij} \tag{1}$$

where M_{AL} is the annual litterfall flux (g m^{-2}) in the primary forest, i represents the sampling site and/or the tree species, j represents the sampling time, m_{ij} is the dry mass of litterfall at each site in each month, p is tree density ratio and is 46 % for *Castanopsis wattii*, 30 % for *Manglietia insignis*, 15 % for *Lithocarpus xylocarpus*, 6 % for *Lithocarpus chintungensis*, and 4 % for *Vaccinium duclouxii,* respectively.

The annual litterfall amount in the secondary forest was calculated based on the four random sampling sites:

$$\mathrm{M}_{\mathrm{DM}} = \overline{\sum_{i}^{n=4} \sum_{j}^{n=12} m_{ij}} \tag{2}$$

where M_{DM} is the annual litterfall flux (g m^{-2}) in the secondary forest, k is the sampling site, j is the sampling time, m_{kj} is the dry mass of litterfall at each site in each month.

Nutrient pools in litterfall in the primary forest and the secondary forest were calculated following formula (3) and (4):

$$F_{k-\mathrm{AL}} = \sum_{i}^{n=5} \sum_{j}^{n=12} c_{ij}^{k} \times m_{ij} \tag{3}$$

$$F_{k-\mathrm{DM}} = \sum_{i}^{n=4} \sum_{j}^{n=12} c_{ij}^{k} \times m_{ij} \tag{4}$$

where $F_{k\text{-AL}}$ and $F_{k\text{-DM}}$ is the annual nutrient amount returned to soil from litterfall in the primary forest and the secondary forest (mg m^{-2}), k represents the nutrient element, i represents the sampling site, j represents the sampling site, c is the mean concentration of nutrient element (mg kg^{-1}) at each site in each month, and m is dry mass of litterfall (g m^{-2}).

LUNE was defined as the ratio of dry mass of litterfall (M) to annual litterfall nutrient content deposition (F_k) (Vitousek 1982). The calculation of LNUE was following formula (5):

$$\mathrm{LNUE} = M/F_k \tag{5}$$

Results

Litterfall deposition

Total annual litterfall flux was 1124 g m^{-2} in the primary forest. The monthly litterfall fluxes ranged from 25 to 207 g m^{-2} for 41 months (Fig. 2). The annual average litterfall flux of *Manglietia insignis* (1731 g m^{-2}) is the highest among the litterfall in these five species, while the smallest litter flux for *Vaccinium duclouxii* is 872 g m^{-2}. Marked seasonal variations were noted in the amount of litterfall. Maximum (68 % of the annual) litterfall occurred in dry period (from November to May) and the remaining in wet season wet season (from July to October) (Fig. 2a). The climatic records for the primary forest show that spring is characterized by low humidity, low rainfall and higher temperatures with evaporation greater than rainfall (Fig. 2a). The seasonal patterns of the litterfall production

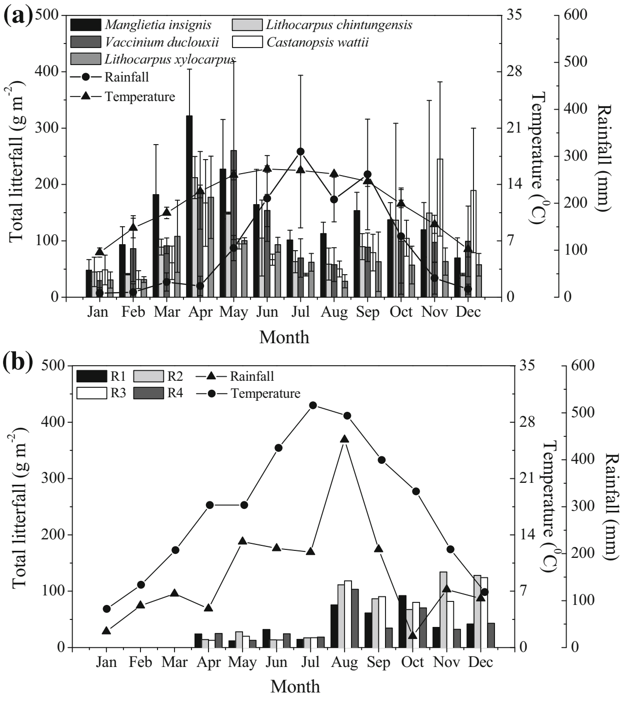

Fig. 2 Monthly variations of litterfall in the primary forest from Jun 2011 to November 2014 (**a**) and the secondary forest from April 2012 to March 2013 (**b**). R1, R2, R3 and R4 were the four litterfall collected in the four random sampling sites of the secondary forest

were similar with high litterfall in the dry season and low litterfall in wet season. The inter-annual variability of total litterfall for 3.5 years was not significant that varied between 1116 and 1333 g m^{-2} from June 2011 to November 2014.

The litterfall ranged from 350 to 600 g m^{-2}, with the annual mean 490 g m^{-2} in the secondary forest. As showed in Fig. 2, the distinct systematic pattern of intra-annual litterfall deposition is depended on the forest types. The seasonal litterfall fluxes in the secondary forest were a rhythm of a typical deciduous forest, where bud scales were shed from April to July, and the pulse of litterfall began in August, peaks started in October and ends in December.

Carbon and nutrient return to soil

Carbon concentration in litterfall samples from the primary forest and the secondary forest were 446–486 and 438–502 mg g^{-1}, respectively. N concentrations in litterfall samples from the primary forest and the secondary forest were 12.7–17 and 15.5–24.1 mg g^{-1}, respectively. And the other nutrient elements are shown in Fig. 3 and Table 3.

Clear seasonal variations of some nutrient concentrations were found in litterfall. A seasonal variation in N concentration was not recorded in the primary forest. However, in the secondary forest, high N in litterfall was observed in growing season (from March to August) and low N concentrations were recorded from September to December. Seasonal changes for other nutrients were also site-specific. The highest K concentrations in litterfall in the primary forest and the secondary forest were in May and September, respectively, while the lowest K concentrations were recorded in litterfall collected in September in the primary forest and in litterfall collected December in the secondary forest (Fig. 3). In addition, minimal and maximal litterfall Ca concentrations in the primary forest followed the opposite pattern to that of N in the secondary forest. But no clear pattern was appreciable in the secondary forest, which changes over time and were more rhythmic. Seasonal patterns for Mg were synchronized at these two sites expect in summer, during which it showed a distinctive valley in litterfall collected in September.

The mean C input by litterfall was significantly higher ($P > 0.01$) in the primary forest (694.9 g m^{-2} year^{-1}) than that in the secondary forest (224.2 g m^{-2} year^{-1}), and the deposition peaks were similar to litterfall fluxes, which were in spring and autumn, respectively (Fig. 4). There were no significant differences between species in total nutrient fluxes in the secondary forest, but nutrient fluxes tended to be higher in R2 and lower in R4 (Table 3). Dissimilar deposition pattern among tree species was found in the primary forest where litterfall production played a more important role. However, Ca deposition fluxes of *Castanopsis wattii* were not only coinciding with the litterfall quality, but also significantly controlled by concentrations simultaneously, which had the highest Ca concentrations (Table 3). The highest values in nutrient content were observed in August in the secondary forest and in April in the primary forest, coinciding with the peak of litterfall production (Figs. 2, 4).

The LNUE varied for different elements among the two forest types ($P < 0.05$ for N and Ca; Table 3). In both forest types, the highest LNUE was found for Mg, following a descending order of Mg > K > Ca > N > C.

Discussion

Litter production

In the present study, maximum litter production in dry months is consistent with the reports of other forest from similar environmental conditions (Sundarapandian and Swamy 1999; Tang et al. 2010). These findings demonstrate that the variations of seasonal litterfall coincide with the rhythm of leaf senescence of the forest tree species along with the changes in annual environmental parameters (i.e., temperature and moisture) at a regional scale (Sundarapandian and Swamy 1999). In secondary deciduous forest, the peak litterfall (84.3 % of total annual mass) in August to December is because of typhoon Sura landed in this area at the beginning of August in 2013 (Liu and Boukabara 2014). This result was consistent with report of Wang et al. (2013) that maximum litter production (59–81 % for total) occurred during these period due to typhoon in two subtropical forests at Central Taiwan.

Observed annual litterfall (Fig. 2) in the southwestern China was much higher than the mean annual litterfall production (712 g m^{-2}) at the same area of the primary forest natural forests between 1991 and 1999 (Liu et al. 2002). Since the primary forest is a climax rain forest ecosystem with greater variations in canopy architecture and tree species, dead branches usually remain on trees for a long period with occasionally falling on the forest ground (Maass et al. 2002). The time delay could cause great variation in twig litterfall. On the other hand, different tree species with different litterfall deposition in the two study periods may be another reason. Furthermore, previous findings around the world (Qiu et al. 1998; Liu et al. 2003; Tripathi et al. 2006) have revealed that litterfall in different forests is strongly driven by rainfall patterns and flushing among dominant canopy species. Further, substantial reduction (1358 mm) in annual precipitation in the studied

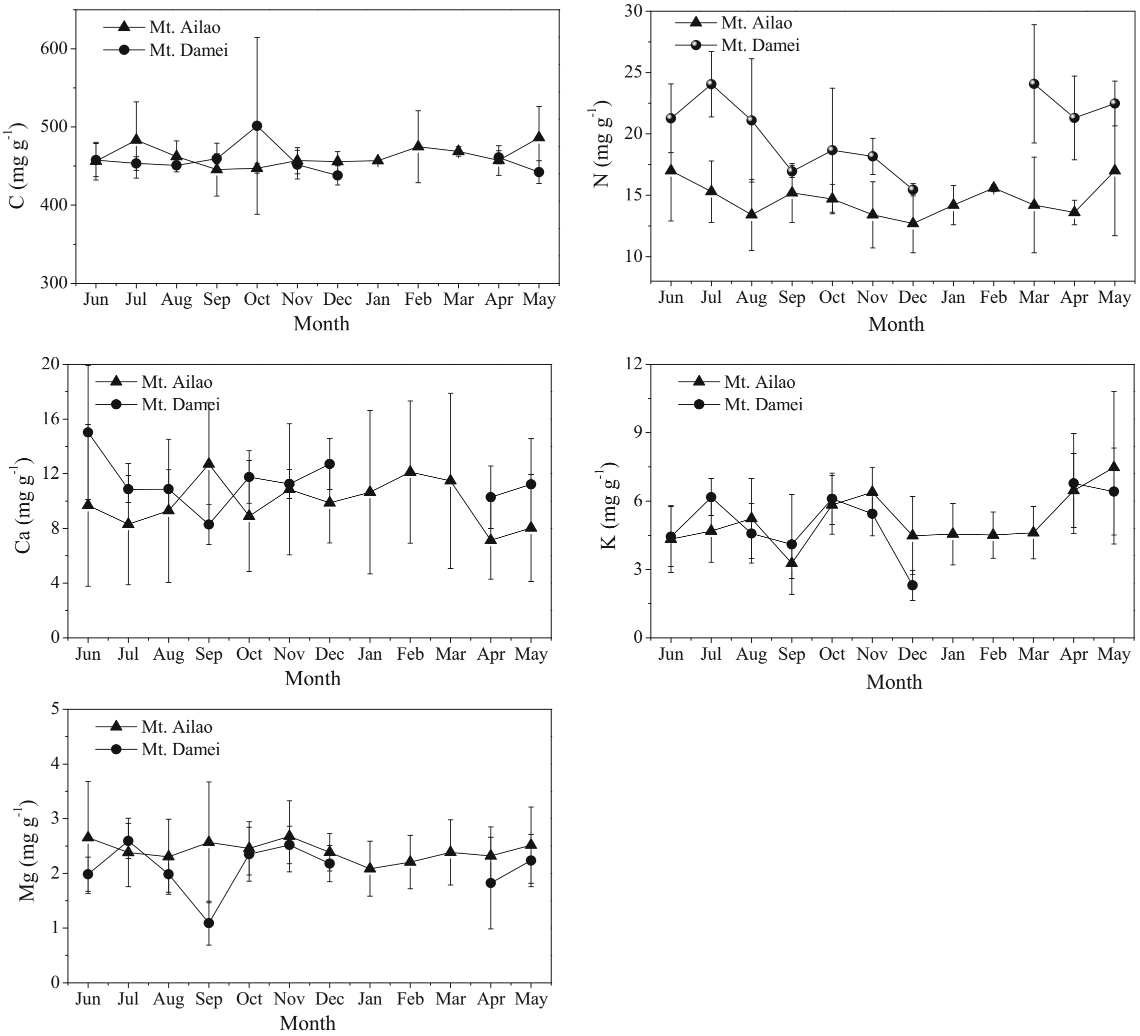

Fig. 3 Mean (±SD) monthly C and nutrient element concentrations of litterfall in the primary forest in Southwestern China and the secondary forest in Eastern China

period (June 2011–May 2012) compared to the normal precipitation (1947 mm) could be another reason.

Carbon in litterfall and return fluxes to soil

In the primary forest, C return of 350.2 ± 47.9 (Liu et al. 2002) was much lower than that in this study due to much higher litterfall amount. Litterfall is the main source of C for forest soils. The organic C storage in soil was only accounted for a small total C storage in the forest ecosystem (Yang et al. 2014), but litterfall production is a good indicator of forest productivity and indicates forest carbon pools and soil organic carbon contents (Silva et al. 2011). C in the litterfall is more dynamic because the residence time of C is shorter than in mineral soil (Guo et al. 2004). Additionally, forest litter organic C comprises an intermediate pool in the global carbon cycle and plays an important role in regulating the atmospheric CO_2 concentration (Houghton et al. 2001; Ataka et al. 2014). Our study indicated that carbon sink in the primary evergreen forest was much larger than that in the deciduous forest. Simultaneously, decreased C returns greatly reduced the stocks of C in forest floor, thus reduce the potential C sequestration of forests, when the primary forest were converted to the secondary forest. In return, the enhanced total organic C in forest soils by increased litter production may benefit the maintenance of soil fertility in natural forest ecosystems.

Nutrient return to soil

The N concentration peaked in spring and summer, implying a high nutrient demand in new leaves. By contrast, the lowest N concentrations in litterfall collected in

Table 3 Statistical summary of C and nutrient elements in litterfall in the primary forest from Jun 2011 to May 2012 and the secondary forest from April 2012 to March 2013

Study site	Tree species	Mass-weighted mean concentration (mg g^{-1})					Annual deposition fluxes (g m^{-2})				
		C	N	Ca	K	Mg	C	N	Ca	K	Mg
The primary forest	*Manglietia insignis*	462	13.9	9.7	5.2	2.8	889.1	26.7	18.7	10.0	5.3
	Lithocarpus chintungensis	452	15.4	6.8	6.9	2.1	486.6	16.6	7.3	7.4	2.3
	Vaccinium duclouxii	468	11.5	8.3	5.4	3.0	420.6	10.3	7.5	4.8	2.7
	Castanopsis wattii	453	15.1	15.2	6.3	2.5	610.0	20.3	20.5	8.4	3.4
	Lithocarpus xylocarpus	477	15.8	6.7	4.0	1.7	677.1	22.4	9.6	5.7	2.4
	mean	462	14.3	9.4	5.5	2.4	694.9	22.1	17.2	8.4	3.8
The secondary forest	R1	448	17.4	11.0	5.0	2.1	174.7	6.8	4.3	21.5	45.0
	R2	468	20.1	11.9	3.8	2.2	281.0	12.1	7.1	27.1	59.7
	R3	448	20.0	10.6	4.8	2.1	255.5	11.4	6.0	29.0	60.9
	R4	449	17.0	11.1	6.0	1.8	157.3	6.0	3.9	23.3	42.0
	Mean	453	18.6	11.2	4.9	2.0	224.2	9.3	5.5	2.3	1.0

autumn and early winter appear to be a strategy to reduce nutrient losses through retranslocation to the new tissue production or storage in twigs (Fife et al. 2008). However, N showed a relative stable pattern in the primary forest, which may be significantly related to litterfall quality. The opposite phenomenon for Ca was observed, and the possible reason would be that litterfall collected in autumn was composed mainly by old litterfall, which had higher Ca concentrations than young litterfall fell in later spring and summer. Previous studies suggested that litterfall quality can be characterized by the ratio of carbon to nitrogen (C:N) since the C:N represents the balance between potentially limiting energy and nutrient resources for microbial communities (Zhou et al. 2013; Gower and Son 1992). With the available data, the most important reason may be that the litterfall in the primary forest retranslocated N to the new tissues and litterfall was mainly older leaves and twigs through the year.

Killingbeck (1996) investigated nutrient resorption proficiency based on the mean concentration of N in litterfall. It is considered that if N concentrations were lower than 0.7 %, it represents a complete resorption, but if N concentrations were higher than 1.0 %, it represents an incomplete resorption in senesced leaves in an evergreen species. Based on the results of the different tree species at two sites (Table 3) with the critical value, we found that the two forests showed incomplete N resorption. However, it is not consistent with the retranslocation as the seasonal variation in the secondary forest, and the reason may be the non-limiting (or weakly limiting) N availability at these sites.

Nutrient inputs in the primary forest are quite high, particularly for Ca, which were due to a combination of high rates of return fluxes of litterfall to the soil surface and high concentrations of nutrients in the fallen material. Such results are consistent with the high concentration of nutrients, particularly Ca, in the loamy soils of these forests (Yang et al. 2008).

Litterfall nutrient use efficiency

The LNUE was found to be element-dependent and site-dependent indicating that forest type 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 that ecosystem LNUE depends mainly on the identity of the species making up the system, but not on a considerable diversity of species per se (Tang et al. 2010). Duchesne et al. (2001) stated that woody deciduous plant species could be more efficient in nutrient transfers than evergreen plant species to avoid losing nutrients through litterfall, which is consistent with our observations of nutrient K and Mg. The LNUE of Mg and K in the present study of the primary forest is within the lower range previously reported for subtropical forests (Gonzalez-Rodriguez et al. 2011), which may reflect a slower circulation of nutrients in the primary forest. The litterfall N concentration was significantly higher in the secondary forest. However, significantly lower LNUE of N was found at the deciduous forest of the secondary forest (Table 4), which is not consistent with Duchesne et al. (2001) stated above. The reason could be that high local N deposited in this area (Zhao et al. 2013) that reduced LNUE. The influence of N deposition on litterfall N concentrations was supported by the low nitrogen use efficiency. These indicate that the excess N in the secondary forest has not been used for growth probably due to limitation of other nutrients. The LNUE of Ca was not different

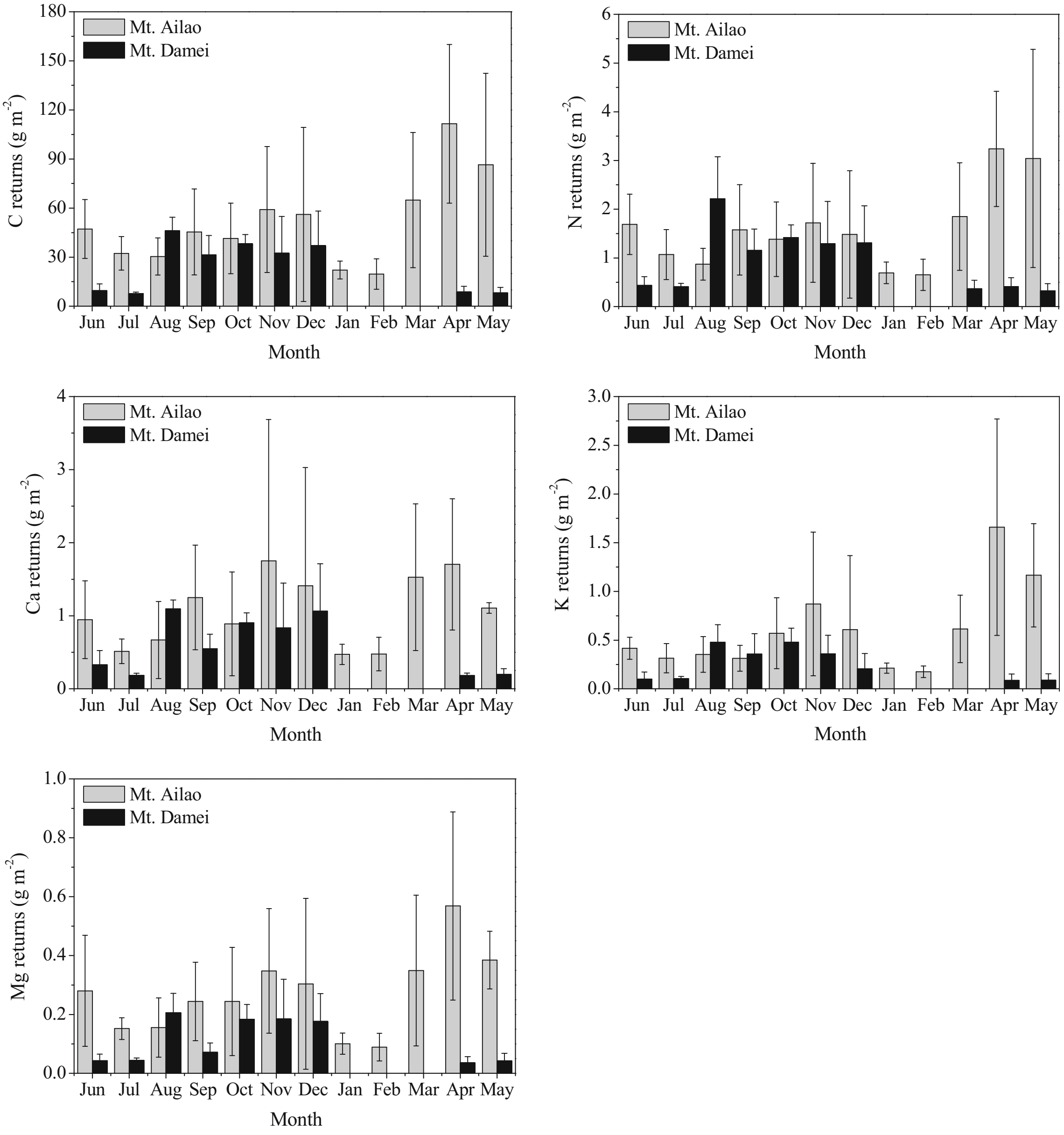

Fig. 4 Mean (±SD) monthly element inputs of litterfall at in the primary forest in Southwestern China and the secondary forest in Eastern China

Table 4 Annual means of LNUE in the primary forest in SW China and the secondary forest in East China

Forest type	C	N	Ca	K	Mg
The primary forest	2.2 ± 0.1a	70.7 ± 9.6b	116.9 ± 34.3a	186.5 ± 39.8a	431.8 ± 106.2a
The secondary forest	2.2 ± 0.1a	54.0 ± 4.8a	89.8 ± 4.4a	209.9 ± 41.5a	493.1 ± 43.6a

Different letters indicate statistically significant ($P < 0.05$) differences within each category among the two forests

between the two forests, because Ca was not retranslocated and stabled or accumulated in the foliage throughout the year (Blanco et al. 2008). These results of the present study could be used to implement site-specific management practices in different forest type responses to nutrient loss.

Conclusions

We conclude that litterfall was highly seasonal and markedly influenced by dry period of the year in these forests. The defoliation in dry period is characterized by retranslocation of significant amount of nutrients to make the trees independent for the supply of nutrients from the soil in summer. These retranslocated supplies of nutrients may be remobilized by the trees for their normal functioning. Significantly lower N use efficiency in the secondary forest compared to other elements in both study indicating a site-specific management practices that should be implemented in different forest types.

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