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Research article

Fine root presence and increased phosphorus availability stimulate wood decay in a central Amazonian rainforest

Nathielly P. Martins[1], Oscar Valverde-Barrantes[2], Lucia Fuchslueger[1,3], Laynara. F. Lugli[1,4], Adriana Grandis[5], Florian Hofhansl[6], Bruno Takeshi[1], Gabriela Ushida[1] and Carlos. A. Quesada[1]

[1]Coordination of Environmental Dynamics (CODAM), National Institute of Amazonian Research, Manaus, AM, Brazil
[2]International Center of Tropical Biodiversity, Florida International University, Miami, FL, USA
[3]Centre of Microbiology and Environmental Systems Sciences, University of Vienna, Vienna, Austria
[4]Land Surface – Atmosphere Interactions, Technical University of Munich, Freising, Bavaria, Germany
[5]Department of Botany, Biosciences Institute, University of São Paulo, SP, Brazil
[6]Biodiversity, Ecology, and Conservation (BEC) Research Group, Biodiversity and Natural Resources (BNR) Program, International Institute for Applied Systems Analysis (IIASA), Laxenburg, Austria

Correspondence: Nathielly P. Martins (nathiellymartins9@gmail.com)

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In the Amazon basin, approximately 60% of rainforest thrives on geologically old and highly weathered soils, thus decomposition represents an important mechanism for recycling nutrients from organic matter. Although dead logs and branches constitute up to 14% of the carbon stored in terrestrial ecosystems, woody debris decomposition and mainly the effect of direct nutrient cycling by plant root interaction is poorly studied and often overlooked in ecosystem carbon and nutrient budgets. Here we monitored the decomposition of five different local woody species covering a range of wood density by conducting a long-term wood decomposition experiment over two years with factorial root presence and phosphorous (P) addition treatments in a central Amazonian rainforest. We hypothesized that woody debris decomposition is accelerated by colonizing fine roots mining for nutrients, possibly strongly affecting wood debris with lower density and higher nutrient concentration (P). We found that root colonization and P addition separately increased wood decay rates, and although fine root colonization increased when P was added, this did not result in a change in wood decay. Nutrient loss from wood was accelerated by P addition, whereas a root presence effect on nutrient mobilization was only detectable at the end of the experiment. Our results highlight the role of fine roots in priming wood decay, although direct nutrient acquisition by plants seems to only occur in more advanced stages of decomposition. On the other hand, the positive effect of P addition may indicate that microbial nutrient mobilization in woody material is driven mainly by wood stoichiometry rather than priming by root activity.

Keywords: Amazon rainforest, coarse wood debris, fine root presence, P limitation, wood decomposition, wood density

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Introduction

Tropical forests are the main global terrestrial carbon (C) sink, with an estimated uptake of 1.2 Pg C $year^{-1}$ from 1990–2007 (Pan et al. 2011). The forests in the Amazon basin alone contribute around 25% to the global terrestrial C sink (Phillips et al. 2009, Pan et al. 2011, Feldpausch et al. 2012), but their sink strength seems to decline, mainly caused by a sustained long-term increase in tree mortality due to rising temperatures and greater drought frequency (Brienen et al. 2015, Hubau et al. 2020). This surge in extreme climate events is predicted to increase dead wood stocks; subsequently, the decomposition of woody material could strongly alter the forest's C balance (Seidl et al. 2017, McDowell et al. 2018).

In tropical forests wood is a major nutrient pool (Heineman et al. 2016, Bauters et al. 2022), and nutrients stored in woody debris are critical to maintaining ecosystem productivity (Grau et al. 2017, Bauters et al. 2022). This is of particular importance in many forests across the Amazon basin, where approximately 60% of the rainforests are growing on geologically old and highly weathered soils, depleted in phosphorus (P) and cations (Quesada et al. 2010, 2011) that can limit primary productivity (Cunha et al. 2022). However, we still need to better understand the factors controlling the decomposition and nutrient release from woody debris.

Wood decomposition is influenced by temperature, moisture (Bradford et al. 2014), and tissue quality, particularly by wood density and nutrient stoichiometry (Parton et al. 2007, Cornwell et al. 2008, Hu et al. 2018). Plants with rapid resource acquisition strategies, characterized for instance, by high specific leaf area, and high leaf nitrogen (N) or P content, tend also to construct softer stems with lower wood density and lignin content than slow-growing species (Cornwell et al. 2008, Chave et al. 2009, Weedon et al. 2009, Freschet et al. 2010), which results in faster decay rates of low-density wood (Baraloto et al. 2010, Van Geffen et al. 2010, Freschet et al. 2012).

Simultaneously, wood decomposition is strongly modulated by fragmentation and degradation processes modulated by faunal, fungal and bacterial communities (Hättenschwiler et al. 2005, Powers et al. 2009). Microbial activity is regulated by substrate quality and the demand of C relative to other nutrients of decomposer communities, with the scarcest nutrient(s) limiting decomposition (Manzoni et al. 2010, Mooshammer et al. 2012). Woody debris has a higher C:N:P ratio (103:40:1; global average) than leaf and root litter, and moreover, the C present in wood is bound in complex and large molecules, such as lignin or cellulose (Weedon et al. 2009, Mooshammer et al. 2014). The breakdown of these compounds requires high energetic costs, slowing down the decay of high-density wood (Mooshammer et al. 2014, Nottingham et al. 2018), suggesting that wood decomposition is a C-limited process (Sinsabaugh et al. 1992). However, the general high stoichiometric C:P ratio of wood, and even higher C:P ratio of wood in forests with low mineral P availability (Heineman et al. 2016), could even further limit woody debris decomposition rates. This was also corroborated by Chen et al. (2016) where P addition increased wood decay in a P-limited secondary tropical forest.

A characteristic feature of the Amazonian rainforest is the presence of large root mats on the soil surface that are responsible for taking up mineralized nutrients from the litter layer and maintaining a tight nutrient cycling (Went and Stark 1968, Herrera et al. 1978, Cuevas and Medina 1988, Martins et al. 2021). While fine roots can increase the mobilization of mineral nutrients from leaf litter (Martins et al. 2021), much less is known whether fine roots also acquire nutrients from woody material, and if they accelerate wood decay rates. Fine roots could enhance woody debris decomposition as they physically disrupt the tissues in their pursuit of nutrients, increasing the specific area for microbial community colonization (Lu et al. 2019). They can release enzymes or mine for specific nutrients (Martins et al. 2021) but they also could accelerate decomposition by releasing labile C as exudates, which could stimulate microbial saprotrophic activity (Kuzyakov et al. 2000). For instance, it has been shown that specialist saprotrophic fungi could use these labile exudates to produce extracellular lignocellulolytic enzymes and enhance the breakdown of more recalcitrant lignin (i.e. positive priming) (Blanchette 2000, Malik 2019, Yang et al. 2022). On the other hand, the decomposition of complex organic compounds can be reduced if microbial decomposers preferentially use labile substrate, e.g. labile root-derived C rather than more complex C compounds present in the organic material, without changing the degradation of the woody substrate (Cheng 1999, Cheng and Kuzyakov 2005).

We here explore whether woody debris characteristics, such as initial density and changes in nutrient stoichiometry induced by P addition, affect fine root colonization and if intensive fine root colonization accelerates wood decomposition rates and nutrient loss. We hypothesized that 1) fine root colonization would accelerate wood decay of species with lower-density wood, as they are structurally more accessible for roots and have a lower C:N:P ratio. Moreover, we hypothesized that 2) wood decomposition is constrained by nutrient availability and predicted that P additions will increase root colonization, as well as that 3) alleviating potential P limitations of decomposers will result in faster wood decay. We tested our hypotheses by conducting a wood decomposition experiment using logs of five tree species constituting a gradient of wood density in a Central Amazonian rainforest over two years (2016–2018), with factorial root presence and P addition treatments.

Material and methods

Site description

The study site is in the Cuieiras Reserve, about 60 km north of Manaus (Amazonas, Brazil), and is managed by the National Institute of Amazonian Research (INPA). The forest is composed of a dense, mature, and well-preserved rainforest typical

of a central Amazonian *Terra-Firme* vegetation, the climate is classified as a rainy tropical climate with average monthly temperatures varying from 24 to 27°C, mean annual rainfall is 2400 mm, with lower precipitation levels (< 100 mm per month) from July to September (Alves et al. 2016). The soil is characterized as Geric Ferralsol, clay-rich, and highly weathered with a low concentration of rock-derived nutrients, such as P, Ca, Mg and K. In these soils, a large proportion of P is bound to secondary soil minerals, such as iron and aluminum oxides (Quesada et al. 2010, 2011).

Experimental design

Woody material was collected from branches of recently fallen trees (identified by a botanist) after an intense storm near the experimental site. We sampled woody branches measuring between 6 to 12 cm in diameter from at least three separated individuals of five canopy species abundant in the area (*Dimorphandra coccinea*, *Croton lanjouwensis*, *Inga alba*, *Byrsonima duckeana* and *Licania heteromopha)* covering a range of wood densities from soft to heavy (Table 1) (Chave et al. 2006). All wood samples' diameter and length (about 10 cm) were measured using a digital caliper and tape. After that, samples were dried at 65°C for 72 h or until constant weight to calculate the wood density of each log used for the decomposition experiment. Among the collected species *Dimorphandra* sp. had the lowest wood density, with an average of 0.19 ± 0.01 g cm^{-3}, and *Licania* sp., had the highest wood density, with an average of 0.38 ± 0.06 g cm^{-3}. The other three species were classified as intermediate, with wood density varying between 0.24 ± 0.01 g cm^{-3} and 0.28 ± 0.04 g cm^{-3} (Table 1).

To test the effects of both root presence (R) and nutrient availability (P) on the rates of wood decomposition and nutrient release, we established a factorial experiment in a paired block design in June 2016. Before the samples were installed in the forest, the total 200 logs were split in P addition (+P) and without P addition (−P). For the + P treatment, wood samples were submerged in a solution containing 570 g of $NH_4H_2PO_4$ in 60 liters of water (0.81 M $NH_4H_2PO_4$ solution) for three days, corresponding in total to 347.7 g of PO_4^{3-}. The samples for the −P treatment was submerged in water for three days. Three samples per species and +P or −P treatments were dried and used to characterize their initial wood chemical composition (Supporting information).

In the forest, the samples were divided equally into two blocks, each under the canopy of a large *Caryocar pallidum* tree separated by ~300 m (giving an n = 2 per species and treatment combination). Each block was divided into five sub-blocks, one for each collection time. Each sub-block contained samples from all five species exposed to the respective treatments: half of the samples were left untouched to allow root colonization (+R), and neither roots nor fauna colonization changed until samples were harvested. The other half of the samples was inspected every two weeks and if roots were colonizing the wood debris they were carefully removed (i.e. reference treatment −R). In addition, P was added to the +P treatment samples by sprinkling 3 ml of the PO_4^{3-} solution (0.017 g of P) on each sample, while 3 ml of water was added to the treatment without P (i.e. reference treatment −P). These additions were done every two weeks during the two years (2016–2018), resulting in four different treatment combinations: +R−P ('natural'), −R−P, −R+P, +R+P. The samples were tied approximately 20 cm from each other directly on the forest floor (Fig. 1).

Sample collection and laboratory analyses

For each collection time, a total of 40 samples (2 blocks, 5 species, 4 treatment combinations) were collected after 3, 6, 12, 18 and 24 months after the onset of the experiment. In the treatments with root presence (+R−P, +R+P), roots were carefully removed from the woody debris, washed and dried at 65°C for 72 h to calculate the total colonizing root biomass.

Woody samples were cleaned with a brush to remove soil residues and dried at 65°C for 72 h. To calculate wood decomposition rates, we first calculated the proportion of remaining wood mass (RM) per collection time as the difference of initial wood mass by remaining wood mass (%) as follows:

$$RM = \left(W_{tn} / W_{t0}\right) \times 100 \quad (1)$$

where W_{t0} is the initial dry weight of wood debris before the start of the experiment, and W_{tn} is the dry weight at a

Table 1. Characterization of woody debris of the five species used in the wood decomposition experiment. Wood density was characterized for all individual samples that were placed into the forest (values are means ± SE for n = 50). The other variables were determined subsamples at t_0 (mean ± SE of 3 samples (n = 3 by species). The wood density is expressed as g cm^{-3}, lignin, and cellulose are expressed in %, N, P are given in g kg^{-1}, N:P ratio is expressed in molar and lignin: NP ratio is expressed in %. Different superscript letters indicate significant differences by species (for multiple comparisons by post hoc Tukey test).

	Dimorphandra coccinea	*Croton lanjouwensis*	*Inga alba*	*Byrsonima duckeana*	*Licania heteromopha*
Wood density	0.19 ± 0.01^{a}	0.24 ± 0.01^{b}	0.26 ± 0.05^{b,c}	0.28 ± 0.04^{c}	0.38 ± 0.06^{d}
Lignin	16.39 ± 0.79^{a}	29.72 ± 4.18^{b}	27.61 ± 2.49^{b}	30.69 ± 0.80^{b}	32.05 ± 1.22^{b}
Cellulose	64.15 ± 1.39^{a}	50.02 ± 0.64^{c}	46.25 ± 0.91^{c,d}	58.98 ± 0.79^{b}	43.01 ± 1.55^{d}
N	4.10 ± 0.11^{a}	2.59 ± 0.21^{b,c}	2.91 ± 0.21^{b}	2.23 ± 0.07^{c}	2.60 ± 0.08^{b,c}
P	0.30 ± 0.01^{a}	0.30 ± 0.01^{a}	0.35 ± 0.01^{b}	0.28 ± 0.01^{a}	0.19 ± 0.01^{c}
N:P	31.88 ± 0.28^{a}	19.00 ± 2.00^{b}	18.08 ± 0.47^{b}	17.48 ± 0.70^{b}	29.87 ± 0.48^{a}
Lignin:N	38.51 ± 2.80^{a}	115.94 ± 0.67^{b,c}	96.53 ± 15.89^{b}	137.65 ± 8.10^{c}	123.07 ± 4.75^{b,c}
Lignin:P	547.58 ± 21.81^{a}	995.92 ± 176.49^{b}	783.90 ± 111.31^{a,b}	1083.52 ± 33.16^{b}	1659.05 ± 45.59^{c}

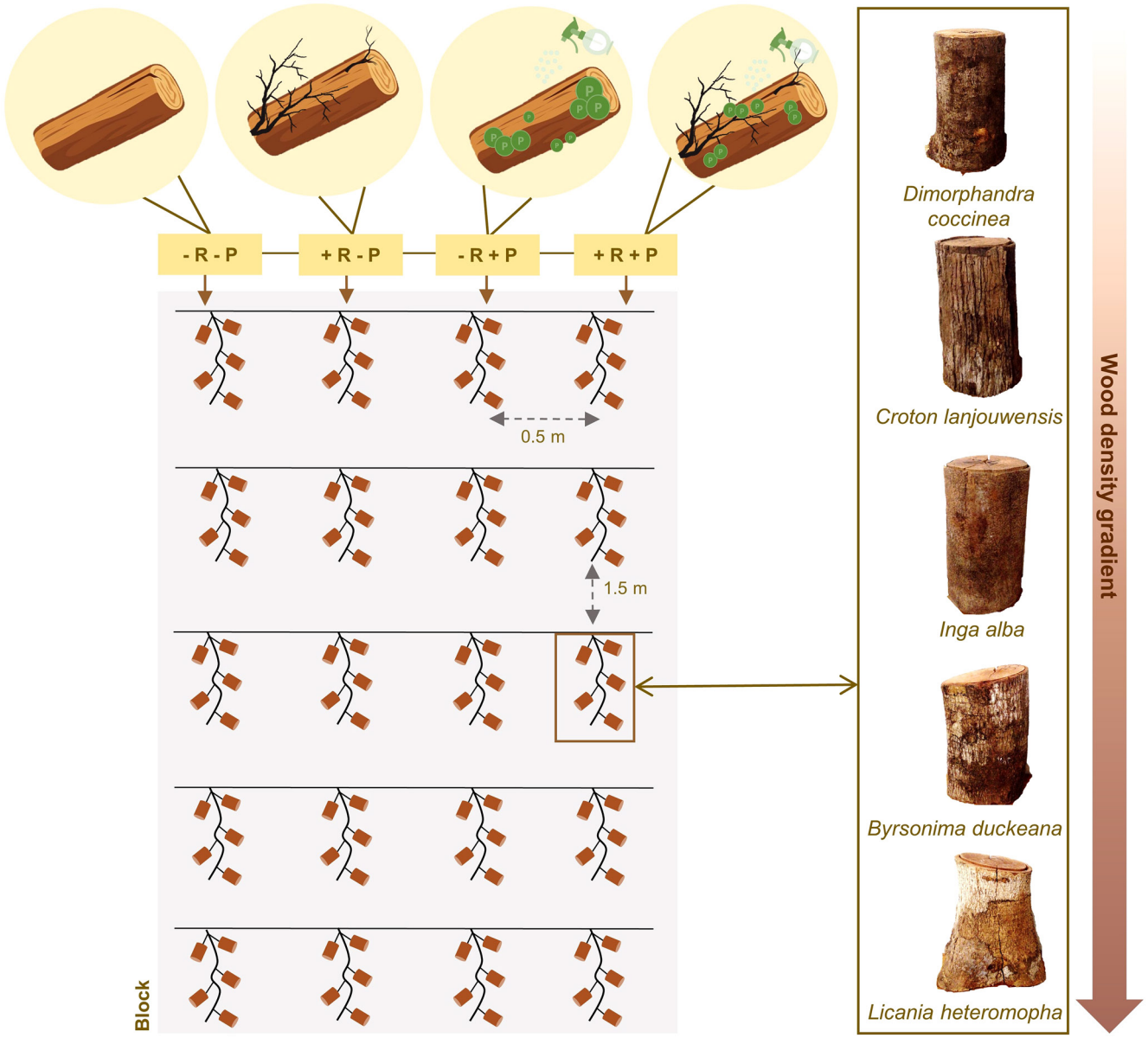

Figure 1. A conceptual overview of the experimental design of one block of the wood decomposition experiment. The decomposition experiment consisted of two blocks approximately 300 m apart, in each of these two blocks, five sub-blocks were set up, approximately 1.5 m from each other (at each sampling, one sub-block per experiment block was collected). Each sub-block included all treatment combinations in a factorial design: root presence, no P addition (+R−P; 'natural'), without roots, no P addition (−R−P), without roots, plus P addition (−R+P), and with root presence plus P addition (+R+P), for five different species (*Dimorphandra coccinea, Croton lanjouwensis, Inga alba, Byrsonima duckeana* and *Licania heteromopha)* separated from each other by approximately 20 cm.

given collection time (t_n). Then, we calculated mass loss as the difference between 100% from the initial mass and the remaining wood mass in percentage at t_n. In addition, decomposition rate constants (k values; fractional mass loss per year) were calculated using a single pool, exponential decay model (Olson 1963):

$$k = \left(-\ln\left(x_t / x_0\right)/t\right) \quad (2)$$

where t represents the time (year), X_t is the wood weight mass on time collection, and X_0 is the initial wood mass.

Chemical analysis

Samples from time zero (t_0, treated with +P or −P) and woody pieces sampled along the decomposition experiment duration were ground to fine powder for chemical analyses. Total nitrogen (N) was determined via Kjeldahl digestion using sulfuric acid digestion. Concentrations of total phosphorus (P) and cations (potassium (K), calcium (Ca) and magnesium (Mg)) were analyzed after digesting samples with a nitro-perchloric acid solution as described by Malavolta et al. (1989). Total P was determined colorimetrically (Murphy and Riley 1962, Olsen and Sommers 1982) and read on a

UV spectrophotometer (model 1240, Shimadzu). Cation concentrations were measured by atomic absorption spectrophotometry as described by Anderson and Ingram (1993). Wood lignin and cellulose contents were determined with the method proposed by Soest (1963) using an acid-detergent fiber. The proportion of remaining structural compounds and nutrient contents in the wood throughout the wood decomposition experiment was calculated as described in Eq. 3 (McGroddy et al. 2004):

$$RE = \left(X_t \times W_t\right) / \left(X_0 \times W_0\right) \times 100 \quad (3)$$

where RE are the remaining elements (%), X_0 is the initial mean concentration of wood elements, X_t is the concentration of elements at a given collection time (t), W_0 is the initial wood dry weight and W_t is wood dry weight at a given collection time (t). Since P concentrations drastically changed when we applied the P treatment, we used the mean of the initial P concentration per species and per treatment (+ P and − P additions), but since no differences between treatment (+ P and − P additions) were detected for N, K, Ca and Mg, we used the mean by species (Supporting information).

Statistical analyses

All analyses were performed in R ver. 4.0.4 (www.r-project.org). We tested differences in the initial wood density and chemical composition between the species by one-way ANOVA and a post hoc Tukey's test for multiple comparisons. We used Pearson's correlation analysis to identify if fine root biomass colonization was associated with physical or chemical properties of woody debris (initial or during the wood decomposition), such as wood density, mean log diameter, as well as N, P and lignin content remaining (Supporting information). We applied linear mixed effect models (LMMs) using the *lmer* function from the 'lme4' package (Bates et al. 2020), to test the effect of root presence, P addition, and their interactive effects. First, we used a simple model (no interaction) to determine how fine root biomass colonizing wood samples was affected by P additions. We selected only data with root presence (+R), using P treatments (+P and −P) as fixed factors. In addition, we included initial wood density as a covariate to account for species-specific differences. Second, we tested the interaction between root presence (+R/−R) and P addition (+P/−P) for wood decomposition and nutrient dynamics. Since no significant interactions were detected, the root presence and P addition were tested in factorial models, that is the effect of root presence (i.e. +R; n = 4) compared to all samples where roots were excluded (i.e. −R; n = 4) and the same pattern was used for P addition (i.e. +P; n = 4) compared to without P addition (i.e. −P; n = 4). This approach allowed us to test potential interactive effects with species identity (e.g. fixed factors: treatment × species identity). We used the simple model (treatment + species identity) if there was no interaction effect. For all models, we tested collection dates and blocks as random factors. Finally, we filtered only the data from the final sample collections after 24 months to account for possible cumulative effects of root presence using species as a random factor. The final selected model was then re-run, and only the significant effects were reported. Post hoc tests for multiple comparisons were conducted using Tukey's test by 'emmeans' package (Lenth et al. 2020) when significant interaction was observed. In all statistical analyses, we used $p < 0.05$ as a threshold for statistical significance.

Results

Wood debris characterization

The five species significantly differed in their initial wood density and chemical composition. *Dimorphandra* sp. had the lowest wood density, lignin content, lignin:N, lignin:P, but the highest cellulose content, and N and P concentration, while *Licania* sp. had the highest wood density, lignin content, lignin:N, lignin:P, but lowest cellulose content, and N and P concentration (Table 1, Supporting information). The woody material of the other three species (*Croton* sp., *Inga* sp., *Byrsonima* sp.) was more similar to each other (Table 1, Supporting information). Before placing logs in the forest, half of the samples were treated with a P solution, which significantly increased P content by 259% in the woody debris. Consequently, N:P and lignin:P ratios across all species decreased on average by 66.58% and 69%, respectively (Supporting information).

Root biomass dynamic

Supporting hypothesis 1, we observed that the highest root colonization of woody debris occurred in the lowest wood density of *Dimorphandra* sp. across control (+R−P) and treated wood (Supporting information; R = −0.31, p = 0.02; i.e. 3.13 mg roots g^{-1} wood). In contrast, wood debris from *Licania* sp., the species with the highest wood density, showed the lowest root colonization (1.13 ± SE 0.59 mg roots g^{-1} wood). Across all species, the amount of fine roots colonizing wood debris ranged between 0.18 ± 0.13 mg roots g^{-1} wood in the first three months of the experiment, reaching a peak of 3.36 ± 1.28 mg roots g^{-1} wood after 24 months (Fig. 2a, without P).

P additions significantly stimulated fine root colonization of wood debris after six months with 5.57 ± 3.08 mg roots g^{-1} wood, reaching a peak of 10.65 ± 3.05 mg roots g^{-1} wood after 24 months (Fig. 2a). Across all sample collections, wood treated with P was 320% more colonized by fine roots than wood that did not receive P ($F_{1:87.8} = 8.71$, p = 0.004; −P; 1.86 ± 0.48 versus +P: 7.83 ± 1.83 mg roots g^{-1} wood). Moreover, we observed an interaction between P addition and initial wood density, where the impact of P additions on root colonization was stronger for the species with lower to intermediate wood density compared to species with dense wood (Supporting information; $F_{1:88} = 3.71$, p = 0.05).

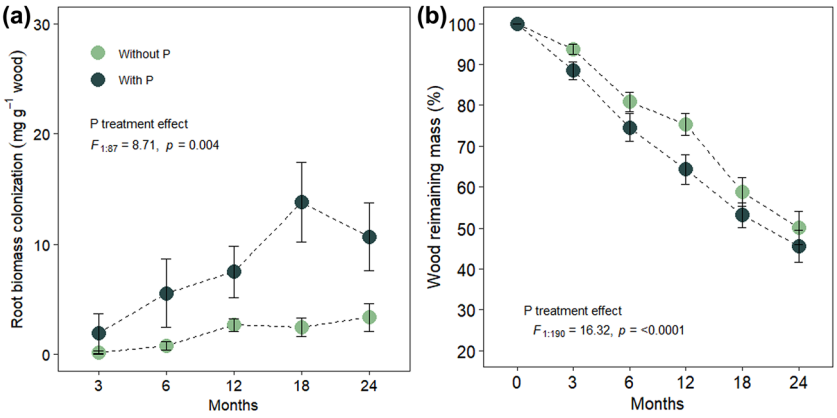

Figure 2. The influence of P additions on (a) fine roots colonization wood debris (mg roots g^{-1} dry wood) over the course of the wood decomposition (means of all species by time) and (b) wood remaining mass (%) showed by mean of the five species and two blocks by collection time (months) resulting in a without/with P addition factorial design. Error bars indicate errors for (a) n = 10 and (b) n = 20. Statistical results of the P addition effect were obtained by linear mixed models, reported by p-value, F-value$_{NumDF,\ DenDF}$ (numerator degrees of freedom and denominator degrees of freedom) for the fixed effect term.

Wood decomposition rates

In control wood material (+R−P), the decomposition rates ranged between 0.56 ± 0.08 year^{-1} for the low-density *Dimorphandra* sp. to 0.25 ± 0.04 year^{-1} for high-density *Licania* sp. Fine root presence, independently of P treatment, reduced remaining wood mass by 12.4% after 24 months (Fig. 3a; –R = 50.9 ± 3.5% and +R = 44.6 ± 4.2% of remaining mass; $F_{1:186} = 6.37$, p = 0.001), with significant interaction with species identity (root effect × species; $F_{4:186} = 4.51$, p = 0.0001). We found that the species with the lowest density *Dimorphandra* sp. had a higher mass loss when colonized by roots compared to root-free wood, specifically for the first six months (−R = 82.0 ± 9.2% and +R = 66.3 ± 12.4%; Fig. 3b). A similar trend was detected for the species with the second lowest density *Croton* sp., after 18 months (18 months, −R = 61.01 ± 7.1% and +R = 40.5 ± 2.8%; 24 months: −R = 56.8 ± 5.2% and +R = 31.0 ± 4.6%; Fig. 3b).

Similarly, P addition induced a reduction in the remaining mass by 9% after 24 months compared to without P (Fig. 2b; −P = 50.0 ± 4% and +P = 45.5 ± 3.9% of remaining mass respectively; $F_{1:190} = 16.32$, $p < 0.0001$). Furthermore, P additions also significantly reduced the remaining cellulose fraction in wood debris by 6.54% (Supporting information; $F_{1:108} = 13.8$, p = 0.003). We did not observe an interaction between fine root colonization and P additions (Table 2) or between P addition and plant species identity ($p > 0.05$).

Wood nutrient dynamics over time

We observed a higher temporal variability in the remaining wood nutrient content, mainly when fine roots were present

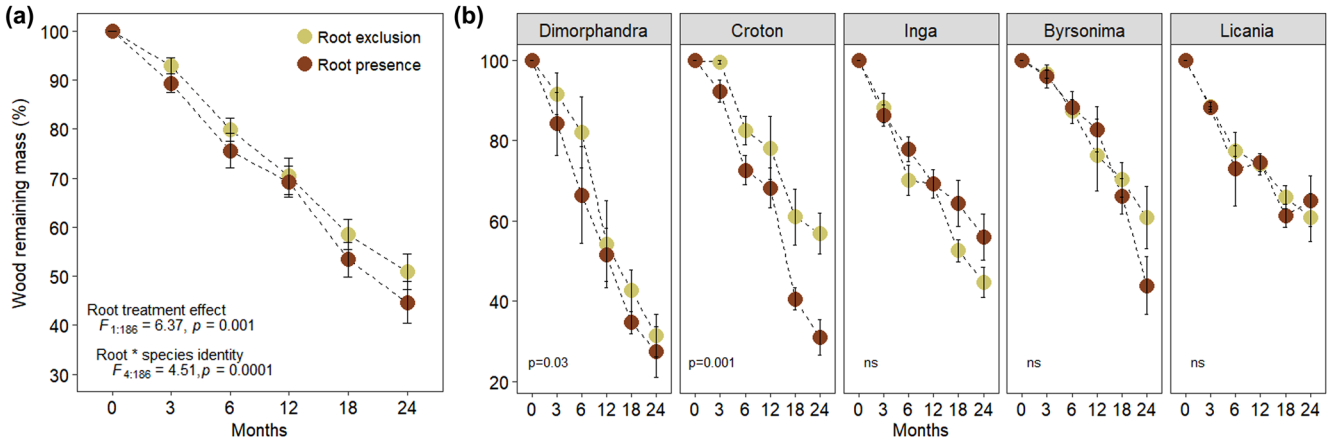

Figure 3. Root presence effect on wood remaining mass (%) over the course of the wood decomposition experiment: (a) showed by mean of the five species and two blocks by collection time (months) resulting in a without/with root presence factorial design (n = 20), and (b) interaction with the specie identity (n = 10). Error bars indicate standard errors of the mean. Statistical results of root presence effect and the interaction with specie identity was obtained by linear mixed models (LMM), reported by p-value, F-value$_{NumDF:DenDF}$ (numerator degrees of freedom and denominator degrees of freedom) for the fixed effect term, and the specific effect of root presence by species was tested using post hoc Tukey's tests of the LMM reported by p-value.

(Fig. 4–5). However, we did not detect a significant influence of fine root presence on the relative remaining N, P, K, Ca and Mg contents ($p > 0.05$; Fig. 4a–b, 5a–c) over time. Only after 24 months, remaining K (−23.6%) and Ca (−30.9%) contents were significantly reduced with fine root presence ($F_{1:34} = 6.02$, $p = 0.01$; $F_{1:34} = 4.74$, $p = 0.03$, respectively; Fig. 5a–b).

P additions did not influence the remaining wood N content (Fig. 4c), but we observed a significant reduction of the remaining wood P content by 52.5% along sample collections ($F_{1:189} = 311.62$, $p < 0.0001$, Fig. 4d). Over time, P additions also significantly reduced the remaining K ($F_{1:188} = 5.47$, $p = 0.02$), Ca ($F_{1:189} = 20.33$, $p < 0.0001$) and Mg ($F_{1:189} = 49.42$, $p < 0.0001$) content by 10.7%, 27.4% and 32.2% respectively (Fig. 4d–f). The effects of fine roots and P additions were not interactive (Table 2) and were independent of species identity.

Discussion

In this study, we found a stimulative effect of fine roots on wood debris decomposition that strongly depended on the wood's initial physical and chemical properties. In line with our first hypothesis, fine root colonization was higher and had a stronger stimulative effect on wood decay in lower wood density species. We found partial support for our second and third hypothesis, that P additions increased wood decay. Although P additions also increased root colonization, this did not translate into faster wood decay or nutrient loss. The lack of such an additive response indicate to a potential preferential substrate utilization by decomposers Qiao et al. (2016), rather avoiding lower-quality material (e.g. wood) towards more C-labile compounds potentially originating from fine root activity. We found the strongest effect of root colonization on nutrient release of specific nutrients (i.e. K and Ca) in species with lower density (i.e. *Dimorphandra* sp. and *Croton* sp.) and generally during later stages of wood decay (after 24 months). This suggests that the ability of roots to acquire nutrients from decomposing wood depends on the stoichiometry of the substrate.

Fine roots accelerate wood decay and nutrient mobilization depending on wood properties

Fine roots play an essential role in acquiring and conserving scarce nutrients, especially in infertile, highly weathered soils (Herrera et al. 1978, Stark and Jordan 1978, St. John 1983). For instance, plants can grow finer roots in the uppermost litter layer and take nutrients from leaf and woody materials before leaching deeper into the mineral soil layers (Sayer et al. 2006). However, little is known about the mechanisms of releasing nutrients stored in wood. In this study, we expected that high-density (i.e. more lignified) wood with a high C:N ratio would take longer to decompose, whereas softer wood material (with a lower C:N ratio) would decompose faster and would be a more attractive substrate for fine roots. In accordance with our hypothesis that the biological activity and physical presence of fine roots would increase wood decay rates and nutrient release, our results confirmed that initial wood density is an important factor both for predicting decay rates, but also for root colonization (Supporting information). Furthermore, we observed that the fine root colonization was negatively correlated with the remaining lignin:P ratio, corroborating those changes in structural and chemical properties during wood decay influence root colonization (Supporting information). Our results showed strong evidence that not only wood density but also wood nutrient composition is driving the colonization by roots, which is mirrored by the three-fold increase in the response of fine root colonization to P additions, especially in softer woods.

Table 2. Test interaction effect between root presence and P addition on wood debris remaining mass, structural compounds, and nutrient dynamics dynamic over the wood decomposition experiment. The statistical parameters are obtained from a linear mixed model (LMM) that considers the entire dataset controlling the 'time' as a random factor. Statistical results of root presence, P addition and the interaction effect were obtained by an analysis of variance of the LMM using Satterthwaite's method, reported by p-value, F-value$_{NumDF:DenDF}$ (numerator degrees of freedom and denominator degrees of freedom) for the respective fixed effect term.

	LMM (response variable ~ P addition × root presence (1|time)		
Parameter	P addition effect	Root presence effect	P addition × Root presence
Remaining mass (%)	**$F_{1:192}$ = 12.39, p = 0.0005**	**$F_{1:192}$ = 4.74, p = 0.03**	$F_{1:192}$ = 1.00, p = 0.31
Cellulose (%)	**$F_{1:114}$ = 3.91, p = 0.05**	$F_{1:114}$ = 2.03, p = 0.15	$F_{1:114}$ = 0.00, p = 0.94
Lignin (%)	$F_{1:114}$ = 0.21, p = 0.64	$F_{1:114}$ = 0.94, p = 0.33	$F_{1:114}$ = 0.02, p = 0.86
N (g kg^{1})	$F_{1:190}$ = 0.11, p = 0.74	$F_{1:190}$ = 2.22, p = 0.13	$F_{1:190}$ = 0.00, p = 0.92
P (g kg^{-1})	**$F_{1:191}$ = 119.18, p = <0.0001**	$F_{1:191}$ = 0.27, p = 0.59	$F_{1:191}$ = 0.00, p = 0.96
K (g kg^{-1})	$F_{1:191}$ = 0.07, p = 0.78	$F_{1:191}$ = 0.35, p = 0.55	$F_{1:191}$ = 0.00, p = 0.98
Ca (g kg^{-1})	**$F_{1:191}$ = 6.87, p = 0.009**	$F_{1:191}$ = 0.28, p = 0.59	$F_{1:191}$ = 0.00, p = 0.96
Mg (g kg^{-1})	**$F_{1:191}$ = 10.58, p = 0.001**	$F_{1:191}$ = 0.37, p = 0.53	$F_{1:191}$ = 0.23, p = 0.63
Remaining cellulose	**$F_{1:114}$ = 11.93, p = 0.0007**	$F_{1:114}$ = 0.08, p = 0.77	$F_{1:114}$ = 0.00, p = 0.93
Remaining lignin	$F_{1:114}$ = 1.13, p = 0.28	$F_{1:114}$ = 1.17, p = 0.27	$F_{1:114}$ = 0.02, p = 0.87
Remaining N	$F_{1:191}$ = 2.79, p = 0.09	$F_{1:191}$ = 0.43, p = 0.51	$F_{1:191}$ = 0.11, p = 0.73
Remaining P	**$F_{1:191}$ = 161.13, p = <0.0001**	$F_{1:191}$ = 0.26, p = 0.61	$F_{1:191}$ = 0.07, p = 0.79
Remaining K	**$F_{1:191}$ = 4.85, p = 0.02**	$F_{1:191}$ = 2.29, p = 0.13	$F_{1:191}$ = 0.00, p = 0.97
Remaining Ca	**$F_{1:191}$ = 19.27, p = <0.0001**	$F_{1:191}$ = 2.22, p = 0.13	$F_{1:191}$ = 0.30, p = 0.58
Remaining Mg	**$F_{1:191}$ = 39.62 p = <0.0001**	$F_{1:191}$ = 2.25, p = 0.13	$F_{1:191}$ = 0.82, p = 0.36

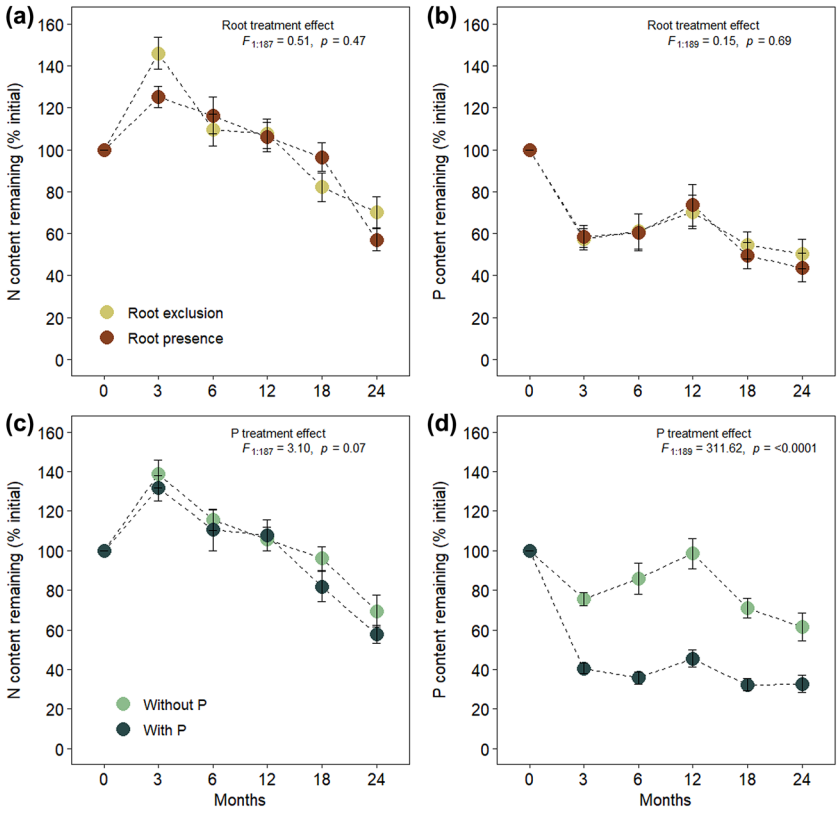

Figure 4. The influence of fine root presence and P addition on the percentage of nitrogen (a, c) and phosphorus (b, d) in the wood remaining mass over the course of the wood decomposition experiment. For each panel and collection time (months), the mean of the five species and two blocks are shown, resulting in root presence/exclusion and with/without P addition factorial design (n = 20). Error bars indicate standard errors of the mean. Statistical results of root presence and P addition effect were obtained by linear mixed models (LMM), reported by p-value, F-value$_{\text{NumDF:DenDF}}$ (numerator degrees of freedom and denominator degrees of freedom) for the respective fixed effect term.

Our findings suggest that fine roots play a stimulative role in wood decomposition, as the decomposition rate was 22.8% higher with roots present (0.43 ± 0.1 year^{-1}) compared to when roots were absent (0.35 ± 0.07 year^{-1}). Confirming our first hypothesis, we found that fine roots had a particularly strong effect on softer woods (i.e. *Dimorphandra* sp. and *Croton* sp., Fig. 3a–b). Similar as reported for other ecosystems (Weedon et al. 2009), we found that softer wood with relatively higher nutrient contents decomposed faster compared to dense wood. In addition, here we first time show that this was even accelerated by root colonization highlighting those fast-growing fast decaying woody materials as crucial resources for plants. We also observed a reduction in the lignin: P ratio of the remaining wood with increases in root colonization in denser woods but at a much slower rate than in softer woods (Supporting information). That may suggest an overall positive effect of root presence on wood decay of higher density wood, but the effect may take longer than the 24 months of decomposition of this study for denser woods (Supporting information).

Fine roots can increase wood fragmentation, increasing the exposure area for microbes, especially fungal colonization, thereby indirectly contributing to wood decay (Hendel and Marxsen 2000, Lu et al. 2019). On the other hand, fine root exudates can introduce labile C and N compounds (i.e. sugars and amino acids) in the wood debris rhizosphere. This input of labile C by root exudates could change the community composition of decomposers or directly stimulate microbial activity, providing the energy needed to break down complex molecules, inducing an increase in nutrient demand and leading to increased wood decomposition (Kuzyakov et al. 2000, Cheng and Kuzyakov 2005). A similar positive effect of fine roots on wood decomposition has been observed in temperate forests, where their presence promoted decay by increasing mycelial colonization (Malik 2019). In contrast, in an experiment simulating enhanced fine root exudates by adding labile C and N, Qiao et al. (2016) observed a negative priming effect and a slowed down woody debris decay that was attributed to preferential labile substrate utilization by microbial decomposers. In this higher N availability scenario, the microbial decomposers may have switched from utilizing complex compounds (i.e. lignin) to more readily available components exuded by roots, which may slow decomposition. In our study, we speculate that fine roots could have provided a significant amount of labile C for the microbial community on top of the rather complex C compounds (i.e. cellulose, lignin) in woody debris. This additional C could have, however, increased microbial decomposers' demand to mine for inorganic nutrients (e.g. N, or P)

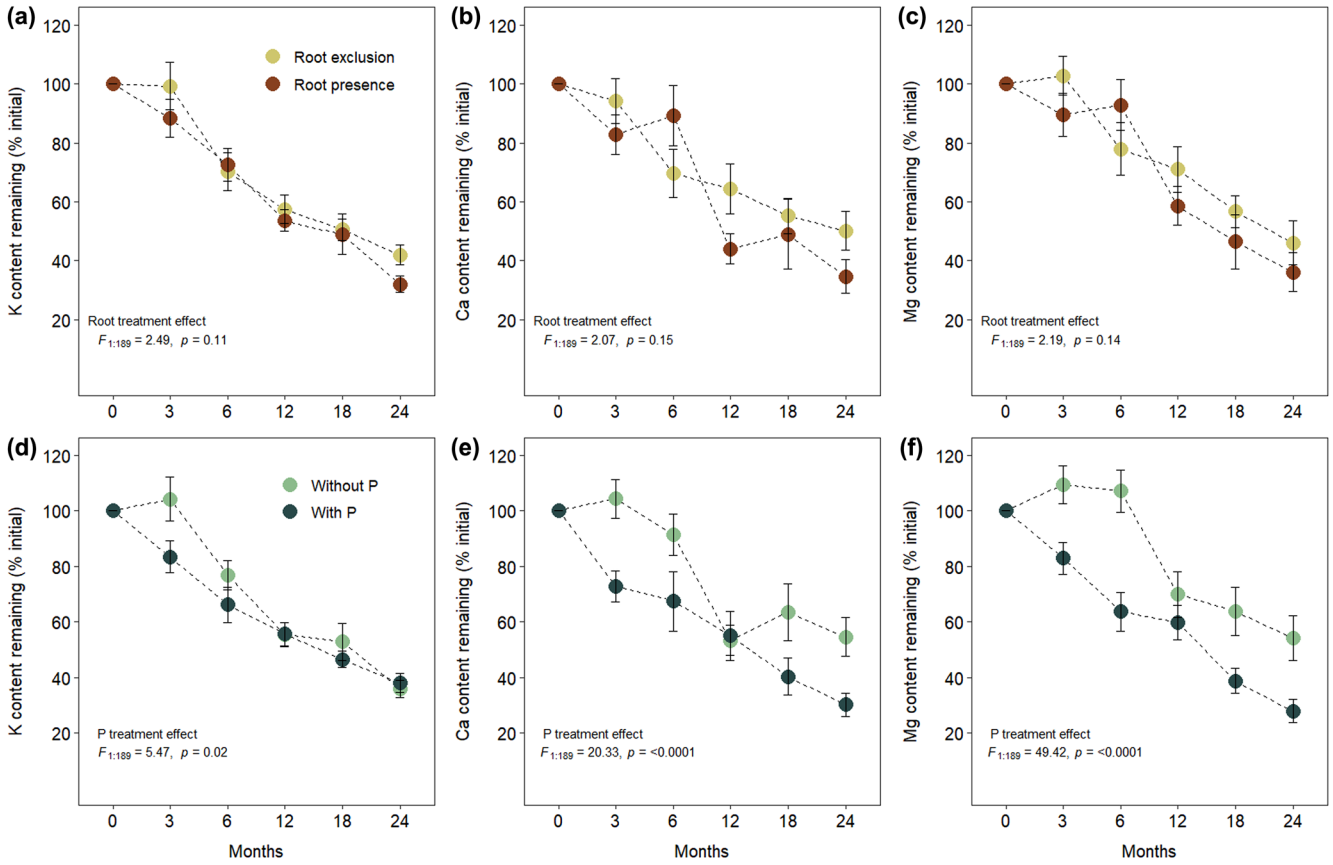

Figure 5. The influence of fine root presence and P addition on the percentage of potassium (a; d), calcium (b, e), and magnesium (c; f) contents remaining in the wood's remaining mass over the course of the wood decomposition experiment. For each panel and collection time (months), the means of the five species and two blocks are shown, resulting in root presence/exclusion and with/without P addition factorial design (n = 20). Error bars indicate standard errors of the mean. Statistical results of root presence and P addition effect were obtained by linear mixed models (LMM), reported by p-value, F-value$_{\text{NumDF:DenDF}}$ (numerator degrees of freedom and denominator degrees of freedom) for the respective fixed effect term.

to maintain their stoichiometric balance (Mooshammer et al. 2014). On the other hand, root colonization increased substantially with P addition (Fig. 2a), but we did not observe a significant additive effect between fine root presence and P addition on wood decay as we expected. In that case, the abundant supply of the most limiting nutrient (by P addition) and the labile C by root exudation could have been the preferential source of energy for microbes, therefore reducing or not changing wood decomposition, similar to what was observed by Qiao et al. (2016).

In addition to stimulating litter decomposition rates and mass loss, fine roots at the soil surface are highly efficient in acquiring nutrients (Herrera et al. 1978, Stark and Jordan 1978, Cuevas and Medina 1988). Previous studies in the central Amazon showed that the presence of roots in the litter layer significantly increased the uptake of P and cations (K, Ca and Mg) without increasing fine litter decomposition (Luizão et al. 2007, Martins et al. 2021). We observed an opposite effect for woody debris, with fine roots increasing wood decay, but not the release of P. We found an increase in the release of K by 17% and Ca by 31% when roots were present, but this effect only occurred at advanced stages of wood decay. These differences may be mainly related to the quality/composition of the wood versus leaf litter substrates. Leaf litter has more labile C to stimulate microbial activity and promote faster nutrient cycling resulting, therefore, in more nutrients returned via fine root colonization before immobilization by microorganisms or leaching into the soil. In contrast, labile exudations from fine roots could promote wood decomposition and sustain nutrient cycling, but in a smaller proportion and with a slower turnover. These results suggest that wood can be an important nutrient source, but only at the late stages of decomposition, and it could take years (for the decay of high-density wood) before nutrients can be readily available for plants. Nevertheless, our findings indicate that the decay of woody debris exhibits a long-term alternative for plants dwelling in such a scarce environment, such as the Amazon forest.

P addition effects on wood decay and nutrient dynamics

Previous studies showed that reduced soil nutrient availability (e.g. N, P and K) decreased wood decomposition rates in a lowland

tropical forest. Still, the moderate increases in soil nutrients by natural litter input did not influence long-term wood decomposition (Gora et al. 2018). To elucidate the processes involved in long-term wood decay, we conducted a P addition experiment that significantly increased the decomposition constant k by 5.5% (−P: 0.38 ± 0.1 $year^{-1}$ and +P: 0.40 ± 0.1 $year^{-1}$), independent of the initial wood properties. This response to P additions suggests that the decomposers benefited from increased P availability and increased activity, and more importantly, indicates that P may limit decomposition in this forest ecosystem. Higher wood mass loss in response to P additions was also reported by Chen et al. (2016) in a secondary mixed tropical forest in China.

Sinsabaugh et al. (1992) showed that wood decomposition is a C-limited process (i.e. higher energy demand) and then highly dependent on lignocellulose degrading enzymes (i.e. β-1,4-glucosidase, phenol oxidase, peroxidase). Here, we observed increased cellulose degradation with P addition (i.e. reduction of remaining wood cellulose content, Supporting information). This faster cellulose loss could indicate that P additions enhanced enzymatic activity by the decomposers to break down specific compounds, which would accelerate wood decomposition and supply their stoichiometric imbalance (Mooshammer et al. 2014).

We expected that in a nutrient poor system higher P availability would increase P immobilization by the microbial community (Stark and Jordan 1978, Cleveland et al. 2006), as was also observed by Chen et al. (2016). However, surprisingly, remaining P in wood decreased faster with P additions compared to control wood logs (Fig. 4d). Such a strong P release may be related to faster total wood mass loss induced by constant P additions or caused by the fact that +P wood debris had higher concentrations of more labile and more easily accessible inorganic P (P_i) from experiment onset (Supporting information). Moreover, P additions also increased the release of cations (K, Ca and Mg) but not of N, highlighting the importance of P and other rock-derived limiting nutrients for microbial processes driving decomposition in tropical rainforests.

Conclusion

We found that fine root colonization and the potential alleviation of P limitation stimulated wood decomposition in Amazonian forests. Our findings indicate that the strength of this effect depends on initial substrate quality, i.e. the wood type, but also on the decomposition stage. Our results highlight the importance of the role of woody debris as a nutrient resource to plants and of monitoring fine root dynamics in tropical forests. Further experiments clarifying the mechanistic linkage between C, N and P cycle processes and the association of fine root presence with microbial decomposer activity for a more robust set of species (plant functional characteristics) will be required to increase our understanding of the mechanisms regulating nutrient imbalances in tropical forest ecosystems.

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Author contributions

Nathielly P. Martins: Conceptualization (equal); Data curation-Lead, Formal analysis (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (lead). **Oscar Valverde-Barrantes**: Conceptualization (lead); Formal analysis (equal); Methodology (lead); Writing – original draft (supporting); Writing – review and editing (equal). **Lucia Fuchslueger**: Conceptualization (lead); Formal analysis (equal); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Laynara F. Lugli**: Formal analysis (supporting); Methodology (supporting); Writing – review and editing (equal). **Adriana Grandis**: Data curation (supporting); Formal analysis (supporting); Writing – review and editing (equal). **Florian Hofhansl**: Conceptualization (supporting); Formal analysis (supporting); Writing – review and editing (equal). **Bruno Takeshi**: Data curation (supporting); Funding acquisition (lead); Project administration (lead); Writing – review and editing (supporting). **Gabriela Ushida**: Data curation (supporting); Formal analysis (equal); Writing – review and editing (equal). **Carlos A. Quesada**: Conceptualization (lead); Data curation (supporting); Funding acquisition (lead); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.rr4xgxdfj (Martins et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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