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Leaf nutrient concentration, nutrient resorption and litter decomposition in an evergreen broad-leaved forest in eastern China

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Abstract

While plant mineral nutrition has been well addressed in temperate ecosystems, our knowledge of this topic in subtropical evergreen broad-leaved forests remains weak. We examined various plant leaf traits and litter decomposition rates among three groups—deciduous species (DB) and evergreen broad-leaved species with leaf life span $<$1.5 years (EBS) and $>$1.5 years (EBL) in a secondary evergreen broad-leaved forest in eastern China. Relative to DB, EBS and EBL classes contained 33 and 44% less leaf N, and 28 and 45% less leaf P, respectively. N resorption efficiency varied from 27 to 65%, 21 to 52% and 22 to 51% in DB, EBS and EBL, respectively. P resorption efficiency varied from 38 to 77% in DB, 6 to 58% in EBS and 15 to 55% in EBL. P resorption efficiency was greater in DB than in EBS and EBL while N resorption efficiency did not differ among the three classes. N resorption efficiency was not correlated with either leaf N or N:P ratio. In contrast, P resorption efficiency was positively correlated with leaf P. Litter decomposition rates were 2.45, 1.33 and 2.30 year^{-1} for DB, EBS and EBL, respectively, but the rates did not significantly differ between groups. Litter decomposition rate was positively correlated with specific leaf area (SLA) and initial litter N but not litter P. In conclusion, there were no significant differences between EBS and EBL for any of the leaf traits measured, but these two classes were different from DB. Plants with long leaf life span tend to minimize nutrient loss more by reducing N concentration in leaf litter than by increasing N resorption efficiency.

Keywords: Decomposition; Deciduous; Evergreen broad-leaved; Leaf life span; Nutrient resorption; Specific leaf area (SLA)

1. Introduction

At the community level, plant species with longer leaf life span tend to have lower leaf nutrient concentrations. During leaf senesence, these species are often assumed to have higher nutrient resorption efficiency than species with short life span so as to reduce nutrient loss (Aerts and Chapin, 2000). Consequently, species with long leaf life span are expected to have lower litter quality (higher in leaf litter toughness, C:N, lignin concentration) and decomposition rate.

As an important mechanism of nutrient conservation in plants, nutrient resorption from senescing leaves has been widely studied in relation to soil fertility, soil humidity, plant growth-forms, leaf life span and forest succession (Boerner, 1984; Boerner, 1986; Chapin and Moilanen, 1991; Wright and Westoby, 2003; Yan et al., 2006). We now know that nutrient resorption may not relate to soil fertility or leaf life span. However, there are two unresolved issues regarding nutrient resorption. First, there is no agreement on the relationship between nutrient resorption efficiency (the percentage of the nutrient pool withdrawn from the foliage before leaf abscission) and leaf nutrient concentration (Chapin and Kedrowski, 1983; Shaver and Melillo, 1984; Schlesinger et al., 1989; Del Arco et al., 1991; Rejmánková, 2005). Second, most of the previous studies compared the extant species growing in high-fertility environments with extant species from low-fertility environments; therefore, species effects are confounded with environment effects (Aerts, 1990; Kobe et al., 2005).

While leaf mineral traits and their relations with leaf life span have been studied and reviewed in various ecosystems (Killingbeck, 1996; Aerts, 1997; Eckstein et al., 1999; Aerts and Chapin, 2000; Wright et al., 2004; Kobe et al., 2005), our knowledge of this topic in evergreen broad-leaved forests (EBLFs) in eastern China still remains poor. EBLFs are the zonal vegetation type in the subtropical area of China, with

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forests characterized by a high diversity of species and functional groups. Unfortunately, these EBLFs now contain areas of severe ecological degradation due to long-term human disturbance. In order to restore forest structure and function, suitable species must be introduced to various degraded places such as areas of bare soil and abandoned quarries. However, poor information about the nutrient status of local tree species hinders forest management in this area.

Therefore, to yield insight into the unresolved relationship between nutrient resorption efficiency and leaf nutrient concentration and to provide nutrient information to forest managers, we conducted a study of foliar nutrient dynamics and decomposition among functional groups of the species in a secondary EBLF. The specific objectives include: (1) quantify foliar nutrient concentrations of the common species in this area to facilitate selection of suitable target species to be used for forest restoration activities; (2) determine whether nutrient resorption efficiency relates to leaf nutrient status in this particular ecosystem; (3) compare leaf nutrient traits and litter decomposition rates among plants with different leaf age classes; (4) determine how litter quality affects litter decomposition rates.

2. Materials and methods

2.1. Study area and species classification

This study was conducted in Tiantong National Forest Park (29°52′N, 121°39′E), Zhejiang Province, China. The climate of this region is subtropical monsoon with mean annual temperature and precipitation of 16.2 °C and 1374.7 mm. The substrate parent materials are mesozoic sediments and acidic intrusive rocks, including quartzite and granite. The soil texture is mainly medium-heavy loam, and soil pH ranges from 4.4 to 5.1 (Song and Wang, 1995). The forests are occupied by evergreen broad-leaved species, deciduous species, coniferous species developed following repeated cutting for charcoal production. The canopy is dominated by *Pinus massoniana* Lamb, *Castanopsis fargesii* Franch, and *Schima superba* Gardn. et Champ.

Fifty species from 22 taxa were selected near the central forest area of the park. These species were first classified as either deciduous (DB) or evergreen species. Since many leaf traits vary continuously with leaf life span (Reich et al., 1992; Wright et al., 2004), Craine and Mack (1998) argued that evergreen species with a short leaf life span (<1.5 years) might be more similar to deciduous species than to evergreen species with longer life span (>1.5 years). Therefore, based on a previous leaf longevity study in this area (Wang et al., 2000), we further divided the evergreen species into two age classes: broad-leaved evergreen species with life span <1.5 years (EBS) and those with life span >1.5 years (EBL).

2.2. Leaf collection

The majority of the species were sampled in or near a permanent 30 m × 30 m *S. superba* community plot (Appendix A). *P. massoniana*, the only conifer species present in this area, was sampled but not included in the data analysis due to its distinct differences from broad-leaved species.

Fresh leaves of evergreen species were collected from May 2000 through July 2000. Fresh leaves of deciduous species were collected in early August 2000, when the leaves were fully expanded. We assumed that the leaf nutrients in summer represented the highest mature leaf nutrient level to facilitate the later calculation of nutrient resorption efficiency. Generally two to three trees for each species were selected and marked. Fresh leaves were sampled from lower and middle outer canopy and then pooled for each tree.

Senesced leaves of seven deciduous species (used in estimation of nutrient resorption) were obtained from area near originally marked trees by gently shaking the branches in early November 2000. Since phenology is not synchronic among evergreen species, we spent 1–2 weeks each month from September 2000 through May 2001 collecting senesced leaves. The harvest of senesced leaves (or fresh litter) was coordinated with the peak of leaf drop of each species over this period. We planned to sample senesced leaves from the original marked trees to minimize variation caused by sampling different plants. However, the quantity of litter produced by some marked evergreen plants, especially shrubs, was insufficient for the purposes of nutrient analysis and litter decomposition experiments. Therefore, litter was also collected from plants that were not original marked and the collected leaf litter was pooled for each species. In these cases, we assumed intraspecific variation was not large because all leaves were sampled from plants located in close proximity to each other. Senesced leaves were collected either from fresh litter on the ground (for most trees) or directly off plants (for most shrubs).

Senesced leaves from each individual tree were well mixed and then ~10 g subsamples per species were dried to a constant weight at 70 °C for nutrients analysis. Remaining senesced leaves were air dried and then used for litter decomposition experiment.

In total, we measured mature leaf nutrient concentration for 38 species and nutrient resorption efficiency for 31 species. Due to limited litter availability, the litter decomposition experiment was conducted for only 23 species.

2.3. Calculation of leaf traits and litter decomposition rate

Specific leaf area (SLA) represents the light-intercepting area of a leaf per unit dry mass and has been shown to relate with many important physiological characteristics, such as leaf nutrient concentration, photosynthetic capacity, and plant relative growth rate (Reich et al., 1999). A flat-bed scanner was used to scan 50–100 fresh leaves per plant, after which scanned leaves were dried for >48 h at 70 °C. Dried leaves were weighed, and SLA was calculated as the ratio of leaf area to dry leaf weight.

Fresh and senesced leaves from each sample were ground and then digested using concentrated H_2SO_4. N concentration

Table 1
Leaf traits and litter decomposition rates among three different functional groups

	Leaf age classes					
	Deciduous species	*n*	Evergreen species with leaf life span <1.5 years	*n*	Evergreen species with leaf life span >1.5 years	*n*
SLA (cm^2/g)	226.60(25.90) a	7	123.88(6.80) b	16	114.80(5.40) b	15
N_{live} (mg/g)	25.06(2.36) a	7	16.84(0.81) b	16	14.11(0.68) b	15
P_{live} (mg/g)	1.31(0.08) a	7	0.94(0.13) ab	16	0.72(0.04) b	15
N_{dead} (mg/g)	15.25(1.31) a	14	11.53(0.62) b	15	9.78(0.67) b	12
P_{dead} (mg/g)	0.70(0.07) a	14	0.66(0.06) a	15	0.49(0.07) a	12
NRE (%)	38.72(4.78) a	7	34.02(2.86) a	11	33.91(2.79) a	11
PRE (%)	55.37(5.87) a	7	35.84(5.12) b	11	36.67(3.46) b	11
k ($year^{-1}$)	2.45(0.72) a	8	1.33(0.28) a	10	2.30(0.53) a	5

Means with S.E. and sample size are presented. Different letters in rows indicate significant differences between groups at Bonferroni adjusted $p < 0.05$. N_{live}, P_{live}: N or P concentration in mature leaves; N_{dead}, P_{dead}: N or P concentration in leaf litter; NRE, PRE: N or P resorption efficiency; *k*: first year leaf litter decomposition rate. *k* was log transformed before data analysis while all other variables are left untransformed.

of the digest was determined using the semi-micro Kjeldahl method. P concentration was determined using the stannous chloride method (APHA, 1976).

Nutrient resorption efficiency can be expressed either on leaf area basis or mass basis. Since senescent leaves of some deciduous species become folded and shrunken, the leaf area of the senescing leaves was likely to be underestimated. Therefore, although we acknowledged that leaf nutrient resorption efficiency might be underestimated due to considerable weight loss during senesce, as discussed by Van Heerwaarden et al. (2003), we expressed N (or P) per unit weight rather than per unit leaf area in order to estimate the percentage of N (or P) resorbed prior to leaf abscission. Nutrient resorption efficiency from senescing leaves was calculated as:

$$\mathrm{NRE} = \left[\frac{\mathrm{Nu}_{\mathrm{live}} - \mathrm{Nu}_{\mathrm{dead}}}{\mathrm{Nu}_{\mathrm{live}}}\right] \times 100,$$

where NRE is the nutrient (N or P) resorption efficiency, Nu_{live} the N (or P) concentration of mature leaves, and Nu_{dead} is the N (or P) concentration of leaf litter.

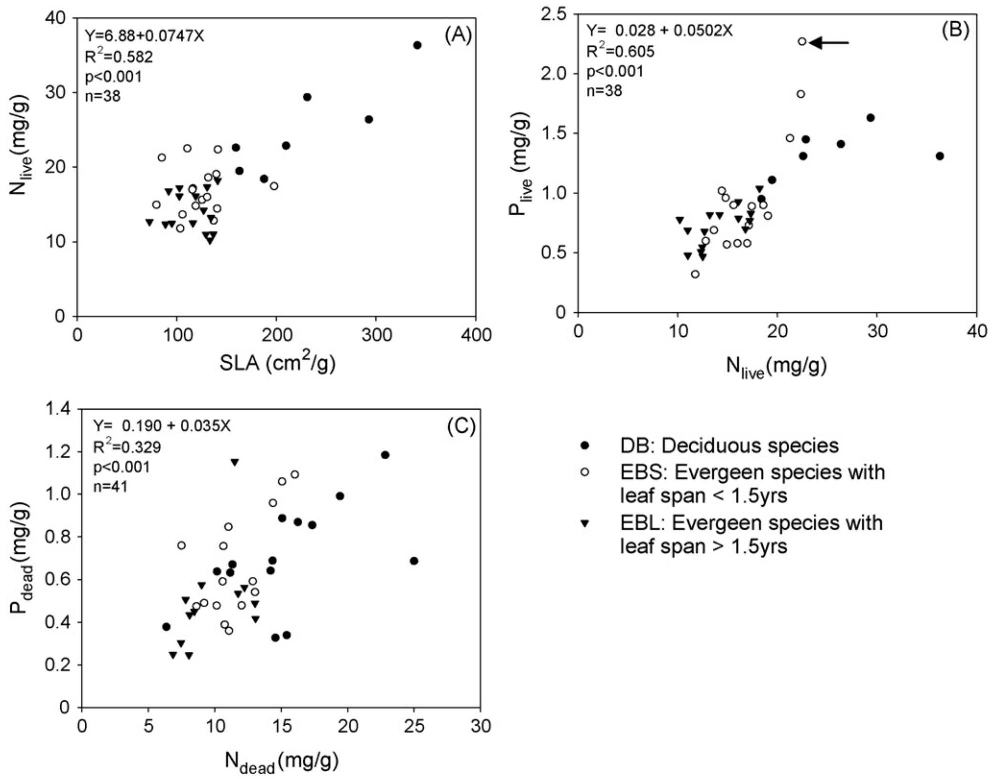

Fig. 1. Relationship between (A) SLA and N_{live}; (B) N_{live} and P_{live}; (C) N_{dead} and P_{dead}. Each point represents a different species. In panel (B), one point as indicated by an arrow is removed as the statistical outlier in the regression analysis.

We used the litter bag method to study litter decomposition. Samples of 4.5 g air dried leaf litter were placed in 15 cm × 20 cm nylon mesh bags made of 2 mm mesh. Since litter was collected at different time, the litter bags were initially put in the field on three different dates: January 2001, May 2001 and June 2001. In total, there were >300 bags (23 species × 4 (or 5) retrieval times × 3 replications). All litter bags were put in one permanent study plot dominated by *S. superba*. Litter bags were later retrieved every 2 or 3 months during 9–12 months period. Harvested bags were quickly washed to remove extraneous materials, arthropods and soil, and litter was dried at 70 °C to constant weight.

The decomposition rate constant (k) was calculated using the modified exponential relationship $X_t/X_0 = a\,e^{-kt}$, where X_0 is the initial dry-weight and X_t the remained litter weight at collection time (t); a the constant of the equation; k is the decomposition rate (Olson, 1963; Swift et al., 1979). Initial weight at $t = 0$ was also included in the modeling. The decay rate constant k provided a single, functionally relevant parameter for describing decomposition.

2.4. Statistical analysis

Analysis of variance (ANOVA) was performed to test the main effects of leaf age-class on each leaf trait and litter decomposition rate. Normality and homogeneity of variance of the residuals were examined using PROC UNIVARIATE in SAS (2001). Leaf and litter N, P and nutrient resorption efficiency were considered normal and left untransformed. Litter decomposition rate was log transformed in ANOVA to meet the normality assumption. For parameters for which there was a significant age-class effect, *a posteriori* least-squares mean separation with Bonferroni correction ($\alpha = \alpha/3$) was used to test for the difference among different age classes.

Linear regression was used to examine the relationship between nutrient resorption efficiency and initial foliar nutrient. To characterize the multivariate pattern of correlations and to help visualize the holistic characteristics of different age classes, a principal component analysis (PCA) was performed using SAS/INSIGHT. All data were left untransformed for the linear regression and PCA analysis.

3. Results

3.1. SLA and nutrient status in fresh and dead leaves

DB has significantly larger specific leaf area (SLA), higher nutrient concentration in fresh and dead leaves than

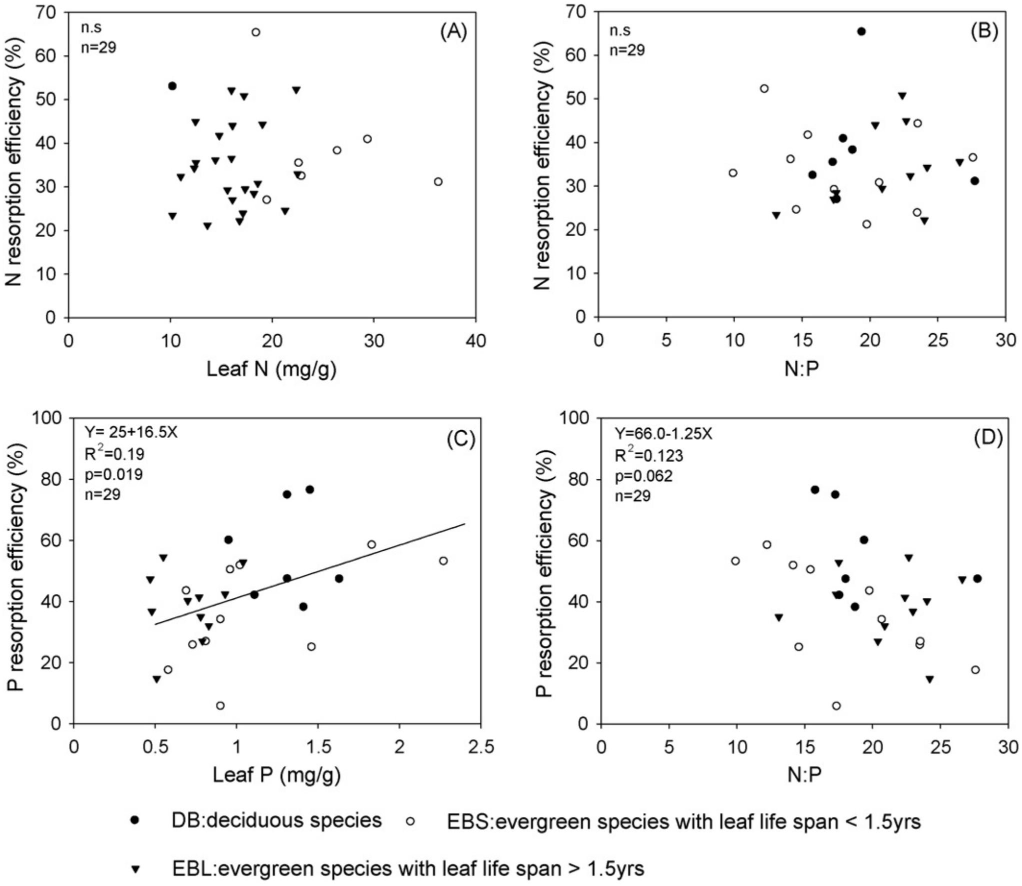

Fig. 2. Relationship between (A) N resorption efficiency and N_{live}; (B) N resorption efficiency and N:P; (C) P resorption efficiency and P_{live}; (D) P resorption efficiency and N:P. In panels (A) and (B), N resorption efficiency is not significantly correlated with either N or N:P ratio in mature leaves. n.s. represents not significant.

either EBS or EBL (Table 1). SLA varied from 159 to 342 cm^2/g in DB, 80 to 198 cm^2/g in EBS, and 73 to 141 cm^2/g in EBL (Appendix A). N concentration in the mature leaves (N_{live}) was 33 and 44% less in plants from EBS and EBL classes than in plants from DB class, respectively. Similarly, P concentration in the mature leaves (P_{live}) was 28 and 45% less in plants from EBS and EBL than in plants from DB class, respectively (Table 1). Litter N (N_{dead}) was significantly higher in plants from DB class whereas litter P (P_{dead}) did not differ among the three functional groups. SLA and leaf N were positively correlated (Fig. 1A). Litter N and litter P were also positively correlated ($R^2 = 0.328$, $p < 0.001$), but not as strongly as in green leaves ($R^2 = 0.605$, $p < 0.001$).

3.2. Nutrient resorption

N resorption efficiency (NRE) varied from 27 to 65%, 21 to 52% and 22 to 51% in DB, EBS and EBL, respectively (Appendix A). P resorption efficiency (PRE) varied from 38 to 77% in DB, 6 to 58% in EBS and 15 to 55% in EBL. DB had higher P resorption efficiency than either EBL or EBS, while N resorption efficiency did not differ among the three groups (Table 1).

N resorption efficiency was not correlated with either N_{live} or N:P ratio (Fig. 2A and B) whereas P resorption efficiency was positively correlated with P_{live} ($p = 0.019$, Fig. 2C). When different age classes were considered separately, P resorption efficiency exhibited borderline correlation ($p = 0.085$) with P_{live} in EBS species, but no such correlation was found in either DB or EBL species. P resorption efficiency tended to decrease with increased N:P ratio (Fig. 2D, $p = 0.062$).

3.3. Litter decomposition

Litter mass loss generally exhibited two trends. First, litter tended to decompose quickly in the initial decomposing stage (0–6 months) and at a lower rate during the later stage (6–12 months) (Table 2); second, litter decomposed quickly during the summer when the temperature and the moisture were more suitable for microbial activity.

Litter mass loss was highly dependent on time and appeared to approximate a negative exponential pattern for most of the studies species (Table 2). Therefore, we calculated the annual litter decomposition rate for each species by fitting a negative exponential function. Litter decomposition rates (k) were 2.45, 1.33 and 2.30 $year^{-1}$ for DB, EBS and EBL, respectively, but the rates did not significantly differ among these groups (Table 1). Deciduous species showed much larger variation in decomposition rate than evergreen broad-leaved species (Appendix A). Litter decomposition rate was positively related with SLA and initial litter N (N_{dead}) but not litter P (Fig. 3).

Table 2
Leaf litter decomposition (expressed as percent mass remaining) in a secondary evergreen broad-leaved forest in eastern China

Species placed on January 2001	Day 100	Day 181	Day 273	Day 365
Castanea mollissima	83.1(1.0)	62.2(8.2)	17.0(6.5)	13.5(2.5)
Castanopsis fargesii	87.5(3.5)	66.7(1.4)	29.6(8.2)	22.6(11.3)
Castanopsis sclerophylla	85.8(2.3)	69.6(3.1)	55.9(11.1)	38.1(4.9)
Celtis tetrandra ssp. *sinensis*	65.2(0.7)	39.5(3.1)	24.9(2.8)	19.0(2.1)
Ficus erecta var. *beecheyana*	34.9(1.7)	11.6(1.7)	2.8(0.4)	0.8(0.3)
Liquidambar formosana	83.1(2.8)	70.6 (3.0)	32.3(0.1)	29.8(4.9)
Lithocarpus glaber	89.9(1.6)	59.4(11.5)	56.1(3.5)	35.7(14.9)
Litsea cubeba	72.5(1.9)	13.5(2.1)	1.4(0.2)	0.3(0.1)
Prunus serrulata	79.8(0.7)	72.5(2.2)	47.8(3.1)	30.7(0.7)
Quercus fabri	90.3(1.8)	75.2(4.0)	45.7(4.3)	32.3(4.3)
Sassafras tzumu	92.0(0.8)	91.4(0.8)	65.7(7.3)	50.2(8.9)
Schima superba	82.0(3.5)	58.3(3.8)	43.2(5.3)	25.7(3.1)

Species placed on May 2001	Day 60	Day 121	Day 182	Day 242	Day 300
Cinnamomum comphora	83.9(1.8)	69.8(3.7)	56.9(3.5)	53.9(2.2)	51.9(0.7)
Cyclobalanopsis glauca	85.0(0.5)	73.8(2.9)	56.7(–)	27.6(2.8)	25.9(4.9)
Cyclobalanopsis gracilis	90.4(0.3)	83.3(1.8)	69.7(7.1)	64.8(5.0)	61.6(2.1)
Cyclobalanopsis myrsinaefolia	63.9(3.5)	47.9(12.2)	33.9(2.8)	30.0(5.6)	29.9(0.5)
Cyclobalanopsis nubium	83.2(0.3)	75.1(0.1)	72.3(1.4)	69.8(11.6)	58.8(3.3)
Daphniphyllum oldhamii	56.9(1.8)	16.4(12.5)	10.4(0.3)	4.2(0.2)	3.5(1.4)
Elaeocarpus decipiens	48.4(3.8)	9.4(1.9)	3.6(1.1)	6.2(0.4)	5.5(0.2)
Lithocarpus harlandii	87.2(0.1)	74.2(0.6)	21.5(3.1)	20.9(1.4)	19.2(3.2)
Phoebe sheareri	85.6(2.2)	49.6(5.1)	39.6(5.0)	34.2(9.6)	28.0(5.7)
Photinia glabra	76.4(0.1)	59.2(9.3)	45.2(4.7)	26.3(6.0)	25.0(3.7)

Species placed on June 2001	Day 30	Day 91	Day 152	Day 212	Day 273
Helicia cochinchinensis	69.4(2.1)	60.1(0.6)	54.5(2.9)	51.5(6.8)	48.2(5.9)

S.D. are in parentheses ($n = 3$). –: S.D. is not estimated due to missing of two retrieved litter bags.

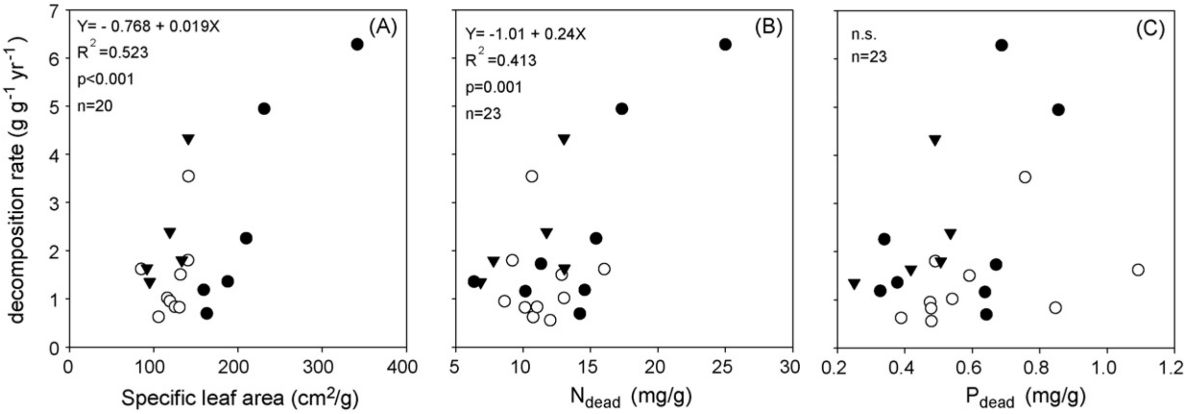

Fig. 3. Relationship between litter decomposition rate and (A) specific leaf area; (B) litter N concentration; (C) litter P concentration (see Fig. 2 for explanation of symbols).

3.4. Multivariate patterns of leaf traits

PCA analysis was used to illustrate how the different variables were associated in the multivariate analysis. The first and second axis represented 50.3 and 23.9% of the total variation. The analysis revealed strong positive correlation among N_{live}, P_{live}, N_{dead} SLA and litter decomposition rate (k) (Fig. 4A).

Loadings of species on axis 1 varied significantly between species of different leaf life span ($F_{2,17} = 5.88$, $p = 0.011$; Fig. 4B): EBS and EBL had lower values of N_{live}, P_{live}, N_{dead}, SLA and decomposed slower than species from DB. Leaf traits of EBS were more similar to EBL than to DB.

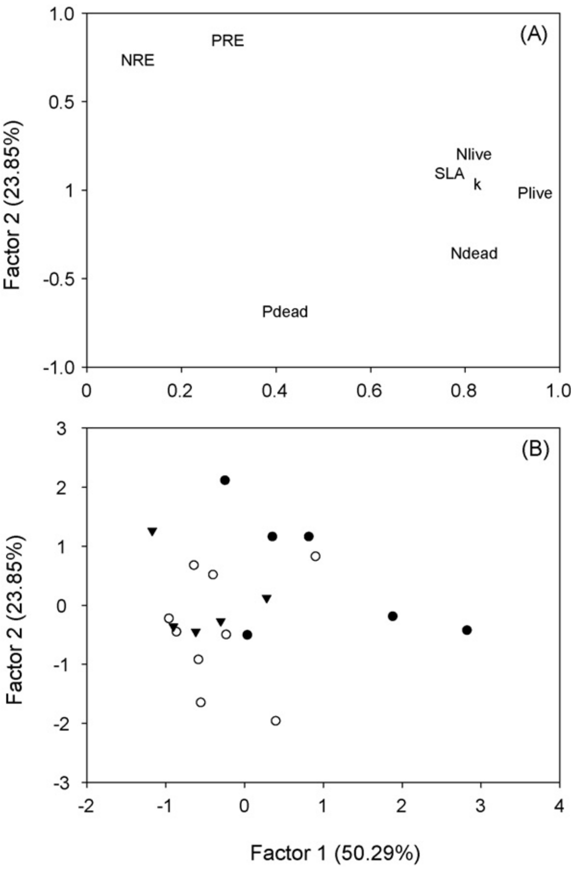

Fig. 4. Principal components analysis combining data on plant leaf traits. Only the first two axes, which account for 74.1% of the total variance, are retained here. (A) Loadings of the variables. It shows the multivariate pattern of correlations among the leaf traits measured. Abbreviations follow Table 1. (B) Function scores of the 20 species (see Fig. 2 for explanation of symbols in panel).

4. Discussion

4.1. Nutrient resorption

Species with long leaf life span, such as evergreen trees and shrubs, are often assumed to have high nutrient resorption efficiency to reduce nutrient loss. However, several recent reviews (Aerts, 1990; Eckstein et al., 1999; Aerts and Chapin, 2000) concluded nutrient resorption efficiency did not differ among growth-forms (e.g. deciduous versus evergreen species). Our study showed that N resorption did not differ between leaf age classes while P resorption efficiency was greater in deciduous species than that in evergreen broad-leaved species.

When nutrient resorption efficiency was correlated with initial leaf traits, we found that N resorption efficiency was not correlated with either leaf N concentration or N:P ratio. In contrast, P resorption efficiency was positively correlated with leaf P concentration. In a recent literature review based on a global database, Kobe et al. (2005) found resorption efficiency generally declined with increasing leaf nutrient status, both within and among species. One explanation for our contradictory result is that the species with high leaf nutrients may be subjected to more intensive leaching loss. For example, most of the evergreen species have low leaf nutrient, thick leaves, smooth (or waxy) leaf surface which might minimize the leaching loss. Since our studies may overestimate the nutrient resorption efficiency by incorporating leaching loss into nutrient resorbed, we had the tendency to overestimate the nutrient resorption efficiency for deciduous species. In addition, several other issues such as large inter- and intra-year variation, large mass loss during nutrient resorption may also account for the contradiction. If P loss due to leaching is greater than N loss, we speculate that leaching also play an important role in explaining why P resorption efficiency was greater in DB species while N resorption did not differ among these three classes.

4.2. Litter decomposition

Litter decomposition is an important process in forest nutrient cycling and has been well studied in various terrestrial ecosystems (Meentemeyer, 1978; Vitousek et al., 1994; Aerts, 1997). At a global scale, litter decomposition rate is mainly determined by climate; at a particular climatic region, litter quality (including leaf toughness, N, P concentration, lignin content, etc.) plays the most important role in determining litter decomposition rate (Aerts, 1997). Numerous studies have well documented that N is one of the most common factors limiting litter decomposition as it determines the growth and turnover of microbial biomass mineralizing the organic C (Talor et al., 1989). Our study did confirm that litter decomposition rates were positively correlated with litter N. However, litter P concentration was a poor indicator of litter decomposition rate in this study area, which contradicted some previous studies (Vitousek et al., 1994).

SLA was positively correlated with litter decomposition rate. Leaves with small SLA are physically tough and leaf toughness has been proven to be a good negative indicator of decomposition rate in various ecosystems (Gallardo and Merino, 1993; Cornelissen et al., 1999); In addition, SLA is negatively correlated with foliar structural and chemical compounds (such as lignin, Cornelissen et al., 1999), which might also contribute to the positive relationship between SLA and litter decomposition rate.

4.3. Leaf nutrient traits among different leaf age classes

Species with shorter leaf life span are associated with higher foliar N concentration, SLA, and mass-based maximum photosynthetic rates (Field and Mooney, 1986; Wright et al., 2004). Our results failed to detect any significant differences in EBS and EBL for any of the leaf traits measured, but these two classes were distinguished from DB.

Evergreen species (or species with long leaf life span) are assumed to reduce nutrient loss by adopting ‘‘conservative’’ nutrient use strategies (Aerts and Chapin, 2000) such as high nutrient resorption and long nutrient resident time. Our results showed that N resorption efficiency did not differ among the three age classes, and P resorption efficiency was lower in evergreen species than deciduous species. In contrast, N concentration in senesced leaves was lower in species with longer leaf life span. Therefore, having lower nutrient concentration in leaf litter might be a more important strategy for plants to minimize nutrient loss than having higher nutrient resorption efficiency.

4.4. Implications in the forest management in eastern China

In eastern China, the zonal evergreen broad-leaved forests have been changing to include more areas of bare soil and areas dominated by degraded secondary forests, shrubs, and/or xeric grassland with low soil nutrient availability (Yan et al., 2006). In recent decades, one major forest management practice in this area was to plant *P. massoniana* because of its drought-resistance and ability to grow in very stressful environments such as shallow soils and in abandoned quarries. However, monocultural *P. massoniana* forests are highly unstable and subject to many infestations (e.g. pinewood nematode). Current practices include the introduction of some late-successional evergreen species (e.g. *C. fargesi*) into these degraded areas and *P. massoniana* forests to accelerate forest succession and to construct diverse vegetation composition. However, these areas can also be altered in ways that may not support the original goal of accelerating forest succession since the soil physical and chemical conditions might not be optimal for these introduced species. Our study shows the evergreen broad-leaved plants have different nutrient use strategies: (1) ‘‘nutrient conservative’’ species with low leaf nutrient and high nutrient resorption efficiency, such as *S. superba*; (2) ‘‘nutrient spending’’ species with relatively high leaf nutrient and low nutrient resorption efficiency, such as *C. fargesii*, the climax species in this area. We suggest ‘‘nutrient conservative’’ species can be optimal candidates to plant in the nutrient poor sites while ‘‘nutrient spending’’ species can be considered for use in less degraded sites. Overall, our study on the nutrient status and litter decomposition rate of the common species in EBLFs can provide the necessary information to facilitate the selection of tree or shrub species for forest restoration.

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Appendix A. Nutrient concentration in fresh and dead leaves, nutrient resorption efficiency and litter decomposition rate in a secondary evergreen broad-leaved forest in eastern China

Species	Family	Location[a]	SLA (cm^2/g)	N_{live} (mg/g)	P_{live} (mg/g)	N_{dead} (mg/g)	P_{dead} (mg/g)	NRE (%)	PRE (%)	*k* ($year^{-1}$)
Deciduous species										
Carpinus viminea	Betulaceae	4				15.08	0.89			
Cornus kousa	Cornaceae	4				19.43	0.99			
Castanea mollissima	Fagaceae	1	210	22.86	1.45	15.42	0.34	32.55	76.63	2.256
Quercus fabri	Fagaceae	4	159	22.60	1.31	14.56	0.33	35.56	75.06	1.186
Liquidambar formosana	Hamamelidaceae	1	188	18.41	0.95	6.37	0.38	65.42	60.24	1.359
Lindera glauca	Lauraceae	1A	293	26.38	1.41	16.26	0.87	38.35	38.33	
Lindera reflexa	Lauraceae	1				14.36	0.69			
Litsea cubeba	Lauraceae	1A	342	36.32	1.31	25.00	0.69	31.17	47.57	6.280
Sassafras tzumu	Lauraceae	1A	163	19.47	1.11	14.21	0.64	27.03	42.22	0.695
Ficus erecta var. *beecheyana*	Moraceae	1A	231	29.37	1.63	17.34	0.86	40.96	47.53	4.944
Prunus serrulata	Rosaceae	5				10.17	0.64			1.162
Celtis tetrandra ssp. *sinensis*	Ulmaceae	4				11.33	0.67			1.730
Zelkova schneideriana	Ulmaceae	4				11.17	0.63			
Premna microphylla	Verbenaceae	4				22.83	1.18			
Evergreen broad-leaved species with leaf life span <1.5 years										
Ilex kengii	Aquifoliaceae	1				11.08	0.36			
Elaeocarpus decipiens	Elaeocarpaceae	2	141	22.37	1.83	10.66	0.76	52.37	58.66	3.542
Vaccinium mandarinorum	Ericaceae	1	104	11.77	0.32					
Castanopsis sclerophylla	Fagaceae	1	119	14.81	0.96	8.62	0.47	41.77	50.56	0.952
Cyclobalanopsis gilva	Fagaceae	3	80	14.94	0.57					
Cyclobalanopsis glauca	Fagaceae	1	141	14.43	1.02	9.20	0.49	36.21	51.97	1.800
Cyclobalanopsis gracilis	Fagaceae	1	106	13.64	0.69	10.74	0.39	21.23	43.68	0.624
Cyclobalanopsis myrsinaefolia	Fagaceae	1	132	18.60	0.90	12.86	0.59	30.85	34.28	1.503
Cyclobalanopsis nubium	Fagaceae	3				12.02	0.48			0.558
Lithocarpus glaber	Fagaceae	1	116	17.14	0.73	13.03	0.54	23.96	25.94	1.020
Cinnamomum comphora	Lauraceae	1	125	15.61	0.90	11.04	0.85	29.30	5.91	0.835
Litsea coreana var. *sinensis*	Lauraceae	2				14.39	0.96			
Machilus leptophylla	Lauraceae	1	111	22.50	2.27	15.07	1.06	33.00	53.33	
Phoebe sheareri	Lauraceae	2	85	21.27	1.46	16.03	1.09	24.63	25.19	1.621
Myrica rubra	Myricaceae	1	116	16.98	0.58					
Osmanthus cooperi	Oleaceae	1				7.50	0.76			
Helicia cochinchinensis	Proteaceae	1	131	16.00	0.58	10.15	0.48	36.57	17.67	0.824
Randia cochinchinensis	Rubiaceae	1	140	19.05	0.81	10.60	0.59	44.38	27.07	
Symplocos lancifolia	Symplocaceae	1	198	17.44	0.89					
Camellia fraterna	Theaceae	1	137	12.82	0.60					
Evergreen broad-leaved species with leaf life span >1.5 years										
Daphniphyllum oldhamii	Daphniphyllaceae	1	141	18.22	1.04	13.03	0.49	28.48	52.96	4.337
Rhododendron ovatum	Ericaceae	1	129	11.02	0.69					
Castanopsis carlesii	Fagaceae	1	127	14.22	0.82					
Castanopsis fargesii	Fagaceae	1	92	16.81	0.70	13.07	0.42	22.25	40.34	1.636
Lithocarpus harlandii	Fagaceae	2	119	16.11	0.93	11.75	0.53	27.04	42.50	2.389
Machilus thunbergii	Lauraceae	1	73	12.69	0.68					
Neolitsea aurata var. *chekiangensis*	Lauraceae	2	103	16.11	0.79	9.01	0.58	44.06	27.13	
Photinia glabra	Rosaceae	1	133	10.22	0.78	7.82	0.51	23.53	35.06	1.801
Meliosma oldhamii	Sabiaceae	2				11.50	1.15			
Styrax suberifolia	Styracaceae	2	131	17.35	0.83	12.23	0.56	29.51	32.11	
Symplocos anomala	Symplocaceae	1	137	11.03	0.48	7.46	0.30	32.37	36.85	
Symplocos heishanensis	Symplocaceae	1	134	13.23	0.82					
Symplocos laurina	Symplocaceae	1	103	17.24	0.77	8.47	0.45	50.86	41.47	
Symplocos stellaris	Symplocaceae	1	89	12.35	0.51	8.11	0.43	34.31	14.89	
Eurya rubiginosa var. *attenuata*	Theaceae	1	116	12.51	0.47	8.06	0.25	35.59	47.43	
Schima superba	Theaceae	1	95	12.47	0.55	6.86	0.25	44.99	54.63	1.353

[a] The species were sampled as—(1) *S. superba* community: altitude 163 m, total soil N 2.60 ± 0.28 mg/g, total soil P 0.39 ± 0.01 mg/g; (1A) the extended area of *S. superba* community ($\sim$30–60 m from each border of the permanent plot); (2) *C. fargesii* community: altitude 200 m, total soil N 5.16 ± 0.09 mg/g, total soil P 0.48 ± 0.01 mg/g; (3) *C. nubium* community: altitude $\sim$350 m; (4) neighboring area of *S. superba* community or *C. nubium* community; (5) near valley. Far away from all other sampling sites.

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