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4 种阔叶树种叶中氮和磷的季节动态及其转移

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摘要:从叶完全展开到生长季结束,对常绿阔叶树种日本米槠(*Castanopsis cuspidata* (Thunb.) Schottky)和具柄冬青(*Ilex pedunculosa* Miq)及落叶阔叶树种枹栎(*Quercus serrata* Murr.)和栓皮栎(*Quercus variabilis* Blume)叶片的 N 和 P 浓度、含量和养分转移进行了测定. 在生长期中日本米槠新叶的 N 浓度在 5 月为 36.6 g/kg,然后降到 15.5 和 17.5 g/kg 之间,其老叶的 N 浓度波动 于 10.4 和 13.1 g/kg 的范围内,而具柄冬青新叶的 N 浓度从 27.3 下降到 16.0 g/kg,接着上升到 18.3 g/kg,其老叶的 N 浓度在 12.0 到 15.5 g/kg 的范围内。枹栎和栓皮栎的叶 N 浓度分别从 28.8 下降到 18.1 g/kg 和从 28.5 下降到 17.5 g/kg。日本米槠新叶的 N 含量从 1.54 下降到 1.35 g/m^2,接着上升到 1.50 g/m^2,其老叶 N 含量从 1.36 下降到 1.00 g/m^2,接着上升到 1.21 g/m^2,而具柄冬青新叶的 N 含量从 2.25 下降到 1.60 g/m^2,接着上升到 2.20 g/m^2,其老叶的 N 含量从 2.13 下降到 1.65 g/m^2。枹栎和栓皮栎的叶 N 含量分别从 2.10 下降到 1.28 g/m^2和从 2.95 下降到 2.13 g/m^2。日本米槠新叶的 P 浓度由 3.39 g/kg 降到 1.12 和 1.15 g/kg 之间,其老叶的 P 浓度变化于 0.66 和 0.88 g/kg 的范围内,而具柄冬青新叶的 P 浓度从 2.39 下降到 0.69 g/kg,接着上升到 1.05 g/kg,其老叶的 P 浓度变化于 0.50 到 0.60 g/kg 之间。枹栎和栓皮栎的叶 P 浓度分别从 1.60 下降到 1.00 g/kg 和从 1.29 下降到 1.11 g/kg。日本米槠新叶的 P 含量从 0.14 下降到 0.09 和 0.10 g/m^2 之间,其老叶的 P 含量波动 于 0.06 到 0.09 g/m^2 之间,而具柄冬青新叶的 P 含量从 0.13 下降到 0.07 g/m^2,接着上升到 0.13 g/m^2,其老叶的 P 含量波动 于 0.07 到 0.09 g/m^2 之间。枹栎和栓皮栎的叶 P 含量分别从 0.09 下降到 0.07 g/m^2和在 0.13 到 0.14 g/m^2 之间变化。叶的 N 和 P 浓度随不同树种的叶的类型和取样时间不同而发生显著变化。常绿阔叶树种日本米槠新叶和具柄冬青新叶的 N 和 P 浓度高峰与其落叶高峰一致。以干重为基础的叶 N 和 P 浓度的季节变化和以叶面积为基础的叶 N 和 P 含量的季节变化模式相似。落叶阔叶树种的 N 平均转移率大于常绿阔叶树种,而它的 P 平均转移率与常绿阔叶树种相近。所有树种的 P 平均转移率大于 N 平均转移率。

关键词:常绿树种;落叶树种;氮;磷;养分转移;季节变化

Seasonal patterns in nitrogen and phosphorus and resorption in leaves of four tree species

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Abstract: The leaves of evergreen *Castanopsis cuspidata* (Thunb.) Schottky and *Ilex pedunculosa* Miq and deciduous *Quercus serrata* Murr., *Quercus variabilis* Blume were collected from the time of full leaf expansion to the end of growing season to describe the seasonal patterns of concentrations and contents of N and P in leaves of these species. N and P resorption rates from the leaves of the four species were also measured. The concentrations of N and P in leaves of deciduous *Q. serrata* and *Q. variabilis* and P concentration in new leaves of evergreen *C. cuspidata* were the highest at the first sampling data, and then tended to decrease with time, whereas N concentration in new leaves of evergreen *C. cuspidata* and concentrations of N and P in new leaves of evergreen *I. pedunculosa* decreased from maximum and then increased during the growing season. The

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changes of N and P concentrations in old leaves of *C. cuspidata* and *I. pedunculosa* were small. Both leaf type and sampling time significantly affected leaf nutrient concentrations. The maximums of N and P concentrations for new leaves of the evergreen species agree with their litter peak. The seasonal patterns of N and P concentrations on percentage of dry weight basis were generally similar to N and P contents on leaf area basis. Mean N resorption in the deciduous species was higher than in the evergreen species, whereas their P resorption was similar. There is lower resorption for N than for P, suggesting compared with N, all species translocated greater percentage P out of senescing leaves.

Key words: evergreen tree; deciduous tree; nitrogen; phosphorus; resorption; seasonal pattern

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1 Introduction

The nutrient concentration in leaves of forest trees varies during the growing season. Nutrients associated with metabolism, such as N and P, have the highest concentrations when a leaf is first produced, then decline, first as the concentration becomes diluted by increasing quantities of cell-wall material during leaf expansion, then by resorption of nutrients during senescence[1]. Studies on leaf nutrient dynamics have been used to determine resorption in forest ecosystems[2,3]. Nutrient resorption is defined as the mobilization and removal of substances from senescing plant tissues and the subsequent transport of these substances to surviving tissues[4,5]. Because N and P are nutrients that are frequently deficient and limiting to tree growth, many studies have focused on N and P resorption[6~13].

Seasonal changes of N and P concentrations in leaves of many tree species are well known, some data exist on N and P contents of leaves on an area basis[14]. Leaf dry weight increases as leaves mature due principally to accumulation of cellulose and lignin and it declines during senescence. If nutrient concentration is expressed as a percentage of dry weight, the accumulation of carbon compounds in more mature leaves and its decline in senescing leaves alter the basis of nutrient resorption comparison. After leaves have expanded fully, variation in leaf shape and size is very little, and seasonal changes in absolute amounts of N and P (on a leaf area basis) provide evidence for movement of the two nutrients to or from leaves[15], so that an accurate assessment for seasonal changes of N and P amounts and their resorption in leaves can be derived.

Plants generally resorb about half of total N and P from senescing leaves[6,9,11], and the resorption of nutrients ranges from 0 to 90% depending on habitat and species[10]. Nutrient resorption from senescing leaves may reduce dependence on soil *nutrient supply*[6,12,16,17] *and counter the effect of nutrient loss from annual litterfall*[18,19]. *Resorbed Nutrients are used to* support further plant growth[2,9,20], and resorption has been viewed as an important nutrient conserving mechanism[8,21,22].

Recently, Duchesne *et al.* researched nutrient transfers by leaf resorption, leaching and litterfall in a hardwood forest[23]. Covelo and Gallardo studied leaf nutrient resorption in recovering oak trees from harvesting pine plantations and reported the higher P resorption rate on the harvested site compared with undisturbed site[24]. Xue and Luo researched leaf nutrient resorption in a Japan Cedar stand and found a spring nutrient resorption peak and a fall nutrient resorption peak, which could be attributed to high nutrient translocation to new leaves in the spring and to translocation from old leaves before senescence in the fall[25].

Castanopsis cuspidata (Thunb.) Schottky, *Ilex pedunculosa* Miq., *Quercus serrata* Murr. and *Quercus variabilis* Blume are main evergreen broadleaved species in Japan. Nevertheless, little information exists about seasonal changes of N and P concentrations and nutrient resorption in leaves of these species. Such knowledge will be of fundamental importance in our understanding of the nutrient characteristics of these species and how we might manage and conserve nutrients.

The objectives of the present work are to (1) measure seasonal changes in N and P concentrations in leaves of *C. cuspidata*, *I. pedunculosa*, *Q. serrata* and *Q. variabilis* on a leaf dry weight basis; (2) compare these values with N and P contents expressed on a leaf area basis and (3) evaluate N and P resorption efficiencies of these species.

2 Material and methods

The two study sites were evergreen broadleaved *C. cuspidata* and evergreen and deciduous broadleaved secondary forests in the eastern suburbs of Nagoya, Japan (35°10′N, 136°58′E) in a warm temperate climate. Mean annual temperature, monthly mean minimum temperature (January) and monthly mean maximum temperature (August) are 15, 3.7 and 27.1℃, respectively. Mean annual rainfall is 1259 mm, occurring mainly between April and August. The *C. cuspidata* forest occurred on a 24° southeast-facing slope on soil developed from the Quaternary deposits. *Castanopsis cuspidata* formed dense, closed canopies with its leaf area distributed mainly in the upper canopy. The sparse understory was dominated by *I. pedunculosa*, *Cleyera japonica* Thunb. and *Eurya japonican* Thunb. The evergreen and deciduous broadleaved secondary forest occurred on a 20° northwest-facing slope on soil developed in the Quaternary deposits. The forest is dominated by deciduous broadleaved *Q. serrata*, in association with evergreen broadleaved *I. pedunculosa* and deciduous broadleaved *Q. variabilis* (basal area of 13.5, 8.2 and 2.3 m^2/hm^2, respectively). Maximum rates of litterfall occur in May for *C. cuspidata*, in April and October for *I. pedunculosa*, and in December for *Q. serrata* and *Q. variabilis*.

Five individuals of each species were selected for the study. Sampling of green leaves was conducted from the time of full leaf expansion to the end of the growing season in 1996, which was from May 25 to November 25 for the evergreen species, and from May 15 to November 25 for the deciduous species. A crane was used for sampling. Leaves were collected from different crown positions of each crown. Leaf collection was consistent among these selected individuals. On each of four sampling dates, approximately 20 leaves/tree were collected, and each sampling was replicated three times and the difference in leaf weight among three replications was smaller than 15 percent. The leaves from the evergreen species were divided into new leaves (<1-year old) and old leaves (≥ 1-year old). Leaf area was measured with an area meter (AAC 100, Hayashi, Japan). A 1-m^2 litter trap was placed under each of the selected trees to collect litterfall. Litterfall was harvested once every two weeks. The traps consisted of a frame with a nylon mesh screen bottom, positioned 30 cm above the ground.

Both green leaf and fallen leaf samples were oven-dried at 85℃ for 48 hours, and weighed after 24 h, and then ground with a vibrating sample mill. Subsamples were analyzed for N on a C-N analyzer (MT 500, Yanagimoto MFG. Co., Kyoto, Japan). For P analyses, subsamples were wet digested with HNO_3-HCL-$HCLO_4$-HF, and then determined by phosphomolybdic blue colorimetric method[26,27]. Nutrient resorption from senescing leaves was calculated as the difference between the highest value of nutrient content found in green leaves on a leaf area basis and the value of nutrient content in leaf litter on a leaf area basis. Nutrient resorption efficiency was calculated as the value of nutrient resorption divided by the highest value of nutrient content of green leaves on a leaf area basis[9,10,24,25].

Significance of nutrient concentrations within leaf type or sampling time was tested by two-way analysis of variance (ANOVA). In cases where there was a significant leaf type or sampling time effect, this was followed by Duncan multiple-comparison test.

3 Results

Both leaf type and sampling time significantly affected leaf nutrient concentrations (Table 1). The variance of nutrient concentrations for leaf type (F=3.14～21.88) was generally greater than that for sampling time (F=4.12～7.95). During the whole year, the greater difference of N and P concentrations was found in different leaf type compared with sampling time, this could results in a more significant different level of nutrient concentration for leaf type than for sampling time.

Table 1 A two-way analysis of variance (ANOVA) on nutrient concentrations of leaf type and sampling time

	Source of variation	df	SS	MS	F-value	p level
N (g/kg)	Leaf type	5	481.5900	96.3180	7.34	* *
	Sampling time	3	313.1633	104.3878	7.95	* *
	Error	15	196.8467	13.1232		
N (g/m^2)	Leaf type	5	5.0221	1.0044	21.88	* *
	Sampling time	3	0.5680	0.1893	4.12	*
	Error	15	0.6886	0.0459		
P (g/kg)	Leaf type	5	3.3102	0.6620	3.14	*
	Sampling time	3	2.7051	0.9017	4.28	*
	Error	15	3.1591	0.2106		
P (g/m^2)	Leaf type	5	0.0113	0.0023	11.50	* *
	Sampling time	3	0.0029	0.0010	5.00	*
	Error	15	0.0028	0.0002		

The significant levels are given by: * $p<0.05$ and * * $p<0.01$.

New leaves of *C. cuspidata* showed a high N concentration of 36.6 g/kg in May and then varied between 15.5 and 17.5 g/kg (Fig. 1). N concentration in new leaves of *I. pedunculosa* declined from 27.3 to 16.0 g/kg and then rose to 18.3 g/kg. By contrast, a relatively stable pattern for N concentration was observed in old leaves for the two evergreen species, and leaf N concentration ranged from 10.4 to 13.1 g/kg in *C. cuspidate* and from 12.0 to 15.5 g/kg in *I. Pedunculosa*. For the deciduous species, leaf N concentration decreased from 28.8 to 18.1 g/kg in *Q. serrata* and from 28.5 to 17.5 g/kg in *Q. variabilis*.

N concentration (g/kg) was high in new leaves and low in old leaves for both evergreen species. N concentration of old *C. cuspidata* leaves was very significantly lower than those of *Q. serrata* and *Q. variabilis* leaves ($p<0.01$) and significantly lower than those of new *C. cuspidata* and *I. pedunculosa* leaves ($p<0.05$). N concentration of old *I. pedunculosa leaves* was significantly lower than those of *Q. serrata* and *Q. variabilis* leaves ($p<0.05$). Leaf N concentration in May was very significantly and significantly higher than those in November ($p<0.01$) and in September ($p<0.05$).

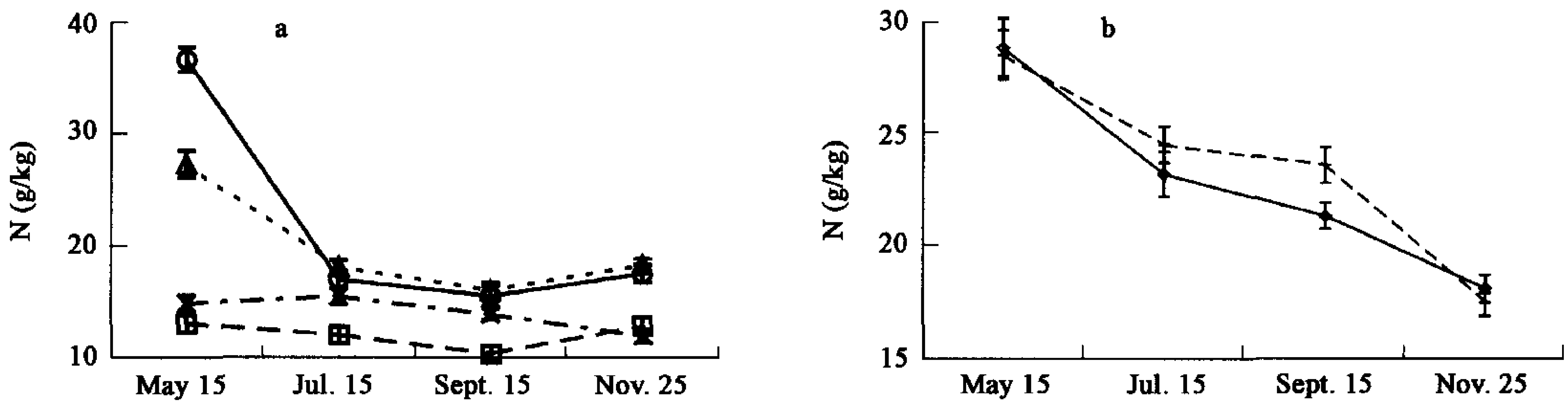

Fig. 1 Seasonal patterns of N concentration in leaves on leaf dry weight basis (g/kg)

(a) evergreen species: ○, new leaves of *Castanopsis cuspidata*; □, old leaves of *Castanopsis cuspidata*; △, new leaves of *Ilex pedunculosa*; ×, old leaves of *Ilex pedunculosa*; (b) deciduous species: ◇, leaves of *Quercus serrata*; +, leaves of *Quercus variabilis*. Mean ±SE, $n=5$ trees

N content in new leaves of *C. cuspidate* declined slightly from 1.54 to 1.35 g/m^2 and then rose to 1.50 g/m^2, whereas in new leaves of *I. Pedunculosa* it declined from 2.25 to 1.60 g/m^2 and then rose to 2.20 g/m^2(Fig. 2). N content declined from 1.36 to 1.00 g/m^2 and then rose to 1.21 g/m^2 in old leaves of *C. cuspidata* and decreased from 2.13 g/m^2 to 1.65 g/m^2 in old leaves of *I. peduncul0sa*. Leaf N content decreased from 2.10 to 1.28 g/m^2 in *Q. serrata* and from 2.95 to 2.13 g/m^2 in *Q. variabilis*.

Leaf N content of *I. pedunculosa* was higher than that of *C. cuspidata* throughout the growing season. Leaf N content of *Q. variabilis* was very significantly higher than leaf N contents of other species ($p<0.01$), and new and old leaf N contents of *C. cuspidata* were very significantly and significantly lower than those of *I. pedunculosa* ($p<0.01$ or $p<0.05$) and leaf N contents of *Q. serrata* ($p<0.05$). A significant difference of leaf N content existed between leaves in May and in November ($p<0.05$).

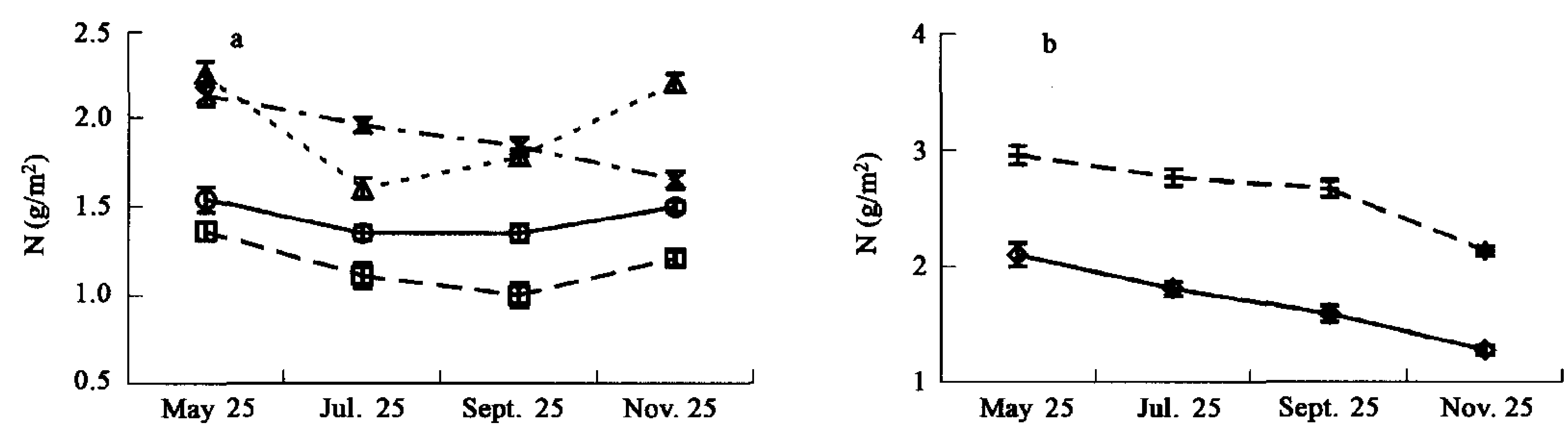

Fig. 2 Seasonal patterns of N content in leaves expressed on leaf area basis (g/m^2)

(a) evergreen species: ○, new leaves of *Castanopsis cuspidata*; □, old leaves of *Castanopsis cuspidata*; △, new leaves of *Ilex pedunculosa*; ×, old leaves of *Ilex pedunculosa*; (b) deciduous species: ◇, leaves of *Quercus serrata*; +, leaves of *Quercus variabilis*. Mean±SE, $n=5$ trees

The seasonal pattern of P concentration (g/kg) for each evergreen species was generally similar to that of nitrogen concentration (Fig. 1), but was consistently low during the growing season (Fig. 3). P concentration in new leaves of *C. cuspidata* initially decreased from a maximum of 3.39 g/kg, and then fluctuated between 1.12 to 1.15 g/kg, whereas in new leaves of *I. pedunculosa*, it declined from a maximum of 2.39 to 0.69 g/kg and then rose to 1.05 g/kg. P concentrations fluctuated between 0.66 and 0.88 g/kg in old leaves of *C. cuspidata* and between 0.50 and 0.60 g/kg in old leaves of *I. pedunculosa*. There was a steady decrease in leaf P concentration in *Q. serrata* from 1.60 g/kg in May to 1.00 g/kg in November, whereas in *Q. variabilis* it decreased gradually from 1.29 to 1.11 g/kg throughout the growing season.

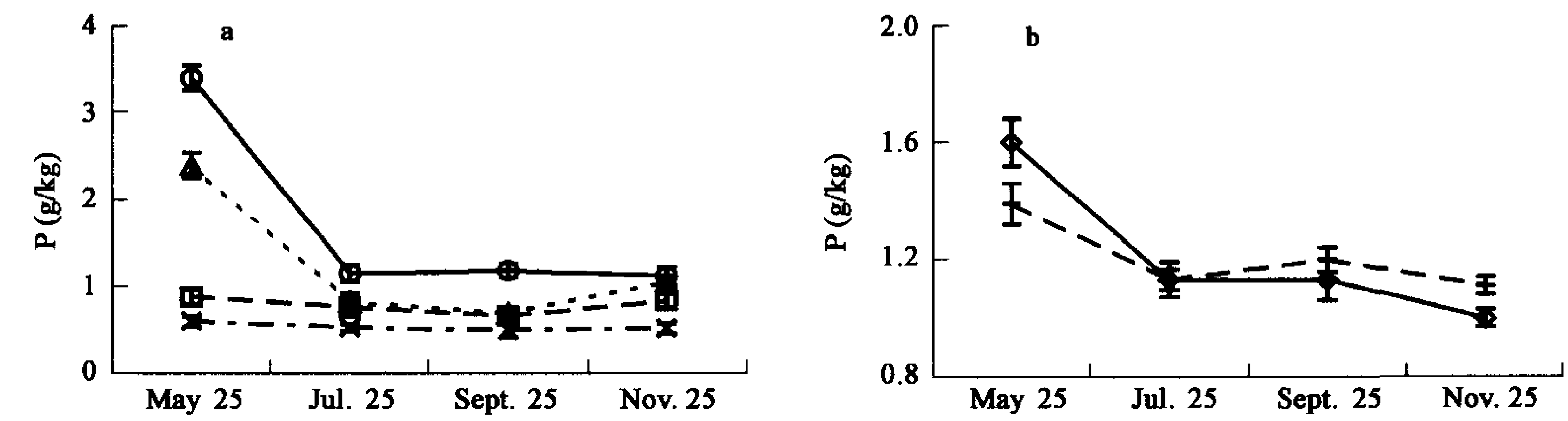

Fig. 3 Seasonal patterns of P concentration in leaves on leaf dry weight basis (g/kg)

(a) evergreen species: ○, new leaves of *Castanopsis cuspidata*; □, old leaves of *Castanopsis cuspidata*; △, new leaves of *Ilex pedunculosa*; ×, old leaves of *Ilex pedunculosa*; (b) deciduous species: ◇, leaves of *Quercus serrata*; +, leaves of *Quercus variabilis*. Mean ±SE, $n=5$ trees

P concentrations for new and old leaves of *C. cuspidata* were respectively higher than those of *I. pedunculosa* during the growing season. P concentration of new *C. cuspidata* leaves was significantly higher than that of old *I. pedunculosa* leaves ($p<0.05$). Leaf P concentration in May was significantly higher than those in November and in September ($p<0.05$).

P content in new leaves of *C. cuspidata* decreased from 0.14 g/m^2, and then varied between 0.09 and 0.10 g/m^2, while in new leaves of *I. pedunculosa*, it declined from 0.13 to 0.07 g/m^2 and then rose to 0.13 g/m^2(Fig. 4). The season pattern of P content in old leaves of each evergreen species was similar to that of N content (Fig. 2), but changes in content were less pronounced. P content fluctuated between 0.06 and 0.09 g/m^2 in old leaves of *C. cuspidata* leaves and between 0.07 and 0.09 g/m^2 in old leaves of *I. pedunculosa*. Leaf P content in *Q. serrata* decreased gradually from 0.09 to 0.07 g/m^2, whereas in *Q. variabilis* it remained a more or less stable level, which ranged from 0.13 to 0.14 g/m^2 throughout the growing season.

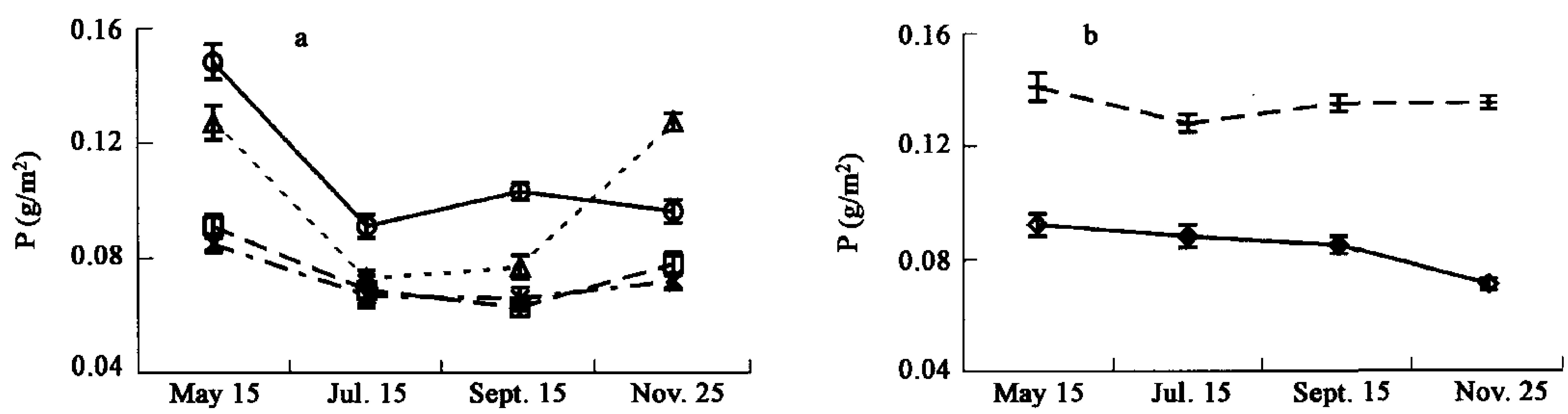

Fig. 4 Seasonal patterns of P concentration in leaves expressed on a leaf area basis (g/m^2)

(a) evergreen species: ○, new leaves of *Castanopsis cuspidata*; □, old leaves of *Castanopsis cuspidata*; △, new leaves of *Ilex pedunculosa*; ×, old leaves of *Ilex pedunculosa*; (b) deciduous species: ◇, leaves of *Quercus serrata*; +, leaves of *Quercus variabilis*. Mean±SE, $n=5$ trees

New leaves contained more P than old leaves in unit area for the evergreen species. P content of *Q. variabilis* leaves was very significantly higher than those of *Q. serrata* leaves and old *C. cuspidata* and *I. Pedunculosa* leaves ($p<0.01$) and significantly higher than that of new *I. Pedunculosa* leaves ($p<0.05$). P content of new *C. cuspidata* leaves was significantly higher than those of old *C. cuspidata* and *I. Pedunculosa* leaves ($p<0.05$). Leaf P content in May was significantly higher than those in November and in September ($p<0.05$).

Maximum green leaf N content varied from 1.54 g/m^2 in *C. cuspidata* to 2.95 g m^{-2} in *Q. variabilis* (Table 2). Except for a low value of 0.09 in *Q. serrata*, maximum green leaf P content of other species was between 0.13 and 0.15 g/m^2. Litter N content for the four tree species ranged from 0.71 to 1.01 g/m^2, and litter P concentration for the four species was 0.02 g/m^2 for *Q. serrata* and 0.03 g/m^2 for the other species. The deciduous species resorbed greater amounts of N (1.39, 1.90 g/m^2) than did the evergreen species (0.66, 1.15 g/m^2). Except for a low value of 0.07 g/m^2 in *Q. serrata*, resorbed amounts of P for the other species was between 0.10 and 0.12 g/m^2. The evergreen species resorbed 43 and 51% of maximum leaf N, which were lower than did the deciduous species (66 and 64%). P resorption efficiency was very significantly greater than N resorption efficiency ($p<0.01$), ranging from 77 to 80% for the four species.

4 Discussion

N content in leaves of the deciduous species and in old leaves of *I. Pedunculosa* as well as P content in leaves of *Q. serrata* were the highest at the first sampling data, and then decreased with time, whereas N and P contents decreased from maximum and then increased for in new leaves of the evergreen *I. Pedunculosa* and in old leaves of *C. cuspidata* (Fig. 2 and Fig. 4). Chapin[28] interpreted that the seasonal decline in N and P concentrations (g/kg) in leaves of deciduous species is due initially to the diluting effect of cell wall material being accumulated more rapidly than cell contents and later to translocation nutrients out of leaves, whereas the seasonal decline in N and P concentrations in evergreen species is due entirely to dilution by cell walls. If the decline in N and P concentrations in leaves of deciduous species is divided into two phases, the first occurs during leaf expanding period. During this phase, decline of N and P concentrations in leaves may be caused by the diluting effect. The second phase of decline of N and P occurs during the period from the leaves being fully expanded to senescence. During the second phase, N and P are translated out of leaves, which is the case showed in this study. The reasons for the seasonal decline in N and P concentrations in leaves of evergreen species are more complicated than Chapins' suggestion. The facts that N and P contents in new leaves of *I. peduncuIosa* decrease and then increase and N content decreases in old leaves of *I. Pedunculosa* during the growing season (Figs. 2 and 4) indicate that seasonal changes in N and P concentrations (g/kg) in leaves of evergreen species are not only due to the diluting effect, but also due to N and P translocation.

Table 2　Nutrient contents in mature leaves and litter, and nutrient resorption. Nutrient contents are the quantity of nutrients per unit leaf area

	Castanopsis cuspidata	*Ilex pedunculosa*	*Quercus serrata*	*Quercus variabilis*
Maximum leaf nutrient content (g/m^2)				
Nitrogen	1.54	2.25	2.10	2.95
Phosphorus	0.15	0.13	0.09	0.14
Litter nutrient content (g/m^2)				
Nitrogen	0.88	1.10	0.71	1.05
Phosphorus	0.03	0.03	0.02	0.03
Nutrient amount resorbed (g/m^2)				
Nitrogen	0.66	1.15	1.39	1.90
Phosphorus	0.12	0.10	0.07	0.11
Nutrient resorption efficiency (% of maximum leaf nutrient content)				
Nitrogen	43	51	66	64
Phosphorus	80	77	78	79

The maximums of N and P concentrations for new leaves of the evergreen species agree with their litter peak. The *C. cuspidata* has a litter peak in May, whereas it occurs in April and October for *I. Pedunculosa*[29], so that higher N and P concentrations occur in May for *C. cuspidata* and in May and November for *I. pedunculosa*, respectively. This indicates that a great amount of nutrient is translocated into new leaves during litter peak. N and P translocated into new leaves could be used for the demand of for production of new leaves at litter peak, whereas N and P at other time translocated from leaves move into developing fruits or support root growth as well as replenishing stores due to the asynchrony of growth of different plant parts[28].

N is gradually translated out of leaves for deciduous species (Fig. 2). However, from the end of the growing season (November) to the litter peak, N translocation accelerates, so that N content drops from 1.28 g/m^2 in green leaves to 0.71 g/m^2 in litter for *Q. serrata* and from 2.13 g/m^2 in green leaves to 1.05 g/m^2 in litter for *Q. variabilis*, respectively, causing 41% and 57% of total amount of N translocation for *Q. serrata* and *Q. variabilis*, respectively. This indicates the time prior abscission of the leaves is a main period of N translocation for the deciduous species. Although the decline trend of P content is not so clear as N concentration during growing season (Fig. 4), it drops faster than N during senescence. The 71% and 89% of the total amount of P translocation are moved out of leaves at the time prior abscission of the leaves, demonstrating main P translocation occur at this time.

N resorption from senescing leaves differs between the evergreen and deciduous species. Mean N resorption in the evergreen species is lower than in the deciduous species (Table 2), this is consistent with a conclusion proposed by Lamber *et al.*[1]. N resorption efficiency is always lower than P resorption (Table 2). This is in agreement with results of other studies[13,30]. The higher P resorption efficiency suggests that compared with N, all species translate greater percentage P out of leaves. This high P resorption may be a response to low P environments[12]. About half of the N and 80% of the P contained in mature leaves are resorbed, suggesting that nutrient resorption is an important nutrient conservation mechanism.

The seasonal patterns of N and P concentrations on dry weight basis are generally similar to those on leaf area basis (Fig. 1~Fig. 4). This is in agreement with the study in three miombo tree species conducted by Ernst[31]. The seasonal patterns of N and P contents on leaf area basis are affected by resorption, whereas the seasonal patterns of N and P concentrations on percentage of dry weight basis are commonly affected by resorption and change of leaf dry weight. For example, on leaf area basis, the ratio of N content of *Q. serrata* to that of *Q. variabilis* increases from 86% to 100% during the growing season (Fig. 1), indicating the decline in leaf N content of *Q. serrata* is slower than that of *Q. variabilis*. On percentage of dry weight basis, it decreases from 71% to 60%, indicating the increase in leaf dry weight of *Q. serrata* is faster than that of *Q. variabilis*. Although increase in leaf dry weight cause different changes in the leaf N concentration (g/kg) for the two species, the effect of leaf dry weight is not great enough to cause the seasonal patterns of N and P concentrations on dry weight basis to be different from N and P contents on leaf area basis.

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