

Research paper

Dynamics of Foliar Nutrients in Major Species of a Broadleaf Forest in the Fushan Experimental Forest, Northeastern Taiwan

Erh-Yang Lu,^{1,3)} Yu-Yen Liu,¹⁾ Chiang-Her Yen²⁾

【 Summary 】

This study was carried out in a subtropical rainforest of the Fushan Experimental Forest, one of the long-term ecological study sites in Taiwan. The forest is mainly composed of hardwood species of Lauraceae, Fagaceae, and other families, including 8 major species investigated in this study, *Phoebe formosana* (Phfo), *Litsea acuminata* (Liac), *Machilus thunbergii* (Math), *Castanopsis cuspidata* var. *carlesii* f. *sessilis* (Cacu), *Pasania hancei* var. *ternaticupula* f. *ternaticupula* (Paha), *Oreocnide pedunculata* (Orpe), *Meliosma squamulata* (Mesq), and *Pyrenaria shinkoensis* (Pysh). Orpe, the only shrub in this study, was mainly found in the valley along with Phfo. The other 6 tree species grow on the hillsides and hilltops. This study investigated the concentrations and seasonal patterns of foliar nutrients in these species and the relationship between foliar nutrients and soil properties. The concentrations of N and P in 1-yr-old leaves were also used to estimate the resorption rates of N and P.

Foliar nutrient concentrations significantly differed among the 8 species. Orpe, the valley shrub, had higher foliar nutrient concentrations than the other species. Among the 3 species of Lauraceae, Phfo, a valley tree, also had higher foliar N, P, and K levels than Liac and Math. The significant differences in soil properties between the hillside/hilltop and the valley may have contributed to differences in the foliar nutrient composition among species from different topographic locations.

Foliar concentrations of N, P, and K usually decreased and foliar Ca increased as the leaves aged. The seasonal patterns of foliar Mg concentrations differed among species. The foliar concentrations of N, P, K, Ca, and Mg consistently dropped 1 mo after leaf emergence, suggesting the dilution effect of leaf expansion. Nitrogen concentrations in 1-yr-old leaves ranged between 1.12 and 3.02%, and P concentrations between 0.05 and 0.06%. Comparisons with the general thresholds of resorption proficiency suggested that within 1 yr, P was resorbed more completely than N. Therefore, P is probably more limited in the Fushan forest.

Key words: Fushan experimental forest, foliar nutrients, seasonal pattern, topography, nutrient resorption.

¹⁾ School of Forestry and Resource Conservation, National Taiwan University, 1 Roosevelt Rd., Sec. 4, Taipei 10617, Taiwan. 國立台灣大學森林環境暨資源學系, 10617台北市羅斯福路四段1號。

²⁾ Department of Forestry, National Chung Hsing University, 250 Kuo-kuang Rd., Taichung 40227, Taiwan. 國立中興大學森林系, 40227台中市南區國光路250號。

³⁾ Corresponding author, e-mail:erhyang@ntu.edu.tw 通訊作者。

Received January 2007, Accepted June 2007. 2007年1月送審 2007年6月通過。

Lu EY, Liu YY, Yen CH. 2007. Dynamics of foliar nutrients in major species of a broadleaf forest in the Fushan experimental forest, northeastern Taiwan. *Taiwan J For Sci* 22(3):307-19.

研究報告

福山試驗林闊葉林重要樹種葉部養分動態研究

鹿兒陽^{1,3)} 劉育延¹⁾ 顏江河²⁾

摘要

本研究於福山試驗林進行，該天然闊葉林主要組成爲樟科、殼斗科及其他科的植物，本研究涵蓋了其中8種主要植物(台灣雅楠、長葉木薑子、紅楠、鋸葉長尾桫、三斗石櫟、長梗紫芋麻、綠樟、烏皮茶)。其中唯一的灌木長梗紫芋麻與台灣雅楠主要生長於溪谷，其他樹種則分布在中坡及稜線上。本研究的目的在了解這些樹種間及季節間的養分濃度變化，並探討養分與土壤特性的關係，此外以一年生葉部的氮、磷濃度來評估養分再吸收作用。

8種植物之間的葉部養分有顯著的差異，生長在溪谷的灌木長梗紫芋麻葉部養分濃度較其他木本植物爲高。三種樟科植物中，以生長在溪谷的雅楠葉部有較高的N、P、K。除了樹種本身遺傳因子所造成的差異之外，溪谷及中坡/稜線間土壤特性的差異也可能是造成樹種葉部養分組成差異的主因。

8種主要樹種葉部的N、P與K濃度均隨著葉齡增加而減少，相反的，葉部Ca濃度均隨著葉齡增加而上升，葉部Mg濃度在樟科植物(台灣雅楠、長葉木薑子、紅楠)與綠樟會隨著葉齡增加而上升，但是在殼斗科植物(鋸葉長尾桫、三斗石櫟)與烏皮茶卻在不同葉齡間卻無明顯變化趨勢。4月29日到6月3日間は葉部開展成熟階段，稀釋效應可能是此時期植物葉部養分濃度下降的主因。8種樹種一年生葉部的氮濃度在1.12及3.02%之間，磷濃度則在0.05及0.06%之間，以一般再吸收度(resorption proficiency)的臨界值評估後發現磷的再吸收較氮的再吸收完全，顯示在福山試驗林中磷爲生長較重要的限制因子。

關鍵詞：福山試驗林、葉部養分、季節變化形式、地形、養分再吸收。

鹿兒陽、劉育延、顏江河。2007。福山試驗林闊葉林重要樹種葉部養分動態研究。台灣林業科學 22(3):307-19。

INTRODUCTION

Nutrients are essential to the health and productivity of plants in forest ecosystems. Foliar nutrient dynamics is a topic of special interest since foliar nutrient concentrations often change with time. Mobile nutrients like N, P, and K can be resorbed through phloem and thus decrease in aging leaves, whereas immobile nutrient like Ca often accumulate with time (Chapin et al. 1980, Chapin and Kedrowski 1983, Ralhan and Singh 1987, Orgeas et al. 2002, López-Serrano et al. 2005).

In addition to nutrient resorption, dilution and leaching also contribute to reductions in nutrient concentrations of aging leaves (Chapin 1980, Hagen-Thorn 2006). However, nutrient resorption has been considered the most important mechanism in nutrient conservation, and thus has been investigated and discussed in many recent studies (Aerts 1996, Killingbeck 1996, Aerts and Chapin 2000, Wright and Westoby 2003, Milla et al. 2005, Singh et al. 2005, Yuan et al. 2005a, Hagen-

Thorn 2006). Nutrient resorption appears to vary, depending on characteristics of species (Ralhan and Singh 1987, Aerts 1996, Yuan et al. 2005a) and soil fertility (Ralhan and Singh 1987, Pensa and Sellin 2003, Wright and Westoby 2003, Martínez-Sánchez 2005, Richardson et al. 2005, Singh et al. 2005, Yuan et al. 2005b).

In this study, we investigated 8 major plant species at the Fushan Experimental Forest to determine (1) differences in foliar nutrient compositions among species, (2) seasonal patterns of foliar nutrients for each species, (3) differences in nutrient resorption among species, and (4) the correlation between resorption and soil fertility in different topographic locations. In addition, we provide suggestions regarding the timing of leaf sampling for foliar nutrient analysis of tree species in north-eastern Taiwan.

MATERIALS AND METHODS

Study site

The study site is located in the Fushan Experimental Forest, a Long-Term Ecological Research (LTER) site in northeastern Taiwan (24°45'N, 121°35'E). The elevations range between 500 and 1400 m. Fushan belongs to an everwet climate without apparent dry periods (Su 1985). From 1993 to 2000, the average annual temperature was 18.2°C, the average monthly temperature ranged from 12.0°C in January to 24.0°C in July, and the average annual precipitation was 4225 mm. According to Lin et al. (1996), in Fushan, the soil of the hillsides and hilltops was classified as Hapludults and the soil of the valley as Udipsamments.

Soil sampling

The surface soil (0~10 cm, humus excluded) was sampled from 3 topographic

locations (valley, hillside, and hilltop). At each topographic location, 3 plots of 25 × 25 m were established. Within each plot, 3 subsamples were randomly taken to make a composite sample. Subsamples were taken at least 3 m from the edge of the plot and at least 5 m apart.

Plant sampling

This study included 8 major species of the Fushan Experimental Forest, *Oreocnide pedunculata* (Shirai) Masamune (Orpe), *Phoebe formosana* (Hayata) Hayata (Phfo), *Machilus thunbergii* Sieb. & Zucc. (Math), *Litsea acuminata* (Bl.) Kurata (Liac), *Castanopsis cuspidata* (Thunb. ex Murray) Schottky var. *carlesii* (Hemsl.) Yamazaki f. *sessilis* (Nakai) Liao (Cacu), *Pasania hancei* (Benth.) Schottky var. *ternaticupula* (Hayata) Liao f. *ternaticupula* (Paha), *Pyrenaria shinkoensis* (Hayata) Keng (Pysh), and *Meliosma squamulata* Hance (Mesq). Orpe is the only shrub in the study and the other 7 are trees. Orpe and Phfo are found in the valley, and the other species are on the hillsides and hilltops. We sampled leaves from individual trees with DBH (diameter at breast height) larger than 10 cm with the exception of Orpe. Being a shrub, Orpe's DBH rarely reached 10 cm. Generally 2 to 3 shoots were taken from each tree to make a leaf sample for nutrient analysis. On each sampling date, 7 to 18 individual trees were sampled for each species, and these individuals were not always the same to avoid over-sampling some smaller trees.

Leaves were sampled 4 times from April 2005 to November 2005. The first sampling was done on 29 April, when young leaves had begun to expand on the new shoots. The current year's shoots were then sampled again on 3 June, 11 August, and 6 November. The leaves sampled on these 4 dates were

sequentially aged, roughly 1, 2, 4, and 7 mo old, since they had all emerged from breaking buds in the spring (late March to early April) of 2005. On 29 April, we also sampled 1-yr-old leaves which had emerged from breaking buds in the spring of the previous year (2004).

Chemical analyses of soil and leaf samples

Soil samples were thoroughly air-dried and then sieved through 2-mm meshes. The air-dried soil samples were analyzed for soil texture (Gee and Bauder 1986), pH (McLean 1982), total nitrogen (Bremner and Mulvaney 1982), organic matter (SOM) (Nelson and Sommers 1982), available-P (Olsen and Sommers 1982), exchangeable K, Na, Ca, and Mg, and cation exchange capacity (CEC) (Rhoades 1982); base saturation (BS) was estimated using exchangeable cations and CEC.

Leaf samples were rinsed with distilled water and then oven-dried at 80°C until a constant weight was reached. The oven-dried samples were analyzed for nitrogen (N) using the total Kjeldahl method, and for phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) using inductively coupled plasma spectrometry (ICPS) (Moore and Chapman 1986).

Data analysis

Data were analyzed by analysis of variance (ANOVA) to determine whether soil properties significantly differed among the topographic locations and whether the nutrient foliar concentrations significantly differed among species and sampling dates. When a significant difference was detected ($p < 0.05$, by the *F*-test) among the means of 1 parameter, multiple comparisons using the protected least significant difference ($\alpha = 0.05$) were performed to compare and rank the means of this parameter.

RESULTS

Soil properties

Table 1 lists the soil properties of the surface soil (0~10 cm) at 3 topographic locations. Most soil properties significantly differed among topographic locations ($p < 0.05$). Compared to the soil in the valley, those on the hillside and hilltop had lower sand percentage, pH, available-P, exchangeable K, Ca, Mg, and BS, and higher clay percentage, SOM, total N, and CEC.

Foliar nutrient concentrations

Specific variations

Foliar nutrient concentrations significantly differed among species (Table 2). The data of mature leaves collected in June, August, and November were combined in the comparison of foliar nutrient concentrations among species (Table 3). The data collected in April was excluded from the comparison because newly emerged leaves had not yet expanded and thus had exceptionally high nutrient concentrations. Among the 8 species, Orpe had significantly higher foliar N concentration, followed by Paha and Phfo (Table 3). Orpe and Phfo had similar foliar concentrations of P and K, which were significantly higher than those of the other 6 species. Orpe also had significant higher concentrations of Ca and Mg than those of the other 7 species.

Seasonal patterns

The foliar nutrient concentrations also significantly differed among sampling dates (Table 2). The seasonal patterns of foliar N, P, K, Ca, and Mg for the 8 species are shown in Figs. 1~5. Foliar concentrations of N were highest on 29 April, had dropped sharply by 3 June, and remained somewhat constant thereafter. Foliar concentrations of P were also highest on 29 April and had dropped sharply by 3 June. However, in most species, foliar P

Table 1. Soil properties (0–10 cm) of 3 topographic locations at the study site¹⁾

Treatment	Particle size (%)			pH _{water}	pH _{KCl}	SOM	Total N
	Sand	Silt	Clay				
Valley	63.7 ^a (0.9)	23.9 ^a (1.5)	12.4 ^b (0.9)	5.47 ^a (0.13)	4.20 ^a (0.19)	2.49 ^b (0.85)	0.09 ^b (0.03)
Hillside	46.0 ^a (18.9)	24.7 ^a (11.6)	29.4 ^a (7.6)	4.51 ^b (0.16)	3.57 ^b (0.12)	5.09 ^a (0.53)	0.30 ^a (0.03)
Hilltop	22.0 ^b (6.4)	38.1 ^a (0.8)	39.9 ^a (7.2)	4.52 ^b (0.18)	3.67 ^b (0.09)	6.05 ^a (0.60)	0.39 ^a (0.07)
<i>p</i> > <i>F</i>	0.0127	0.0719	0.0041	0.0004	0.0028	0.0016	0.0006

¹⁾ Data are presented as the mean with standard deviation in parenthesis. Means in a column followed by different letters significantly differ at $\alpha = 0.05$.

Table 1. Soil properties (0–10 cm) of 3 topographic types at the study site¹⁾ (continued)

Treatment	Available-P	Exch. K	Exch. Na	Exch. Ca	Exch. Mg	CEC	BS
	mg kg ⁻¹						
Valley	7.19 ^a (0.62)	0.10 ^a (0.03)	0.15 ^a (0.15)	1.99 ^a (0.31)	0.56 ^a (0.07)	9.65 ^b (1.57)	29.91 ^a (8.28)
Hillside	1.20 ^b (0.25)	0.04 ^b (0.01)	0.08 ^a (0.11)	0.02 ^b (0.02)	0.09 ^b (0.02)	20.65 ^a (1.56)	1.13 ^b (0.53)
Hilltop	1.70 ^b (0.10)	0.06 ^{ab} (0.02)	0.10 ^a (0.05)	0.06 ^b (0.07)	0.11 ^b (0.03)	21.85 ^a (2.55)	1.54 ^b (0.25)
<i>p</i> > <i>F</i>	< 0.0001	0.0335	0.7414	< 0.0001	< 0.0001	0.0005	0.0005

¹⁾ Data are presented as the mean with standard deviation in parenthesis. Means in a column followed by different letters significantly differ at $\alpha = 0.05$. Exch., exchangeable; CEC, cation exchange capacity; BS, base saturation; SOM, soil organic matter.

continued to decrease afterwards.

For all but 1 species (Phfo), foliar concentrations of K were highest on 29 April, and then decreased with time. For Phfo, foliar K differed little among sampling dates. Foliar concentrations of Ca generally increased with time. For Phfo, Liac Cacu, and Paha, however, foliar Ca concentrations were slightly lower on 3 June than on 29 April.

For most species, foliar concentrations of Mg were lower on 3 June than on 29 April. After 3 June, foliar Mg concentrations either went up (Phfo, Liac, Math, and Mesq) or remained constant (Cacu, Paha, and Pysh). By

contrast, Orpe was the only species with a continual increase in foliar Mg concentration after 29 April.

For most species, nutrient concentrations in 1-yr-old leaves (from the previous year's buds) were quite similar to those in the current year's leaves sampled on 6 November.

DISCUSSION

Specific variations

This study found significant differences in nutrient compositions among the 8 species (Table 2). Similar results of species differences

Table 2. Analysis of variance on the effects of species and sampling dates on foliar elemental concentrations

Element	Factor	df	F	p value
N	Species	6	419	< 0.0001
	Date	3	202	< 0.0001
	Species x Date	27	13	< 0.0001
P	Species	6	165	< 0.0001
	Date	3	417	< 0.0001
	Species x Date	27	6	< 0.0001
K	Species	6	142	< 0.0001
	Date	3	140	< 0.0001
	Species x Date	27	4	< 0.0001
Ca	Species	6	771	< 0.0001
	Date	3	100	< 0.0001
	Species x Date	27	6	< 0.0001
Mg	Species	6	1157	< 0.0001
	Date	3	20	< 0.0001
	Species x Date	27	9	< 0.0001

df, degrees of freedom.

Table 3. Foliar nutrient concentrations (% dry weight) of 8 species with combined data from June, August, and November¹⁾

Species	n	N	P	K	Ca	Mg
Phfo	27	2.05 ^c ± 0.19	0.21 ^a ± 0.04	1.60 ^b ± 0.40	0.54 ^b ± 0.27	0.12 ^{cd} ± 0.03
Liac	54	1.70 ^d ± 0.16	0.08 ^c ± 0.02	0.88 ^c ± 0.25	0.28 ^d ± 0.15	0.10 ^e ± 0.03
Math	54	1.33 ^f ± 0.15	0.07 ^d ± 0.02	0.72 ^d ± 0.26	0.35 ^c ± 0.12	0.13 ^c ± 0.03
Cacu	54	1.47 ^e ± 0.12	0.06 ^{de} ± 0.02	0.59 ^e ± 0.19	0.36 ^c ± 0.12	0.20 ^b ± 0.04
Paha	21	2.16 ^b ± 0.22	0.09 ^c ± 0.03	0.59 ^{de} ± 0.21	0.28 ^{cd} ± 0.11	0.11 ^{de} ± 0.02
Orpe	27	3.05 ^a ± 0.28	0.20 ^b ± 0.03	1.84 ^a ± 0.40	1.85 ^a ± 0.27	0.77 ^a ± 0.10
Mesq	27	1.23 ^g ± 0.09	0.06 ^{de} ± 0.01	0.89 ^c ± 0.17	0.51 ^b ± 0.14	0.20 ^b ± 0.04
Pysh	53	1.42 ^e ± 0.16	0.06 ^e ± 0.01	0.61 ^{de} ± 0.21	0.47 ^b ± 0.13	0.10 ^e ± 0.03
<i>p</i> > <i>F</i>		< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001

¹⁾ Data are presented as the mean ± standard deviation. Means in a column followed by different letters significantly differ at $\alpha = 0.05$. Phfo, *Phoebe formosana*; Liac, *Litsea acuminata*; Math, *Machilus thunbergii*; Cacu, *Castanopsis cuspidata* var. *carlesii* f. *sessilis*; Paha, *Pasania hancei* var. *ternaticupula* f. *ternaticupula*; Orpe, *Oreocnide pedunculata*; Mesq, *Meliosma squamulata*; Pysh, *Pyrenaria shinkoensis*.

in foliar nutrient concentrations have been well documented in earlier studies (Marschner 1995, Masunaga et al. 1998). Orpe, a shrub, generally had higher foliar concentrations of

N, P, K, Ca, and Mg than the other species which were all trees. Similarly, Yuan et al. (2005a) reported that foliar N concentration was greater in shrubs than in trees. Phfo, Liac,

and Math all belong to the same family, the Lauraceae, but Phfo had significantly higher foliar concentrations of N, P, and K than Liac and Math (Figs. 1~3). Similarly, Cacu and Paha are in the same family, the Fagaceae, but the latter had significantly higher foliar concentrations of N, P, and lower foliar Mg than the former (Figs. 1, 2, 5).

Many studies have reported that foliar nutrient concentrations are influenced by soil fertility (Burke and Raynal 1998, Pensa and Sellin 2003, Richardson et al. 2005). However, we found inconsistent results regarding the effect of soil fertility on foliar nutrient concentrations. Compared to soils on the hillside and hilltop, the soil in the valley was lower in N and richer in P (Table 1). The higher foliar P concentrations in Orpe and Phfo reflected

the higher P availability in valley soil. By contrast, the higher foliar N concentrations in these 2 species did not support the general idea of positive relationships between foliar nutrients and soil fertility. The possible explanation for this discrepancy is the different physiological properties among species regardless of nutrient availability.

Seasonal patterns

Nitrogen, phosphorous, and potassium

In all 8 species, foliar concentrations of N, P, and K usually decreased in aging leaves (Figs. 1~3). The same results were found in earlier studies (Ralhan and Singh 1987, Orgeas et al. 2002, Roca-Pérez et al. 2005). In most species, foliar concentrations of N, P, and K decreased sharply from 29 April to 3

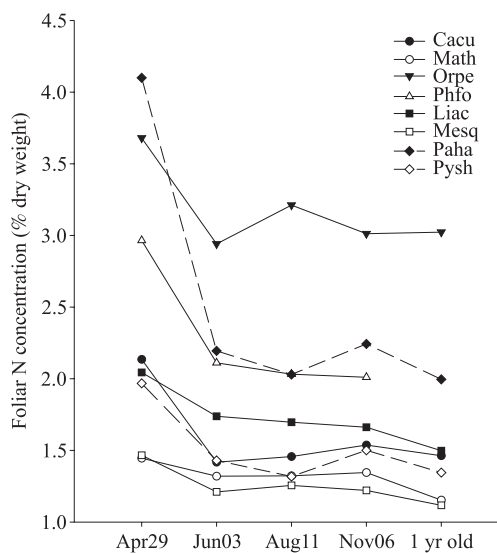


Fig. 1. Seasonal changes in foliar N concentrations (% dry weight) of 8 tree species. Seasonal differences were significant ($p < 0.05$) for all species. For each species, each point represents the mean of 7~18 individuals sampled on each date. Abbreviations for plant species are given in the footnotes to Table 3.

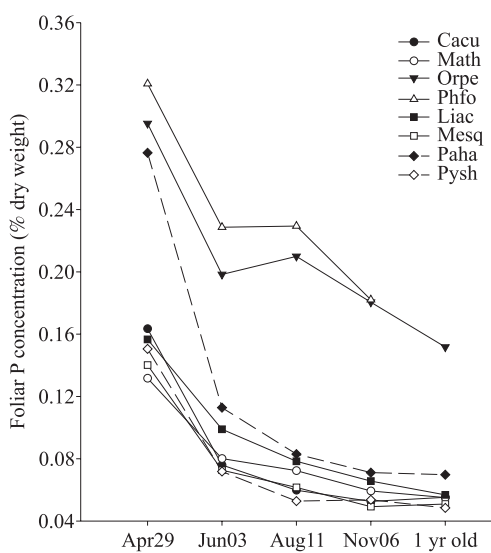


Fig. 2. Seasonal changes in foliar P concentrations (% dry weight) of 8 tree species. Seasonal differences were significant ($p < 0.05$) for all species. For each species, each point represents the mean of 7~18 individuals sampled on each date. Abbreviations for plant species are given in the footnotes to Table 3.

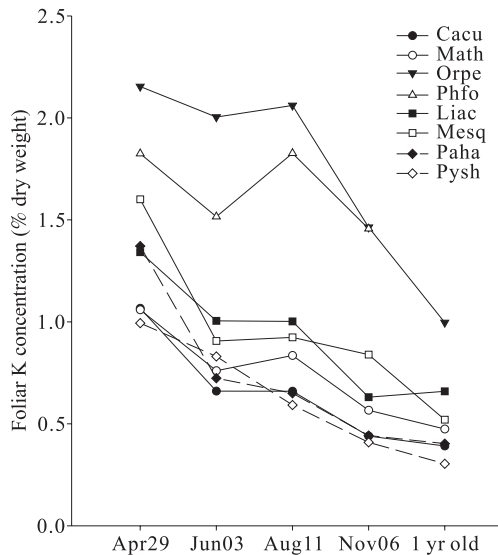


Fig. 3. Seasonal changes in foliar K concentrations (% dry weight) of 8 tree species. Seasonal differences were significant ($p < 0.05$) for all species. For each species, each point represents the mean of 7~18 individuals sampled on each date. Abbreviations for plant species are given in the footnotes to Table 3.

June. A dilution effect might have been the major factor responsible for the sharp decreases in foliar nutrient concentrations at the expansion stage of leaf life, as pointed out by some other studies (Chapin 1980, Chapin and Kedrowski 1983, Bauer et al. 1997, Mediavilla and Escudero 2003). The foliar concentrations of P and K in most species and N in a few species tended to decline further after 3 June. This continuous decrease in foliar nutrient concentrations could have been caused by resorption and/or leaching. Chapin and Kedrowski (1983) found that leaching played an insignificant role in the decline of foliar N and P for 4 Alaskan tree species. In addition, K was found to be more readily leached out of leaves than N and P (Tukey 1970, Bernhard-Reversat 1975, Ryan and Bormann

1982, Hagen-Thorn et al. 2006). The higher rainfall in Fushan could have caused great loss of foliar K by leaching. By contrast, resorption might be the major factor causing the decline in foliar concentrations of N and P after 3 June. On the other hand, the resorption of N, P, and K might be underestimated due to leaf mass (weight) loss often observed during senescence (Heerwaarden et al. 2003).

Niinemets and Tamm (2005) found that foliar concentrations of N, P, and K in deciduous trees dropped dramatically in the short period of time right before leaf-fall. In this study, we traced the foliar nutrient concentrations for less than 1 yr, and did not see a drop in the nutrient concentrations of senescing leaves (Figs. 1~3). We cannot be sure whether such a drop would occur eventually in the later stage of leaf life for evergreen species until more information can be gathered in future studies. However, we will use the data at hand to evaluate the possibility of the drop in foliar nutrient concentrations in a later section.

Calcium and magnesium

In all 8 species, the foliar Ca concentration usually increased in aging leaves (Fig. 4). The same trend had also been shown by other studies (Orgeas et al. 2002, Roca-Pérez et al. 2005). The higher Ca concentration in older leaves mainly results from Ca accumulation with time because the low mobility in phloem prevents Ca from being retranslocated out of leaves (Marschner 1995). Although the higher concentration of foliar Ca could also have resulted from mass loss during leaf senescence, the extent of leaf mass loss, reportedly ranging between 3 and 36% (Heerwaarden et al. 2003), could not account for the increase in Ca concentrations of aging leaves found in this study (Fig. 4).

A dilution effect might also have been

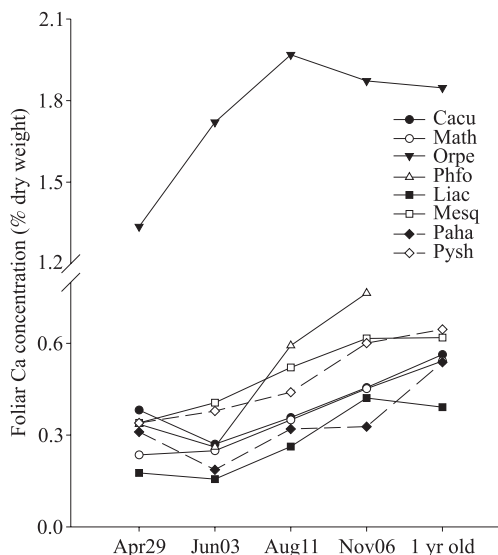


Fig. 4. Seasonal changes in foliar Ca concentrations (% dry weight) of 8 tree species. Seasonal differences were significant ($p < 0.05$) for all species. For each species, each point represents the mean of 7~18 individuals sampled on each date. Abbreviations for plant species are given in the footnotes to Table 3.

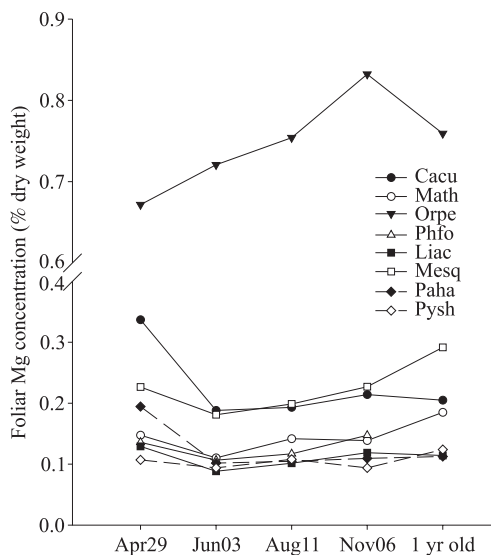


Fig. 5. Seasonal changes in foliar Mg concentrations (% dry weight) of 8 tree species. Seasonal differences were significant ($p < 0.05$) for all species except Pysh ($p > 0.05$). For each species, each point represents the mean of 7~18 individuals sampled on each date. Abbreviations for plant species are given in the footnotes to Table 3.

responsible for the decrease in foliar Mg concentrations of most species (with the exception of Orpe and Pysh) from 29 April to 3 June (Fig. 5). With intermediate mobility in phloem (Marschner 1995), Mg had different seasonal patterns of foliar concentration among species. Magnesium accumulated in aging leaves of Phfo, Liac, Math, Mesq, and Orpe. In Cacu, Paha, and Pysh, foliar Mg concentrations were rather constant after 3 June. It is worth noting that all 3 species of Lauraceae (Phfo, Liac, and Math) had a tendency to accumulate Mg in aging leaves, but 2 species of Fagaceae (Cacu and Paha) had rather constant foliar Mg concentrations after 3 June.

Nutrient conservation

Killingbeck (1996) introduced the concept of resorption proficiency (RP) for woody plants and proposed proficiency values defined by the ultimate concentration in senescent leaves before leaf-fall. The lower nutrient concentration in senescent leaves indicates a higher RP. For evergreen species, the resorption is considered “complete” in senescent leaves with N and P concentrations lower than 0.7 and 0.04%, respectively, and the resorption is “incomplete” in senescent leaves with N and P concentrations higher than 1.0 and 0.05%, respectively (Killingbeck 1996).

For 7 species in this study (no data for Phfo), N concentrations of 1-yr-old leaves ranged between 1.12 and 3.02%, and P con-

centrations between 0.05 and 0.15% (Figs. 1, 2). Compared to the thresholds proposed by Killingbeck (1996), none of the species in this study had reached complete N resorption in 1-yr-old leaves. By contrast, 2 of 7 species, Mesq and Pysh, came close to complete P resorption in 1-yr-old leaves. Phosphorus concentrations in 1-yr-old leaves ranged between 0.06 and 0.15% for the remaining 5 species, certainly indicating incomplete P proficiency. It appeared that we had not witnessed the end of N and P resorption for most species in the duration of this study. The leaves of evergreen tree species generally have life spans extending from 1 to 5 yr (Aerts and Chapin 2000, Pensa and Sellin 2003), and those of some species can even live up to 10 yr (Reich et al. 1992). From our observations, we can safely assume the leaves of the evergreen species in this study had life spans of longer than 1 yr. Therefore, lower foliar concentrations of N and P may be observed in leaves sampled on later dates. Results also suggested that the evergreen species in this study had potentially lower concentrations of N and P in senescent leaves.

If we compared our data with those from evergreen tree species of hardwood forests in central Taiwan (Chu 2005), we could come to somewhat different conclusions. The concentrations of N and P in the fallen leaves that were shed naturally (not prematurely due to mechanic forces such as rain or wind) were presumably the results of complete resorption. Chu (2005) found in the study over 2 yr that N concentrations ranged between 0.9 and 1.1% and P between 0.05 and 0.06% in leaves falling naturally during major peaks of leaf-fall. The ranges seemed to be higher than the thresholds of resorption proficiency proposed by Killingbeck (1996). If we used the average concentrations of N and P (1.0 and 0.06%) in fallen leaves of major peaks reported by

Chu (2005) instead of the thresholds values for evergreen trees in Taiwan, most tree species (except for Paha and Orpe) in this study had reached complete P resorption in 1 yr, but only 2 species (Math and Mesq) had come “close” to complete N resorption (Figs. 1, 2). If plants indeed make greater efforts to conserve limited elements by greater resorption (Aerts and Chapin 2000), in Fushan, P is probably an element more limited than N.

Many reports found that plants growing in soils of higher fertility had lower nutrient resorption (Ralhan and Singh 1987, Aerts and Chapin 2000, Pensa and Sellin 2003, Singh et al. 2005, Yuan et al. 2005b). Older leaves, sampled on 6 November and at 1 yr old, had higher P concentrations in Orpe and Phfo than in the other 6 tree species (Fig. 2). This suggests that Orpe and Phfo might have less-complete P resorption in the valley with higher P availability. While P is a limited element at Fushan, it was even more limited on hillsides and hilltops.

However, the higher foliar N concentrations in older leaves of Orpe and Phfo (Fig. 1) were in conflict with the generally accepted relationship between soil fertility and resorption. It was reported that N concentrations in senescent leaves were related to the concentrations in green leaves (Kobe et al. 2005, Yuan et al. 2005b). Similarly, N concentrations in both young and old leaves were higher in Orpe and Phfo than in other species. As discussed above, physiological traits rather than soil nutrient availability might be the main cause for the higher foliar N concentrations in Orpe and Phfo.

Sampling time

In this study, the foliar concentrations of N, P, and K were rather stable after June (Figs. 1–3). For valid comparisons in future studies on foliar nutrients, we propose that the cur-

rent year's leaves should be sampled during this period of time (from June to November) to avoid issues of dilution in immature leaves and dramatic decline in senescent leaves. Bauer et al. (1997) reported that foliar N of Norway spruce (*Picea abies* (L.) Karst.) was constant after the end of the growing season (autumn). Kim and Wetzstein (2005) found that foliar nutrients of pecan (*Carya illinoensis* Wangenh. K. Koch.) remained relatively stable after leaf maturation. Based on our observation and the study by Lin et al. (1997), leaf expansion of most tree species in Fushan occurred from April to May, and leaves had matured by August. Therefore, we suggest that the best time for leaf sampling for N, P, and K analyses is from August to October. Two species of the Fagaceae had constant foliar Mg concentration from June to November and could also be sampled in this period (Fig. 5). As for Ca and Mg of most species (Figs. 4, 5), continuous changes in foliar concentrations make it difficult to determine an optimal sampling time. For consistent sampling times, however, we still propose to sample leaf tissues for analyses of Ca and Mg at the same time as for N, P, and K.

ACKNOWLEDGEMENTS

Financial support for the project by the National Science Council (NSC94-2313-B-002-113) of the Republic of China is gratefully noted.

LITERATURE CITED

- Aerts R. 1996.** Nutrient resorption from senescing leaves of perennials: are there general patterns? *J Ecol* 84:597-608.
- Aerts R, Chapin FS III. 2000.** The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv Ecol Res* 30:1-67.
- Bauer G, Schulze ED, Mund M. 1997.** Nutrient contents and concentrations in relation to growth of *Picea abies* and *Fagus sylvatica* along a European transect. *Tree Physiol* 17: 777-86.
- Bernhard-Reversat F. 1975.** Nutrients in throughfall and their quantitative importance in rain forest mineral cycle. *Ecol Stud* 11:153-9.
- Bremner JM, Mulvaney CS. 1982.** Nitrogen-total. In: Page AL, editor. *Methods of soil analysis. Part 2, Chemical and microbiological properties*, 2nd ed. Madison, WI: American Society of Agronomy, Inc., Soil Science Society of America, Inc. p 595-624.
- Burke MK, Raynal DJ. 1998.** Liming influences growth and nutrient balances in sugar maple (*Acer saccharum*) seedlings on an acidic forest soil. *Environ Exp Bot* 39:105-16.
- Chapin FS III. 1980.** The mineral nutrition of wild plants. *Ann Rev Ecol Syst* 11:233-60.
- Chapin FS III, Johnson DA, McKendrick JD. 1980.** Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: implications for herbivory. *J Ecol* 68:189-209.
- Chapin FS III, Kedrowski RA. 1983.** Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology* 64:376-91.
- Chu PC. 2005.** Litterfall and nutrient dynamics in two adjacent stands in Shenmuhsi Forest Reserve of Experimental Forest, National Taiwan University [master thesis]. National Taiwan University. p 92. [in Chinese with English summary].
- Gee GW, Bauder JW. 1986.** Particle-size analysis. In: Klute A, editor. *Methods of soil analysis. Part 1, Physical and mineralogical methods*, 2nd ed. Madison, WI: American Society of Agronomy, Inc., Soil Science Society of America, Inc. p 383-411.
- Hagen-Thorn A, Varnagiryte I, Nihlgård B,**

- Armolaitis K. 2006.** Autumn nutrient resorption and losses in four deciduous forest tree species. For Ecol Manage 228:33-9.
- Heerwaarden, LM, Toet S, Aert R. 2003.** Current measures of nutrient resorption efficiency lead to a substantial underestimation of real resorption efficiency: facts and solutions. Oikos 101:664-9.
- Killingbeck KT. 1996.** Nutrients in senesced leaves: key to the search for potential resorption and resorption proficiency. Ecology 77: 1716-27.
- Kim TR, Wetzstein HY. 2005.** Seasonal fluctuations in nutrients and carbohydrates in pecan leaves. J Hort Sci Biotechnol 80:681-8.
- Kobe RK, Lepczyk CA, Iyer M. 2005.** Resorption efficiency decrease with increasing green leaf nutrients in a global data set. Ecology 86:2780-92.
- Lin KC, Horng FW, Cheng WE, Chiang HC, Chang UC. 1996.** Soil survey and classification of the Fushan Experimental Forest. Taiwan J For Sci 11:159-74. [in Chinese with English summary].
- Lin KC, Hwanwu CB, Liu CC. 1997.** Phenology of broadleaf tree species in the Fushan Experimental Forest of northeastern Taiwan. Taiwan J For Sci 12:347-35. [in Chinese with English summary].
- López-Serrano FR, de las Heras J, González-Ochoa AI, García-Morote FA. 2005.** Effects of silvicultural treatments and seasonal patterns on foliar nutrients in young post-fire *Pinus halepensis* forest stands. For Ecol Manage 210:321-36.
- Marschner H. 1995.** Mineral nutrition of higher plants. San Diego, CA: Academic Press.
- Martínez-Sánchez JL. 2005.** Nitrogen and phosphorus resorption in a neotropical rain forest of a nutrient-rich soil. Rev Biol Trop 53:353-9.
- Masunaga T, Kubota D, Hotta M, Wakatsuki T. 1998.** Nutritional characteristics of mineral elements in leaves of tree species in tropical rain forest, West Sumatra, Indonesia. Soil Sci Plant Nutr 44:315-29.
- McLean EO. 1982.** Soil pH and lime requirement. In: Page AL, editor. Methods of soil analysis. Part 2, Chemical and microbiological properties, 2nd ed. Madison, WI: American Society of Agronomy, Inc., Soil Science Society of America, Inc. p 199-223.
- Mediavilla S, Escudero A. 2003.** Relative growth rate of leaf biomass and leaf nitrogen content in several Mediterranean woody species. Plant Ecol 168:321-32.
- Milla R, Castro-Díez P, Maestro-Martínez M, Montserrat-Martí G. 2005.** Does the gradualness of leaf shedding govern nutrient resorption from senescing leaves in Mediterranean woody plants? Plant Soil 278:303-13.
- Moore PD, Chapman SB. 1986.** Methods in plant ecology, 2nd ed. Oxford: Blackwell Scientific Publications.
- Nelson DW, Sommers LE. 1982.** Total carbon, organic carbon, and organic matter. In: Page AL, editor. Methods of soil analysis. Part 2, Chemical and microbiological properties, 2nd ed. Madison, WI: American Society of Agronomy, Inc., Soil Science Society of America, Inc. p 539-79.
- Niinemets Ü, Tamm Ü. 2005.** Species differences in timing of leaf fall and foliage chemistry modify nutrient resorption efficiency in deciduous temperate forest stands. Tree Physiol 25:1001-14.
- Olsen SR, Sommers LE. 1982.** Phosphorus. In: Page AL, editor. Methods of soil analysis. Part 2, Chemical and microbiological properties, 2nd ed. Madison, Wisconsin: American Society of Agronomy, Inc., Soil Science Society of America, Inc. p 403-27.
- Orgeas J, Ourcival JM, Bonin G. 2002.** Seasonal and spatial patterns of foliar nutrients in cork oak (*Quercus suber* L.) growing on siliceous soils in Provence (France). Plant Ecol

164:201-11.

Pensa M, Sellin A. 2003. Soil type affects nitrogen conservation in foliage of small *Pinus sylvestris* L. trees. *Plant Soil* 253:321-9.

Ralhan PK, Singh SP. 1987. Dynamics of nutrients and leaf mass in central Himalayan forest trees and shrubs. *Ecology* 68:1974-83.

Reich PB, Walters MB, Ellsworth DS. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol Monogr* 62:365-92.

Rhoades JD. 1982. Cation exchange capacity. In: Page AL, editor. *Methods of soil analysis. Part 2, Chemical and microbiological properties*, 2nd ed. Madison, WI: American Society of Agronomy, Inc., Soil Science Society of America, Inc. p 149-57.

Richardson SJ, Peltzer DA, Allen RB, McGlone MS. 2005. Resorption proficiency along a chronosequence: responses among communities and within species. *Ecology* 86:20-5.

Roca-Pérez L, Pérez-Bermúdez P, Gavidia I, Boluda R. 2005. Relationships among soil characteristics, plant macronutrients, and cardenolide accumulation in natural populations of *Digitalis obscura*. *J Plant Nutr Soil Sci* 168:774-80.

Ryan DF, Bormann FH. 1982. Nutrient resorption in northern hardwood forests. *BioScience* 32:29-32.

Singh SP, Bargali K, Joshi A, Chaudhry S. 2005. Nitrogen resorption in leaves of tree and shrub seedlings in response to increasing soil fertility. *Curr Sci* 89:389-96.

Su HJ. 1985. Studies on the climate and vegetation types of the natural forests in Taiwan. (III). A scheme of geographical climatic regions. *Q J China For* 18:33-44.

Tukey HB Jr. 1970. The leaching of substances from plants. *Annu Rev Plant Physiol* 21:305-24.

Wright IJ, Westoby M. 2003. Nutrient concentration, resorption and lifespan: leaf traits of Australian sclerophyll species. *Funct Ecol* 17:10-9.

Yuan ZY, Li LH, Han XG, Huang JH, Jiang GM, Wan SQ, Zhang WH, Chen QS 2005a. Nitrogen resorption from senescing leaves in 28 plant species in a semi-arid region of northern China. *J Arid Environ* 63:191-202.

Yuan ZY, Li LH, Han XG, Huang JH, Wan SQ. 2005b. Foliar nitrogen dynamics and nitrogen resorption of a sandy shrub *Salix gordejvii* in northern China. *Plant Soil* 278:183-93.

