Nutrient limitation of woody debris decomposition in a tropical forest: Contrasting effects of N and P addition

Journal:	*Functional Ecology*
Manuscript ID:	FE-2014-01032.R2
Manuscript Type:	Standard Paper
Date Submitted by the Author:	n/a
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Key-words:	CWD, decay, deposition, fertilization, nutrient addition, tropical soil, Fine woody debris

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Running headline: Effects of N and P addition on woody debris decay

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Number of words: 3708

Number of tables: 3

Number of figures: 5

Summary

1. Tropical forests represent a major terrestrial store of carbon (C), a large proportion of which is contained in the soil and decaying organic matter. Woody debris plays a key role in forest C dynamics because it contains a sizeable proportion of total forest C. Understanding the factors controlling the decomposition of organic matter in general, and woody debris in particular, is hence critical to assessing changes in tropical C storage.

2. We conducted a factorial fertilization experiment in a tropical forest in South China to investigate the influence of nitrogen (N) and phosphorus (P) availability onwoody debris decomposition using branch segments (5-cm diameter) of four species (*Acacia auriculaeformis*, *Aphanamixis polystachya, Schefflera octophylla, Carallia brachiata*) in plots fertilized with +N, +P, or +NP, and controls.

3. Fertilization with +P and +NP increased decomposition rates by 5-53% and the magnitude was species-specific. Contrary to expectations, we observed no negative effect of +N addition on decay rates or mass loss of woody debris in any of the four study species. Decomposition rates of woody debris were higher in species with lower C:P ratios regardless of treatment.

4. We observed significant accumulation of P in the woody debris of all species in plots fertilized with +P and +NP during the early stages of decomposition. N-release from woody debris of *Acacia* (N-fixing) was greater in the +P plots towards the end of the study, whereas fertilization with +N had no impact on the patterns of nutrient release during decomposition.

5. Synthesis: Our results indicate that decomposition of woody debris is primarily constrained by P availability in this tropical forest. However, contrary to expectations, +N addition did not exacerbate P-limitation. It is conceivable that decay rates of woody debris in tropical forests can be predicted by C:P or lignin:P ratios but additional work with more tree species is needed to determine whether the patterns we observed are more generally applicable.

Keywords: Coarse woody debris, CWD, decay, deposition, fertilization, fine woody debris, nutrient addition, tropical soil

Introduction

Tropical forests play an important role in the global carbon (C) cycle and are valued globally for the services they provide to human beings. Although tropical forests occupy only *c.*12% of Earth's land surface, they account for nearly 40% of terrestrial net primary production (NPP) and 25% of the world's biomass C (Pan *et al.* 2011; Townsend *et al.* 2011). Tropical forests are also considered to be a major sink for atmospheric carbon dioxide (CO_2); recent research estimates that enhanced growth in tropical forests has resulted in an uptake of around 1.6 Gt C yr^{-1} from 1997 to 2007 (Pan *et al.* 2011), which is equivalent to *c.* 18% of the total global anthropogenic C emissions. The amount of C stored in terrestrial ecosystems is determined by the balance between CO_2 uptake during photosynthesis and C losses via respiration and the decomposition of organic matter. Hence, effective forecasts of the tropical forest C balance require not only estimates of tree growth but also accurate identification of the factors controlling organic matter decomposition.

A substantial proportion of total forest C is contained in woody debris, defined as any dead, woody plant material, including logs, branches and standing dead trees (Harmon *et al.* 1986). Estimates of woody debris mass vary widely according to forest type, from 15.9 Mg ha^{-1} in a central Illinois floodplain forest (Polit & Brown 1996) to more than 200 Mg ha^{-1} in an old-growth redwood forest (Bingham & Sawyer 1988). Globally, the current C stock in woody debris is estimated as 73±6 Pg. Natural disturbances, especially typhoons and hurricanes, often play a central role in the inputs of woody debris (Chokkalingam & White 2001; Muller 2003). In South China and nearby regions, tropical forests are subjected to large-scale disturbances from typhoons and the additional litter generated during these storms can amount to 17%–

80% of the total annual litter production, depending on the frequency and intensity of the typhoon (Lin *et al.* 2011). Despite the large amounts of C stored in woody debris, few studies have investigated the decomposition of woody debris (Harmon *et al.* 1986), especially in tropical forests.

Empirical and conceptual studies suggest that woody debris decomposition is regulated by the quality of substrate (e.g., nutrient and lignin concentrations, wood density, and secondary compounds that trees use to protect their wood when they are still living), the physical environment (e.g., temperature, moisture), the nutrient status of the forest floor environment and decomposer organisms (Harmon *et al.* 1986). Among these factors, the nutrient limitation of organic matter decomposition has received much attention in tropical forests (Hobbie & Vitousek 2000; Cleveland, Reed & Townsend 2006; Cleveland & Townsend 2006; Hobbie 2008) because it is not possible to fully understand tropical forest C cycling without considering nutrient limitations (Townsend *et al.* (2011). In this context, it is important to assess how human activities are affecting nutrient inputs to ecosystems, e.g. through atmospheric nitrogen (N) deposition, as this can affect a number of ecosystem processes, including decomposition.

Atmospheric N deposition in particular has increased dramatically in recent decades and is projected to rise further in tropical and subtropical regions in future (Reay *et al.* 2008; Bala *et al.* 2013). Rates of N deposition already range from 30 to 73 kg N ha^{-1} yr^{-1} in some tropical forests of southern China (Fang *et al.* 2011) but there is very little information on the effects of N deposition on woody debris decomposition in tropical forests. Although N deposition is thought to impede organic matter decomposition (Janssens *et al.* 2010), experimental studies in different forests have produced inconsistent patterns; for example, Hobbie (2005) showed increased decomposition of wood with N addition, whereas Bebber *et al.* (2011) observed enhanced woody debris decomposition at low levels of N deposition but reduced decomposition rates at high levels.

Surprisingly, the effect of P availability on woody debris decomposition in tropical forests has not yet been reported, even though a number of ecosystem processes are thought to be P-limited in tropical forests on highly weathered soils (Cleveland, Townsend & Schmidt 2002; Vitousek *et al.* 2010), and there are multiple lines of evidence for P-limitation of leaf litter decomposition in lowland tropical forests. For instance, elevated P in litter and elevated N and P in soil increased decomposition rates in a Hawaiian tropical forest (Hobbie & Vitousek 2000) and P-fertilization stimulated soil respiration in a lowland tropical rainforest in Costa Rica (Cleveland & Townsend 2006). These results suggest that P constraints on decomposition are critical for understanding the role of tropical forests in a rapidly changing global C cycle.

Hence, despite the importance of woody debris to local and global C budgets, we know little about the nutrient limitations of woody debris decomposition, especially in tropical forests (Harmon *et al.* 1986; Kaspari *et al.* 2008). To address this, we conducted a fertilization experiment using branch segments from four tree species in a tropical forest in southern China to investigate the effects of +N and +P-fertilization on woody debris decomposition and nutrient release. Our previous work demonstrated that soil fungal biomass decreased with +N addition but increased with +P addition (Li *et al.* 2015). Hence, fertilization treatments are likely to affect the decomposition of woody debris because lignin degradation is highly dependent on fungal decomposers (van der Wal *et al.* 2007). Accordingly, we hypothesized that: (1) +N addition would impede woody debris decomposition; whereas (2) +P addition would accelerate woody debris decomposition; and (3) the responses to fertilization treatments would be species-specific.

Materials and methods

Site description

This study was conducted in a secondary mixed tropical forest at the Xiaoliang Research Station for Tropical Coastal Ecosystems, the Chinese Academy of Sciences (21°27′N, 110°54′E), southwest of Guangdong Province, China. The station is located 4 km from the coastline of the South China Sea. The climate is tropical monsoon with a mean annual temperature of 23°C and annual precipitation of 1400 - 1700 mm. The climate is seasonal with a distinct wet season from April to September and a dry season from October to March. The soil is a latosol, formed from highly weathered granite, with a pH of *c.* 4 and low availability of P (Table 1). The site was originally established as a *Eucalyptus exserta* plantation in 1959 but a further 312 species were planted between 1964 and 1975 (Ding *et al.* 1992; Ren *et al.* 2007). Hence, the current diversity and structural complexity of the forest community are considered typical of secondary tropical forest (Yu & Peng 1996).

Experimental Design

A factorial N and P fertilization experiment was established in a complete randomized block design in August 2009; a detailed description of this experiment is given in Wang *et al.* (2014). Briefly, N addition (+N), P addition (+P), N and P addition (+NP), and control treatments (CT), were assigned randomly to four 10-m ×10-m plots within five replicate blocks (Zhao *et al.* 2014). Starting in September 2009, N and P were applied in equal amounts every two months to give 100 kg $ha^{-1}yr^{-1}$. Specifically, for each fertilizer application, 476.6 g NH_4NO_3 (equal to 166.6 g N) and/or 808 g NaH_2PO_4 (equal to 166.6g P) were dissolved in 30 L groundwater and applied to the corresponding plots using a backpack sprayer, spraying as close to the soil surface as possible; 30 L groundwater was applied to each control plot. The amounts of N and P added correspond to studies of experimental N (Lu *et al.* 2010) and P (Liu *et al.* 2012) additions in neighboring forests. Similar large additions of P relative to the biological demand for N and P are standard practice in tropical fertilization experiments because in many tropical soils, a large proportion of the added P is fixed in biologically inaccessible forms (Ostertag 2010; Wright *et al.* 2011).

Four common broadleaf tree species were chosen for this experiment: *Acacia auriculaeformis* (henceforth '*Acacia*'; N-fixing), *Aphanamixis polystachya* ('*Aphanamixis*'), *Schefflera octophylla* ('*Schefflera*') and *Carallia brachiata* ('*Carallia*'). After a serious typhoon disturbance in September 2010, standing dead or recently fallen branches of *c.* 5-cm diameter were harvested and cut into 10-cm long segments with a fine-bladed band saw. The samples were weighed, measured and tagged before being placed in the experimental sites in October 2010. Six branch segments of each species were placed on the soil surface at 5-10-cm intervals in each plot, making a total of 480 samples. For each species and plot, one branch segment (henceforth referred to as woody debris) was collected at random after 6, 12, 18, 24, 30, 36 months and sealed in a plastic bag. Samples were cleaned of soil and litter with a brush, dried to constant mass at 70°C and weighed. Each sample was then cut into *c.* 2-cm thick pieces (including bark) and finely ground for analysis of N and P concentrations.

In October 2010, three samples of freshly fallen branch segments (5-cm diameter, 10-cm length) of each species were analyzed for initial C, N, P, lignin and cellulose concentrations and wood density. The sample volume of fresh woody debris of each species was determined gravimetrically by water displacement (Hatfield & Fukushima 2005); samples were then oven-dried to constant weight at 70°C to calculate wood density. We measured lignin and cellulose concentrations following Goering and Van Soest (1970). N and P concentrations were determined by the micro-Kjeldahl digestion followed by colorimetric determination on a flow injection auto-analyzer (FIA, Lachat Instruments, USA). To assess nutrient accumulation or release during decomposition, we calculated the nutrient content remaining at each collection by multiplying the nutrient concentrations at each time point by the mass remaining and report these values as a proportion of the initial values (McGroddy, Silver & de Oliveira 2004):

$$\text{Nutrient content remaining} = \frac{XtWt}{X0W0}$$

Where X_0 is the mean initial nutrient concentration in woody debris (n = 3), X_t is the nutrient concentration at a given collection time (t), W_0 is the initial dry weight of woody debris and W_t is the dry weight at a given collection time (t). Hence, values greater than 1 reflect an accumulation of nutrients during decomposition, and values below 1 reflect nutrient release.

Data analysis

We used a single negative exponential decay model to estimate woody debris decomposition rates: $y/y_0=e^{-kt}$

where y/y_0 is the fraction of mass remaining at a specific time t (in years), and k is the annual decay rate constant (Olson 1963). Regression analysis was used to test the model fit for mass loss of woody debris over time. Species differences in initial woody debris properties were explored with one-way ANOVA; where overall differences were significant, post-hoc tests (Fisher's least significant differences test, LSD) were used to correct for multiple comparisons among species. Regression analyses and ANOVA were conducted using SPSS 16.0 for Windows (SPSS Inc., Chicago, IL).

We used linear mixed effects models (nmle package in R 3.1.0; (R Core Team 2014)) to investigate the effects of fertilization treatments and species identity on decomposition processes. Treatment and species were considered fixed effects and block as a random effect in models for the decay rate constant *k*; collection time was included as an additional random effect in the models for mass loss, nutrient concentrations and nutrient release during three years of decomposition. The significance of each term was determined by comparing nested models using likelihood ratio tests and AICs to check for model improvement (Pinheiro & Bates 2000); final models were compared to null models to determine main treatment and species effects. Where there was no difference in the model fit with or without the interaction term (treatment*species), we chose the simpler model (treatment + species). However, as there was no significant improvement in any model fit when the interaction term was excluded and all models showed a highly significant effect of tree species identity, species-specific responses to treatments were investigated with individual models. Results are reported as significant at $p<0.05$.

Results

Initial chemistry of woody debris

The initial nutrient concentrations of the woody debris differed among species: woody debris of the N-fixing *Acacia* had a significantly higher total N and lower total P concentrations than the other species, resulting in a higher N:P ratio, and lower C:N and lignin:N ratios (Table 2). The woody debris of *Schefflera* and *Carallia* had higher P concentrations than *Acacia* and *Aphanamixis*. *Acacia* and *Carallia* had greater lignin and cellulose concentrations and higher wood density than the other two species. *Schefflera* had the lowest N, lignin and cellulose concentrations as well as the lowest wood density of all four species (Table 2).

Decomposition rates

The mass loss of woody debris over time fit an exponential equation for all species (R^2 = 0.71 - 0.79, p<0.01) and decay rates differed among species (p<0.01); woody debris decomposed in the order *Schefflera* > *Carallia* > *Aphanamixis* > *Acacia* (Fig. 1 and Table 3). The decomposition of *Scheffleria* woody debris in the CT plots was significantly faster than other species (Table 2, p<0.01), with less than 20% mass remaining after 24 months (Fig. 1c).

Mass loss from woody debris increased in response to fertilization with +P and +NP (p=0.02 and p<0.01, respectively) and the response was strongly species-specific (species effect p<0.01). Fertilization with +P increased mass loss in *Acacia* (p=0.024) and there was a trend towards increased mass loss in *Carallia* (p=0.06; Fig. 1). Fertilization with +NP significantly increased mass loss from woody debris in *Acacia*, *Carallia* and *Scheffleria* (p<0.01, p<0.01 and p=0.012, respectively), whereas mass loss of woody debris of *Aphanmixis* was unaffected by fertilization.

Although the inclusion of the treatment×species interaction significantly improved the model for the decay rate constant k (p<0.01), there was no significant effect of any single treatment relative to the controls across all species. Individual models showed higher decay rates of *Acacia* and *Scheffleria* in +P plots but no effect of fertilization on the decay rates of *Corallia* and *Aphanamixis* (Table 3).

Dynamics of nutrient concentrations and nutrient release

The N concentration of woody debris in the CT plots increased substantially in all species over 36 months (84% to 390%; Fig. 2) and P concentrations increased by 44% to 70% depending on species (Fig. 3). We observed a net release of N from woody debris in the CT plots in all species except *Aphanamixis* (Fig. 4). There was a net increase of N in woody debris of *Aphanamixis* in the first year, which then declined, resulting in a net release of N after two years (Fig. 4b).

The N concentration in woody debris changed significantly in response to +N, +P and +NP fertilization (p<0.01, p=0.04 and p<0.01, respectively) and the direction of the response was species-specific (species effect: p<0.01). N concentrations in the woody debris of *Acacia* increased significantly in +N plots (p<0.01; Fig. 2a) and there was a trend towards increased N in *Schefflera* (p=0.06; Fig. 2c). N concentrations in *Carallia increased* in response to +NP addition (p=0.04) and marginally in response to +N fertilization (p=0.06; Fig. 2d). For *Aphanamixis,* N concentrations decreased with +P fertilization (p=0.015; Fig. 2b). The P concentrations of woody debris were not affected by +N fertilization but increased significantly with +P and +NP fertilization in all species (p<0.01; Fig. 3).

The patterns of N release were significantly influenced by fertilization with +N and +P (p=0.01 and p=0.03, respectively) and the response differed among species (species effect: p<0.001). For *Acacia*, N release from woody debris was greater in +P and +NP plots (p=0.04 and p=0.03, respectively), whereas N accumulated in the +N plots towards the end of the study (p=0.01; Fig. 4a). For *Carallia*, N-release at the end of the study was greater in +NP plots (p=0.02; Fig. 4d) but there was no effect of fertilization on N-release from woody debris of *Scheffleria* or *Aphanamixis* (Fig. 4b,c).

P accumulated in woody debris in response to +P and +NP additions during the first 12-18 months of decomposition in all species (p<0.01 for all species; Fig. 5). There was a marked shift towards nutrient release after two years of decomposition, with both N and P content in woody debris dropping below the initial values for all species in all treatments by the end of the study (Figs 4 and 5).

Discussion

Fertilization effects on decomposition rates

We hypothesized that the decay rate of woody debris would decrease with N addition because previous studies indicate that decomposition of wood by fungi increases at low rates of N addition but decreases under high N availability (Schmitz & Kaufert 1936). Large N inputs can alter the fungal community (Carreiro *et al.* 2000) and inhibit the basidiomycete fungi known as 'white rots', which are highly efficient in utilizing woody litter (Bebber *et al.* 2011). A previous study at our site showed that

+N addition decreased total fungal biomass by 10% compared to controls (Li *et al.* 2015) but despite this, and although our +N additions were more than twice the atmospheric N deposition rates in the studied area, we observed no negative effect of +N addition on decay rates or mass loss of woody debris in any of the four study species.

We found strong evidence to support our hypothesis of P-limitation of woody debris decomposition in this system, as +P and +NP additions increased mass loss from woody debris in all species. Phosphorus is frequently cited as the primary limiting element in tropical forest soils but to our knowledge, this study was the first field study to report the effects of +P addition on woody debris decomposition in a tropical forest. We propose that the positive effect of +P addition in our study is likely a result of shifts in the community composition of decomposer organisms and changes in soil extracellular enzyme activities in response to alleviation of P-limitation. Previous work at the study site showed that soil microbial biomass in general, and fungal biomass in particular, increased with +P addition (Wang *et al.* 2014), and there was greater relative abundance of fungal biomarkers in +P plots (Liu *et al.* 2012; Li *et al.* 2015). Soil fungi play a pivotal role in litter decomposition and nutrient cycling in forest ecosystems (Dick, Cheng & Wang 2000; Enowashu *et al.* 2009) and fungal decomposers are largely responsible for the breakdown of lignin and cellulose (i.e. lignocellulose) derived from woody plant material (van der Wal *et al.* 2007). As microbial resource allocation, and hence decomposition, is subject to fairly strict stoichiometric constraints (Sinsabaugh *et al.* 1993), the high availability of N and the alleviation of P-limitation at our site would provide a strong incentive for microbes to invest in C acquisition (Allison et al. 2011), which in turn would accelerate decomposition processes. Taken together, these different lines of evidence suggest that P addition has enhanced the decomposition of woody debris by stimulating the growth and activity of soil fungal decomposers.

Fertilization effects on nutrient retention and release

Numerous studies in more N-limited systems reported accumulation of N during decomposition of wood (Sollins *et al.* 1987; Arthur & Fahey 1990; Laiho & Prescott 1999), whereas in our control plots the woody debris of all species except *Aphanamixis* acted as a net N source during the 36 months of decomposition. Interestingly, the woody debris of *Aphanamixis* had the highest C:N:P ratio of all the species in our study, and it is likely that initial N concentrations were low relative to decomposer requirements. The observed pattern of initial N accumulation followed by a shift to net N release after 24 months (Fig. 4) is consistent with immobilization of N until it reached a critical concentration for decomposition.

The patterns in P release from woody debris in control plots during decomposition varied among species but the high initial P accumulation in +P and +NP plots in all species is striking (Fig. 5). Microbial immobilization and active uptake of limiting elements is regarded as an important nutrient retention mechanism in nutrient-poor systems (Olander & Vitousek 2004; Cleveland, Reed & Townsend 2006) and fungal decomposers can actively forage for P and import it into carbon-rich, low-nutrient substrates such as decaying wood (Wells, Hughes & Boddy 1990). In our study, it is conceivable that greater P availability in the surrounding soil allowed fungal decomposers to allocate more P to the decomposing substrate. Although this remains to be tested, we propose that fungal import of P presents a plausible mechanism for accelerated woody debris decomposition in +P-fertilized plots.

It is noteworthy that +P-fertilization increased N concentrations in *Aphanamixis*, the species with the lowest N:P ratio (Fig. 2), and net N release from woody debris of the N-fixing species *Acacia*, which had the highest initial N concentration (Table 2; Fig. 4). Further, the effects of +NP fertilization on mass loss and nutrient release were often stronger than the effects of +P alone. These results demonstrate the regulation of stoichiometric balance during decomposition and possible imbalances caused by extraneous nutrient inputs, which in turn will alter patterns of nutrient accumulation and release.

Interspecific differences in woody debris decay rates

For a given site and climate, litter mass-loss is primarily related to chemical and physical properties of the litter (Berg, Steffen & McClaugherty 2007). Wood density is a key physical trait affecting the decomposability of woody debris; decomposition is faster in low-density wood because it provides a favorable microenvironment for decomposer organisms (Chave *et al.* 2009). Although lignin:N ratios are often cited as good predictors of litter decomposability (Aerts (1997), litter from tropical sites generally has lower lignin:N ratios, higher N and lower P concentrations compared to other climatic regions (Yuan & Chen 2009). It is therefore noteworthy that the rates of woody debris decomposition for the four species in our study (*Schefflera* > *Carallia* > *Aphanamixis* > *Acacia*) were inversely related to C:P ratios (Table 2), even though the species with the highest decomposition rates (*Scheffleria*) also had the highest lignin:N ratio. As our sample size is limited, further study with a larger number of species is needed to test whether woody debris decomposition in tropical forests can be predicted by C:P or lignin:P ratios.

Conclusions

To our knowledge, this is the first study to provide direct evidence of P limitation of woody debris decomposition in a tropical forest. Our results demonstrate that N and P additions have variable effects on woody debris decomposition and many of the observed patterns can be explained by the stoichiometry of the substrate and activity of decomposer organisms. It is therefore conceivable that the decomposition of woody debris may become inhibited by nutrient imbalances as a result of e.g. increasing atmospheric CO_2 concentrations and N deposition in many tropical forests in future. Our results provide a solid foundation for further, more detailed work on microbial community composition and enzyme activities during decomposition to gain a more complete picture of nutrient regulation of the tropical C cycle.

Acknowledgements

This work was funded by Natural Science Foundation of China (31300419), NSFC-Guangdong Joint Project (U1131001), National Basic Research Program of China (2011CB403200), Innovation Foundation of Guangdong Forestry (2012KJCX013-02, 2014KJCX021-03) and the "Strategic Priority Research Program" of the Chinese Academy of Sciences (XDA05070307).

References

Aerts, R. (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A triangular relationship. *Oikos,* **79,** 439-449.

Arthur, M.A. & Fahey, T.J. (1990) Mass and nutrient content of decaying boles in an engelmann spruce-sub-alpine fir forest, rocky-mountain-national-park, colorado. *Canadian Journal of Forest Research,* **20,** 730-737.

Bala, G., Devaraju, N., Chaturvedi, R.K., Caldeira, K. & Nemani, R. (2013) Nitrogen deposition: how important is it for global terrestrial carbon uptake? *Biogeosciences,* **10,** 7147-7160.

Bebber, D.P., Watkinson, S.C., Boddy, L. & Darrah, P.R. (2011) Simulated nitrogen deposition affects wood decomposition by cord-forming fungi. *Oecologia,* **167,** 1177-1184.

Berg, B., Steffen, K.T. & McClaugherty, C. (2007) Litter decomposition rate is dependent on litter Mn concentrations. *Biogeochemistry,* **82,** 29-39.

Bingham, B.B. & Sawyer, J.O. (1988) Volume and mass of decaying logs in an upland old-growth redwood forest. *Canadian Journal of Forest Research,* **18,** 1649-1651.

Carreiro, M.M., Sinsabaugh, R.L., Repert, D.A. & Parkhurst, D.F. (2000) Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. *Ecology,* **81,** 2359-2365.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters,* **12,** 351-366.

Chokkalingam, U. & White, A. (2001) Structure and spatial patterns of trees in old-growth northern hardwood and mixed forests of northern Maine. *Plant Ecology,* **156,** 139-160.

Cleveland, C.C., Reed, S.C. & Townsend, A.R. (2006) Nutrient regulation of organic matter decomposition in a tropical rain forest. *Ecology,* **87,** 492-503.

Cleveland, C.C. & Townsend, A.R. (2006) Nutrient additions to a tropical rain forest drive substantial soil carbon dioxide losses to the atmosphere. *Proc Natl Acad Sci U S A,* **103,** 10316-10321.

Cleveland, C.C., Townsend, A.R. & Schmidt, S.K. (2002) Phosphorus limitation of microbial processes in moist tropical forests: Evidence from short-term laboratory incubations and field studies. *Ecosystems,* **5,** 680-691.

Dick, W.A., Cheng, L. & Wang, P. (2000) Soil acid and alkaline phosphatase activity as pH adjustment indicators. *Soil Biology & Biochemistry,* **32,** 1915-1919.

Ding, M., Yi, W., Liao, L., Martens, R. & Insam, H. (1992) Effect of afforestation on microbial biomass and activity in soils of tropical China. *Soil Biology & Biochemistry,* **24,** 865-872.

Enowashu, E., Poll, C., Lamersdorf, N. & Kandeler, E. (2009) Microbial biomass and enzyme activities under reduced nitrogen deposition in a spruce forest soil. *Applied Soil Ecology,* **43,** 11-21.

Fang, Y.T., Gundersen, P., Vogt, R.D., Koba, K., Chen, F.S., Chen, X.Y. & Yoh, M. (2011) Atmospheric deposition and leaching of nitrogen in Chinese forest ecosystems. *Journal of Forest Research,* **16,** 341-350.

Goering, H.K. & Van Soest, P.J. (1970) Forage fiber analysis (Apparatus, reagent, procedures and some applications). *Agric. Handbook, No. 379, ARS-USDA, Washington, DC.*

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. & Cummins, K.W. (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research,* **15,** 133-302.

Hatfield, R. & Fukushima, R.S. (2005) Can lignin be accurately measured? *Crop Science,* **45,** 832-839.

Hobbie, S.E. (2005) Contrasting Effects of Substrate and Fertilizer Nitrogen on the Early Stages of Litter Decomposition. *Ecosystems,* **8,** 644-656.

Hobbie, S.E. (2008) Nitrogen effects on decomposition: a five-year experiment in eight temperate sites. *Ecology,* **89,** 2633-2644.

Hobbie, S.E. & Vitousek, P.M. (2000) Nutrient limitation of decomposition in Hawaiian forests. *Ecology,* **81,** 1867-1877.

Janssens, I.A., Dieleman, W., Luyssaert, S., Subke, J.A., Reichstein, M., Ceulemans, R., Ciais, P., Dolman, A.J., Grace, J., Matteucci, G., Papale, D., Piao, S.L., Schulze, E.D., Tang, J. & Law, B.E. (2010) Reduction of forest soil respiration in response to nitrogen deposition. *Nature Geoscience,* **3,** 315-322.

Kaspari, M., Garcia, M.N., Harms, K.E., Santana, M., Wright, S.J. & Yavitt, J.B. (2008) Multiple nutrients limit litterfall and decomposition in a tropical forest. *Ecology Letters,* **11,** 35-43.

Laiho, R. & Prescott, C.E. (1999) The contribution of coarse woody debris to carbon, nitrogen, and phosphorus cycles in three Rocky Mountain coniferous forests. *Canadian Journal of Forest Research,* **29,** 1592-1603.

Li, J., Li, Z., Wang, F., Zou, B., Chen, Y., Zhao, J., Mo, Q., Li, Y., Li, X. & Xia, H. (2015) Effects of nitrogen and phosphorus addition on soil microbial community in a secondary tropical forest of China. *Biol Fert Soil,* **51,** 207-215.

Lin, T.C., Hamburg, S.P., Lin, K.C., Wang, L.J., Chang, C.T., Hsia, Y.J., Vadeboncoeur, M.A., McMullen, C.M.M. & Liu, C.P. (2011) Typhoon Disturbance and Forest Dynamics: Lessons from a Northwest Pacific Subtropical Forest. *Ecosystems,* **14,** 127-143.

Liu, L., Gundersen, P., Zhang, T. & Mo, J.M. (2012) Effects of phosphorus addition on soil microbial biomass and community composition in three forest types in tropical China. *Soil Biology & Biochemistry,* **44,** 31-38.

Lu, X., Mo, J., Gilliam, F., Zhou, G. & Fang, Y. (2010) Effects of experimental nitrogen additions on plant diversity in an old-growth tropical forest. *Global Change Biology,* **16,** 2688-2700.

McGroddy, M.E., Silver, W.L. & de Oliveira, R.C. (2004) The effect of phosphorus availability on decomposition dynamics in a seasonal lowland Amazonian forest. *Ecosystems,* **7,** 172-179.

Muller, R.N. (2003) Landscape patterns of change in coarse woody debris accumulation in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. *Canadian Journal of Forest Research,* **33,** 763-769.

Olander, L.P. & Vitousek, P.M. (2004) Biological and geochemical sinks for phosphorus in soil from a wet tropical forest. *Ecosystems,* **7,** 404-419.

Olson, J.S. (1963) Energy-storage and balance of producers and decomposers in ecological-systems. *Ecology,* **44,** 322-&.

Ostertag, R. (2010) Foliar nitrogen and phosphorus accumulation responses after fertilization: an example from nutrient-limited Hawaiian forests. *Plant and Soil,* **334,** 85-98.

Pan, Y.D., Birdsey, R.A., Fang, J.Y., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S.L., Rautiainen, A., Sitch, S. & Hayes, D. (2011) A Large and Persistent Carbon Sink in the World's Forests. *Science,* **333,** 988-993.

Pinheiro, J.C. & Bates, D.M. (2000) *Mixed-Effects Models in S and S-PLUS*. Springer New York, New York. USA.

Polit, J.I. & Brown, S. (1996) Mass and nutrient content of dead wood in a central Illinois floodplain forest. *Wetlands,* **16,** 488-494.

R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reay, D.S., Dentener, F., Smith, P., Grace, J. & Feely, R.A. (2008) Global nitrogen deposition and carbon sinks. *Nature Geoscience,* **1,** 430-437.

Ren, H., Li, Z.A., Shen, W.J., Yu, Z.Y., Peng, S.L., Liao, C.H., Ding, M.M. & Wu, J.G. (2007) Changes in biodiversity and ecosystem function during the restoration of a tropical forest in south China. *Science in China Series C-Life Sciences,* **50,** 277-284.

Schmitz, H. & Kaufert, F. (1936) The effect of certain nitrogenous compounds on the rate of decay of wood. *American Journal of Botany,* **23,** 635-638.

Sinsabaugh, R.L., Antibus, R.K., Linkins, A.E., McClaugherty, C.A., Rayburn, L., Repert, D. & Weiland, T. (1993) Wood decomposition - nitrogen and phosphorus dynamics in relation to extracellular enzyme-activity. *Ecology,* **74,** 1586-1593.

Sollins, P., Cline, S.P., Verhoeven, T., Sachs, D. & Spycher, G. (1987) Patterns of log decay in old-growth douglas-fir forests. *Canadian Journal of Forest Research,* **17,** 1585-1595.

Townsend, A.R., Cleveland, C.C., Houlton, B.Z., Alden, C.B. & White, J.W.C. (2011) Multi-element regulation of the tropical forest carbon cycle. *Frontiers in Ecology and the Environment,* **9,** 9-17.

van der Wal, A., de Boer, W., Smant, W. & van Veen, J.A. (2007) Initial decay of woody fragments in soil is influenced by size, vertical position, nitrogen availability and soil origin. *Plant and Soil,* **301,** 189-201.

Vitousek, P.M., Porder, S., Houlton, B.Z. & Chadwick, O.A. (2010) Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecological Applications,* **20,** 5-15.

Wang, F., Li, J., Wang, X., Zhang, W., Zou, B., Neher, D.A. & Li, Z. (2014) Nitrogen and phosphorus addition impact soil N_2O emission in a secondary tropical forest of South China. *Scientfic Reports,* **4,** 5615.

Wells, J.M., Hughes, C. & Boddy, L. (1990) The Fate of Soil-Derived Phosphorus in Mycelial Cord Systems of *Phanerochaete Velutina* and *Phallus Impudicus*. *New Phytologist,* **114,** 595-606.

Wright, S.J., Yavitt, J.B., Wurzburger, N., Turner, B.L., Tanner, E.V., Sayer, E.J., Santiago, L.S., Kaspari, M., Hedin, L.O., Harms, K.E., Garcia, M.N. & Corre, M.D. (2011) Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology,* **92,** 1616-1625.

Yu, Z. & Peng, S. (1996) Ecological studies on vegetation rehabilitation of tropical and subtropical degraded ecosystems. *Guangdong Science and Technology Press, Guangzhou.*

Yuan, Z. & Chen, H.Y.H. (2009) Global trends in senesced-leaf nitrogen and phosphorus. *Global Ecology and Biogeography,* **18,** 532-542.

Zhao, J., Wang, F., Li, J., Zou, B., Wang, X., Li, Z. & Fu, S. (2014) Effects of experimental nitrogen and/or phosphorus additions on soil nematode communities in a secondary tropical forest. *Soil Biology & Biochemistry,* **75,** 1-10.

Tables

Table 1. Means of soil physical and chemical characteristics (0-10cm depth) before the start of fertilization in 2009. values are means ± SE for n=5; aP is available P.

Variables	CT	+N	+P	+NP
pH	3.99±0.06	3.97±0.05	3.95±0.05	4.02±0.09
SOC (%)	2.54±0.16	2.90±0.12	2.86±0.27	2.90±0.17
Total N (g kg^{-1})	2.71±0.15	2.34±0.21	2.66±0.10	2.68±0.19
Total P (g kg^{-1})	0.40±0.03	0.38±0.02	0.42±0.02	0.43±0.03
aP (mg kg^{-1})	4.10±0.56	3.79±0.42	4.06±0.37	3.70±0.03
NO_3^--N (mg kg^{-1})	2.88±0.35	2.72±0.11	2.68±0.31	2.35±0.33
NH_4^+-N (mg kg^{-1})	2.12±0.12	1.85±0.13	1.81±0.11	2.03±0.17

Table 2. Initial chemical and physical properties of woody debris of the four study species in a fertilization experiment in a secondary mixed tropical forest**:** *Acacia auriculaeformis*, *Aphanamixis polystachya*, *Schefflera octophylla,* and *Carallia brachiate*; where TOC is total organic carbon, TN is total nitrogen, TP is total phosphorus; nutrient ratios (C:N, C:P, N:P, Lignin/N, Lignin/P) are mass-based; values are means ± SE for *n*=5; different superscript letters within a column indicate significant differences among species at $p<0.05$ (after correction for multiple comparisons).

Species	TOC (mg g^{-1})	TN (mg g^{-1})	TP (mg g^{-1})	Lignin (%)	Cellulose (%)	Density (g cm^{-3})	C:N	C:P	N:P	Lignin/N	Lignin/P
Acacia	434^{a}±9.2	4.4^{a}±0.3	0.11^{c}±0.01	24.1^{b}±0.4	46.5^{b}±0.4	0.70^{a}±0.01	100^{d}±2.1	3336^{a}±70	33.5^{a}±0.3	55^{c}±0.8	2181^{a}±43
Aphanamixis	439^{a}±7.6	2.5^{c}±0.1	0.13^{b}±0.01	22.5^{b}±0.5	50.0^{a}±0.6	0.54^{b}±0.02	175^{b}±7.2	2661^{b}±130	15.2^{c}±2.1	90^{b}±2.1	1700^{b}±50
Schefflera	411^{a}±10	1.9^{d}±0.1	0.18^{a}±0.02	28.0^{a}±0.8	39.1^{c}±0.9	0.34^{c}±0.01	212^{a}±8.2	2333^{c}±83	11.0^{d}±0.1	143^{a}±6.8	1552^{b}±45
Carallia	426^{a}±17	2.8^{b}±0.2	0.18^{a}±0.02	24.5^{b}±2.1	43.7^{b}±2.6	0.74^{a}±0.01	149^{c}±6.1	2406^{c}±113	16.3^{b}±0.1	86^{b}±7.3	1361^{c}±66

Table 3. Decay rate constants k (year^{-1}) for woody debris of four species. values are means ± SE for n=5 and p-values for treatment effects based on individual species models are given; species names follow Table 2.

Species	CT	+N	+P	+NP	Treatment effects		
					N	P	NP
Acacia	0.30 ±0.03	0.24 ±0.04	0.46 ±0.07	0.40 ±0.04	0.32	***0.03***	0.17
Aphanamixis	0.68 ±0.08	0.67 ±0.08	0.71 ±0.06	0.73 ±0.04	0.92	0.72	0.59
Schefflera	1.12 ±0.06	1.10 ±0.06	1.56 ±0.13	1.13 ±0.06	0.82	***<0.01***	0.95
Carallia	0.71 ±0.06	0.68 ±0.08	0.83 ±0.11	0.95 ±0.07	0.81	0.33	0.06

Figures

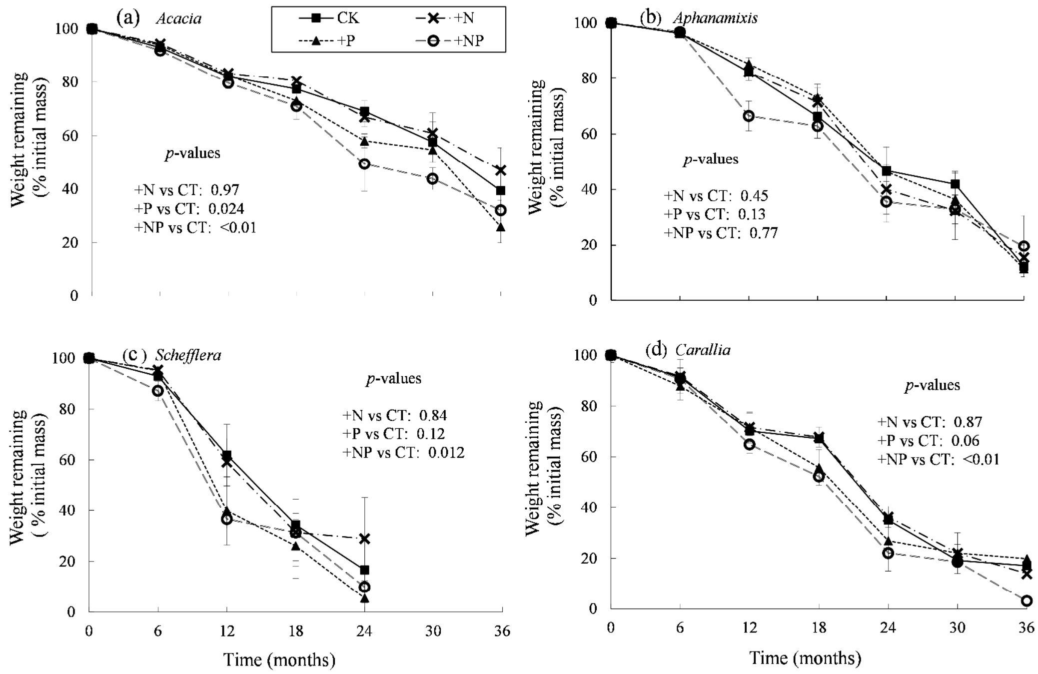

Fig. 1. Patterns of mass loss of woody debris of four species during 36 months of decomposition in a fertilization experiment in a secondary mixed tropical forest; error bars show standard errors of means for n=5 and p-values for treatment effects based on individual species models are given; species names and abbreviations follow Tables 2 and 3.

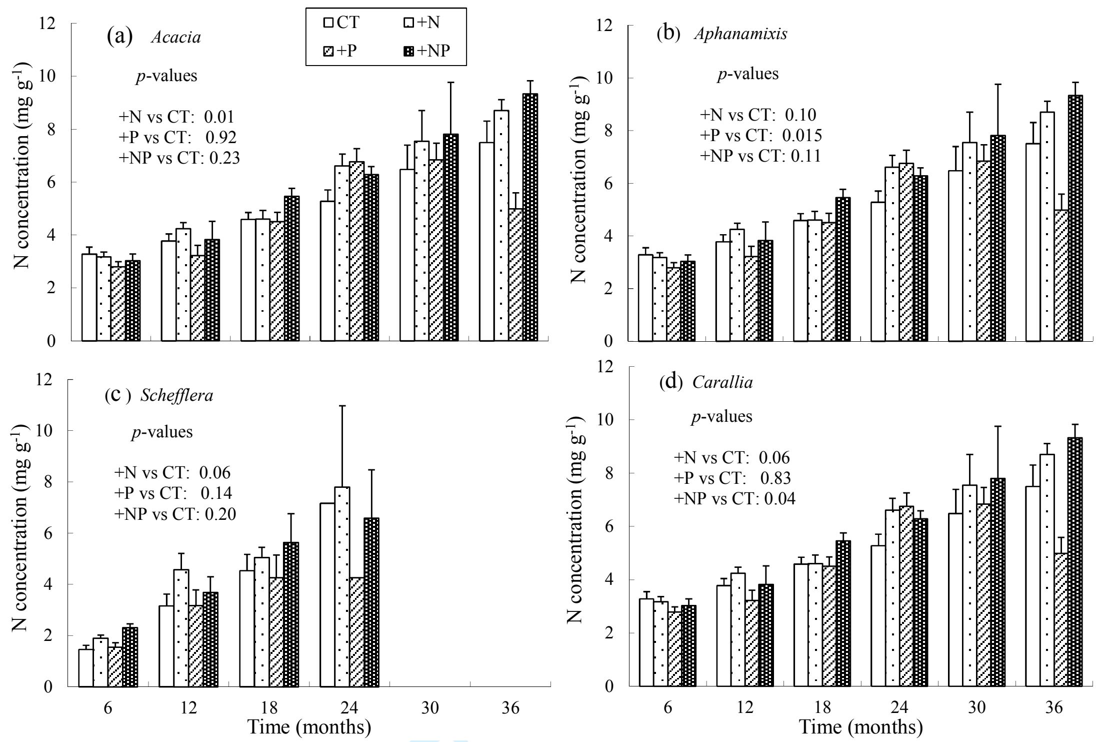

Fig. 2. Nitrogen (N) concentrations of woody debris of four species during 36 months of decomposition in a fertilization experiment in a secondary mixed tropical forest; error bars show standard errors of means for n=5 and p-values for treatment effects based on individual species models are given; species names and abbreviations follow Tables 2 and 3.

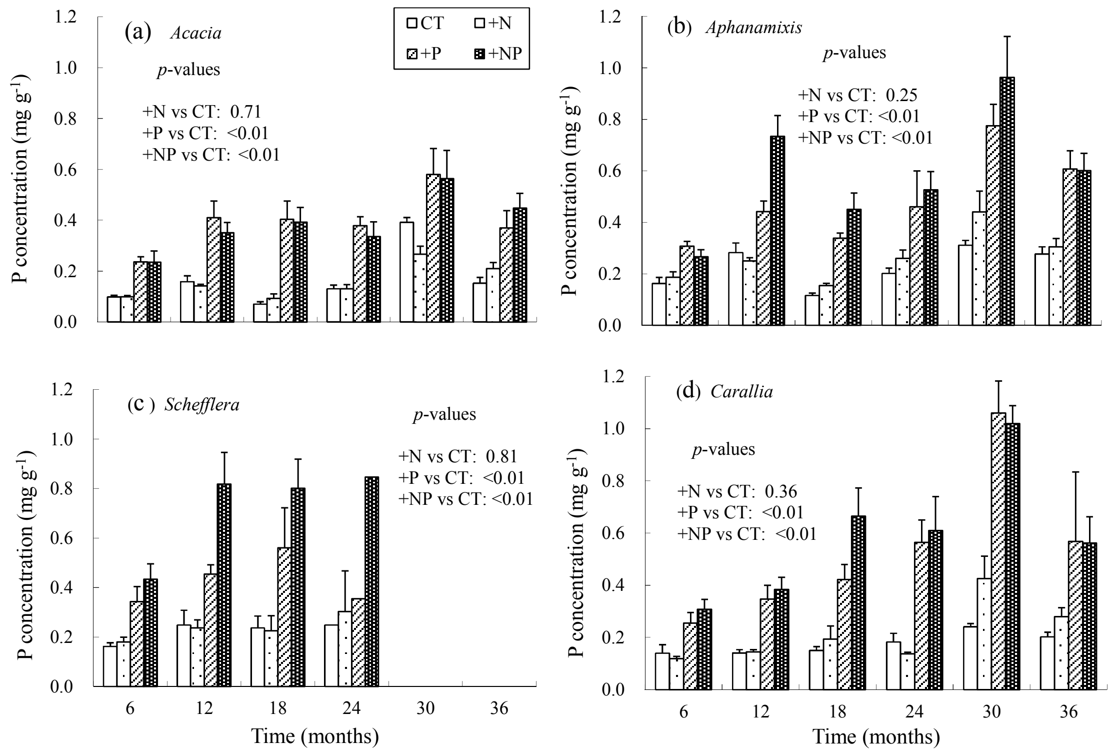

Fig. 3. Phosphorus (P) concentrations of woody debris of four species during 36 months of decomposition in a fertilization experiment in a secondary mixed tropical forest; error bars show standard errors of means for n=5 and p-values for treatment effects based on individual species models are given; species names and abbreviations follow Tables 2 and 3.

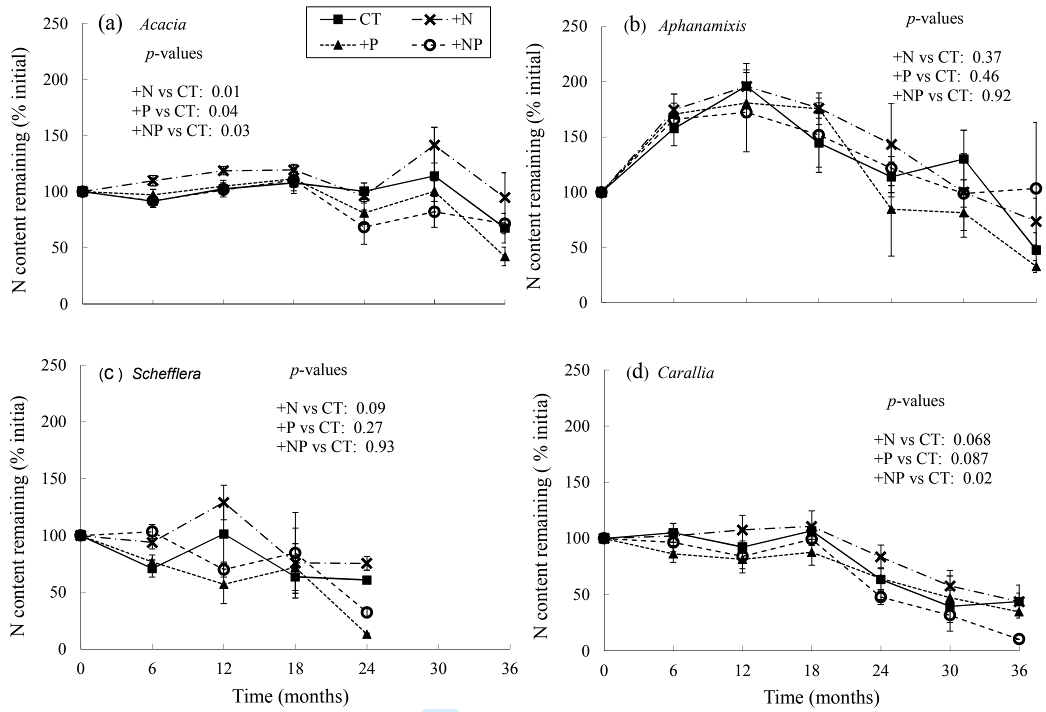

Fig. 4. Patterns of nitrogen (N) accumulation and release in woody debris of four species during 36 months of decomposition in a fertilization experiment in a secondary mixed tropical forest; error bars show standard errors of means for n=5 and p-values for treatment effects based on individual species models are given; species names and abbreviations follow Tables 2 and 3.

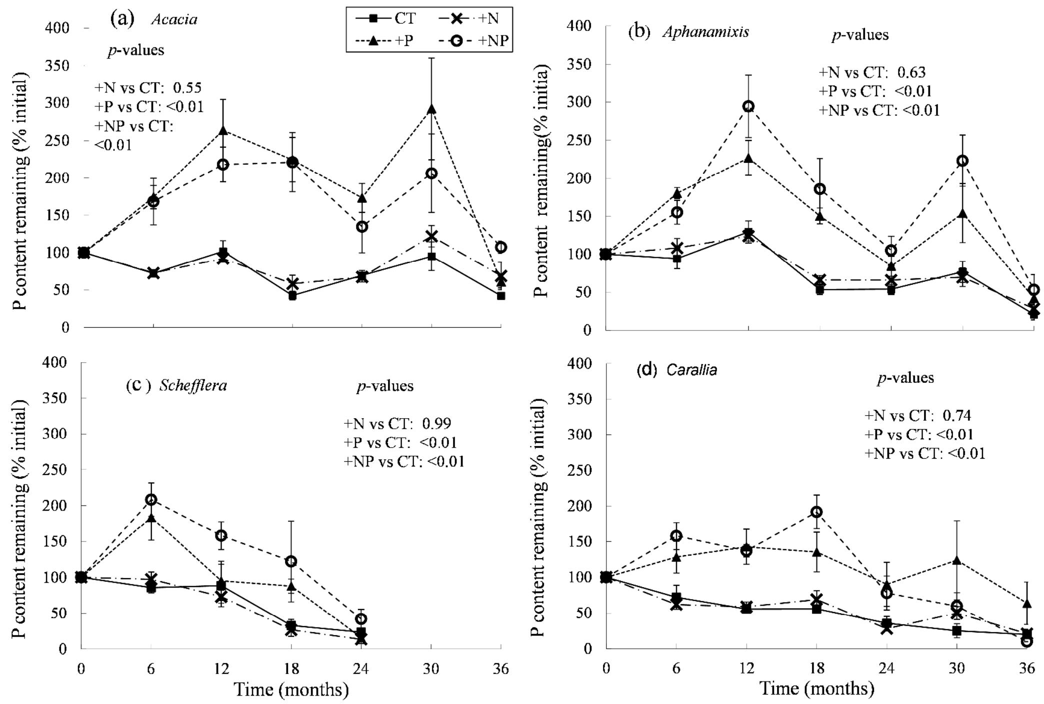

Fig. 5. Patterns of phosphorus (P) accumulation and release in woody debris of four species during 36 months of decomposition in a fertilization experiment in a secondary mixed tropical forest; error bars show standard errors of means for *n*=5 and *p*-values for treatment effects based on individual species models are given; species names and abbreviations follow Tables 2 and 3.