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ORIGINAL PAPER

Changes in ecological stoichiometry and nutrient resorption in *Castanopsis hystrix* plantations along an urbanization gradient in the lower subtropics

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Abstract The stoichiometry of carbon, nitrogen and phosphorous in plants can reflect the interactions between plants and their environment. The interplay between plant nutrients, climatic factors, and soil properties and the underlying regulatory mechanisms are pillars of ecology but remain underexplored. In this study of plant C–N–P stoichiometry and nutrient resorption in *Castanopsis hystrix* groves in three cities (Guangzhou, Zhongshan, and Lechang) that represent an urban–rural gradient in Guangdong Province, South China, we explored potential relationships among NO_2 concentrations, diameter at breast height (DBH), and resident human population. Mean annual temperature, mean annual precipitation, insolation duration per year, and the human resident population differed significantly among the three cities. Soil C-N-P was always highest in suburban Lechang, and the concentration of NO_2 was highest in urban Guangzhou (55.33 ± 0.67 μg m^{-3}) and positively correlated with the resident population and leaf N:P. Our findings suggest that C–N–P stoichiometry of *C. hystrix* was better explained by NO_2 than by soil C–N–P stoichiometry and that nutrient resorption was better explained by leaf nutrients and DBH than by NO_2 and soil stoichiometry. Our study supports the hypothesis that rapid urbanization influences NO_2 concentrations and microclimate, which may jointly change the stoichiometry of plant nutrients in the forest ecosystems.

Keywords Ecological stoichiometry · Nutrient cycling · Plant-environment interaction · Subtropical forest · Urban–rural gradient

Introduction

Ecological stoichiometry has been described as the bridge linking species with ecosystems (Elser et al. 1996; Zhang et al. 2019). In terrestrial ecosystems, the variations in the carbon (C), nitrogen (N) and phosphorous (P) stoichiometry in different plant organs can be used as reliable indicators of ecological function (Elser et al. 2000; Xie et al. 2020). For example, C-N-P stoichiometry can be used to predict plant growth, nutrient cycling and nutrient limitation in forest communities (Sterner and Elser 2002; Elser et al. 2007). Plant N:P ratios can help us understand the responses of vegetation to nutrient supply, phytometabolic processes, and community assembly (Vitousek 1982; Güsewell 2004). At the global scale, patterns of N and P are closely related with climatic factors such as temperature and environmental variables such as latitude (Reich and Oleksyn 2004). Numerous studies have found that human activities (e.g., urbanization, deforestation, release of fossil fuels) influence nutrient cycles, such as carbon from CO_2 and nitrogen from NO_2 (Jonasson et al. 1999; Lamsal et al. 2013). As a major source of N deposition influencing nutrient cycle of plant, NO_2 is

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mainly derived from fossil energy combustion processes like transportation; thus, NO_2 concentration is highly correlated with the resident human population due to increased industrialization caused by population growth (Lamsal et al. 2013). C:N:P ratios (the stoichiometry of C, N and P) are of great importance to understand nutrient cycles and biotic feedbacks in both marine and terrestrial ecosystems worldwide (McGroddy et al. 2004; Sardans et al. 2012; Bell et al. 2014). However, the mechanisms responsible for ecological stoichiometry and nutrient resorption of plant organs and soil in a specific region along an urban–rural gradient remain unclear, but are key to understanding plant responses in an era defined by rapid climate evolution and urbanization.

Soil nutrients are not only essential for plant growth, but also influence the expression of physiological and ecological functions as well (Nye 1960; Schoenholtz et al. 2000) and can be used to assess nutrient limitation in terrestrial ecosystems. Globally, the C:N:P atomic ratio of soils has been shown to be roughly 186:13:1 (Cleveland and Liptzin 2007). This general estimated ratio of nutrient allocation provides a background value for specific investigations. However, C:P and N:P ratios are highly variable across space, climatic zone, soil depth and type (Millard and Grelet 2010), and weathering stage (Tian et al. 2010). Ecological stoichiometry can explain the state of plant nutrient resorption in ecosystem dynamics and functioning (Sterner and Elser 2002; Fan et al. 2015; Zechmeister-Boltenstern et al 2015). Plant nutrient resorption, the process by which nutrients from aged tissues are mobilized to other tissues, prolongs nutrient retention by the plant, improves the utilization efficiency of the nutrients, and may reduce plant dependency on soil nutrients (Vergutz et al. 2012; Zhang et al. 2015). Multiple studies have found that a large portion of the nutrient requirements of perennial plants are obtained through resorption (Aerts 1996; Reed et al. 2012).

Castanopsis hystrix, one of the most important evergreen tree species in South China, is primarily distributed throughout the provinces of Fujian, southern Hunan, Guangdong, Guangxi, and southwestern Guizhou, as well as in southeastern Tibet (Li et al. 2007). *C. hystrix* is a dominant landscape species often grown in commercial stands for luxury furniture (Li 1996; Li et al. 2007). In this study, we focused on *C. hystrix* groves in three Chinese subtropical forests along urban–rural gradients to answer two fundamental questions: (1) How do NO_2 concentrations correlate with the C–N–P stoichiometry in the plant? (2) How is the C-N-P stoichiometry in different organs related to soil and climatic factors? The answers will improve our understanding of nutrient cycling in *C. hystrix* plantations in subtropical regions, South China. Determining the C-N-P status in different organs and soil of *C. hystrix* forests will help us understand nutrient cycling processes in the plantations in South China and design appropriate management strategies.

Materials and methods

Study site

We selected five sampling locations in three subtropical forests along the urban–rural gradients in Guangdong Province, South China (Fig. 1). Specifically, a mixed population of *C. hystrix* and *S. superba* (G1), a monoculture of *C. hystrix* (G2), and a mixed population of *C. hystrix* and *Acacia mangium* (G3) of Longdong Forest Farm in Guangzhou city (highly urbanized); a mixed population of *C. hystrix* and *S. superba* (Z1) of Wugui Mountain in Zhongshan city (moderately urbanized); and a monoculture of *C. hystrix* (L1) of Longshan Forest Farm in Lechang city (less urbanized). Stand age for the sampled populations were relatively similar: 18 years in Lechang and Zhongshan and 20 years in Guangzhou according to records from earlier field investigations. All stands were fertilized and managed for 2 years before being allowed grow naturally, and all soil types were classified as red soil with similar acid pH (4.47, 4.58 and 4.86 in the city of Guangzhou, Zhongshan and Lechang, respectively). All sites have a subtropical monsoon climate with an annual mean precipitation between 1336–1777 mm and a mean annual temperature between 18.7–23.4 °C.

Sample collection and data processing

The plots in Guangzhou city, Zhongshan city and Lechang city were 20 m × 30 m, 20 m × 20 m and 30 m × 40 m, respectively. At each site, three replicate plots with similar topography and minimal human interference were established. The position and direction of slope

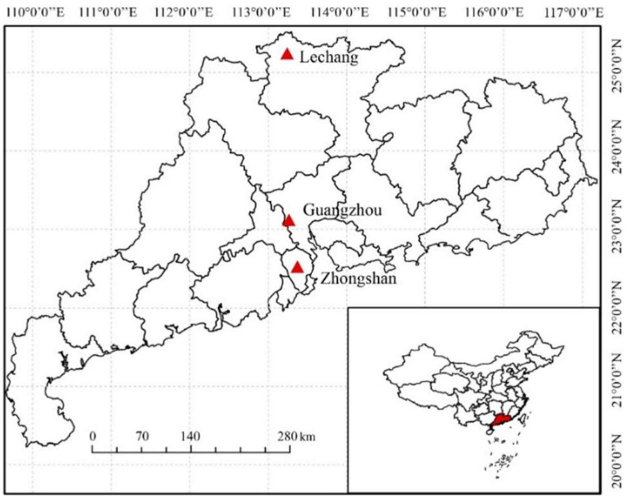

Fig. 1 Research areas and sites of the Castanopsis hystrix plantations sampled in Guangdong Province, South China. Red triangles represent the Longdong Forest Farm in Guangzhou, Wugui Mountain in Zhongshan, and Longshan Forest Farm in Lechang

for these plots were the same, and *C. hystrix* individuals of similar age were selected. We measured the diameter at breast height (DBH > 2 cm), tree height, and height under branches (HUB). Three representative trees were selected to sample leaves and branches for each forest plot from five places. Samples were taken from healthy pest-free foliage and branches from the upper and outer portions of the crown. Three litter samples of fresh and undecomposed material were randomly collected from the soil surface to better understand nutrient resorption in the forest site. Three soil cores (6 cm in diameter) in each stand were taken 0–20 cm depth after removing the surface litter.

Regional data of mean annual temperature (MAT), mean annual precipitation (MAP), insolation duration per year, and resident human population (RP) were compiled from China's National Bureau of Statistics (http://www.stats.gov.cn/) for the years of 2015–2017. Simultaneously, regional NO_2 concentrations were retrieved from the Municipal Eco-Environment Bureau of Guangzhou (http://www.gzepb.gov.cn/), Zhongshan (http://www.zsepb.gov.cn) and Shaoguan (http://epb.sg.gov.cn/) during the same period.

C, N, and P analyses

Branches and leaves were dried at 105 °C for 15 min and then at 75 °C for 72 h to constant mass (Zheng et al. 2010). Soil samples were sieved (2 mm mesh) and air-dried. Leaf and soil C were measured via external heating of potassium dichromate (Kalembasa and Jenkinson 1973). Leaf N and P were measured using $H_2SO_4 + H_2O_2$ digestion, then distillation titration for N and vanadium molybdenum yellow colorimetry for P (Parkinson and Allen 1975). Total soil N and P were measured by the micro-Kjeldahl distillation titration method and the NaOH melting molybdenum-antimony anticolorimtric method, respectively (Parkinson and Allen 1975).

Data analyses

Nutrient resorption efficiency (NuRE) of N and P were calculated as:

$$\text{NuRE} = \left(\frac{N_{le} - N_{li}}{N_{le}}\right) MLCF \times 100$$

where MLCF (0.780) is the mass loss correction factor for evergreen woody angiosperms (Vergutz et al. 2012), and N_{le} and N_{li} represent the concentrations of leaf and litter, respectively. SPSS 19.0 (IBM, Armonk, NY, USA) was used for one-way analyses of variance (ANOVAs) to compare the variation of C, N, P stoichiometry and NuRE of plant-soil. Origin 2017 (OriginLab, Northampton, Massachusetts, USA) was used to draw graphs. R-studio (Public Benefit Corporation, Boston, Massachusetts, USA) was used for hierarchical partitioning analysis (HP), which was used to measure the explanatory value of independent variables.

Results

Variation of regional climatic and social factors

NO_2 concentrations in Guangzhou city (55.33 ± 0.67 μg m^{-3}; mean ± SE) were higher than in Zhongshan city (46.00 ± 1.53 μg m^{-3}) and Lechang city (50.67 ± 0.88 μg m^{-3}), based on public data from 2015 to 2017. Climatic factors of MAP, MAT, insolation duration per year and resident population (RP) were significantly different across the three localities ($p < 0.05$) (Table 1).

Soil C-N-P stoichiometry in *C. hystrix* plantations

Significant differences were detected in soil C–N–P stoichiometry at the 0–20 cm depth among the three forests. Soil C-N-P was highest in Lechang and lowest in Zhongshan, while soil C:N, C:P and N:P were lowest in Lechang and highest in Zhongshan. Soil N concentration was not significantly different between Guangzhou and Zhongshan (Table 2).

Table 1 Means (± SE) for climate and population metrics (2015–2017) for the three sampled plantations of *Castanopsis hystrix* in South China

Sites	MAT (°C)	MAP (mm)	RP (million)	Insolation duration per year (h)
Guangzhou	22.57 ± 0.09b	2306.33 ± 176.74b	14.01 ± 0.28c	1634.13 ± 67.48b
Zhongshan	23.23 ± 0.29c	1707.13 ± 80.54a	3.22 ± 0.02b	1936.37 ± 16.72c
Lechang	20.47 ± 0.09a	1645.83 ± 110.2a	0.41 ± 0.00a	1308.3 ± 93.35a

MAT, mean annual temperature; *MAP*, mean annual precipitation; *RP*, resident population. *MAP* was anomalous in Zhongshan in 2016 and replaced with data from 2014. Means followed by different lowercase letters within a column differed significantly in a one-way ANOVA ($p < 0.05$)

Table 2 Mean (±SE) soil C-N-P stoichiometry of the stand types at the three sampled plantations of *Castanopsis hystrix* in South China

Metric	Guangzhou stands			Zhongshan stand	Lechang stand
	G1	G2	G3	Z1	L1
C	28.85±4.15ab	23.60±2.52a	28.10±2.40ab	23.01±3.72a	34.74±3.09b
N	1.00±0.12a	0.88±0.08a	1.11±0.07a	0.81±0.14a	1.56±0.12b
P	0.19±0.01b	0.19±0.01b	0.17±0.01b	0.09±0.01a	0.43±0.03c
C/N	28.43±0.71cd	26.28±0.81bc	25.14±1.05b	28.97±0.88d	22.09±0.55a
C/P	155.28±23.85 b	120.18±10.46ab	167.59±10.63b	297.48±48.42c	81.87±6.73a
N/P	5.37±0.67ab	4.53±0.33ab	6.66±0.29b	10.49±1.87c	3.67±0.25a

G1, mixed *C. hystrix* and *Schima superba*; G2, *C. hystrix* only; G3, mixed *C. hystrix* and *Acacia mangium* (G1–G3, highly urbanized). Z1, mixed *C. hystrix* and *S. superba* (moderately urbanized). L1, *C. hystrix* (least urbanized). Means followed by different lowercase letters within a row differed significantly in a one-way ANOVA ($p<0.05$)

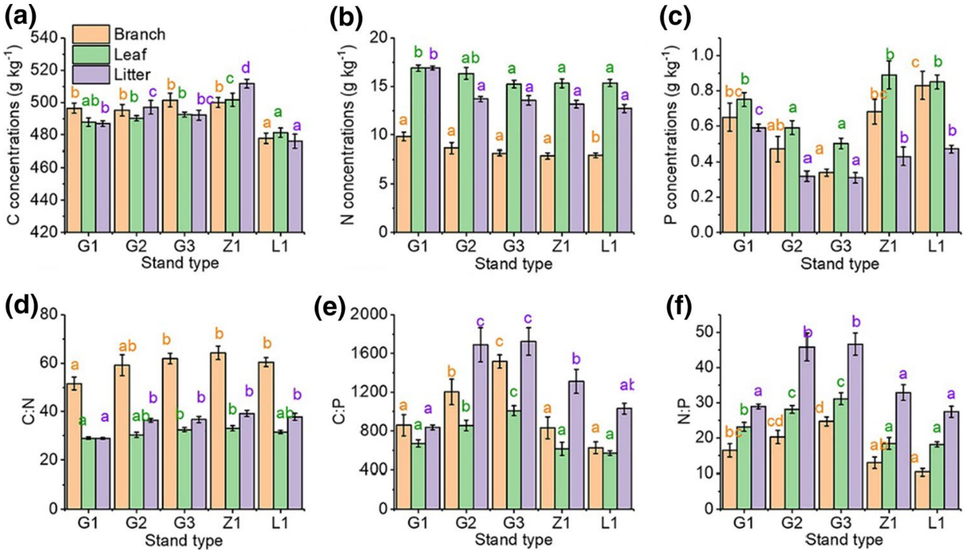

Fig. 2 Plant C-N-P stoichiometry in branch, leaf, and litter samples from plantations of Castanopsis hystrix at three sites in South China. See Notes with Table 2 for stand types and urbanization level. Different letters above bars for the same sample type (n = 3) indicate a significant difference among stand types (n = 5) based on a one-way ANOVA ($p = 0.05$)

Plant C-N-P stoichiometry in *C. hystrix* plantations

N and P concentrations and C:N, C:P and N:P ratios varied among branch, leaf, and litter samples, but did not differ significant among the cities (Fig. 2b–f). Plant C concentration and C:N were higher in Zhongshan than in Lechang and Guangzhou (Fig. 2a, d). Plant N and N:P were higher in Guangzhou than in Lechang and Zhongshan (Fig. 2b, f). Plant P concentrations were higher and C:P were lower in Lechang compared to Guangzhou (Fig. 2c, e).

Regression and HP analysis (Table 3) showed that most plant stoichiometric measures could be explained by a model including DBH, NO_2, and soil stoichiometry. Furthermore, of the measures that could be explained by our model, DBH and NO_2 explained the majority of the variance, with the exception of leaf C concentration, where soil stoichiometry had the strongest predictive power. Branch C, branch C:P and leaf N:P increased linearly with NO_2 (Fig. 3a, f, g). Branch/leaf P and C:P decreased linearly with NO_2 (Fig. 3b, c) and with DBH (Fig. 3d, e).

Characteristics of nutrient resorption

Litter N concentrations were higher in Guangzhou than in Zhongshan and Lechang, while litter C:N was higher in Zhongshan than in Lechang and Guangzhou (Fig. 2b, d). NRE (N nutrient resorption efficiency) and PRE (P nutrient resorption efficiency) differed significantly among the three sites (Fig. 4). With the exception of litter N:P, the full model that included DBH, NO_2 and leaf and soil stoichiometries explained the majority of the variance in litter stoichiometry and NuRE (Table 4). DBH and leaf stoichiometry were the most predictive independent variables for all dependent variables except for litter N:P, for which the model had poor predictive power. Soil stoichiometry was not the most predictive variable. Litter C, N and P concentrations were negatively correlated with DBH, leaf N concentration, and DBH, respectively (Fig. 5a–c). Litter and leaf C:N were also negatively correlated (Fig. 5d). NRE was positively correlated with leaf N concentration (Fig. 5e), and PRE was positively correlated with DBH (Fig. 5f).

Table 3 Hierarchical partitioning analysis of fraction of total variance in C–N–P stoichiometry of *Castanopsis hystrix* explained by DBH, NO_2, and soil stoichiometry

Elements	Sample	Full model R^2	Percentage of total variance explained		
			DBH	NO_2	Soil stoichiometry
C	Branch	0.40	26.1	58.0	15.9
	Leaf	0.25	34.0	6.6	59.4
N	Branch	0.41	30.8	55.2	14.0
	Leaf	0.26	42.9	20.3	36.8
P	Branch	0.56	41.5	50.0	8.5
	Leaf	0.83	37.8	55.0	7.1
C:N	Branch	0.27	42.3	51.4	6.3
	Leaf	0.21	62.0	37.2	0.8
C:P	Branch	0.65	49.1	46.7	4.2
	Leaf	0.73	52.6	46.7	0.7
N:P	Branch	0.69	38.7	58.6	2.7
	Leaf	0.77	40.4	58.1	1.5

Soil stoichiometry refers to the same element in a given row, representing soil nutrient elements that correspond to plant nutrient elements. Bold values represent significant differences ($p < 0.05$)

Discussion

C-N-P stoichiometry and interactions in soil

Soil characteristics are influenced by the diversity of soil microbes, spatial heterogeneity, and structural complexity. Although the global C:N:P ratios (186:13:1) of soils may be stable (Cleveland and Liptzin 2007), local climate and soil formation affect the stoichiometry in soils (Tian et al. 2010), creating regional and local heterogeneity. Furthermore, the same plant species in different stand types may have different nutrient concentrations. Here we found that C:N ranged from 22.09 to 28.97, C:P from 81.87 to 297.48, and N:P from 3.67 to 10.49, values that differed significantly from previous means of 14.4, 136 and 9.3 in China's soil (Tian et al. 2010). These differences may be caused by differences in tree species and climate zones. Soil C-N-P concentrations were highest in Lechang and lowest in Zhongshan, which may be due to latitudinal differences (Sardans et al. 2011), vegetation age (Bui and Henderson 2013), and understory vegetation diversity (Small and McCarthy 2005). Hence, soil stoichiometry was likely influenced by complex factors (Huang et al. 2016).

Our study shows that soil stoichiometry played a minor role in the C–N–P content in branches and leaves, and NO_2 was often the most predictive variable. However, many studies have found that plant nutrients are sensitive to soil nutrients (Schreeg et al. 2014; Tang et al. 2018). Although plant and soil nutrient concentrations are usually correlated, at least in some organs (He et al. 2016; Erinle et al. 2020), the relationship maybe confounded by air pollution and other climatic factors that influence forest nutrient cycling. Nutrient cycling has been shown to be a complicated process involving plant-soil interactions (Zechmeister-Boltenstern et al. 2015).

Ecological stoichiometry of plant organs and relationships with environmental factors

N concentrations and N:P ratios in branches and leaves were higher in Guangzhou than in Zhongshan and Lechang, but P concentration in branches was lower in Guangzhou. P concentrations in branches and leaves were significantly negatively correlated with NO_2. N:P ratios of branches and leaves were significantly positively correlated with NO_2, indicating that NO_2 can reflect the status of plant nutrient P. Global change, N deposition and anthropogenic activities are primary factors affecting N:P ratios in leaves (Güsewell 2004; Sardans et al. 2016). A regional study showed a positive correlation between MAT and C:P and N:P in branches of 803 plant species in China (Zhang et al. 2018b). In our study of the three sites, mean leaf N–P ranged from 0.75 to 0.89 g kg^{-1}, and N:P from 18.17 to 31.11. Leaf P concentration was lower than found in a meta-analysis of leaf P in terrestrial species in China (1.21 g kg^{-1}) (Han et al. 2005). In addition, leaf N concentrations were lower than the mean for 753 Chinese terrestrial species (18.6 g kg^{-1}; Han et al. 2005), except for the mixed population of *C. hystrix* and *A. mangium* from Longdong Forest Farm in Guangzhou city (25.62 g kg^{-1}). However, the leaf N:P ratio was higher than in the Han et al. (2005) study (14.4).

N:P ratios in plants are influenced by species composition, community, plant age, etc. (Güsewell 2004). In our study, in leaves, C:N ranged from 28.99.28 to 33.03 and C:P from 571.10 to 1007.40. We also found that leaf C:N in this study was lower than the global mean for broadleaf forests (35.1 ± 3.7), but C:P (922.3 ± 77.3) was within the global range (McGroddy et al. 2004). N:P ratios of plant above 16 suggest P limitation; those below 14 indicate N limitation (Meuleman 1996; Wang et al. 2018). The N:P ratios of leaves collected from the *C. hystrix* populations were greater than 16 across all sites, suggesting that P limitation is widespread in the region. Our results show that NO_2 correlates with plant N content and significantly influences P content and N:P ratios. Therefore, NO_2 concentration may be used as an indicator of plant N and P status.

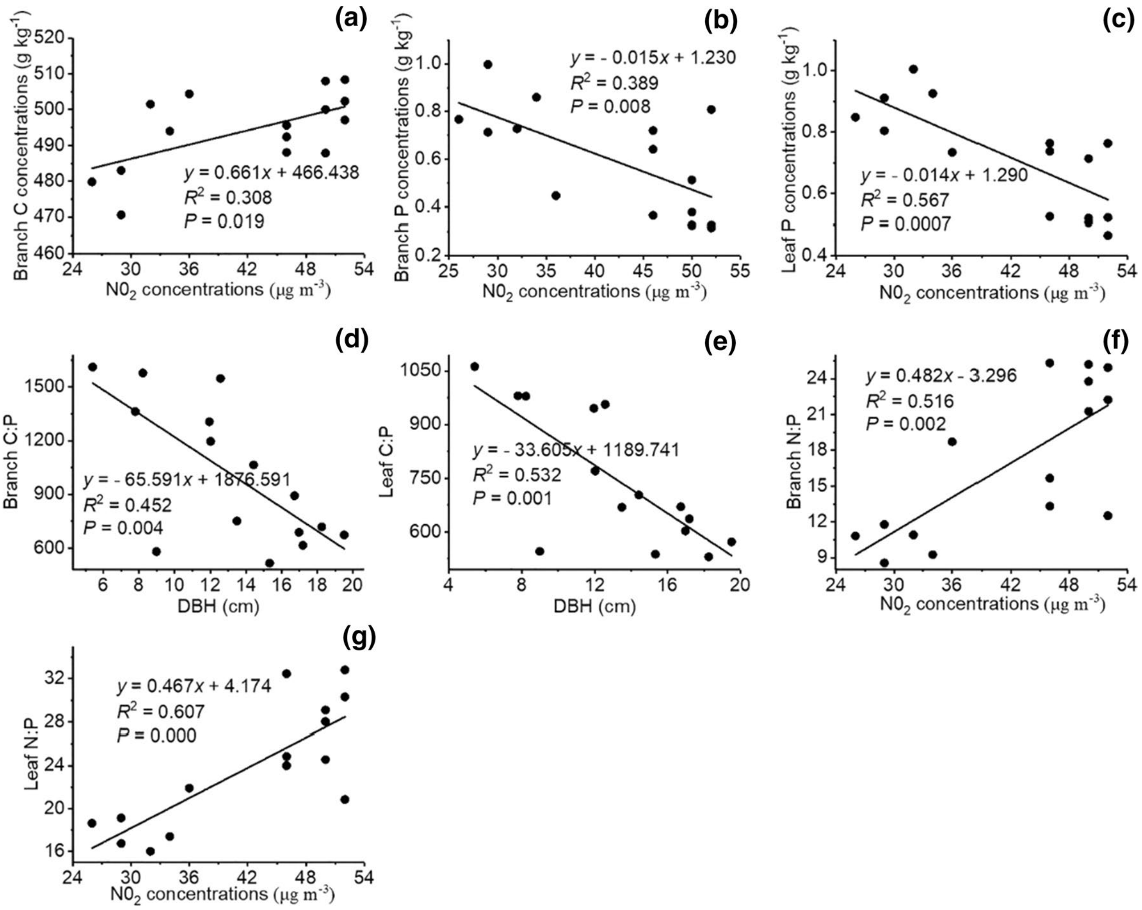

Fig. 3 Relationships between NO_2 (**a**–**c**, **g**, **f**) and DBH (**d**, **e**) with plant stoichiometry from plantations of *Castanopsis hystrix* at three sites in South China. See Notes with Table 2 for stand types and urbanization level

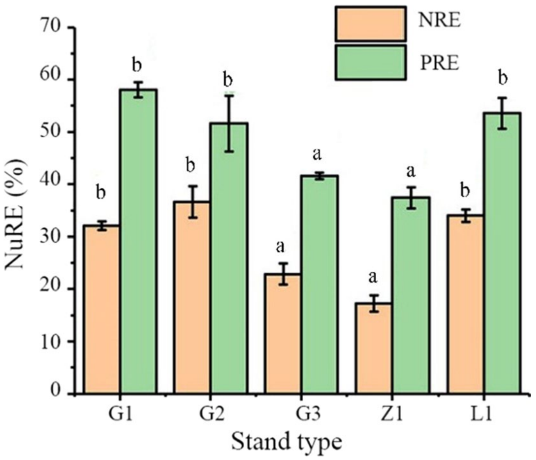

Fig. 4 Variation in nutrient resorption efficiency (NuRE) in *Castanopsis hystrix* plantations in Guangzhou, Zhongshan, and Lechang, which differed in their urbanization levels. See Notes with Table 2 for stand types

Nutrient resorption and influencing factors

Atmospheric NO_2 concentrations often exhibit variations across diverse cities, as in Guangdong Province in South China. Our study confirmed that NO_2 was highest in Guangzhou and increased significantly with population growth. Plants distribute nutrients to leaves for growth (Sardans and Peñuelas 2013) and often use the nutrients stored in branches when nutrients are limited (Heineman et al. 2016; Yan et al. 2016). Litter P content was lower in our study compared to the global mean (0.85 g kg^{-1}) (Kang et al. 2010). In contrast, N content and N:P ratios were both higher than the global means (10.9 g kg^{-1} and 18.3, respectively) (Kang et al. 2010). Litter composition and stoichiometry are important factors in litter decomposition. Specifically, N content and C:N of litter strongly affects decomposition (Leitner et al. 2012). Usually, net N release from litter decomposition

Table 4 Percentage of total variation in litter stoichiometry and nutrient resorption efficiency from plantations of *Castanopsis hystrix* at three sites in South China explained by DBH, NO_2, leaf and soil stoichiometry. See Notes with Table 2 for stand types and urbanization level

Sample	Full model R^2	Percentage of total variance explained			
		DBH	NO_2	Stoichiometry	
				Leaf	Soil
LitterC	**0.63**	**30.6**	20.1	28.7	20.6
LitterN	**0.77**	35.4	**11.2**	**36.6**	16.8
LitterP	**0.67**	**41.9**	29.3	10.0	18.8
LitterC:N	**0.70**	30.4	**14.8**	**47.2**	7.6
LitterC:P	0.66	**35.7**	32.0	11.8	20.5
LitterN:P	0.12	4.8	53.1	10.2	31.9
NRE	**0.71**	22.1	**14.2**	**37.8**	25.9
PRE	**0.64**	**36.0**	25.3	10.6	28.1

Stoichiometry values are for the sample metric in a given row. Bold values represent significant differences at α = 0.05. Hierarchical partitioning (HP) analysis was used to examine the effects of DBH, NO_2, leaf and soil stoichiometry on litter stoichiometry and nutrient resorption

begins when litter C:N is less than 40 (Parton et al. 2007). Litter decomposition rate is negatively correlated with C:N and C:P; lower C:N and C:P typically correspond to faster decomposition rates (Enríquez et al. 1993). MAP and NO_2 are key factors influencing litter N content, and litter N content follows a linear relationship with MAP (Liu et al. 2006; Yuan and Chen 2009b). Old leaves and branches may be more sensitive than young ones to N content (Di et al. 2018), and here, N and P were higher in leaves than in branches and litter.

Foliar N content was significantly positive correlated with NRE ($p = 0.042$), but PRE was not correlated with leaf P content. However, some studies have found the opposite trend, with P concentrations in leaves positively correlated with PRE, and a lack of correlation between NRE and N content in a *Metasequoia glyptostrobodies* forest (Zhang et al. 2018a). Here, we did not find any significant correlations between either NRE or PRE and MAP. However, a contrasting report suggested that NRE increases, while PRE decreases, with MAP at a global scale (Yuan and Chen 2009a).

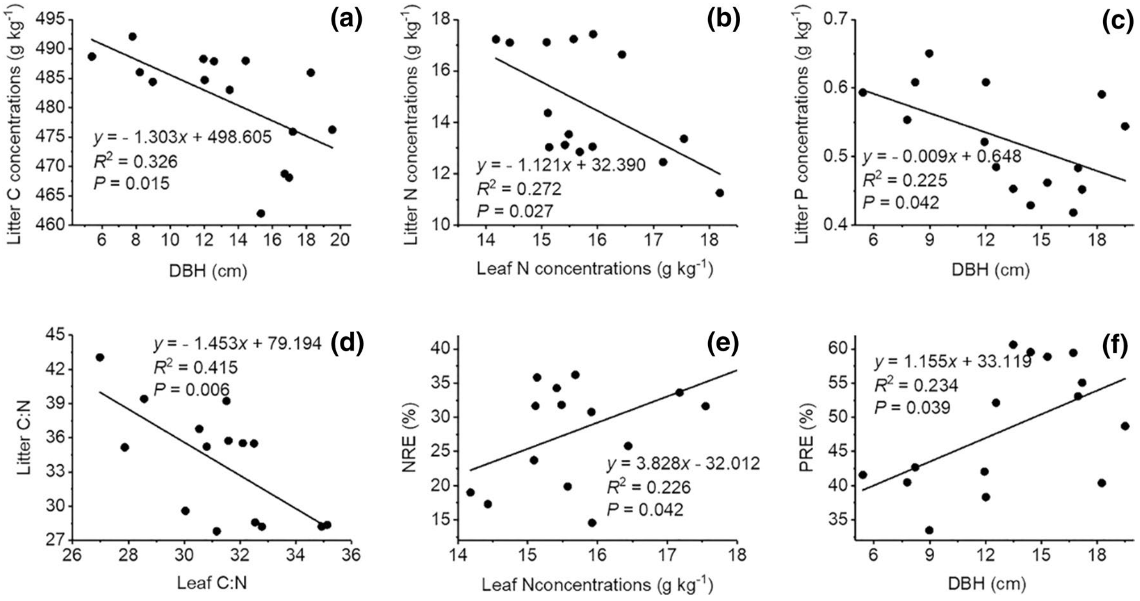

Fig. 5 The relationships from plantations of *Castanopsis hystrix* at three sites in South China between DBH and litter stoichiometry (**a**, **c**), litter and leaf stoichiometries (**b**, **d**), and nutrient resorption and leaf stoichiometry and DBH (**e**, **f**). See Notes with Table 2 for stand types and urbanization level

Conclusions

Plant N:P in branches and leaves were positively correlated with NO_2 in *C. hystrix* populations. Variance in nutrient resorption was better explained by leaf nutrients and DBH than by NO_2 and soil ecological stoichiometry. Our results highlight that NO_2 concentration decreased along the urban–rural gradient exemplified by Guangzhou–Zhongshan–Lechang in Guangdong Province, South China. The effect of NO_2 concentration was greater than soil stoichiometry on plant nutrient cycling.

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