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SHORT COMMUNICATION

Contrasting nitrogen and phosphorus resorption efficiencies in trees and lianas from a tropical montane rain forest in Xishuangbanna, south-west China

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Tropical montane rain forest is widely considered to be a highly threatened hotspot of global diversity (Brummitt & Nic Lughadha 2003), and one of the least understood humid tropical forest ecosystems in terms of nutrient cycling (Bruijnzeel & Proctor 1995). There is, therefore, an urgent need to improve our understanding of nutrient cycling processes in this ecosystem, including the absorption of nutrients (mainly N and P) from senescing leaves, which may be a key component of adaptive mechanisms that conserve limiting nutrients (Killingbeck 1996). Nutrients which are not resorbed, however, will be circulated through litterfall in the longer term (Aerts 1996). The degree of nutrient resorption affects litter quality, which consequently affects decomposition rates and soil nutrient availability (Aerts & Chapin 2000). The importance of resorption in nutrient conservation has led to general hypotheses that species adapted to nutrient-poor environments have high resorption efficiencies (Richardson *et al.* 2005), and that low leaf nutrient concentrations are associated with high resorption efficiencies within species (Aerts 1996, Kobe *et al.* 2005). Nutrient resorption has also been shown not to differ greatly between growth forms (e.g. shrubs, grasses, forbs and trees) (Aerts 1996). However, its relative importance among plant functional groups is still highly controversial (Richardson *et al.* 2005).

Lianas, which are important and less-understood components of tropical forests (Schnitzer & Bongers 2002), support substantially more leaves per unit basal area than do trees and can account for 20–40% of the canopy foliage (Gerwing & Farias 2000, Putz 1983), although their total biomass per unit area is usually only 2–4% of the woody biomass of trees. Moreover, the abundance of lianas and the amount of liana leaf litter as a proportion of total litter production has generally increased in tropical forests in recent years (Wright *et al.* 2004). The study presented here investigated changes in leaf size, leaf mass and foliar nutrient concentrations during leaf senescence in two groups of woody species (liana and tree) in a tropical montane rain forest in Xishuangbanna, south-west China. Our objectives were to assess leaf area shrinkage and mass loss during senescence in woody species, and to compare the nutrient conservation strategies of the two plant growth forms.

The study site was located in the undisturbed tropical montane rain forest in Mengsong (21°27′N, 100°25′E), Xishuangbanna, Yunnan. The climate of Xishuangbanna is dominated by the south-west monsoon with distinct wet (May–October) and dry (November–April) seasons. Mean annual rainfall was 1379 mm, of which about 80% occurs in the wet season. The potential natural vegetation at the Mongsong site is described in detail in Zhu *et al.* (2004). Species sampled (listed in Table 1, nomenclature follows Li *et al.* 1996) were the dominants in their respective growth-form groups, and all of them are evergreen species. Mature individuals of each species with comparable diameters at breast height (dbh) were marked. During the late wet season (September 2004), corresponding to the peak vegetative growth period, fully expanded sun canopy mature leaves were collected using a tree pruner attached to a long handle. In the dry season (March 2005) during the peak of leaf drop for individual species, similar collections were made for senescing leaves. Senesced leaves were collected directly

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Table 1. Leaf area (LA, cm^2 per leaf), leave mass ratio (LMA, $g\ m^{-2}$ per leaf), leaf area shrinkage (LAS = 1 – senesced leaf area/mature leaf area, %), leaf mass loss (LML = 1 – senesced leaf mass/mature leaf mass, %), nutrient concentrations ($mg\ g^{-1}$) in mature and senesced leaves, and leaf resorption efficiency (%) of 26 woody species in the tropical montane forest. Resorption efficiency = 1 – nutrient concentration of senesced leaves/nutrient concentration of fresh leaves per leaf (Gusewell 2005, van Heerwaarden *et al.* 2003). NRE, nitrogen resorption efficiency; PRE, phosphorus resorption efficiency. Each leaf area and LMA value presented is a mean of 6–8 replicates. The nutrient concentration values are means of four replicates. Significance levels: ns, non-significant ($P > 0.05$); *, $P < 0.05$.

	Mature leaves					Senesced leaves							
Tree species	LA	LMA	N	P	N:P	LA	LMA	N	P	LAS	LML	NRE	PRE
Alangium chinensis	126.5	53.5	31.5	1.79	17.6	121.0	51.9	12.0	0.66	4.3	7.2	64.6	65.9
Alseodaphne petiolaris	163.1	128.3	17.8	0.77	23.1	149.8	95.5	7.4	0.36	8.1	31.6	71.5	68.0
Calophyllum polyanthum	27.2	177.9	16.8	0.84	20.0	26.5	153.8	16.0	0.47	2.4	15.7	19.4	53.1
Cryptocarya densiflora	85.2	187.9	21.0	0.88	23.9	79.7	172.5	18.1	0.35	6.5	14.2	25.9	66.2
Cyclobalanopsis sp.	25.9	129.4	17.1	0.72	23.8	23.7	118.8	13.3	0.35	8.8	16.3	34.9	59.1
Diospyros kerrii	86.1	190.0	18.4	0.78	23.8	85.3	178.6	7.8	0.35	0.9	6.9	60.4	57.8
Elaeocarpus sylvestris	98.7	76.2	24.0	1.03	23.2	76.7	71.0	9.6	0.47	22.3	27.6	71.0	67.0
Engelhardtia roxburghiana	67.2	102.2	23.6	1.13	20.9	56.9	95.7	20.8	0.59	15.2	20.6	30.2	58.8
Euodia trichotoma	56.2	86.1	30.6	1.65	18.5	47.5	76.8	24.5	0.90	15.5	24.7	39.7	59.9
Hovenia acerba	68.8	51.7	37.2	1.94	19.2	65.5	44.5	16.2	0.68	4.8	18.1	64.4	71.1
Michelia floribunda	38.1	79.1	20.0	1.51	13.3	34.6	67.8	8.3	0.38	9.1	22.1	67.6	80.3
Schima superba	70.3	122.1	18.6	0.87	21.4	64.5	104.9	13.3	0.46	8.4	21.3	43.5	58.3
Toxicodendron succedaneum	27.9	89.6	18.1	1.19	15.2	24.4	84.4	7.0	0.39	12.7	17.9	68.3	72.9
Toxicodendron sp.	58.8	136.5	24.1	1.78	13.5	56.9	128.2	19.1	0.97	3.2	9.1	27.8	50.3
Liana species													
Akebia trifoliata	30.0	149.0	18.1	0.89	20.4	25.5	161.7	11.2	0.51	15.2	8.0	42.9	46.8
Artabotrys hongkongensis	31.8	76.1	23.6	1.23	19.2	24.8	61.5	17.7	1.15	21.9	36.9	44.7	41.0
Craspedolobium schochii	68.2	96.4	21.5	1.27	16.9	63.5	85.2	15.5	0.72	6.9	17.7	40.6	53.5
Gnetum pendulum	54.8	110.3	31.1	1.41	22.1	51.3	89.5	27.1	0.81	6.4	24.0	33.9	56.2
Melodinus henryi	35.6	107.1	22.8	1.90	12.0	31.3	93.0	12.4	0.85	12.1	23.7	58.3	66.0
Melodinus suaveolens	32.3	91.6	26.9	1.31	20.5	25.8	81.3	18.8	0.90	20.3	29.2	50.6	51.3
Millettia pachycarpa	41.5	101.5	33.6	1.19	28.3	37.2	91.3	20.4	0.77	10.2	19.1	50.8	47.8
Smilax corbularia	62.1	100.2	15.8	1.45	10.9	53.2	87.6	10.2	0.81	14.3	25.1	51.6	58.0
Smilax hypoglauca	15.2	63.2	19.6	0.86	22.8	15.0	60.1	11.6	0.52	1.3	6.1	30.2	43.7
Smilax microphylla	69.5	87.6	22.9	0.96	23.9	61.6	73.5	16.2	0.71	11.4	25.7	38.5	44.9
Spatholobus suberectus	114.7	123.5	38.2	1.68	22.7	93.2	103.5	20.4	0.52	18.7	31.9	63.7	79.0
Uncaria rhynchophylla	27.2	105.9	20.8	0.73	28.4	23.7	96.6	9.5	0.26	12.9	20.6	63.7	71.7
Mean values													
Tree species	71.4	115	22.8	1.21	19.8	65.2	103.2	13.8	0.53	8.8	18.1	49.2	63.5
(SD)	39.3	46.4	6.3	0.44	3.8	36.5	42.5	5.5	0.21	5.9	7.3	19.3	8.2
Liana species	48.6	101	24.6	1.24	20.7	42.2	90.4	15.9	0.71	12.6	22.3	47.5	55.0
(SD)	24.9	24.4	7.6	0.37	6.5	21.1	26.5	5.4	0.25	5.7	8.8	12.2	15.9
Significant levels	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	*

off plants rather than from leaf litter, as we were concerned that decomposition of litter and leaching of leaf nutrients would lead to underestimates of nutrient concentrations in senesced leaves. These leaves are easily identified as they are generally a different colour from live leaves (often red or yellow), and can be removed by a gentle flicking of the branch or leaf. Sets of 6–8 mature leaves and 6–8 senesced leaves of each species were collected and analysed in order to assess changes in leaf area, mass and nutrient concentrations that occurred during the senescence process. The surface areas of mature and senesced leaves were determined using a leaf area meter (LI-3000, Li-Cor, USA). The samples were brought to the laboratory in polyethylene bags and oven-dried at 70 °C to a constant weight, and leaf mass ratio (LMA) was then calculated for both mature and senesced leaves of each species. Changes in leaf size and leaf mass during senescence were determined for each species as the percentage differences in mean values between the mature and senesced leaves. Nutrient concentrations (N, P) of mature and senesced leaves were determined in the Biogeological Laboratory of the Kunming Division of the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. Green and senesced leaves were analysed by the semi-micro-Kjeldahl method (for N) and the plasma emission spectrometry technique (for P; Benton Jones *et al.* 1991). Since changes in leaf structure during senescence (due to losses of mass or shrinkage in leaf area) can heavily bias estimates of resorption efficiency (van Heerwaarden *et al.* 2003), leaf-level nutrient resorption efficiencies were calculated on a leaf unit basis (Gusewell 2005, van Heerwaarden *et al.* 2003). Leaf and litter nutrient concentrations were log-transformed and resorption data were square-root-transformed prior to statistical analyses to satisfy ANOVA assumptions. The relationships between mature leaf nutrient concentrations and nutrient resorption were evaluated by Spearman rank correlation analysis.

The mature leaves of the woody species investigated in the tropical montane rain forest differed considerably in size and LMA, which showed 6-fold and 3-fold variations, respectively (Table 1). Although the average leaf area and LMA in mature leaves were slightly larger in trees than in lianas, no significant differences were found between the two groups (two t-tests, each $P > 0.05$). During senescence, leaf shrinkage and leaf mass losses were higher in tree species than in liana species, but there were no significant differences between the two growth forms in these respects (two t-tests, each $P > 0.05$). Compared to previously published values for leaf litter in about 50 tropical forests (Proctor 1984) the P concentrations of the senesced leaves (mean $= 0.62$ mg g^{-1}) of woody plants in our study we examined were generally higher, but the N concentrations (mean $= 14.9$ mg g^{-1}) were similar. There were no significant differences between the liana and tree groups in terms of the N concentrations of either their mature or senesced leaves ($P > 0.05$), but the liana species produced leaf litter with higher P concentrations than the tree species (one-way ANOVA, $F = 4.3$, $P = 0.048$). N:P ratios in mature leaves of lianas and trees ranged from 12.0 to 28.4 (average value 20.2), suggesting the presence of strong community-level P limitation in this forest (since N:P ratios > 16.0 indicate P limitation according to Tessier & Raynal 2003). High phosphorus resorption efficiency (PRE) should be favoured under P-limited conditions, and according to Killingbeck (1996), P resorption mechanisms in plants can be regarded as highly efficient if the P concentrations in their senesced leaves are < 0.05 mg g^{-1}. More than half the species we examined met this criterion, in accordance with the hypothesis that high PRE are likely to be promoted by P-limited conditions. The nitrogen resorption efficiency (NRE), calculated on a leaf basis, varied from 19.4% to 71.0% (mean = 48.9%), and PRE varied from 41.0% to 79.0% (mean = 58.5%) for liana and tree species. Liana species showed similar NRE to tree species ($P > 0.05$), but had significantly lower PRE ($F = 5.1$, $P = 0.033$) than the tree species. In accordance with findings of other studies of nutrient relations during leaf senescence (Aerts 1996, Wright & Westoby 2003, Zotz 2004), nutrient resorption was not correlated with the nutrient status of green leaves prior to senescence ($r = 0.19$–0.37, $P > 0.05$) in either lianas or trees. These findings indicate that the efficiency of the resorption process is not determined by plant nitrogen status, as previously concluded in an analysis of data from temperate species (Aerts 1996) and demonstrated for various tropical forest tree species (Del Arco *et al.* 1991, Lal *et al.* 2001, Wright & Westoby 2003).

NRE and PRE were significantly positively correlated in both lianas ($r = 0.78$, $P = 0.003$) and trees ($r = 0.67$, $P = 0.008$). These correlations suggest that N resorption may be controlled by biochemical processes similar to those that control P resorption, in accordance with the results of studies of woody species in tropical forests (Lal *et al.* 2001) and wetland graminoids (Gusewell 2005). However, other studies have found no significant correlations between the N and P resorption efficiencies of certain plants (Chapin & Kedrowski 1983, Shaver & Melillo 1984). These discrepancies may be due, at least in part, to differences in the methodologies used by the different authors. Reductions in leaf mass during senescence could cause mass-based resorption efficiency to be underestimated by about 20% because the translocation of carbon is not taken into account, while area-based measures can underestimate resorption efficiency by about 10% (van Heerwaarden *et al.* 2003).

In conclusion, the relative leaf shrinkage and mass loss during senescence did not differ significantly, on average, between lianas and trees. The nutrient concentrations in the mature leaves and nitrogen resorption efficiency of the liana species were similar to those of the tree species, but the phosphorus concentrations of the liana litter were higher, and their phosphorus resorption efficiencies were lower, in the strongly P-limited montane rain forest we examined. Our results therefore provide clear evidence in favour of a novel mechanism whereby lianas may influence the ecosystems in which they occur. Through the production of nutrient-rich litter, they have the potential to greatly enhance the availability of nutrients within paths where they are abundant, and thus have significant possible effects on small-scale biodiversity.

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