

Shifts in plant nutrient use strategies under secondary forest succession

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Abstract In evergreen broad-leaved forests (EBLFs) in Tiantong National Forest Park, Eastern China, we studied the soil chemistry and plant leaf nutrient concentration along a chronosequence of secondary forest succession. Soil total N, P and leaf N, P concentration of the most abundant plant species increased with forest succession. We further examined leaf lifespan, leaf nutrient characteristics and root–shoot attributes of *Pinus massoniana* Lamb, the early-successional species, *Schima superba* Gardn. et Champ, the mid-successional species, and *Castanopsis fargesii* Franch, the late-successional species. These species showed both intraspecific and interspecific variability along succession. Leaf N concentration of the three dominant species increased while N resorption tended to decrease with succession; leaf P and P resorption didn't show a consistent trend along forest succession. Compared with the other two species, *C. fargesii* had the shortest leaf lifespan, largest decay rate

and the highest taproot diameter to shoot base diameter ratio while *P. massoniana* had the highest root–shoot biomass ratio and taproot length to shoot height ratio. Overall, *P. massoniana* used 'conservative consumption' nutrient use strategy in the infertile soil conditions while *C. fargesii* took up nutrients in the way of 'resource spending' when nutrient supply increased. The attributes of *S. superba* were intermediate between the other two species, which may contribute to its coexistence with other species in a wide range of soil conditions.

Keywords Evergreen broad-leaved forests · Leaf lifespan · Nutrient resorption · Nutrient use strategies · Root /shoot ratios · Soil nutrients

Abbreviations

<i>C. fargesii</i>	<i>Castanopsis fargesii</i>
EBLF	evergreen broad-leaved forest
<i>P. massoniana</i>	<i>Pinus massoniana</i>
RSBR	root–shoot biomass ratio
RSDR	root–shoot diameter ratio
RSLR	root–shoot length ratio
<i>S. superba</i>	<i>Schima superba</i>

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Introduction

Species from nutrient poor sites usually have 'conservative consumption' nutrient use strategy

such as long-lived leaves, low nutrient concentration, high nutrient resorption, and slow litter decomposition (Aerts 1997; Aerts and Chapin 2000; Escudero et al. 1992; Kobe et al. 2005; Reich et al. 1991; Wright and Cannon 2001; Wright and Westoby 2003). Plants from nutrient rich-sites, on the other hand, usually use nutrient in the way of ‘resource spending’ such as having high nutrient concentration in green leaves and low nutrient resorption efficiency in senesced leaves (Aerts and Chapin 2000; Grime 2001; Reich et al. 1992; Wright and Cannon 2001; Wright and Westoby 2003). Therefore, it has been assumed that there is a relationship between soil nutrient conditions and the leaf-level characteristics among various vegetation types (Cordell et al. 2001; Kobe et al. 2005; Wright et al. 2002).

Many previous studies have also shown that species from infertile habitats have relatively higher root–shoot ratio than do species from fertile sites (Aerts et al. 1991; Aerts and Chapin 2000). When light is limited, plants tend to allocate more for aboveground biomass (Grime 2001). When nutrients are more limited than light, however, the pattern shifts to allocate more for belowground biomass (Comas et al. 2002). The optimal shoot–root ratio, therefore, depends on the availability and ratio of light and nutrients (Agren and Franklin 2003; McConnaughay and Coleman 1999; Sami and Anna 2002). Although the allocation pattern is only poor indicator of resource capture when different growth-forms are compared (Craine 2005; Tilman 1985), it is still recognized as an important trait to reflect species competition strategies at different resource availability (Aerts and Chapin 2000; Tilman 1991). Therefore, understanding of the leaf traits and root–shoot ratio of the dominant species in forest is crucial to understand species replacement during forest dynamics (Gedroc et al. 1996; Reynolds and D’Antonio 1996).

Evergreen broad-leaved forest (EBLF), covering a lot of area in China, is the zonal vegetation type in subtropical area. Unfortunately, under long-term human disturbances, this forest is shifting to include more degraded areas dominated by early-successional forests and shrubs (Wang et al. 2005). Soil nutrient concentration, especially N, is usually very poor

in the early-successional forests. *Pinus massoniana* is a pioneer coniferous species occupying a lot of disturbed habitats such as the abandoned fields (Wang and Song 1999). Although this species grows rapidly, it retains some characteristics of slow-growing species such as low leaf nutrient concentration, long leaf life span and slow litter decomposition rate (Wang and Song 1999; Huang and Wang 2002; Wang et al. 2004). When the secondary succession proceeds, this species is gradually replaced by *Schima superba*, and *Castanopsis fargesii* (Ding and Song 1998), which have high leaf nutrient concentration and short leaf life-span (Huang and Wang 2002; Wang et al. 2000). Therefore, we speculate that the early successional species is more “nutrient conservative” than late successional species in this study area. However, empirical studies have shown the opposite-late-successional species tend to have lower resource uptake and loss rate (Garnier et al. 2004; Hegarty 1990; Vile et al. 2006) when soil nutrient accumulates with succession. Therefore, in order to shed light into the plant nutrient use strategies and soil chemistry dynamics with succession in this region, we conducted a study to address the following questions: (1) Does leaf nutrient concentration vary among different successional forests? (2) Does soil N, P content vary among different successional forests? (3) How plant nutrient use strategies, especially considering the dominant species, change along forest succession? (4) Can nutrient use strategies of the dominant species reflect soil nutrient conditions?

Materials and methods

Study area

This study was done in Tiantong National Forest Park (29°52′N, 121°39′E, 200 m a.s.l.). Mean annual temperature in this area is 16.2 °C. Average annual precipitation is 1374.7 mm (Song and Wang 1995). Soils are mainly red and yellow earths with pH ranging from 4.4 to 5.1. The substrate of parental material is mesozoic sediments and acidic intrusive rocks, including quartzite and granite. Soil texture is mainly medium to heavy

loam (Song and Wang 1995). The mature forests around a Buddhist temple in the center of the park are considered as climax monsoon EBLF because this area has been protected from clear cutting (Song and Wang 1995). Outside of this area, *P. massoniana* Lamb dominated community and *S. superba* Gardn. et Champ dominated community are representative of early- and mid-successional forests respectively (Song and Wang 1995). These two forest communities have similar species composition, but the dominant species shift (Appendix 1). Compared with them, forest dominated by *C. fargesii* Franch has more closed canopy and includes more shade-tolerant species.

Experimental design

We chose *C. fargesii* community (mature climax EBLF), *S. superba* community, and *P. massoniana* community as study stands, which represent three successional stages of EBLF. Within each community, we set up one sampling plot (30 × 30 m).

In order to achieve our objectives, we split the study into two steps. The first step was to study the nutrient use strategies of *P. massoniana*, *S. superba* and *C. fargesii* at these three successional stages. Species and successional stages were considered as two main factors. Since *P. massoniana* was not presented in *C. fargesii* forest, we had incomplete 2 × 2 factorial design. Due to the limitation of labor and sapling availability, leaf lifespan, litter decomposition and root–shoot attributes were determined for each species at their own dominated successional stages instead of whole successional series. The second step was to examine the leaf nutrient concentration of most abundant species in each successional stage to understand the interspecific leaf nutrient variations along succession.

Leaf collection

In the first step, fresh leaves and leaf litter were collected from July 2004 to October 2004. In July 2004, three to five trees for each of the three species were selected and marked in each plot. Three branches per tree were cut from upper, middle and lower canopy positions. Leaves were

pooled for each tree. Specific leaf area and leaf N, P were later measured. In October and November 2004, senesced leaves of these three species were obtained from originally marked trees by gently shaking the branches. Senesced leaves from each individual tree were well mixed and then 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 July 2005, leaf life span was estimated by examining ~60 branches per plant from these 15 marked trees.

In the second step, we selected 7 to 8 most abundant species in each successional stage in summer 2005. Three to five plant individuals per species were randomly chosen. Mature leaves were collected using the method discussed above.

Calculation of leaf traits

Approximately 50–100 fresh-leaves (or senesced leaves) per plant were scanned using a flat-bed scanner. Scanned leaves were then dried for >48 h at 70 °C. Since needles don't have flat leaf area, we record needle length and cross-section width and needle leaf area was estimated as:

$$S = \pi * L * D / 2$$

Where S is leaf area; L is needle length and D is needle width at the half needle length.

Fresh and senesced leaves were ground and digested. Leaf N and P concentrations were determined using flow-injection autoanalyser (Skalar, Netherland). In estimating the percentage of nutrient resorbed from senesced leaves, N (or P) was expressed per unit leaf area rather per unit weight. This corrects for the fact that weight may change considerably during senescence due to differential resorption or the deposition of materials onto the leaf surface. Nutrient resorption efficiency was calculated as:

$$Nur_{res} = ((Nu_{fre} - Nu_{sen}) / Nu_{fre}) * 100$$

Where Nur_{res} is nutrient resorption efficiency, Nu_{fre} and Nu_{sen} are nutrient concentration in fresh leaves and senesced leaves, respectively.

Litter bag method was used to study litter decomposition. Approximately 4.5 g air dried leaves were placed in 2 mm mesh nylon bags of 15 × 20 cm. In total, there were 75 (3 species × 25 bags). On 4 January 2005, Litter bags were placed in each of the three plots. Bags were later retrieved every 3 months during one year period. Harvested bags were cleaned with water to remove extraneous materials, arthropods and soil. Litter was dried at 70 °C to constant weight. Decomposition rate constant (k) was calculated using the exponential relationship $X_t/X_0 = e^{-kt}$, where X_0 is initial dry-weight and X_t is the remained litter weight at collection time (t), (Olson 1963).

Approximately 60 branches per plant species were sampled to estimate leaf life span using life table method (Wang et al. 2000). For each twig, a leaf ‘sequence’ was defined from the youngest leaf backwards along the twig to the oldest primary leaf found, whether on the same twig or on a branch one or more branching-orders back from the twig (Wright et al. 2002). The number of primary leaves in the sequence was counted. In evergreen conifers, the apex of a long branch produces a yearly growth increment that bears a single age class of needles. We counted back leaf age classes from branch tips, which were validated by counting tree-rings at the base of the branches. In broad-leaved evergreen trees, leaf age classes were determined by counting back the internodes from the branch tips (Luo et al. 2005; Wang et al. 2000). Leaf age of current leaves was determined as the duration between leaf onset and sampled date. The expected leaf life span was estimated as:

$$E = \left(\sum_x^{\infty} L_x \right) / N_x$$

$$L_x = (N_x + N_{x+1}) / 2$$

where E is the expected leaf life span; x is the leaf age class; N_x is the number of the leaves presented at age class x ; L_x is the average number of survived leaves from age x to age $x+1$.

Root–shoot attributes

Due to limited sapling availability, we measured root–shoot attributes for these three species only

at their own successional stages. In May 2004, fifteen small saplings of each species were selected around the border of these three plots using the following criteria: (1) saplings were 1–2 m tall; (2) saplings had only one stem, no obvious damage on either leaf or stem. After vertical height, shoot diameters at base, and total length of all branches were determined, saplings were excavated carefully. Special care was taken to avoid breaking fine roots. Roots, shoots, and leaves were separated in the field. Roots were cleaned to remove surface soil in lab. The diameter and length of the major root, and stem length, were determined using vernier caliper. All parts of each sapling were oven dried at 70 °C for 72 h and weighted to 0.001 g.

Soil variables

In August 2004, five soil samples were taken with a metallic tube (20 cm height and 7.5 cm in diameter) from randomly chosen spots in each of the three plots. Litter layer was removed before soil was taken. Then subsample in each of the 15 soil samples were air-dried, sieved to 0.5 mm to analyze total nitrogen concentration (Kjeldahl), and further ground to pass through 0.25 mm mesh to analyze total P using the chloromolybdophosphonic blue color method. Total N and total P concentration were estimated using the flow-injection autoanalyser (Skalar, Netherland).

Statistical analysis

To determine whether leaf nutrient concentration of the most abundant species changed over different successional stages, Leaf N and P were first averaged for each species sampled from different successional forests and species means were then analyzed as response variables using one-way analysis of variance (ANOVA). Successional stage was included as fixed effect. Different plant species were considered as samples. If there was a significant effect of successional stage, least-squares mean separation with Tukey correction was used to test for differences among successional stages. In order to determine whether dominant species of each successional

stages exhibited different nutrient use strategies and further determine whether same species showed different strategies at different successional stages, leaf N, P concentration, N, P resorption were analyzed as two-way ANOVA. Species and successional stages were considered as fixed effects. Each sampled plant was included as replications. We acknowledged that the experiment design was pseudoreplicated because we had one plot for each successional stage; therefore, special care should be taken for any inferences. All statistical tests were conducted using SPSS 10.0 (SPSS Inc., Chicago, IL, USA). Normality and homogeneity of variance of the residuals were tested. Data were log-transformed, if homogeneity of the variance was not met.

Results

Leaf nutrient dynamics along forest succession

Leaf N was significantly different among different successional forests ($F_{2,19} = 4.14$, $P = 0.012$; Appendix 2). Leaf N was higher in *C. fargesii* Community than in *P. massoniana* community (Fig. 1A). In contrast, leaf P didn't differ among these different successional stages ($F_{2,19} = 2.20$, $P = 0.139$).

Leaf nutrient traits of dominant species along forest succession

Over these three dominant species, leaf N, and leaf N resorption rate exhibited significant difference among different successional stages while leaf P and P resorption didn't differ (Table 1). Leaf N tended to increase while N resorption tended to decrease with succession (Fig. 2). These three dominant species exhibited significant interspecific differences in nutrient concentration and resorption efficiency (Table 1). *C. fargesii*, the dominant species in the mature forest, had higher leaf N than *P. massoniana* and *S. superba*, which were the dominant species in the early- and mid-successional stages (Fig. 2A). Compared with *P. massoniana* and *C. fargesii*, *S. superba*, had lower leaf P (Fig. 2B). *C. fargesii* and *P. massoniana* tended to decrease N resorption with

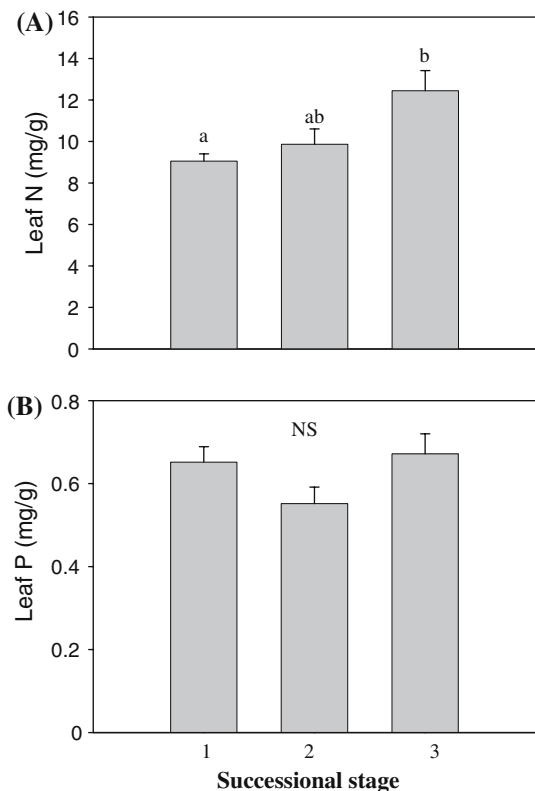


Fig. 1 Leaf nutrient characteristics among different successional stages. Means and SE were presented. Bars with different letter were significant different at Tukey adjusted $P < 0.05$. In horizontal axis, 1: *P. massoniana* community, $n = 7$ species; 2: *S. superba* community, $n = 7$ species; 3: *C. fargesii*. Community, $n = 8$ species

succession while *S. superba* exhibited highest N resorption at the mid-successional stage (Fig. 2C). P resorption didn't show a clear trend along succession (Fig. 2D).

Leaf life span, litter decomposition and root–shoot attributes

Leaf life span ($P < 0.001$) and litter decomposition rates ($P < 0.001$) varied among species (Table 2). *P. massoniana*, had the highest leaf longevity while *C. fargesii* and *S. superba* didn't differ significantly. Leaf litter decomposition was fastest in *C. fargesii* and slowest in *P. massoniana*.

Root–shoot biomass ratio (RSBR, hereafter) was significantly greater in *P. massoniana* than that in *S. superba* and *C. fargesii* ($P = 0.001$). Root–shoot length ratio (RSLR) showed a similar

Table 1 Results of two-way ANOVA's for plant nutrient concentration

Factor	df	N		P		N resorption		P resorption	
		F	P	F	P	F	P	F	P
Stage	2	3.93	0.033	2.66	0.09	9.01	0.002	3.08	0.072
Species	2	5.26	0.012	4.30	0.025	21.69	< 0.001	20.06	< 0.001
Stage-species	3	0.82	0.496	0.28	0.836	7.06	0.003	20.44	< 0.001

The *F*-values and *P*-values are presented for effects of succession stages, species, and species-stage. Error df is 25 for N, P and 17 for N, P resorption. Since *P. massoniana* was not present in *C. fargesii* community. Stage-species interaction degree of freedom was reduced to 3

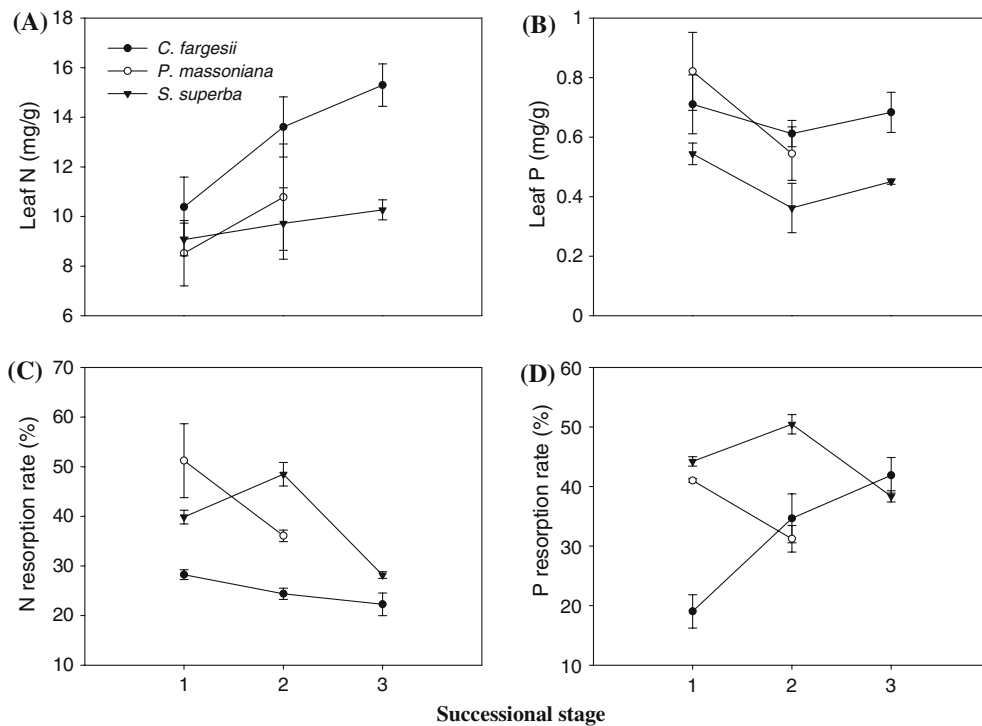


Fig. 2 Leaf nutrient characteristics of dominant species at different successional stages. Means and SE were presented. See Fig. 1 for explanation of numbers on horizontal axis

pattern as RSBP ($P < 0.001$). RSLR didn't differ between *S. superba* and *C. fargesii*. *C. fargesii* had the highest taproot diameter to shoot base diameter ratio (RSDR) while *P. massoniana* had the lowest ($P = 0.03$) (Table 2).

Soil variables

Soil total N ($P < 0.001$) and total P ($P < 0.001$) was higher in *C. fargesii* community than in the other two successional stages. In the shifting from *P. massoniana* community to *S. superba*

community, soil N and the total soil P displayed a slight decrease, but of no statistical significance (Table 3).

Discussion

Soil chemistry and plant nutrient

Soil total N and P were found to be higher in the mature forest than the other two successional forests. Previous studies have well documented

Table 2 Leaf life span, leaf litter decay rate and root–shoot attributes of dominant tree species at different succession stages in the evergreen broad-leaved forests, Eastern China

Species	Leaf life span (yr)	Decay rate ($\text{g g}^{-1}\text{yr}^{-1}$)	Root–shoot biomass ratio	Root–shoot length ratio	Root–shoot diameter ratio
<i>Castanopsis fargesii</i>	1.21 ± 0.49^a	1.64 ± 0.08^a	0.90 ± 0.28^a	0.79 ± 0.24^a	1.40 ± 0.32^a
<i>Schima superba</i>	1.35 ± 0.63^a	1.35 ± 0.06^b	1.04 ± 0.28^a	0.98 ± 0.41^a	1.20 ± 0.38^{ab}
<i>Pinus massoniana</i>	2.35 ± 0.14^b	0.69 ± 0.03^c	1.55 ± 0.52^b	2.12 ± 0.44^b	1.06 ± 0.26^b

Data are means \pm SE, $n = 5$ for leaf life span and decay rate. $n = 15$ for root–shoot attributes. Different letters on the same column indicate significant differences at $P < 0.05$ (Tukey test)

Table 3 Soil nutrient contents at different succession stages in the evergreen broad-leaved forests, Eastern China

Community types	Total N (mg g^{-1})	Total P (mg g^{-1})
<i>Castanopsis fargesii</i> community	5.16 ± 0.09^a	0.48 ± 0.01^a
<i>Schima superba</i> community	2.60 ± 0.28^b	0.39 ± 0.01^b
<i>Pinus massoniana</i> community	2.12 ± 0.17^b	0.38 ± 0.01^b

Data are means \pm SE, $n = 5$. Different letters on the same column indicate significant differences at $P < 0.05$ (Tukey test)

that succession on nutrient poor site resulted in increased N mineralization and enhanced N pool (Berendse et al. 1998). In the early successional forests, soil nutrient availability is relatively poor due to the large biomass removal from clear cutting, and high nutrient leaching from exposed soils. With succession, soil nutrient, especially N increased significantly.

How plant foliar nutrient variation along succession relates to soil nutrient conditions has long been of interest to forest ecologists. Many studies have attempted to relate foliar nutrient concentration to site quality and soil nutrient availability and provided conflicting results (Boerner 1984; Ellsworth and Reich 1996; Hobbie and Gough 2002; Shukla and Ramakrishnan 1984; McIendon and Redente 1992; Garnier et al. 2004; Wright et al. 2001). Our study showed that plant leaf N was higher in mature forest, which corresponds to soil nutrient dynamics (Fig. 1). Therefore we concluded that with succession, leaf-level N concentrations and soil nutrient availability tended to increase in this study area. Though soil P also increased with secondary succession, leaf P didn't show similar trend. Since most of the soil P

is not available to plants, it is therefore not surprising to find that leaf P is not a useful indicator of soil P pool.

Nutrient use strategies of the dominant species

Pinus massoniana, *S. superba* and *C. fargesii* are the dominant species in early-, mid- and late-successional stages, respectively. *P. massoniana* exhibits 'conservative nutrient use strategies' such as long leaf life span, low leaf nutrient concentration, high N resorption efficiency from senescing leaves and slow litter decomposition while *C. fargesii*, the late-successional species, has the opposite characteristics (Fig. 2, Table 2).

Long leaf life span and high nutrient resorption are assumed to be particularly beneficial in infertile habitats (Eckstein et al. 1999; Escudero et al. 1992; Wright and Cannon 2001). In the present study, *P. massoniana* had longer leaf life span than other two species. It suggests that, in the nutrient-poor habitats, longer leaf life span was adopted as an important nutrient use strategy to reduce nutrient losses (Eckstein et al. 1999; Wright and Cannon 2001), to produce more leaf biomass at a given level of nutrient availability (Aerts 1999; Killingbeck 1996), and to increase the nutrient use efficiency (Cordell et al. 2001; Reich et al. 1991). However, some other studies have shown that early successional species had shorter leaf life span (Garnier et al. 2004; Hegarty 1990; Navas et al. 2003; Shukla and Ramakrishnan 1984; Vile et al. 2006). Therefore, we think the nutrient use strategy is shaped by the complex interactions among plant growth form and changes in light and soil nutrient availability following forest succession.

Considering root–shoot attributes of these three species, we found that *P. massoniana* had the highest RSBR and taproot RSLR, and the lowest taproot RSDR. It suggests that *P. massoniana* allocates more biomass in belowground than aboveground in nutrient-poor habitats. This finding is consistent with the hypothesis that high biomass allocation to roots is beneficial in infertile habitats (Aerts 1999; Comas et al. 2002).

Castanopsis fargesii, the late successional species, took up nutrients in the way of ‘resource spending’ where soil nutrients were rich. This characteristic was demonstrated by a set of leaf traits, such as shorter leaf life span, higher N concentration in green leaves, and the smaller proportional resorption of N, compared to other two species. It is assumed that, in the nutrient-rich habitats, there is no need for *C. fargesii* to employ ‘conservative’ strategies.

As a dominant tree in the climax EBLF, successfully obtaining light resource is crucial for sustaining dominant niche. Although Ding and Song (1998) have suggested that shade-tolerant trait (e.g. with the relative lower light compensation point) provided the greatest competitive advantage for *C. fargesii* to ensure its dominance in climax community, but the lower light compensation point is not the whole reason. Since nutrients are abundant at the mature successional stage, other traits, such as strong competitive ability for light, are more important (Garnier et al. 2004; Lambers et al. 1998; Vile et al. 2006). For instance, *C. fargesii* has the lowest RSBR and the shortest RSLR among these three study species. It suggests that high shoot–root biomass ratio and shoot–root height ratio can help it capture more light and therefore is superior competitor comparing with neighboring plants. Many previous studies have shown that high biomass allocation to shoots is advantageous in fertile habitats (Agren and Franklin 2003; Grime 2001; Reynolds and D’Antonio 1996). Some other studies further suggested that allocation to shoot should exceed allocation to roots when light is more limiting than nutrients (Aerts and Chapin 2000; Grime 2001). *C. fargesii* from nutrient-rich habitats has set of traits that lead to quick capture of light, thus it can eventually sustain its’ dominant niche in the climax EBLF.

Ding and Song (1998) suggested that *S. superba* presented in all these successional stages but with more dominance in the middle stages of succession in EBLF. Our results showed that the attributes of *S. superba* are intermediate between the other two species, which may contribute to its coexistence with other species in a gradient of nutrient conditions.

Concluding remark

Overall, plant leaf nutrient concentration and soil chemistry improve with the secondary succession in our study area. Nutrient use strategies of the dominant species shifted from ‘conservative consumption’ to ‘intermediate’ and finally ‘nutrient spending’. We acknowledge that different function-type of the dominant species might also contribute to the explanation of the altered nutrient use strategies; therefore, any generalization of this study or inferences towards other ecosystems or study areas should be carefully taken.

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Appendix

Appendix 1 The importance value of common species along a chronosequence of secondary forest succession in evergreen broad-leaved forests in Tiantong National Forest Park, Eastern China

	Successional communities		
	I	II	III
Field age (a)	30	90	150
Altitude (m)	115	130	207
Height of community (m)	15	15–20	25
Total coverage (%)	90	95	95
Species	Importance value* (%)		
Tree layer			
<i>Castanopsis fargesii</i>	0.85	2.17	75.58
<i>Schima superba</i>	41.68	66.24	9.03
<i>Pinus massoniana</i>	53.93	20.65	•
<i>Liquidambar formosana</i>	1.35	•	7.16
<i>Diospyros lotus</i>	•	•	2.55

Appendix 1 continued

<i>Cyclobalanopsis myrsinaefolia</i>	•	•	2.17
<i>Lithocarpus glaber</i>	1.85	6.95	2.12
<i>Castanopsis sclerophylla</i>	0.34	3.9	1.41
Shrub layer			
<i>Castanopsis fargesii</i>	4.56	4.58	5.25
<i>Schima superba</i>	0.91	3.92	0.65
<i>Pinus massoniana</i>	5.38	•	•
<i>Camellia fraterna</i>	2.31	4.7	18.55
<i>Eurya nitida</i>	•	0.64	9.56
<i>Symplocos glauca</i>	•	•	6.74
<i>Daphniphyllum macropodium</i>	•	0.26	4.96
<i>Eurya loquaiana</i>	•	•	4.58
<i>Symplocos lancifolia</i>	•	0.82	3.53
<i>Elaeocarpus japonica</i>	•	0.42	3.14
<i>Styrax suberifolius</i>	•	•	3.11
<i>Neolitsea aurata var. chekiang</i>	0.2	•	3.04
<i>Symplocos laurina</i>	•	0.22	3.01
<i>Cinnamomum japonicum</i>	•	•	2.96
<i>Ilex buergeri</i>	•	•	2.77
<i>Symplocos sumuntia</i>	11.55	8.41	2.2
<i>Symplocos stellaris</i>	•	•	2.2
<i>Acer olivaceum</i>	•	0.28	2.18
<i>Eurya rubiginosa var. attenuata</i>	4.57	10.22	2.12
<i>Tricalysia dubia</i>	•	0.28	2.1
<i>Cyclobalanopsis glauca</i>	•	•	1.62
<i>Cyclobalanopsis myrsinaefolia</i>	0.69	0.72	1.48
<i>Myrica rubra</i>	7.01	1.98	1.45
<i>Machilus thunbergii</i>	0.38	0.42	1.33
<i>Eurya muricata</i>	1.38	1.92	1.31
<i>Ilex kengii</i>	•	•	1.13
<i>Lasianthus lancilimbus</i>	•	•	0.95
<i>Meliosma regida</i>	•	•	0.92
<i>Lithocarpus harlandii</i>	•	•	0.79
<i>Helicia cochinchinensis</i>	•	1.87	0.68
<i>Ilex rotunda</i>	•	•	0.65
<i>Cleyrea japonica</i>	0.26	•	0.59
<i>Photinia serrulata</i>	•	•	0.53
<i>Litsea elongata</i>	•	8.28	0.46
<i>Prunus phaeosticta</i>	•	•	0.43
<i>Lithocarpus glaber</i>	3.47	1.51	0.43
<i>Ilex purpurea</i>	0.23	•	0.28
<i>Styrax confusus</i>	0.28	•	0.26
<i>Diospyros kaki var. sylvestris</i>	•	•	0.25
<i>Symplocos anomala</i>	•	•	0.24
<i>Vaccinium mandarinorum</i>	5.07	1.74	0.23
<i>Rhododendron ovatum</i>	13.44	20.27	0.22
<i>Cunninghamia lanceolata</i>	4.58	•	0.22
<i>Toxicodendron succedaneum</i>	0.49	•	0.21
<i>Elaeocarpus decipiens</i>	0.21	•	0.21
<i>Symplocos stellaris</i>	1.88	5.53	•
<i>Symplocos heishanensis</i>	0.2	5.39	•
<i>Castanopsis carlesii</i>	•	4.75	•
<i>Castanopsis sclerophylla</i>	1.13	4.55	•
<i>Loropetalum chinensis</i>	27.21	1.83	•
<i>Syzygium buxifolium</i>	•	1.29	•
<i>Carpinus fargesii</i>	•	0.94	•
<i>Cyclobalanopsis stewardiana</i>	0.27	0.86	•
<i>Ormosia henryi</i>	•	0.34	•
<i>Vaccinium bracteatum</i>	•	0.34	•

Appendix 1 continued

<i>Symplocos setchuensis</i>	•	0.33	•
<i>Clerodendrum cyrtophyllum</i>	0.57	0.16	•
<i>Liquidambar formosana</i>	0.94	0.13	•
<i>Alangium platanifolium</i>	0.42	•	•
<i>Diospyros lotus</i>	0.31	•	•
Herb layer			
<i>Castanopsis fargesii</i>	2.39	2.87	2.52
<i>Schima superba</i>	0.8	2.87	2.52
<i>Smilax china</i>	1.59	2.15	2.52
<i>Stauntonia leucantha</i>	•	•	2.52
<i>Ficus pumila</i>	•	•	0.63
<i>Symplocos anomala</i>	•	0.72	•
<i>Sarcandra glabra</i>	•	•	26.74
<i>Camellia sinensis</i>	3.18	2.87	•
<i>Lithocarpus henryi</i>	•	•	2.52
<i>Syzygium buxifolium</i>	1.59	•	1.26
<i>Clerodendrum cyrtophyllum</i>	•	•	0.63
<i>Lophatherum gracile</i>	2.39	•	•
<i>Maesa japonica</i>	•	•	1.89
<i>Elaeocarpus decipiens</i>	•	•	2.52
<i>Ilex buergeri</i>	•	•	1.26
<i>Carpinus fargesii</i>	•	0.72	•
<i>Liquidambar formosana</i>	0.8	•	•
<i>Acer olivaceum</i>	•	•	1.26
<i>Tricalysia dubia</i>	•	•	1.89
<i>Wookwardia japonica</i>	14.91	7.83	5.96
<i>Cyclobalanopsis stewardiana</i>	•	•	0.63
<i>Symplocos heishanensis</i>	•	7.11	0.63
<i>Ardisia crenata f. hortensis</i>	•	0.72	2.52
<i>Machilus thunbergii</i>	1.59	2.15	4.08
<i>Helicia cochinchinensis</i>	•	0.72	0.63
<i>Damnacanthus indicus</i>	0.8	•	•
<i>Ormosia henryi</i>	0.8	•	•
<i>Machilus leptophylla</i>	•	•	0.63
<i>Litsea elongata</i>	•	1.43	1.26
<i>Symplocos laurina</i>	•	•	1.26
<i>Loropetalum chinensis</i>	3.18	0.72	•
<i>Viburnum dilatatum</i>	•	•	•
<i>Daphniphyllum macropodium</i>	•	•	0.63
<i>Gynostemma pentaphyllum</i>	•	•	1.89
<i>Arthraxon hispidus</i>	0.8	•	•
<i>Castanopsis sclerophylla</i>	3.18	2.87	0.63
<i>Carex spp.</i>	1.6	•	0.63
<i>Lasianthus lancilimbus</i>	•	•	0.63
<i>Symplocos stellaris</i>	•	2.87	•
<i>Diplopterygium laevissium</i>	•	•	5.96
<i>Camellia fraterna</i>	2.39	7.83	1.89
<i>Dryopteris spp.</i>	1.6	•	•
<i>Trachelospermum jasminoides</i>	0.8	•	2.52
<i>Rhododendron ovatum</i>	3.18	2.87	•
<i>Vaccinium sbracteatum</i>	4.52	•	0.63
<i>Castanopsis carlesii</i>	•	2.15	0.63
<i>Kadsura longipedunculata</i>	0.8	•	•
<i>Osmanthus cooperi</i>	•	0.72	•
<i>Symplocos lancifolia</i>	•	1.43	•
<i>Cyclobalanopsis myrsinaefolia</i>	0.8	1.43	0.63
<i>Indocalamus tessellatus</i>	•	2.15	•
<i>Symplocos sumutia</i>	14.91	7.83	0.63
<i>Lindera glauca</i>	0.8	•	•

Appendix 1 continued

<i>Randia cochinchinensis</i>	•	•	1.26
<i>Litsea cubeba</i>	0.8	•	•
<i>Cunninghamia lanceolata</i>	0.8	1.43	•
<i>Rhaphiolepis indica</i>	0.8	•	0.63
<i>Lithocarpus glaber</i>	3.18	7.83	1.26
<i>Photinia serrulata</i>	•	•	0.63
<i>Elaeocarpus japonica</i>	•	0.72	0.63
<i>Dioscorea opposita</i>	4.52	•	0.63
<i>Symplocos setchuensis</i>	2.39	•	•
<i>Cinnamomum japonicum</i>	4.7	7.83	1.26
<i>Smilax glabra</i>	3.18	2.15	1.26
<i>Vaccinium bracteatum</i>	•	2.87	•
<i>Eurya loquaiana</i>	•	•	0.63
<i>Dalbergia millettii</i>	•	2.15	•
<i>Morinda umbellata</i>	3.18	2.15	0.63
<i>Symplocos glauca</i>	•	•	0.63
<i>Myrica rubra</i>	0.8	2.15	•
<i>Styrax japonicus</i>	0.8	0.72	•
<i>Rhododendron simsii</i>	•	2.15	•
<i>Eurya rubiginosa</i>	5.5	2.87	0.63
<i>Cinnamomum chekiangense</i>	•	•	0.63
<i>Ilex kengii</i>	•	•	0.63
<i>Ardisia crenata</i>	•	•	2.52
<i>Osmundaceae japonica</i>	•	•	0.63

I. *Pinus massoniana* Community; II. *Schima superba* Community; III. *Castanopsis fargesii* Community

• indicate this species is not present

* Tree layer and shrub layer:importance value(%)=(relative abundance+relative dominance+relative frequency)/3

Herb layer:importance value(%)=(relative abundance+relative dominance)/2

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Appendix 2 Leaf nutrient contents of most abundant species along a chronosequence of secondary forest succession in evergreen broad-leaved forests in Tiantong National Forest Park, Eastern China

Species	Growth form	Leaf_N content (mg g ⁻¹)			Leaf_P content(mg g ⁻¹)		
		I	II	III	I	II	III
<i>Pinus massoniana</i>	Tree	8.52 (1.32)	10.78 (1.67)	•	0.82 (0.13)	0.54 (0.09)	•
<i>Schima superba</i>	Tree	9.07 (0.66)	9.72 (1.44)	10.27 (0.41)	0.54 (0.04)	0.41 (0.08)	0.45 (0.01)
<i>Castanopsis fargesii</i>	Tree	10.38 (1.21)	13.61 (1.21)	15.29 (0.86)	0.71 (0.08)	0.61 (0.04)	0.69 (0.05)
<i>Lithocarpus glaber</i>	Tree	8.11 (1.47)	9.69 (0.73)	•	0.55 (0.06)	0.70 (0.11)	•
<i>Castanopsis sclerophylla</i>	Tree	9.42 (0.59)	8.56 (1.83)	•	0.70 (0.08)	0.46 (0.07)	•
<i>Camellia fraterna</i>	Shrub	7.94 (1.71)	7.44 (1.31)	10.43 (2.32)	0.63 (0.09)	0.65 (0.13)	0.54 (0.08)
<i>Symplocos sumuntia</i>	Shrub	9.95 (1.26)	9.25 (0.92)	•	0.61 (0.06)	0.49 (0.03)	•
<i>Eurya nitida</i>	Shrub	•	•	17.57 (1.18)	•	•	0.90 (0.06)
<i>Litsea elongata</i>	Shrub	•	•	11.95 (1.33)	•	•	0.74 (0.07)
<i>Cinnamomum japonicum</i>	Shrub	•	•	12.1 (0.97)	•	•	0.71 (0.04)
<i>Daphniphyllum macropodum</i>	Shrub	•	•	12.59 (1.55)	•	•	0.61 (0.08)
<i>Symplocos glauca</i>	Shrub	•	•	9.37 (0.38)	•	•	0.73 (0.03)

I. *Pinus massoniana* Community; II. *Schima superba* Community; III. *Castanopsis fargesii* Community

Means and SE are presented, n=5

• No data

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