

Leaf traits and relationships differ with season as well as among species groupings in a managed Southeastern China forest landscape

Fu-Sheng Chen · Karl J. Niklas ·
Guang-Sheng Chen · Dali Guo

Received: 1 December 2011 / Accepted: 24 July 2012 / Published online: 4 August 2012
© Springer Science+Business Media B.V. 2012

Abstract The relationships among leaf traits often reflect plant adaptation for coping with nutrient resources. However, the seasonal variations in leaf traits and their relationship with soil nutrients are not well understood. We sampled seven major functional traits of thirty trees and nine shrubs (sorted into different plant functional groups, PFGs, based on their growth form, leaf lifespan, and leaf shape) at different seasons in a managed forest plantation of Southeastern China. Both green leaf nitrogen and phosphorus concentrations (N_{green} and P_{green}) decreased significantly from spring and summer to autumn, and varied significantly with PFGs ($P < 0.05$) at different times of the year. Across all plants, specific leaf area

correlated positively with N_{green} and P_{green} in spring, summer, and winter, but not in autumn; N resorption proficiency generally correlated positively with N_{green} in each season, while P resorption efficiency correlated positively with P_{green} in spring and summer, but not in autumn and winter. Soil nitrogen availability correlated negatively with leaf nutrient traits in some seasons. In conclusion, leaf trait relationships varied among the seasons and among PFGs. Seasonal dynamics of leaf traits as well as soil nutrients' relations must be considered when exploring plant feedback to soil nutrients.

Keywords Garden plantation · Leaf nutrient concentration · Mid-subtropical region · Nutrient resorption · Plant functional group (PFG) · Specific leaf area (SLA)

Electronic supplementary material The online version of this article (doi:10.1007/s11258-012-0106-5) contains supplementary material, which is available to authorized users.

F.-S. Chen (✉)
College of Life Sciences, Nanchang University, No. 999,
Xuefuda Road, Honggutan New District, Nanchang
330031, People's Republic of China
e-mail: chenfush@yahoo.com

F.-S. Chen
College of Forestry, Jiangxi Agricultural University,
Nanchang 330045, People's Republic of China

K. J. Niklas
Department of Plant Biology, Cornell University, Ithaca,
NY 14853, USA

G.-S. Chen
School of Forestry and Wildlife Sciences, Auburn
University, Auburn, AL 36830, USA

D. Guo
Key Laboratory of Ecosystem Network Observation and
Modeling, Synthesis Research Center of Chinese
Ecosystem Research Network, Institute of Geographic
Sciences and Natural Resources Research, Chinese
Academy of Sciences, Beijing 100101, People's Republic
of China

Introduction

Leaves are the primary photosynthetic organs for the majority of vascular plants. Consequently, their functional traits have co-evolved in complex and species-specific ways (Cunningham et al. 1999; Niklas 1999). Among the many important leaf traits, specific leaf area (SLA), nutrient concentrations, and nutrient resorption play critical roles in the ability of plants to capture and retain resources (Niinemets and Kull 2003; Wright et al. 2004a, 2005b), and thus influence many central ecosystem processes (Schulze et al. 1994; Grime et al. 1997; Ackerly et al. 2000). Thus, the relationships among SLA, leaf nutrients, and nutrient resorption are considered the most effective (as well as convenient) tools for evaluating nutrient use strategies (Aerts and Chapin 2000; Chen et al. 2011) and for understanding soil–plant interactions (Niinemets and Kull 2003; Wright et al. 2001, 2005a, b).

Nevertheless, assessing the generality of leaf trait relationships is a challenge because many factors contribute to the variability observed among these relationships (Niinemets 2001; Reich and Oleksyn 2004; Wright et al. 2005a, b; He et al. 2006; Chen et al. 2011). For example, nitrogen (N) and phosphorus (P) concentrations of mature green leaves (N_{green} and P_{green}) generally increase with SLA (Reich et al. 1997; Niinemets 2001; Westoby et al. 2002; Wright et al. 2004b) presumably because larger fractions of N and P are required simultaneously for the construction of photosynthetic as opposed to non-photosynthetic tissues (Sobrado and Medina 1980; Reich et al. 1992). However, in some instances, the correlation between SLA and N_{green} or P_{green} is weak or even negative. For example, the SLA vs. N_{green} relationship differs across communities growing under different water availabilities (Wright et al. 2001). Based on a global observational dataset, Kobe et al. (2005) found that N resorption efficiency (NRE) and P resorption efficiency (PRE) decreased with increasing N_{green} and P_{green} . Yet, Wright and Westoby (2003) found no such relationship in a National Park Reserve dominated by evergreen, sclerophyllous trees and shrubs. Because leaf nutrient status, soil fertility, climatic conditions, and even differences between individual trees can influence nutrient resorption (Niinemets and Kull 2003; Kobe et al. 2005), the relationship between soil nutrient status and leaf nutrient concentrations or nutrient resorption remains controversial (Aerts 1996;

Niinemets and Kull 2003) particularly when considering different spatial and temporal scales of sampling.

Two other important factors are the plant functional groups (PFGs) that characterize a particular community and the seasonal variations of leaf traits, both of which contribute to the variations of leaf nutrient concentrations and resorption (e.g., Chapin and Kedrowski 1983). Research has shown that the selection of PFGs influences whether statistical trends are observed for functional traits such as SLA (Reich et al. 1992; Santiago and Wright 2007; Chen et al. 2011). This finding is somewhat intuitive, since a “functional trait” must be (at least to some extent) correlated with the “functional plant group” it helps to characterize or define. For this reason, many ecologists have categorized species into discrete PFGs that share the same biological traits and that perform similar roles in ecosystem processes (Lavorel et al. 1997; Westoby et al. 2002) to identify and understand central tendencies in the ecological variation of leaf functional traits from an ecosystem to across the major biomes on the earth (Wright et al. 2004a, 2005a). For example, the tree vs. shrub PFGs, which are pooled to classify two major plant growth forms, are one of the primary axes of the “leaf economics spectrum” because it spans species with the potential for quick vs. slow returns on investments of nutrient and dry mass in leaves (Wright et al. 2004a). Likewise, the evergreen vs. deciduous tree PFGs, which are pooled to classify leaf lifespan (LL), are effective in identifying differences in nutrient use strategies since evergreens have longer LL, lower leaf nutrient concentrations, and generally reduce soil fertility, while deciduous trees have shorter LL, higher leaf nutrient concentrations, and generally increase soil fertility (Aerts and Chapin 2000; Cornelissen et al. 2003; Mueller et al. 2012). By the same token, the coniferous vs. broadleaved tree PFGs, which are pooled to classify leaf shape, help to identify potential differences in light and water use efficiencies (Reich et al. 1997, 1998). For these and other reasons, the analysis of leaf functional traits is critically dependent upon both the manner in which species are sorted into functional groups and the manner in which the species comprising a particular community naturally sort into PFGs.

Although the influence of PFGs on the analysis of leaf functional traits is widely recognized and researched, comparatively little is known about how

nutrient levels change over the growing season within well-defined PFGs. By definition, the response of leaf traits and their relations to seasonality must depend to some degree on PFGs. For example, we might anticipate that deciduous tree species would manifest generally a higher nutrient resorption efficiency compared to their evergreen counterparts (Wright and Westoby 2003; Kobe et al. 2005). But, this begs the question regarding variations in the efficiency of nutrient resorption during the growing season of both of these PFGs. Thus, it is likely that the average leaf N concentrations will differ during the growing season of deciduous broadleaved trees and evergreen broadleaved trees since the season schedule for nutrient resorption in the former must adaptively anticipate leaf fall, whereas that of the evergreen trees must include leaf functionality during the autumn and winter. Consequently, we hypothesize that seasonal variations in leaf functional traits, such as nutrient concentrations and resorption, will differ according to seasonality as well as how species are grouped or classified according to functional traits.

The goal of this paper was to explore seasonal variations in foliar functional traits at different time periods of a year. To achieve this, a managed forest plantation in a mid-subtropical region of Southeastern China was selected to determine the following: (1) whether and how N_{green} , P_{green} , and $N_{\text{green}}/P_{\text{green}}$ ratio changed seasonally within different PFGs under the same soil and climatic conditions and (2) whether and how SLA, nutrient resorption efficiency, and proficiency correlated with green leaf nutrient concentrations in each season. We also explored the possible existence of a “plant–soil feedback” in which nutrients released into the soil through leaf litter could be taken up by plants and thus change leaf-level concentrations of N or P at different time periods of a year. For this purpose, seasonal patterns in leaf nutrient traits and soil nutrient supplies (represented by C/N, C/P, NH_4^+ , NO_3^- , and mineral N and P availabilities) were measured.

Materials and methods

Study area

The research site is located in the new campus of Nanchang University (115°48'E, 28°39'N), Nanchang

City, Southeastern China. The soil type is a hilly red soil belonging to the Ultisol soil order, a typical soil type in the central subtropical region of China. The site has a total area of approximately 240 ha and a subtropical warm humid climate with an annual mean air temperature of 17.5 °C and a frost-free period of 291 day year⁻¹. Mean annual precipitation is about 1,600–1,800 mm with mean annual relative humidity about 77 %. The average elevation is 25 m.

More than 100 plant species have been planted on the campus since 2004. One hundred 100-m² plots were randomly selected and surveyed in 2007. The average diameter at breast height (DBH) and the height for 2,176 trees (belonging to 54 species, 42 genera, and 28 families) are 8.8 cm and 4 m, respectively. The average height of 1,619 shrubs (belonging to 36 species, 31 genera, and 21 families) is 1.1 m. Currently, the selected managed plantation includes most of the typical tree and shrub species for the subtropical region of China. The vegetation coverage is approximately 59 % in the plantation (Yu 2010).

Site and species selections

A total of 13 tree and shrub species in the study plantation were selected for extensive analyses. All of the selected species are dominant locally and were planted between 2004 and 2005. The plants were not managed except for irrigation shortly after planting. The species are classified into different PFGs based on their growth forms (tree vs. shrub species), leaf lifespan (evergreen vs. deciduous species), and leaf shape (scale/needle vs. broadleaved species) (Table 1). Three representative trees or shrubs for each species (three replicates) were selected from four different campus sites (residential, teaching, recreational, and lakeside areas) which were established during a previous field investigation.

Specific leaf area and leaf nutrient concentrations

Approximately 0.5 kg of fully expanded and mature leaves were collected in spring, summer, autumn, and winter for the evergreen species and in spring, summer, and autumn for the deciduous species from different canopy positions at each of the four cardinal directions, mixed together, stored in closed bags, and

Table 1 Species, geography, and species characteristics

Species	Species groups	Sites	Diameter (cm) ^a	Height (m)	Leaf lifespan (months) ^b
<i>Magnolia grandiflora</i>	Evergreen broadleaved tree (EBT)	TA(2), RA(1)	13.4 ± 5.2	5.5 ± 1.3	26
<i>Cinnamomum camphora</i>	Evergreen broadleaved tree (EBT)	TA(1), LA(1), RA(1)	26.5 ± 2.4	8.1 ± 0.6	18
<i>Osmanthus fragrans</i>	Evergreen broadleaved tree (EBT)	LA(1), RA(1), LA(1)	9.5 ± 1.0	4.2 ± 0.3	42
<i>Liriodendron chinense</i>	Deciduous broadleaved tree (DBT)	RA(2), LA(1)	7.9 ± 0.5	7.0 ± 0.1	7
<i>Prunus persica</i>	Deciduous broadleaved tree (DBT)	TA(1), RA(2)	10.5 ± 0.6	4.8 ± 0.3	6
<i>Salix babylonica</i>	Deciduous broadleaved tree (DBT)	RA(1), LA(1), LA(1)	11.5 ± 0.7	6.0 ± 0.8	8
<i>Pinus massoniana</i>	Evergreen coniferous tree (ECT)	RA(2), TA(1)	18.5 ± 3.2	8.6 ± 1.1	23
<i>Cedrus deodara</i>	Evergreen coniferous tree (ECT)	RA(1), TA(1), LA(1)	16.4 ± 1.5	5.3 ± 0.4	62
<i>Pseudolarix kaempferi</i>	Deciduous coniferous tree (DCT)	TA(2), LA(1)	12.0 ± 0.6	6.0 ± 0.3	8
<i>Metasequoia glyptostroboides</i>	Deciduous coniferous tree (DCT)	TA(1), LA(2)	10.8 ± 0.7	7.3 ± 1.5	9
<i>Michelia figo</i>	Evergreen broadleaved shrub (EBS)	LA(2), RA(1)	5.6 ± 0.3	1.5 ± 0.1	22
<i>Pyracantha fortuneana</i>	Evergreen broadleaved shrub (EBS)	LA(1), RA(1), LA(1)	2.5 ± 0.2	1.1 ± 0.1	21
<i>Rhododendron simsii</i>	Evergreen broadleaved shrub (EBS)	TA(1), RA(1), LA(1)	1.6 ± 0.2	0.5 ± 0.1	13

Mean ± SE ($n = 3$) for diameter and height

LA residential area, TA teaching area, RA recreational area, LA lakeside area. The *digit in parenthesis* is the number of replicate samples in this site

^a Average diameter at breast height and average ground diameter refer to trees and shrubs, respectively

^b Leaf lifespan data for each species are from Yu (2010)

brought back to the laboratory for analysis. In order to insure equivalent leaf ages, leaves were collected from first order branches. Senesced leaves were also collected every day using nylon mesh boxes (six 50 × 50 cm boxes in each location) placed under plant canopies during the key periods of defoliation, which ranged between 20 and 30 days from October to February. The sample per individual plant was mixed together to be analyzed for the nutrient traits.

The average leaf lifespan (LL) for species used in this study was reported by Yu (2010) (Table 1). We calculated SLA as the ratio of leaf area to dry mass. About 30–50 fresh leaves from the broadleaved species were randomly selected from each sample bag and scanned digitally to determine leaf area. These leaves were subsequently cleaned with deionized water and oven dried at 70 °C to constant weight. The total mass of all the dried leaves was measured and divided by the total leaf number to determine the average leaf dry mass for each sampling time except for the coniferous trees. Because the leaves of coniferous trees are acerose, their exact leaf areas could not be obtained by scanning. Their SLA therefore was not determined.

Oven-dried green and senesced leaves were ground for analyzing nutrient concentrations. The concentrations of organic C (OC), total N (TN), and total P (TP) in green leaves (C_{green} , N_{green} , and P_{green}) and senesced leaves ($C_{\text{senescent}}$, $N_{\text{senescent}}$, and $P_{\text{senescent}}$) were measured by the potassium dichromate oxidation–ferrous sulfate titrimetry method, the Kjeldahl method, and the colorimetric method, respectively (Allen 1989). These data were used to calculate green leaf C/N, C/P, and N/P.

Leaf-level nutrient resorption (i.e., nutrient retranslocation from senescing leaves) is recognized as an efficient mechanism of nutrient conservation in various plant species (Killingbeck 1996). Nutrient resorption proficiency and nutrient resorption efficiency are two indices of nutrient conservation from the proportion of nutrients resorbed (Wright and Westoby 2003). Nutrient resorption proficiency is defined as the concentration of the nutrient remaining in senesced leaves (litter fall) throughout a year (Killingbeck 1996). In this study, N and P resorption proficiencies (NRP and PRP) are the average N and P concentrations of the litter fall collected between October and February. The nutrient resorption efficiency was calculated by means of the formulas of Aerts (1996):

Table 2 ANOVA for effects of plant functional group (PFG) and seasonality on green leaf N and P concentrations (N_{green} and P_{green}), and green leaf C:N:P stoichiometric ratios in the forest plantation

Factors	df	<i>F</i> value				
		N_{green}	P_{green}	C/N	C/P	N/P
PFG	4	52.62***	35.04***	51.65***	17.44***	5.60***
Season	3	2.74*	16.63***	5.52**	12.35***	10.45***
PFG × season	12	3.26***	2.75**	2.13*	0.38 ^{NS}	2.87**

NS not significant

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

$$\text{NRE (\%)} = \frac{(N_{\text{max-green}} - N_{\text{senescent}})}{N_{\text{max-green}}} \times 100 \quad (1)$$

$$\text{PRE (\%)} = \frac{(P_{\text{max-green}} - P_{\text{senescent}})}{P_{\text{max-green}}} \times 100 \quad (2)$$

where $N_{\text{max-green}}$ and $P_{\text{max-green}}$ are the observed maximum N and P concentrations of green leaves in a year and $N_{\text{senescent}}$ and $P_{\text{senescent}}$ are the average N and P concentrations of the senescent leaves. In this study, the effect induced by leaf mass change on nutrient resorption was not considered since the change in leaf mass (varied from 5 to 10 %; Aerts 1996) during senescence was not easily measured. In addition, it is difficult to reliably measure the area of senesced leaves because of curling and deformations of the laminae.

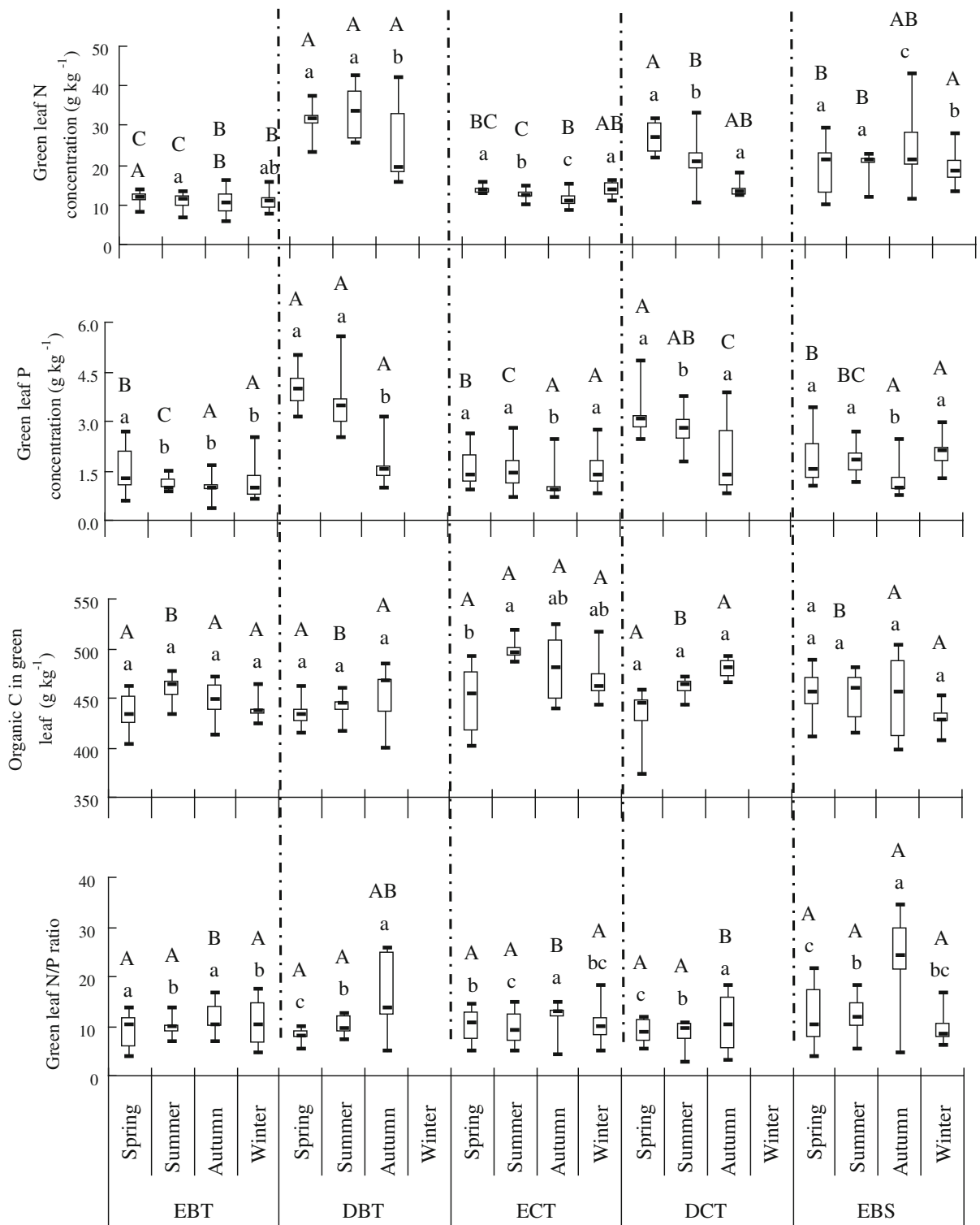
Soil nutrient levels

Between April 2008 and January 2009, soil samples were collected seasonally at 30 locations for trees (under tree canopies) and 9 locations for shrubs. Eight soil cores (4.8 cm in diameter) at a depth of 0–15 cm were collected per individual plant per season and homogenized into a single soil sample (total of 39 samples each season). After removing visible plant residues, the samples were sieved through a 2-mm screen and then immediately used to measure soil NH_4^+ , NO_3^- , mineral N (NH_4^+ plus NO_3^-), and available P. We used 2 mol L^{-1} KCl solution to extract NH_4^+ -N and NO_3^- -N and the colorimetry method to measure NH_4^+ and NO_3^- concentrations. We used 0.5 mol L^{-1} NaHCO_3 solution to extract available P and the phosphomolybdic acid blue color method to measure its concentration (Allen 1989).

Subsamples of fresh soil samples taken in summer were air-dried and stored at room temperature to analyze concentrations of OC, TN, and TP. These subsamples were oven dried and sieved with a 0.5-mm screen before taking measurements. The potassium dichromate oxidation–ferrous sulfate titrimetry method was used to determine soil OC concentration. TN was determined subsequently by the Kjeldahl method. A colorimetric method was used to determine TP (Allen 1989). These data were used to calculate soil C/N, C/P, and N/P.

Data processing and statistical analysis

All the data were tested for homogeneity of variance (Brown and Forsythe's variation of Levene's test) before statistical analysis. Soil variables were \log_{10} -transformed to achieve a nearly normal distribution. Two-way analysis of variance (ANOVA) was used to identify the effects of functional species groupings and season on leaf nutrient concentrations and stoichiometric ratios. One-way ANOVA and least significant difference (LSD) methods were used to compare leaf traits among functional species groupings as well as soil nutrient properties among different sites and functional species groupings. Standardized major axis tests and routines (SMATR) was used to compare the significance of correlations among major leaf traits and to test the soil nutrient properties vs. leaf nutrient traits' relations (Warton et al. 2006). All statistical analyses were conducted by SPSS 11.0 (SPSS Inc. 2001) except the correlation analyses by SMATR Version 2.0 (Falster et al. 2006). The standard 0.05 level of significance was used to represent a statistical significance.



◀ **Fig. 1** Variations of green leaf nutrient traits within plant functional groups (PFGs) and seasons in a forest plantation. *Box plots* characterize the distribution of green leaf nutrient traits with the *bottom* and *top* of each box indicating the 25th and 75th percentile, respectively. The *two whiskers* denote the smallest and largest values of the dataset and the *horizontal line* within each box denotes the median value. Different *lowercase* and *capital letters* indicate significant differences ($P < 0.05$) of mean values among the different seasons within a plant functional group and among the five PFGs in a season, respectively. *EBT* evergreen broadleaved trees, *DBT* deciduous broadleaved trees, *ECT* evergreen coniferous trees, *DCT* deciduous coniferous trees, *EBS* evergreen broadleaved shrubs

Results

Green leaf nutrient concentrations and SLA

Green leaf nutrient concentrations and their stoichiometric ratios differed significantly among seasons within the different PFGs (Table 2; Fig. 1). Both N_{green} and P_{green} generally decreased from spring and summer to autumn within each PFG, but differed in winter depending on the PFGs considered. Organic C concentration in green leaves ranged from 380 to 520 g kg⁻¹ and was relatively constant within each PFG across the entire growing season. The pattern observed for the seasonal variations in green leaf N/P ratio differed among the PFGs in no clearly discernible manner (Fig. 1).

During spring, summer, and autumn, the average N_{green} was always the highest for deciduous broadleaved trees and the lowest for evergreen broadleaved trees. However, no consistent ordering (e.g., from high to low) was observed for N_{green} among the species of deciduous coniferous trees, evergreen broadleaved shrubs, and evergreen coniferous trees. In winter, the average N_{green} for evergreen broadleaved shrubs was

higher than for evergreen broadleaved trees, but not significantly different from evergreen coniferous trees (Fig. 1). In contrast, the average P_{green} in spring and summer was generally higher for deciduous broadleaved and deciduous coniferous trees compared to evergreen broadleaved trees, evergreen coniferous trees, and evergreen broadleaved shrubs. No significant difference in P_{green} was observed during autumn and winter (Fig. 1).

Although C_{green} was higher in summer for evergreen coniferous trees compared to all of the other PFGs, no significant difference in C_{green} was observed among the different PFGs during spring, autumn, and winter (Fig. 1). The annual average C/N ratio was the highest for evergreen broadleaved trees (63.65) and evergreen coniferous trees (41.93) followed by deciduous coniferous trees (34.05), evergreen broadleaved shrubs (33.88), and deciduous broadleaved trees (18.16). The average C/P ratio was higher in evergreen broadleaved trees (773) and evergreen coniferous trees (510) than in deciduous broadleaved trees (252) and deciduous coniferous trees (320). The green leaf C/N and C/P ratios for evergreen broadleaved shrubs (394) were not significantly different from the other PFGs (Table 2).

No differences were observed in the green leaf N/P ratio among the different PFGs during spring, summer, and winter. However, the average N/P ratio was higher during autumn for evergreen broadleaved shrubs than for evergreen broadleaved trees, evergreen coniferous trees, and deciduous coniferous trees, all of which did not differ significantly from the annual average N/P ratio of deciduous broadleaved trees (Fig. 1).

The average SLA was the highest for deciduous broadleaved trees followed by evergreen broadleaved shrubs; the lowest average SLA was observed for

Table 3 Mean \pm SE of specific leaf area (SLA), N and P resorption proficiency (NRP and PRP), and N and P resorption efficiency (NRE and PRE) with different plant functional groups in the forest plantation

Groups	SLA (cm ² g ⁻¹)	NRP (g kg ⁻¹)	NRE (%)	PRP (g kg ⁻¹)	PRE (%)
EBT	75.04 \pm 7.21c	7.02 \pm 0.50c	47 \pm 2a	1.03 \pm 0.11b	45 \pm 4b
DBT	157.58 \pm 9.12a	22.73 \pm 1.54a	41 \pm 4ab	1.13 \pm 0.12b	73 \pm 2a
ECT	–	11.18 \pm 0.30bc	25 \pm 3b	1.81 \pm 0.25a	8 \pm 4c
DCT	–	13.91 \pm 0.58b	48 \pm 3a	1.42 \pm 0.05ab	55 \pm 5ab
EBS	116.98 \pm 5.99b	15.71 \pm 2.02b	39 \pm 6ab	1.29 \pm 0.19ab	45 \pm 7b

Different *lowercase letters* indicate significant differences ($P < 0.05$) of mean values among the five plant functional groups

EBT evergreen broadleaved tree species grouping, *DBT* deciduous broadleaved tree species grouping, *ECT* evergreen coniferous tree species grouping, *DCT* deciduous coniferous tree species grouping, *EBS* evergreen broadleaved shrub species grouping

Table 4 Correlation coefficients from standardized major axis regressions among leaf nutrient traits varied with season for different plant functional groups in the forest plantation

Correlations	Season	All	Trees	Evergreens	Broadleaved species
<i>n</i>		13	10	8	9
SLA vs. N_{green}	Spring	0.76*	0.89*	0.55 ^{NS}	0.76*
	Summer	0.75*	0.79*	0.74*	0.75*
	Autumn	0.49 ^{NS}	0.50 ^{NS}	0.52 ^{NS}	0.49 ^{NS}
	Winter	0.85*	1.00*	0.84*	0.85*
N_{green} vs. NRP	Spring	0.83***	0.83**	0.97***	0.88**
	Summer	0.87***	0.97***	0.68*	0.88**
	Autumn	0.59*	0.54 ^{NS}	0.88**	0.57***
	Winter	0.87***	0.68 ^{NS}	0.87**	0.88**
N_{green} vs. NRE	Spring	0.02 ^{NS}	0.20 ^{NS}	-0.44 ^{NS}	-0.37 ^{NS}
	Summer	-0.03 ^{NS}	-0.08 ^{NS}	0.05 ^{NS}	-0.35 ^{NS}
	Autumn	0.11 ^{NS}	0.23 ^{NS}	-0.02 ^{NS}	-0.07 ^{NS}
	Winter	-0.21 ^{NS}	-0.66 ^{NS}	-0.21 ^{NS}	-0.41 ^{NS}
SLA vs. P_{green}	Spring	0.62*	0.75*	0.24 ^{NS}	0.65*
	Summer	0.66*	0.75*	0.53 ^{NS}	0.66*
	Autumn	0.39 ^{NS}	0.49 ^{NS}	0.09 ^{NS}	0.39 ^{NS}
	Winter	0.89*	0.70 ^{NS}	0.88*	0.89*
P_{green} vs. PRP	Spring	0.17 ^{NS}	0.10 ^{NS}	0.69*	0.34 ^{NS}
	Summer	0.17 ^{NS}	0.15 ^{NS}	0.58 ^{NS}	0.22 ^{NS}
	Autumn	0.16 ^{NS}	0.22 ^{NS}	0.48 ^{NS}	0.35 ^{NS}
	Winter	0.27 ^{NS}	0.40 ^{NS}	0.27 ^{NS}	0.45 ^{NS}
P_{green} vs. PRE	Spring	0.55**	0.68*	0.26 ^{NS}	0.50 ^{NS}
	Summer	0.50**	0.59*	-0.30 ^{NS}	0.54 ^{NS}
	Autumn	0.36 ^{NS}	0.38 ^{NS}	-0.20 ^{NS}	0.40 ^{NS}
	Winter	0.07 ^{NS}	-0.21 ^{NS}	-0.07 ^{NS}	0.05 ^{NS}
N_{green} vs. P_{green}	Spring	0.82***	0.89***	0.26 ^{NS}	0.86**
	Summer	0.89***	0.92***	0.62 ^{NS}	0.77*
	Autumn	0.05 ^{NS}	0.18 ^{NS}	0.09 ^{NS}	0.61 ^{NS}
	Winter	0.80**	0.70*	0.80*	0.81*
NRP vs. PRP	–	0.26 ^{NS}	0.11 ^{NS}	0.50 ^{NS}	0.51 ^{NS}
NRE vs. PRE	–	0.52**	0.66**	0.61 ^{NS}	0.08 ^{NS}

NS not significant, *NRP* nitrogen resorption proficiency, *NRE* nitrogen resorption efficiency, *PRP* phosphorus resorption proficiency, *PRE* phosphorus resorption efficiency
 * $P < 0.05$, ** $P < 0.01$,
 *** $P < 0.001$

evergreen broadleaved trees (Table 3). Meanwhile, SLA positively correlated with N_{green} and P_{green} in spring, summer, and winter, but not in autumn across all PFGs except SLA vs. N_{green} for evergreens in spring, SLA vs. P_{green} for trees in winter, and for evergreens in spring and summer (Table 4).

Nutrient resorption and its relationship with green leaf nutrient concentrations

The N and P nutrient resorption proficiencies and efficiencies varied among the five PFGs. NRP was the highest for deciduous broadleaved trees (followed by

deciduous coniferous trees and evergreen broadleaved shrubs) and the lowest for evergreen broadleaved trees and evergreen coniferous trees. NRE was higher for evergreen broadleaved trees and deciduous coniferous trees than for evergreen coniferous trees, and differed little between deciduous broadleaved trees and evergreen broadleaved shrubs. PRP was higher for evergreen coniferous trees than for evergreen broadleaved trees and deciduous broadleaved trees, but did not differ between deciduous coniferous trees and evergreen broadleaved shrubs. PRE was the highest in deciduous broadleaved trees and deciduous coniferous trees followed by evergreen broadleaved trees and

evergreen broadleaved shrubs; the lowest PRE was observed for evergreen coniferous trees (Table 3).

NRP correlated positively with N_{green} within the tree, evergreen, and broadleaved species groupings as well as across all of the species during each season with the exception of the tree species grouping during autumn and winter. In contrast, NRE did not significantly correlate with N_{green} in any season. PRP only correlated positively with P_{green} for the evergreen species in spring. PRE correlated positively with P_{green} across all species and within the tree PFG during spring and summer, but not during autumn and winter. Finally, the N_{green} vs. P_{green} relationship varied among the PFGs and the seasons (Table 4).

Soil nutrient properties

Soil organic C ($F_{4,38} = 1.68, P = 0.18$), total N ($F_{4,38} = 1.22, P = 0.32$), and total P ($F_{4,38} = 0.44, P = 0.78$) concentrations were not significantly different among the five PFGs. Soil mineral N varied with PFGs ($F_{4,52} = 6.45, P < 0.001$) and was the lowest for deciduous broadleaved trees (53.53 mg/kg) followed by evergreen broadleaved trees (61.14 mg/kg), deciduous coniferous trees (64.30 mg/kg), evergreen broadleaved shrubs, and evergreen coniferous trees (102.70 mg/kg). In contrast, there was no significant difference in soil available P among the five PFGs ($F_{4,52} = 1.01, P = 0.41$). Soil mineral N ($F_{3,52} = 3.47, P = 0.02$) and soil available P ($F_{3,52} = 3.17, P = 0.03$) varied seasonally with generally higher mineral N levels in spring and summer; soil available P was the highest during summer, decreased during spring and autumn, and reached the lowest in winter.

In addition, soil organic carbon, total N, NH_4^+ , total P, and available P were not significantly different among the four sites (Table 5). As we anticipated, the annual averages of NO_3^- and mineral N were higher in soils collected from residential areas than in teaching, recreational, and lakeside areas. Consequently, the differences reported for the functional leaf traits measured in this study likely reflected real biological differences among the examined species.

Discussion

Seasonal variation in leaf nutrient traits at the level of the individual plant is well known (Chapin 1980; Aerts

Table 5 Soil nutrient properties at different sites in the forest plantation

Sites	Sample size	pH	Organic C (g kg ⁻¹)	Total N (g kg ⁻¹)	NH ₄ ⁺ -N (mg kg ⁻¹)	NO ₃ ⁻ -N (mg kg ⁻¹)	Mineral N (mg kg ⁻¹)	Total P (g kg ⁻¹)	Available P (mg kg ⁻¹)
Residential area	6	5.4 ± 0.4a	71.3 ± 9.9a	7.6 ± 0.8a	15.2 ± 2.9a	97.1 ± 27.0a	112.2 ± 29.5a	2.4 ± 0.2a	4.4 ± 0.5a
Teaching area	10	5.1 ± 0.2a	64.7 ± 4.8a	8.4 ± 0.7a	15.7 ± 2.1a	58.3 ± 9.3b	74.0 ± 10.7b	2.4 ± 0.1a	5.0 ± 0.8a
Recreational area	14	5.2 ± 0.3a	55.8 ± 5.4a	7.1 ± 0.8a	15.7 ± 1.9a	40.8 ± 2.9b	56.6 ± 3.6b	2.3 ± 0.2a	5.1 ± 0.6a
Lakeside area	9	5.4 ± 0.3a	66.9 ± 4.4a	8.7 ± 0.9a	14.3 ± 2.3a	54.6 ± 8.2b	68.9 ± 10.4b	3.1 ± 0.3a	5.8 ± 0.8a

Mean ± SE. The data for pH, organic C, total N, and total P were obtained from the soils collected in Summer, while NH_4^+ -N, NO_3^- -N, mineral N, and available P averaged on the four seasons of spring, summer, autumn, and winter. Different lowercase letters indicate significant differences ($P < 0.05$) of mean values among the four sites

1996; Aerts and Chapin 2000). However, how leaf traits vary seasonally among plant functional groups (PFGs) under relatively uniform environmental conditions and soil properties is less understood. Our study is one of the first to document significant seasonal variations in leaf nutrient levels within well-defined PFGs, which highlights the importance of selecting the appropriate representative sampling season in order to draw valid conclusions when comparing leaf functional traits among different PFGs.

As expected, we found that seasonal patterns in leaf nutrient traits were significantly different among seasons and PFGs. Our results show that N_{green} is significantly higher in winter than in other seasons for evergreen coniferous trees, lower in winter than in other seasons for evergreen broadleaved shrubs, and unchanged between winter and other seasons for evergreen broadleaved trees. In contrast, P_{green} is higher in winter than in the other seasons for evergreen coniferous trees and evergreen broadleaved shrubs and the lowest in winter for evergreen broadleaved trees. Additionally, the scaling relationships for SLA vs. N_{green} , N_{green} vs. NRP, SLA vs. P_{green} , P_{green} vs. PRE, and N_{green} vs. P_{green} also varied with season and differed among PFGs (Table 4). Differences in nutrient resorption efficiency and proficiency (Table 4) are most likely responsible for these patterns because the observed trends for these functional traits are consistent with those for N and P concentrations. Thus, seasonal patterns of N_{green} , P_{green} , and the $N_{\text{green}}/P_{\text{green}}$ ratio vary with PFGs under the same soil and climatic conditions, resulting in different relationships among SLA, nutrient resorption efficiency and proficiency, and green leaf nutrients across PFGs in different seasons.

Nevertheless, significant seasonal variations in leaf traits do not alter the major inherent biological differences among different PFGs (Reich et al. 1992; Wright et al. 2004b). For example, P_{green} is greater for trees than for shrubs (2.13 mg g⁻¹ for trees vs. 1.73 mg g⁻¹ for shrubs), which is the opposite of the trend observed for the green leaf N/P ratio (10.27 for trees vs. 14.28 for shrubs). In this context, it is worth noting that one strategy to increase foliar nutrient concentrations in response to nutrient deficiency is to increase the investment in root growth (Poorter and Nagel 2000), which can facilitate the acquisition of relatively immobile phosphate (see, however, Sands and Mulligan 1990; Poorter and Bergkotte 1992). It is

reasonable, therefore, to speculate that the greater root distribution space and fine root surface area of trees compared to shrubs may account for the observed differences in P_{green} for the tree and shrub species groups in our study sites (Jackson et al. 1997; Niinemets and Kull 2003).

In addition, we found that SLA, N_{green} , P_{green} , and N and P resorption proficiencies (NRP and PRP) were higher in deciduous than in evergreen tree species, whereas green leaf C/N, C/P, and NRE and PRE manifest the reverse pattern. Negative relationships were observed for SLA vs. LL ($r = -0.93$, $n = 13$, $P < 0.001$) and N_{green} vs. LL ($r = -0.63$, $n = 13$, $P < 0.05$). These trends resonate with previous research showing that longer-lived leaves contain much more carbon-rich (structural and chemical) rather than nitrogen-rich (photosynthetic) components (e.g., Chabot and Hicks 1982; Wright and Westoby 2003). Indeed, carbon fixed per unit nutrient investment increases with leaf lifespan with longer-lived leaves generally yielding greater returns in C fixed per unit N or P than shorter-lived leaves (Falster et al. 2012). Likewise, the observations that the average PRP is higher in coniferous than in broadleaved tree species and that the average PRE has the opposite trend for coniferous and broadleaved trees agree with previous observations (e.g., Aerts and Chapin 2000) that coniferous and broadleaved trees have different P use efficiency strategies.

Our study also explored the plant–soil nutrient relationship since the nutrient levels of leaves may reflect the availability of soil nutrients as well as the ability to absorb them. This topic has been studied extensively (Aerts and Chapin 2000; Chen et al. 2010b), but not in the context of seasonal variations in leaf nutrient levels, which was our principal focus. Our results show that the N_{green} vs. soil total N relationship and the P_{green} vs. soil total P relationship differ little seasonally (Table 6). This invariance supports previous analyses showing that leaf nutrient concentrations are more dependent on PFGs than on seasonal changes in nutrient availability (Chapin 1980). It is likely, therefore, that leaf nutrient concentrations reflect both a plant's ability to internally store and recycle nutrients and the potential to take up new nutrients from the soil. Among long-lived plants, the former may be particularly important for buffering seasonal changes in soil nutrient availability (Chapin and Kedrowski 1983).

Table 6 Correlation coefficients from standardized major axis regressions ($n = 39$) among soil nutrient properties and leaf nutrient traits varied with season in the forest plantation

Correlations	Annual average	Spring	Summer	Autumn	Winter
N_{green} vs. soil OC	-0.19 ^{NS}	-0.22 ^{NS}	-0.30 ^{NS}	0.05 ^{NS}	0.07 ^{NS}
P_{green} vs. soil OC	-0.38*	-0.34*	-0.30	-0.42**	0.07 ^{NS}
Green leaf N/P ratio vs. soil OC	0.26 ^{NS}	0.27 ^{NS}	0.04 ^{NS}	0.25 ^{NS}	-0.01 ^{NS}
NRE vs. soil OC	-0.04 ^{NS}	-	-	-	-
PRE vs. soil OC	-0.24 ^{NS}	-	-	-	-
N_{green} vs. soil TN	0.02 ^{NS}	0.08 ^{NS}	-0.01 ^{NS}	-0.03 ^{NS}	-0.18 ^{NS}
P_{green} vs. soil TN	0.01 ^{NS}	-0.01 ^{NS}	0.08 ^{NS}	0.01 ^{NS}	-0.26 ^{NS}
Green leaf N/P ratio vs. soil TN	-0.03 ^{NS}	0.06 ^{NS}	-0.09 ^{NS}	-0.08 ^{NS}	0.07 ^{NS}
NRE vs. soil TN	0.06 ^{NS}	-	-	-	-
PRE vs. soil TN	0.02 ^{NS}	-	-	-	-
N_{green} vs. soil TP	0.36*	0.32*	0.15 ^{NS}	0.45**	0.28 ^{NS}
P_{green} vs. soil TP	0.02 ^{NS}	0.22 ^{NS}	0.18 ^{NS}	0.01 ^{NS}	0.23 ^{NS}
Green leaf N/P ratio vs. soil TP	0.20 ^{NS}	0.05 ^{NS}	-0.14 ^{NS}	0.33*	-0.03 ^{NS}
NRE vs. soil TP	0.27 ^{NS}	-	-	-	-
PRE vs. soil TP	0.25 ^{NS}	-	-	-	-
N_{green} vs. soil C/N	-0.04 ^{NS}	-0.14 ^{NS}	-0.21 ^{NS}	0.26 ^{NS}	0.34 ^{NS}
P_{green} vs. soil C/N	-0.27 ^{NS}	-0.21 ^{NS}	-0.26 ^{NS}	-0.35 ^{NS}	0.33 ^{NS}
Green leaf N/P ratio vs. soil C/N	0.34*	0.15 ^{NS}	0.05 ^{NS}	0.43**	-0.04 ^{NS}
NRE vs. soil C/N	-0.02 ^{NS}	-	-	-	-
PRE vs. soil C/N	-0.17 ^{NS}	-	-	-	-
N_{green} vs. soil C/P	-0.49**	-0.53***	-0.44**	-0.27 ^{NS}	-0.05 ^{NS}
P_{green} vs. soil C/P	-0.54***	-0.50**	-0.48**	-0.45**	-0.02 ^{NS}
Green leaf N/P ratio vs. soil C/P	0.11 ^{NS}	0.16 ^{NS}	0.17 ^{NS}	0.05 ^{NS}	-0.03 ^{NS}
NRE vs. soil C/P	-0.23 ^{NS}	-	-	-	-
PRE vs. soil C/P	-0.49**	-	-	-	-
N_{green} vs. soil N/P	-0.21 ^{NS}	-0.16 ^{NS}	-0.11 ^{NS}	-0.26 ^{NS}	-0.26 ^{NS}
P_{green} vs. soil N/P	-0.10 ^{NS}	-0.12 ^{NS}	-0.05 ^{NS}	0.00 ^{NS}	-0.26 ^{NS}
Green leaf N/P ratio vs. soil N/P	-0.18 ^{NS}	-0.06 ^{NS}	-0.01 ^{NS}	-0.25 ^{NS}	0.00 ^{NS}
NRE vs. soil N/P	-0.09 ^{NS}	-	-	-	-
PRE vs. soil N/P	-0.18 ^{NS}	-	-	-	-
N_{green} vs. soil NH_4^+-N	-0.33*	-0.36*	-0.27 ^{NS}	-0.10 ^{NS}	-0.02 ^{NS}
P_{green} vs. soil NH_4^+-N	-0.39*	-0.38*	-0.31 ^{NS}	-0.05 ^{NS}	0.06 ^{NS}
Green leaf N/P ratio vs. NH_4^+-N	0.13 ^{NS}	0.18 ^{NS}	-0.20 ^{NS}	0.11 ^{NS}	-0.03 ^{NS}
NRE vs. soil NH_4^+-N	-0.57***	-0.44**	-0.43**	-0.41**	-0.03 ^{NS}
PRE vs. soil NH_4^+-N	-0.52***	-0.52***	-0.50**	-0.13 ^{NS}	-0.19 ^{NS}
N_{green} vs. soil NO_3^--N	-0.06 ^{NS}	-0.09 ^{NS}	-0.02 ^{NS}	-0.12 ^{NS}	0.25 ^{NS}
P_{green} vs. soil NO_3^--N	-0.23 ^{NS}	-0.34*	-0.09 ^{NS}	-0.02 ^{NS}	-0.16 ^{NS}
Green leaf N/P ratio vs. NO_3^--N	0.31 ^{NS}	0.40*	0.10 ^{NS}	0.02 ^{NS}	0.33 ^{NS}
NRE vs. soil NO_3^--N	-0.41**	-0.33*	-0.43**	-0.41*	-0.27 ^{NS}
PRE vs. soil NO_3^--N	-0.20 ^{NS}	-0.39*	-0.13 ^{NS}	-0.17 ^{NS}	-0.13 ^{NS}
N_{green} vs. soil mineral N	-0.11 ^{NS}	-0.18 ^{NS}	-0.09 ^{NS}	-0.13 ^{NS}	0.24 ^{NS}
P_{green} vs. soil mineral N	-0.28 ^{NS}	-0.40*	-0.16 ^{NS}	-0.03 ^{NS}	-0.15 ^{NS}
Green leaf N/P ratio vs. mineral N	0.30 ^{NS}	0.40*	0.14 ^{NS}	0.05 ^{NS}	0.31 ^{NS}
NRE vs. soil mineral N	-0.47**	-0.40*	-0.52***	-0.45**	-0.26 ^{NS}

Table 6 continued

Correlations	Annual average	Spring	Summer	Autumn	Winter
PRE vs. soil mineral N	-0.27 ^{NS}	-0.48**	-0.25 ^{NS}	-0.17 ^{NS}	-0.14 ^{NS}
N _{green} vs. soil available P	0.04 ^{NS}	0.03 ^{NS}	0.18 ^{NS}	0.00 ^{NS}	0.18 ^{NS}
P _{green} vs. soil available P	0.12 ^{NS}	0.09 ^{NS}	0.18 ^{NS}	0.08 ^{NS}	-0.31 ^{NS}
Green leaf N/P ratio vs. available P	-0.07 ^{NS}	-0.11 ^{NS}	0.05 ^{NS}	-0.10 ^{NS}	0.45*
NRE vs. soil available P	-0.10 ^{NS}	-0.05 ^{NS}	0.04 ^{NS}	-0.03 ^{NS}	-0.33*
PRE vs. soil available P	-0.11 ^{NS}	-0.18 ^{NS}	-0.08 ^{NS}	0.01 ^{NS}	-0.09 ^{NS}

NS not significant, *NRP* nitrogen resorption proficiency, *NRE* nitrogen resorption efficiency, *PRP* phosphorus resorption proficiency, *PRE* phosphorus resorption efficiency

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Even though seasonal variations in leaf vs. soil N concentrations and in leaf vs. soil P concentrations were not pronounced, we observed statistically significant negative correlations between N_{green} and soil total P concentrations and between P_{green} and soil organic C concentrations during spring and autumn. Taken at face value, this suggests to us that higher soil nutrient availabilities do not necessarily insure higher leaf nutrient concentrations and that, in turn, the biological attributes of a species can take precedence over its soil nutrient availability. One such attribute may involve species-specific plant–soil feedbacks on nutrient cycles (Ordoñez et al. 2009). In general, plants growing in nutrient-poor environments produce nutrient-poor litter and conserve more nutrients in long-lived and recalcitrant tissues to cope with infertile environments. In contrast, plants growing in nutrient-rich environments tend to produce significant amounts of nutrient-rich litter that sustain higher levels of soil fertility (Aerts and Chapin 2000; Chen et al. 2010a). Certainly, these are only general trends since there are many strategies to cope with nutrient limitations even within the same site (Wright et al. 2004b). In our study sites, more than 100 species and several million individuals (unpublished data) have been planted as garden landscape specimens since 2004. Among these species, the dominants within each of the various PFGs differ both in their responses to and their effects on soil nutrient supply. Therefore, it is possible that some of the correlations reported here for functional traits in terms of soil nutrient (e.g., the amount and quality of C soil input) reflect a spectrum of strategies and that some of the negative correlations we observe are not simply the result of soil nutrient depletion and sequestration in green leaf tissues. The

plants would have a rapid and negative feedback on soil nutrient availability as the nutrients in the dead roots and foliar litters return to the soils (Luxmoore 1991; Ordoñez et al. 2009). This speculation is consistent with the observations that soil organic carbon, total N and P, and the various ratios of these nutrients are not correlated with NRE and PRE, while soil NH₄⁺, NO₃⁻, and mineral N within most, but not all, seasons are negatively correlated with NRE and PRE across all species (Table 6).

In summary, our data indicate that foliar nutrient concentrations vary significantly with season and in a manner that reflects different strategies for coping with N and P resource limitations among different species groupings. Thus, seasonal variations in leaf functional traits, soil nutrient availability, and C, N, and P stoichiometry should be considered which season is the most representative of a species' nutrient level status and when exploring plant–soil interactions.

Acknowledgments This study was supported by Grants from the National Basic Research Program of China (973 Program, 2012CB416903) and the National Natural Science Foundation of China (30960311 and 31160107). We greatly appreciate Xiao-Fei Hu, Kun Yu, Xue Feng, and Wen Ren for their help in sampling and soil analyses and Dr. De-Hui Zeng for manuscript improvement. Several anonymous reviewers and the editor Dr. Rebecca Ostertag have significantly improved the quality of this paper.

References

- Ackerly DD et al (2000) The evolution of plant ecophysiological traits: recent advances and future directions. *Bioscience* 50:979–995
- Aerts R (1996) Nutrient resorption from senescing leaves of perennials: are there general patterns? *J Ecol* 84:597–608

- Aerts R, Chapin FS (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv Ecol Res* 30:1–67
- Allen SE (1989) *Chemical analysis of ecological materials*. Blackwell, Oxford
- Chabot BF, Hicks DJ (1982) The ecology of leaf life spans. *Annu Rev Ecol Syst* 13:229–259
- Chapin FS (1980) The mineral nutrition of wild plants. *Annu Rev Ecol Syst* 11:233–260
- Chapin FS, Kedrowski RA (1983) Seasonal-changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology* 64:376–391
- Chen FS, Fahey TJ, Yu MY, Gan L (2010a) Key nitrogen cycling processes in pine plantations along a short urban-rural gradient in Nanchang, china. *For Ecol Manag* 259:477–486
- Chen FS, Zeng DH, Fahey TJ, Yao CY, Yu ZY (2010b) Response of leaf anatomy of *Chenopodium acuminatum* to soil resource availability in a semi-arid grassland. *Plant Ecol* 209:375–382
- Chen FS, Niklas KJ, Zeng DH (2011) Important foliar traits depend on species-grouping: analysis of a remnant temperate forest at the Keerqin sandy lands, China. *Plant Soil* 340:337–345
- Cornelissen JHC et al (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust J Bot* 51:335–380
- Cunningham SA, Summerhayes B, Westoby M (1999) Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecol Monogr* 69:569–588
- Falster DS, Warton DI, Wright IJ (2006) User's guide to SMATR: standardised major axis tests & routines. Version 2.0. http://bio.mq.edu.au/ecology/SMATR/SMATR_users_guide.pdf
- Falster DS, Reich PB, Ellsworth DS, Wright IJ, Westoby M, Oleksyn J, Lee TD (2012) Lifetime return on investment increases with leaf lifespan among 10 Australian woodland species. *New Phytol* 193:409–419
- Grime JP et al (1997) Integrated screening validates primary axes of specialisation in plants. *Oikos* 79:259–281
- He JS, Wang ZH, Wang XP, Schmid B, Zuo WY, Zhou M, Zheng CY, Wang MF, Fang JY (2006) A test of the generality of leaf trait relationships on the Tibetan plateau. *New Phytol* 170:835–848
- Jackson RB, Mooney HA, Schulze E-D (1997) A global budget for fine root biomass, surface area, and nutrient contents. *Proc Natl Acad Sci USA* 94:7362–7366
- Killingbeck KT (1996) Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. *Ecology* 77:1716–1727
- Kobe RK, Lepczyk CA, Iyer M (2005) Resorption efficiency decreases with increasing green leaf nutrients in a global data set. *Ecology* 86:2780–2792
- Lavorel S, McIntyre S, Landsberg J, Forbes TDA (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends Ecol Evol* 12:474–478
- Luxmoore RJ (1991) A source sink framework for coupling water, carbon, and nutrient dynamics of vegetation. *Tree Physiol* 9:267–280
- Mueller KE, Hobbie SE, Oleksyn J, Reich PB, Eissenstat DM (2012) Do evergreen and deciduous trees have different effects on net N mineralization in soil? *Ecology* 93(6): 1463–1472
- Niinemets U (2001) Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* 82:453–469
- Niinemets U, Kull K (2003) Leaf structure vs. nutrient relationships vary with soil conditions in temperate shrubs and trees. *Acta Oecol* 24:209–219
- Niklas KJ (1999) A mechanical perspective on foliage leaf form and function. *New Phytol* 143:19–31
- Ordoñez JC, van Bodegom PM, Witte JPM, Wright IJ, Reich PB, Aerts R (2009) A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecol Biogeogr* 18:137–149
- Poorter H, Bergkotte M (1992) Chemical-composition of 24 wild-species differing in relative growth-rate. *Plant Cell Environ* 15:221–229
- Poorter H, Nagel O (2000) The role of biomass allocation in the growth response of plants to different levels of light, CO₂, nutrients and water: a quantitative review. *Aust J Plant Physiol* 27:595–607
- Reich PB, Oleksyn J (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc Natl Acad Sci USA* 101:11001–11006
- Reich PB, Walters MB, Ellsworth DS (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol Monogr* 62:365–392
- Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. *Proc Natl Acad Sci USA* 94:13730–13734
- Reich PB, Walters MB, Ellsworth DS, Vose JM, Volin JC, Gresham C, Bowman WD (1998) Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. *Oecologia* 114:471–482
- Sands R, Mulligan DR (1990) Water and nutrient dynamics and tree growth. *For Ecol Manag* 30:91–111
- Santiago LS, Wright SJ (2007) Leaf functional traits of tropical forest plants in relation to growth form. *Funct Ecol* 21:19–27
- Schulze ED, Kelliher FM, Korner C, Lloyd J, Leuning R (1994) Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and plant nitrogen nutrition—a global ecology scaling exercise. *Annu Rev Ecol Syst* 25:629–660
- Sobrado MA, Medina E (1980) General morphology, anatomical structure, and nutrient content of sclerophyllous leaves of the 'Bana' vegetation of Amazonas. *Oecologia* 45: 341–345
- SPSS Inc. (2001) *SPSS for Windows (10.0)*. SPSS Inc., Chicago
- Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. *Biol Rev* 81:259–291
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annu Rev Ecol Syst* 33:125–159
- Wright IJ, Westoby M (2003) Nutrient concentration, resorption and lifespan: leaf traits of Australian sclerophyll species. *Funct Ecol* 17:10–19

- Wright IJ, Reich PB, Westoby M (2001) Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Funct Ecol* 15:423–434
- Wright IJ et al (2004a) Leaf trait relationships in Australian plant species. *Funct Plant Biol* 31:551–558
- Wright IJ et al (2004b) The worldwide leaf economics spectrum. *Nature* 428:821–827
- Wright IJ et al (2005a) Assessing the generality of global leaf trait relationships. *New Phytol* 166:485–496
- Wright IJ et al (2005b) Modulation of leaf economic traits and trait relationships by climate. *Global Ecol Biogeogr* 14: 411–421
- Yu K (2010) Leaf structure and nutrient traits across important garden plants under hilly red soil in mid-subtropical region: the case of the new campus of Nanchang University. Master thesis, Nanchang University (in Chinese)