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Seasonal changes of nutrient levels and nutrient resorption in *Avicennia marina* leaves in Yingluo Bay, China

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***Avicennia marina* is a typical mangrove species of subtropical coastlines of China. However, little is known about the retention of nutrients by this species in oligotrophic, coastal environments. In this study, seasonal changes in nitrogen (N) and phosphorus (P) concentrations, N:P ratio and total phenolic concentration in *A. marina* leaves during senescence were studied. *Avicennia marina* leaves had high N and P concentrations but the seasonal pattern of N concentration was different from that of P concentration. The *A. marina* forest was N-limited as the N:P ratio of mature leaves was less than 14. Nitrogen resorption efficiency was higher than P resorption efficiency, and the concentrations of N and P in senescent leaves indicated that N resorption was mostly complete whereas P resorption was incomplete. *Avicennia marina* leaves contained low tannin concentrations, particularly condensed tannins, as the leaf extracts did not react with acid butanol. Total phenolic concentrations were not correlated with N concentrations in mature and senescent leaves of *A. marina*. These findings suggest that the high N resorption efficiency and low nutrient losses play an important role in nutrient conservation strategies for *A. marina* forests, whereas low tannin concentrations have limited effects on nutrient cycling.**

Keywords: *Avicennia marina*, nutrient limitation, nutrient resorption, total phenolics

Introduction

Mangroves are a special kind of forest occurring on tropical and subtropical coastlines. Mangrove species that flourish in oligotrophic, coastal environments have very efficient mechanisms for retaining and recycling nutrients (Twilley et al. 1986; Alongi et al. 1992).

Many previous studies have shown that the nitrogen (N) and phosphorus (P) availability is an important factor responsible for mangrove growth (Feller 1995; McKee et al. 2002). Although N:P ratios have been widely used to determine plant N and P limitation in wetlands (Güsewell and Koerselman 2002; Güsewell et al. 2003; Rejmánková 2005), but have not been used widely as an indicator in mangrove ecosystems (Lin et al. 2010; Zhou et al. 2010). The plant N:P ratio is a useful variable for consideration in ecological research because it reflects the gradual and dynamic character of nutrient limitation rather than fixed characters such as N-limited versus P-limited (Güsewell 2004).

Growth of perennial plants is determined not only by the amount of nutrients they acquire, but also by the amount of stored nutrients that can be reused (Rejmánková 2005). Nutrient resorption is the process by which nutrients are withdrawn from senescing leaves prior to abscission and stored in other plant tissues (Killingbeck 1986). This increases the use of absorbed nutrients and reduces plant dependence on soil supply (Pugnaire and Chapin 1993). Nutrient resorption has been assumed to be one of the most important strategies by plants to conserve nutrients (Lin et al. 2010; Ye et al. 2012). The degree of nutrient resorption affects litter quality, which consequently affects decomposition rates and nutrient availability (Rejmánková 2005).

Phenolic compounds, including tannins, are a significant component of plant secondary metabolites. Tannins are comprised of hydrolysable tannins and condensed tannins, generally known for their ability to bind N and proteins (Haslam 1989), but the condensed tannins are considered the more reactive of the two groups and hence more influential in decomposition and nutrient dynamics (Hättenschwiler and Vitousek 2000). In mangrove species tannins are an abundant component, constituting as high as 20% dry weight, that prevent damage from herbivory. Leaves and bark may contain up to 30–40% tannins by dry weight (Lin et al. 2010). Because tannins are complex and energetically costly molecules to synthesise, their widespread occurrence and abundance suggest that tannins play an important role in plant function and evolution (Zucker 1983).

Despite growing knowledge of nutrient limitation for mangrove species and how mangroves adapt to low

nutrients (McKee et al. 2002; Lin and Sternberg 2007; Lin et al. 2010; Reef et al. 2010), there is scant information about the relative importance of the N:P ratio and leaf phenolics variability in determining nutrient conservation (Lin et al. 2010). In this study, we evaluated possible nutrient conservation strategies of a mangrove *Avicennia marina* under nutrient limitation on subtropical coastlines of China. The hypotheses tested in this study were that (1) the mature leaves of *A. marina* have higher concentrations of nutrients and tannins than the senescent leaves and (2) strong nutrient limitation will result in higher resorption of the limiting nutrient.

Materials and methods

Study area
The study was carried out in Yingluo Bay, a core zone within the Shankou Mangrove Nature Reserve (21°32′ N, 109°40′ E) in Guangxi province, China. The climate of the region is southern subtropical maritime monsoon. The mean annual temperature is 23.4 °C, the coldest month (January) average temperature ranges from 14.2 to 14.5 °C, and the minimum temperature in January is 2.0 °C. Average annual rainfall and evaporation ranges between 1 500 and 1 700 mm, and 1 000 and 1 400 mm, respectively. The annual relative humidity is about 80% and approximately half of the precipitation is concentrated in summer. The tidal regime in Yingluo Bay is a diurnal tide, a typical tidal regime that prevails in Beibu Gulf. There is no riverine freshwater input, and the mean salinity of the seawater is 28.9‰ (Fan et al. 2005). At the study site, *A. marina* was the dominant species with a few individuals of *Rhizophora stylosa*, *Bruguiera gymnorrhiza*, *Kandelia candel* and *Aegiceras corniculatum*. The mean height of *A. marina* plants was 2.5 m and the canopy density was 0.98.

Leaf sampling
Leaf samples of *A. marina* were collected from a mangrove forest at Shankou, Guangxi province, China in October 2006 (autumn), January 2007 (winter), April 2007 (spring) and July 2007 (summer).

A total of 30 trees with similar height and growth conditions were selected and labelled. The 30 trees were divided into six groups (five trees per group) as six replications. The developmental stages of leaves were demarcated into two stages, i.e. mature leaf (the third to fifth pairs of developmentally matured leaves) and yellow senescent leaf (turning yellow due to senescence). Leaves damaged by insects and disease or mechanical factors were avoided. Fifty leaves at each developmental stage were sampled per group. All samples were taken to the laboratory immediately after sampling and cleaned with distilled water.

Chemical analyses
All chemicals used for the analyses were of analytical reagent grade. An additional standard denoted here was tannic acid obtained from Sigma. Procedures described by Lin et al. (2006) were used to determine total phenolics (TP). The TP concentration was measured with the Prussian blue method (Graham 1992).

Leaf samples were digested with sulphuric acid and hydrogen peroxide. The N concentration of leaf samples was determined by the micro-Kjeldahl method (Yoshida et al. 1972). The P concentration was determined by the ascorbic acid–antimony reducing phosphate colorimetric method (Nanjing Institute of Soil Science 1978).

Calculations
Resorption efficiency (RE) was calculated as the percentage of N or P recovered from the senescing leaves (Aerts 1996; Killingbeck 1996):

$$RE\ (\%) = (A_1 - A_2)/A_1 \times 100$$

where A_1 is the N or P concentration in the mature leaves, and A_2 is the N or P concentration in the senescent leaves.

Resorption efficiency and proficiency are different fundamental attributes of the same process. Killingbeck (1996) modified the concepts of nutrient resorption efficiency and proposed the use of 'resorption proficiency', which is the absolute level to which nutrients are reduced in senescing leaves. Lower final nutrient concentrations in senescent leaves correspond to higher proficiencies, which are usually expressed as percentages (Rejmánková 2005).

Statistical analysis
All measurements were replicated six times. A one-way analysis of variance (ANOVA) was performed with season as the treatment factor. The Student–Newman–Keuls multiple comparison method was used to test significant differences between any two seasons. All analyses were performed with SPSS 13.0 for Windows (SPSS, Chicago, IL, USA).

Results

Seasonal changes in N and P concentrations, N:P ratio and nutrient resorption of A. marina leaves
Mature leaves had significantly higher concentrations of N and P than senescent leaves. The N concentration in mature leaves remained relatively stable with no significant difference among the four seasons, whereas the P concentration in mature leaves changed with season, with the highest concentration in winter and the lowest in summer. The N and P concentrations in senescent leaves were higher in winter than those in other seasons (Table 1).

The N:P ratios in mature leaves were all below 14 with the highest value attained in summer. The nitrogen resorption efficiencies (NRE) in four seasons were mostly above 60% and higher in autumn, spring and summer than in winter. The phosphorus resorption efficiencies (PRE) were generally below 60% with the lowest value recorded in summer (Table 1).

The N concentrations in senescent leaves were less than 0.75% and the P concentrations in senescent leaves were all ≥0.06%, respectively (Table 1).

The N and P concentrations were not correlated in mature leaves, whereas a significant positive correlation between N and P concentrations was observed in senescent leaves. There was no significant relationship between NRE and N concentration in mature leaves, nor between PRE and P

Table 1: Seasonal changes in nitrogen (N) and phosphorus (P) concentrations, N:P ratio, nutrient resorption efficiency and proficiency of *A. marina* leaves at Shankou in Guangxi province, China. Values followed by a different superscript letter indicate significant differences among seasons ($P < 0.05$). ML = mature leaves, SL = senescent leaves; NRE and PRE = N and P resorption efficiency, respectively; NRP and PRP = N and P resorption proficiency, respectively

Variable		Season			
		Autumn	Winter	Spring	Summer
N (mg g⁻¹)	ML	16.49 ± 1.25[a]	17.67 ± 1.35[a]	17.70 ± 1.67[a]	17.19 ± 1.25[a]
	SL	5.27 ± 0.67[b]	7.48 ± 0.91[a]	5.62 ± 0.72[b]	5.40 ± 0.69[b]
P (mg g⁻¹)	ML	1.53 ± 0.02[c]	1.92 ± 0.08[a]	1.64 ± 0.06[b]	1.24 ± 0.02[d]
	SL	0.69 ± 0.03[b]	0.76 ± 0.02[a]	0.61 ± 0.02[c]	0.62 ± 0.03[c]
N:P ratio	ML	10.79 ± 0.90[b]	9.21 ± 0.91[b]	10.81 ± 1.01[b]	13.98 ± 0.94[a]
NRE (%)		67.94 ± 4.39[a]	57.39 ± 5.01[b]	68.11 ± 5.47[a]	68.56 ± 5.06[a]
PRE (%)		54.96 ± 2.03[b]	60.40 ± 3.02[a]	62.90 ± 2.44[a]	49.93 ± 2.01[c]
NRP (%)		0.53 ± 0.07[b]	0.75 ± 0.09[a]	0.56 ± 0.07[b]	0.54 ± 0.07[b]
PRP (%)		0.07 ± 0.00[b]	0.08 ± 0.00[a]	0.06 ± 0.00[c]	0.06 ± 0.00[c]

concentration in senescent leaves. However, there was a significant correlation between NRE and N concentration in senescent leaves, and between PRE and P concentration in mature leaves. NRE was correlated positively with N:P ratio of mature leaves, whereas PRE, NRP and PRP were all correlated negatively with N:P ratio in mature leaves (Table 2).

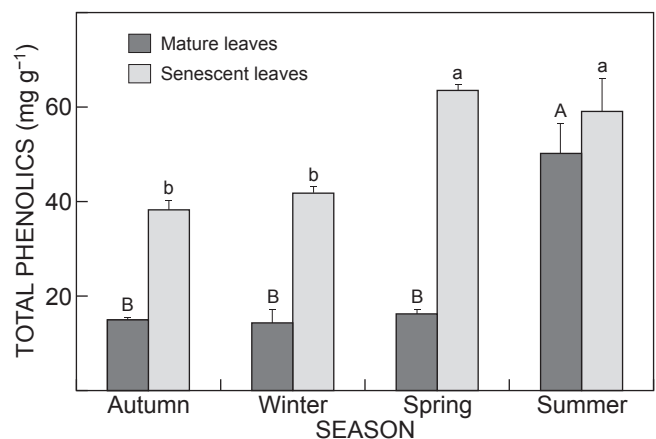### Seasonal changes in total phenolic concentration of *A. marina* leaves

The TP concentration in mature leaves was significantly lower than that in senescent leaves in all seasons. The TP concentration in mature leaves peaked in summer and remained at low concentrations in the other seasons. In senescent leaves the TP concentrations were higher in spring and summer than those in autumn and winter (Figure 1). TP concentrations were not correlated with N concentrations in mature and senescent leaves; however, TP concentrations showed a significantly negative correlation with P concentrations for both mature and senescent leaves. In addition, TP concentrations in mature and senescent leaves were positively correlated with the N:P ratio of mature leaves (Table 3).

Discussion

The most common nutrients limiting plant growth are N and P (Lambers et al. 1998). The concentrations of N and P in mature leaves of *A. marina* were higher than the ranges reported by Aerts and Chapin (2000), who observed that N and P concentrations in green leaves of evergreen species ranged between 10.0 and 15.0 mg g⁻¹, and 0.20 and 1.50 mg g⁻¹, respectively. In particular, N concentrations of mature leaves were almost twice as high as those in *Rhizophora stylosa* grown in the same site conditions (Lin et al. 2010). The N concentration in mature leaves did not change with season (Table 1), which was consistent with the findings in a previous study by Sharma (1983) but inconsistent with those of Ryan and Bormann (1982). Ryan and Bormann (1982) suggested that during spring, growth is accompanied by high mitotic activity due to cellular growth and a strong demand for nutrients, and that N concentration would be higher in spring. In contrast,

Table 2: Correlations between nitrogen (N) and phosphorus (P) concentrations, N:P ratio, and nutrient resorption efficiency and proficiency of *A. marina* leaves at Shankou in Guangxi province, China. N_m and P_m = N and P concentrations in mature leaves, respectively; N_s and P_s = N and P concentrations in senescent leaves, respectively; NRE and PRE = N and P resorption efficiency, respectively; NRP and PRP = N and P resorption proficiency, respectively

Correlation	F	R^2	P
$N_m–P_m$	0.497	0.022	0.489
$N_s–P_s$	5.952	0.115	0.019
$N_m–NRE$	1.956	0.041	0.169
$N_s–NRE$	239.131	0.839	<0.001
$P_m–PRE$	41.733	0.476	<0.001
$P_s–PRE$	2.089	0.043	0.155
$NRP–N_m:P_m$	6.801	0.129	0.012
$PRP–N_m:P_m$	11.506	0.200	0.001
$NRE–N_m:P_m$	15.189	0.248	<0.001
$PRE–N_m:P_m$	33.370	0.420	<0.001

Figure 1: Seasonal changes in total phenolic concentration in leaves of *A. marina* at Shankou in Guangxi province, China. Different letters above bars represent a significant difference ($P < 0.05$)

Table 3: Correlations between total phenolic (TP) and nitrogen (N) and phosphorus (P) concentrations, and N:P ratio of *A. marina* leaves at Shankou in Guangxi province, China. TP_m and TP_s = total phenolic concentrations in mature and senescent leaves, respectively; N_m and P_m = N and P concentrations in mature leaves, respectively; N_s and P_s = N and P concentrations in senescent leaves, respectively; NRE and PRE = N and P resorption efficiency, respectively; NRP and PRP = N and P resorption proficiency, respectively

Correlation	F	R^2	P
$TP_m–N_m$	0.555	0.025	0.464
$TP_s–N_s$	1.772	0.075	0.197
$TP_m–P_m$	31.879	0.592	<0.001
$TP_s–P_s$	26.651	0.548	<0.001
$TP_m–N_m{:}P_m$	21.691	0.496	<0.001
$TP_s–N_m{:}P_m$	4.521	0.170	0.045

P concentrations changed with season, with the highest observed in winter, and the lowest in summer for both mature and senescent leaves (Table 1). This finding was in agreement with the observation of Wang et al. (2003). First, a portion of leaf P was allocated to other portions (e.g. roots and flowers). Second, P concentrations were diluted by leaf biomass accumulation during summer when *A. marina* grew rapidly.

Seasonal changes in leaf nutrients occur in response to resorption before leaf senescence (Chapin 1980). Generally, it is estimated that approximately half of the N and P concentrations are resorbed during senescence and used to support further plant growth (Aerts 1996). In the current investigation, the average NRE and PRE were 65.50 ± 5.63% and 57.05 ± 2.97%, respectively. In *A. marina*, a mangrove species of tropical and subtropical coastlines with a continuous growing season, the active growing foliage probably serves as a sink for nutrients resorbed from senescing leaves (Lambers et al. 1998). The intertidal habitat is a stressful environment and mangroves expend large amounts of their energy on adaptations to those stresses (Tong et al. 2006). This is a further reason why a high RE for essential nutrients is needed. In addition, NRE was highest and PRE was lowest in summer when *A. marina* grew rapidly. This may indicate that *A. marina* mainly resorbed N from senescent leaves and absorbed P from the soil to adapt to the N-limited environment.

The N:P ratio of mature leaves is in response to natural variation in N and P supply, reflecting variation in N and P concentrations (Güsewell 2004). The N:P ratio has been used to identify thresholds of nutrient limitation (Rejmánková 2005; Zhang et al. 2008). Thresholds of foliar N:P ratios have been observed to be <14 for N limitation and >16 for P limitation (Güsewell and Koerselman 2002). The N:P ratio in mature leaves of *A. marina* ranged from 9.21 to 13.98 in all seasons, indicating that the *A. marina* forest was N-limited. The highest values occurred in summer due to the decrease of P concentration in mature leaves, but N concentration changed little among the seasons. The N-limited *A. marina* forests showed higher NRE than PRE (Table 1). Under natural conditions,

because of the anaerobic status of mangrove soils, large amounts of N are lost by denitrification (Hicks and Silvester 1985). Mangroves soils are generally low in nutrient contents, especially N (Alongi et al. 1992). This result supports the hypothesis that a strong nutrient limitation will result in higher resorption of the limiting nutrient.

In contrast to RE, RP is an absolute measure of nutrient withdrawal. It has been suggested that RP is more meaningful and objective than RE for assessing the evolution of the resorption process, because selection acts on traits (such as nutrient contents in senescent leaves) rather than proportions (such as the amount of nutrients in green vs senescent leaves) (Killingbeck 1996). Killingbeck (1996) proposed that in evergreen species, leaves might approach complete, intermediate and incomplete N resorption when the N concentration in senescent leaves is <0.7%, 0.7–1.0% and >1.0%, respectively. For the P concentration in senescent leaves, <0.04%, 0.04–0.05% and >0.05% corresponds to complete, intermediate and incomplete resorption, respectively. In the present study, NRP in senescent leaves ranging from 0.53% to 0.75% through the year were indicative of mostly complete resorption of N; PRP in senescent leaves were all above 0.06%, reflecting that P resorption was incomplete. Nevertheless, PRP was lowest in spring and summer when *A. marina* grew rapidly. This result may indicate that low P concentrations of senescent leaves in spring and summer made it difficult for *A. marina* to resorb additional P.

The N and P concentrations in mature leaves were not correlated, but there was a significantly positive correlation in senescent leaves (Table 2). Chapin and Kedrowski (1983) observed a direct correlation between proportional nutrient retranslocation from the leaves during senescence and nutrient concentration in tree leaves. The present observation of N concentration was inconsistent with that of Chapin and Kedrowski (1983), but PRE had a significantly positive correlation with the P concentration in mature leaves (Table 2). However, no relationship between leaf nutrients status and leaf nutrient resorption was observed by Aerts (1996).

The mature leaves contained low tannin levels (below 6%). Total phenolic concentrations in senescent leaves were higher than in mature leaves of *A. marina*. The highest concentration in mature leaves was observed in summer (Figure 1). The observed changes in total phenolic concentration associated with different developmental stages were in agreement with the findings reported for other mangrove species (Lin et al. 2010). As polyphenols are water-soluble and susceptible to leaching (Hättenschwiler and Vitousek 2000), leaching of polyphenols or tannins by sporadic rain (from green leaves) might be a cause for the net enrichment in senesced leaves (Teklay 2004). However, Mafongoya et al. (1998) indicated that much of the soluble carbon compounds (which also include polyphenols) are expected to be translocated from leaves during senescence. Constantinides and Fownes (1994) found both an increase and a decrease in concentrations of polyphenols.

Tannins produced by plants are divided into two major classes called condensed tannins and hydrolysable tannins. Many plant species contain complex mixtures of hydrolysable and condensed tannins (Schofield et al. 1998).

The extracts from leaves of *A. marina* did not react with acid butanol, suggesting that the extracts did not contain condensed tannins (Zhou et al. 2010). The synthesis of hydrolysable tannins may be a cost-saving defense strategy during a time when condensed tannins are not yet effective for defense (Salminen et al. 2001). In summer, insect herbivory was highly active, resulting in relatively higher total phenolic concentrations. However, the changes in concentration do not necessarily reflect the quantitative allocation of tannins to the leaves, because of rapid turnover of labile compounds (Kleiner et al. 1999) and because the concentrations are affected by concomitant changes in proportions of other components of the leaves, e.g. structural leaf components (Koricheva 1999).

It was observed that total phenolic concentrations were not correlated with N concentrations in mature and senescent leaves of *A. marina* (Table 3). Condensed tannins and proteins have phenylalanine as their precursor (Hättenschwiler and Vitousek 2000), whereas hydrolysable tannins have gallic acid as the precursor (Haukioja et al. 1998). According to the 'protein competition' model (Jones and Hartley 1999), as N is a component of common precursor compounds for phenylalanine, condensed tannins and proteins could compete for the limiting resources phenylalanine in the process of plant growth. Thus the N concentration in the leaves might show a significant relationship with condensed tannin levels. However, the hydrolysable tannins, depending on the relative strength of the synthesis pathway via dehydroshikimic acid to gallic acid, may not trade off directly with protein synthesis (Haukioja et al. 1998). It has been suggested that changes in phenolic concentration may be due to growth dilution or changes in leaf development rather than changes in carbohydrate or nutrient availability (Koricheva 2002).

The role that tannins play in soil processes is believed to occur largely through their ability to precipitate proteins, as well as their relative resistance to decomposition (Kraus et al. 2003). The amount of tannins entering the soil relative to the amount of proteins or N may be the key factor influencing soil nutrient cycling. However, when *A. marina* leaves are deposited on the sediment surface, hydrolysable tannins will be easily and rapidly leached, and would have limited effects on nutrient cycling.

Conclusions

Avicennia marina leaves had high N and P concentrations, but the seasonal pattern of N concentration was different from that of P concentration. Based on the N:P ratio of mature leaves (<14), the *A. marina* forest was N-limited. The NRE was higher than PRE. The resorption proficiency of N and P indicated that N resorption was mostly complete and P resorption was incomplete. *Avicennia marina* leaves contained low quantities of tannins. The extracts from leaves of *A. marina* did not react with acid butanol, suggesting that the extracts did not contain condensed tannins. Total phenolic concentrations were not correlated with N concentrations in mature and senescent leaves of *A. marina*. Low tannin concentrations would have limited effects on nutrient cycling. In conclusion, high nutrient resorption is an important strategy for *A. marina* in coastal environments. As *A. marina* is N-limited, some nutrient input processes, such as N deposition and eutrophication, may promote growth of *A. marina*. On the other hand, N deposition is an important driver of plant community change. Changes in species compositions of ecosystems are related to the relative amounts of N, carbon (C) and P in the plant soil system. Further work is required to address the effects of soil N and (or) P changes on C:N:P stoichiometry of the plant and the function of the mangrove ecosystem.

References

Aerts R. 1996. Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology* 84: 597–608.

Aerts R, Chapin FS. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of patterns and processes. *Advances in Ecological Research* 30: 1–67.

Alongi DM, Boto KG, Robertson AI. 1992. Nitrogen and phosphorus cycles. In: Alongi DM, Robertson AI (eds), *Tropical mangrove ecosystems. Coastal and Estuarine Studies* 41. Washington, DC: American Geophysical Union. pp 251–292.

Chapin FS. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 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.

Constantinides M, Fownes JH. 1994. Nitrogen mineralization from leaves and litter of tropical plants: relationship to nitrogen, lignin and soluble polyphenol concentrations. *Soil Biology and Biochemistry* 26: 49–55.

Fan HQ, Chen GH, He BY, Mo ZC. 2005. *Coastal wetland and management of Shankou mangroves*. Beijing: Ocean Press.

Feller IC. 1995. Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). *Ecological Monographs* 65: 477–505.

Graham HD. 1992. Stabilization of the Prussian blue color in the determination of polyphenols. *Journal of Agricultural Food and Chemistry* 40: 801–805.

Güsewell S. 2004. N:P ratios in terrestrial plants: variation and functional significance. *New Phytologist* 164: 243–266.

Güsewell S, Koerselman W. 2002. Variation in nitrogen and phosphorus. *Plant Ecology, Evolution and Systematics* 5: 37–61.

Güsewell S, Koerselman W, Verhoeven JTA. 2003. Biomass N:P ratios as indicators of nutrient limitation for plant populations in wetlands. concentrations of wetland plants. *Ecological Applications* 13: 372–384.

Haslam E. 1989. *Plant polyphenols: vegetable tannins revisited*. Cambridge: Cambridge University Press.

Hättenschwiler S, Vitousek PM. 2000. The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends in Ecology and Evolution* 15: 238–243.

Haukioja E, Ossipov V, Koricheva J, Honkanen T, Larsson S, Lempa K. 1998. Biosynthetic origin of carbon-based secondary compounds: cause of variable responses of woody plants to fertilization? *Chemoecology* 8: 133–139.

Hicks BJ, Silvester WB. 1985. Nitrogen fixation associated with the New Zealand mangrove (*Avicennia marina* (Forsk.) Vierh. var. *resinifera* (Forst. f.) Bakh.). *Applied and Environmental Microbiology* 49: 955–959.

Jones CG, Hartley SE. 1999. A protein competition model of phenolic allocation. *Oikos* 86: 27–44.

Killingbeck KT. 1986. The terminological jungle revisited: making a case for use of the term resorption. *Oikos* 42: 263–264.

Killingbeck KT. 1996. Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. *Ecology* 77: 1716–1727.

Kleiner KW, Raffa KF, Dickson RE. 1999. Partitioning of ^{14}C-labeled photosynthate to allelochemicals and primary metabolites in source and sink leaves of aspen: evidence for secondary metabolite turnover. *Oecologia* 119: 408–418.

Koricheva J. 1999. Interpreting phenotypic variation in plant allelochemistry: problems with the use of concentrations. *Oecologia* 119: 467–473.

Koricheva J. 2002. The carbon-nutrient balance hypothesis is dead; long live the carbon-nutrient balance hypothesis? *Oikos* 98: 537–539.

Kraus TEC, Yu Z, Preston CM, Dahlgren RA, Zasoski RJ. 2003. Linking chemical reactivity and protein precipitation to structural characteristics of foliar tannins. *Journal of Chemistry Ecology* 29: 703–730.

Lambers H, Chapin FS, Pons TL. 1998. *Plant physiological ecology*. New York: Springer-Verlag.

Lin YM, Liu JW, Xiang P, Lin P, Ye GF, Sternberg LDL. 2006. Tannin dynamics of propagules and leaves of *Kandelia candel* and *Bruguiera gymnorrhiza* in the Jiulong River Estuary, Fujian, China. *Biogeochemistry* 78: 343–359.

Lin YM, Liu XW, Zhang H, Fan HQ, Lin GH. 2010. Nutrient conservation strategies of a mangrove species *Rhizophora stylosa* under nutrient limitation. *Plant and Soil* 326: 469–479.

Lin YM, Sternberg LDL. 2007. Nitrogen and phosphorus dynamics and nutrient resorption of *Rhizophora mangle* leaves in south Florida, USA. *Bulletin of Marine Science* 80: 159–169.

Mafongoya PL, Nair PKR, Dzowela BH. 1998. Mineralization of nitrogen from decomposing leaves of multipurpose trees as affected by their chemical composition. *Biology and Fertility of Soils* 27: 143–148.

McKee KL, Feller IC, Popp M, Wanek W. 2002. Mangrove isotopic (δ^{15}N and δ^{13}C) fractionation across a nitrogen vs. phosphorus limitation gradient. *Ecology* 83: 1065–1075.

Nanjing Institute of Soil Science. 1978. *Physical and chemical analysis of soils*. Shanghai: Science and Techology Press of Shanghai [in Chinese].

Pugnaire F, Chapin FS. 1993. Controls over nutrient resorption from leaves of evergreen Mediterranean species. *Ecology* 74: 124–129.

Reef R, Feller IC, Lovelock CE. 2010. Nutrition of mangroves. *Tree Physiology* 30: 1148–1160.

Rejmánková E. 2005. Nutrient resorption in wetland macrophytes: comparison across several regions of different nutrient status. *New Phytologist* 167: 471–482.

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

Salminen JP, Ossipov V, Haukioja E, Pihlaja K. 2001. Seasonal variation in the content of hydrolysable tannins in leaves of *Betula pubescens*. *Phytochemistry* 57: 15–22.

Schofield JA, Hagerman AE, Harold A. 1998. Loss of tannins and other phenolics from willow leaf litter. *Journal of Chemical Ecology* 24: 1409–1421.

Sharma BM. 1983. Mineral content of leaves of some common tropical forest trees and their associated soils in Ibadan, Nigeria. *Canadian Journal of Forest Research* 13: 556–562.

Teklay T. 2004. Seasonal dynamics in the concentrations of macronutrients and organic constituents in green and senesced leaves of three agroforestry species in southern Ethiopia. *Plant and Soil* 267: 297–307.

Tong YF, Lee SY, Morton B. 2006. The herbivore assemblage, herbivory and leaf chemistry of *Kandelia obvata* (L.) Druce in two contrasting mangrove forests in Hong Kong. *Wetlands Ecology and Management* 14: 39–52.

Twilley RR, Lugo AE, Patterson-Zucca C. 1986. Litter production and turnover in basin mangrove forests in southwest Florida. *Ecology* 67: 670–683.

Wang WQ, Wang M, Lin P. 2003. Seasonal changes in element contents in mangrove element retranslocation during leaf senescence. *Plant and Soil* 252: 187–193.

Ye GF, Zhang SJ, Zhang LH, Lin YM, Wei SD, Liao MM, Lin GH. 2012. Age-related changes in nutrient resorption patterns and tannin concentration of *Casuarina equisetifolia* plantations. *Journal of Tropical Forest Science* 24: 546–556.

Yoshida S, Forno DA, Cock JH, Gomez KA. 1972. *Laboratory manual for physiological studies of rice* (2nd edn). Los Baños, Philippines: International Rice Research Institute.

Zhang LH, Lin YM, Ye GF, Liu XW, Lin GH. 2008. Changes in the N and P concentrations, N:P ratios, and tannin content in *Casuarina equisetifolia* branchlets during development and senescence. *Journal of Forest Research* 13: 302–311.

Zhou HC, Wei SD, Zeng Q, Zhang LH, Tam NFY, Lin YM. 2010. Nutrient and caloric dynamics in the leaves of the mangrove *Avicennia marina* at different age and decay stages in Zhangjiang River Estuary, China. *Estuarine, Coastal and Shelf Science* 87: 21–26.

Zucker WV. 1983. Tannins: does structure determine function? An ecological perspective. *American Naturalist* 121: 335–365.