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Rapid root assimilation of added phosphorus in a lowland tropical rainforest of French Guiana

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Abstract :

Theory states that tree growth in lowland tropical forests on old, weathered soils is limited by low phosphorous (P) availability. However, evidence for P limitation from nutrient manipulation experiments remains unclear, which raises the question whether trees are taking up added P. In French Guianese lowland rainforest, we measured changes in nitrogen (N) and P availability before and up to two months after N and P addition. We measured in soils with intact root systems and soils excluding roots and mycorrhizal fungi with root exclusion cylinders. When the root system was excluded, P addition increased P availability to a much greater extent and for a longer time than where the roots remained undisturbed. N dynamics were unaffected by root presence/absence. These results indicate rapid root uptake of P, but not of N, suggesting very effective P acquisition in these lowland rainforests.

Highlights

► Trees quickly and effectively take up P after fertilization with NxP fertilizer. ► Nitrogen is not rapidly taken up after fertilization. ► Combination of PRS probes and RECs reveals fate of added nutrients.

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Keywords : Tropical Forest, Phosphorus, Nitrogen, Fertilization, Root System, Plant Root Simulator Probes

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One of the long-standing paradigms in terrestrial ecology states that tropical forest productivity is limited by phosphorus (P) availability (Vitousek, 1984; Vitousek and Sanford, 1986) because the old soils that characterize much of the tropics are strongly weathered and hence depleted in P (Walker and Syers, 1976; Wardle et al., 2004). There is also a wealth of indirect evidence for P limitation in tropical forests, including high N:P ratios in leaves and correlations between forest productivity and soil P stocks at continental scale (Quesada et al., 2012; ter Steege et al., 2006). Nutrient addition experiments have shown widespread P limitation of soil microbial communities in tropical forests (Camenzind et al., 2018), but these experiments have produced only limited evidence for P limitation in trees (Cleveland et al., 2011; Wright, 2019). The lack of a clear growth response to P addition in tropical forests on P-poor soils has been taken to suggest that these trees are strongly adapted to the low P conditions (Turner et al., 2018). This has raised the question if the added P is quickly occluded onto the soil mineral fraction or assimilated by microbes (Olander and Vitousek, 2004), making it unavailable to the plants, or if trees are very effective in the uptake of P (e.g. from dead organic matter) and hence are not experiencing P limitation as suggested by Gill and Finzi (2016).

We used a NxP fertilization experiment in the lowland rainforests of French Guiana to explore the effectiveness of added P uptake by plants. To this end, we assessed the fate of added P fertilizer and compared this to the fate of added N, a nutrient that is usually in ample supply in tropical rainforests (Hedin et al., 2009). We hypothesized that the trees, adapted to low P availability soils, are much more effective in the assimilation of added P than in the assimilation of added N, which is more abundant in this forest (Van Langenhove et al., 2019). The fertilization experiment started in 2016 at the Paracou research station in French Guiana and consisted of twelve plots that received a +N, +P, +NP or no treatment (control). Soils are highly weathered and display typical characteristics of low nutrient availability, such as low cation exchange capacity, high acidity and very low total and available P concentrations (Sabatier et al., 1997; Gourlet-Fleury et al., 2004; Grau et al., 2017; see supplementary text). Due to a sesquioxide dominated mineral fraction and the presence of 1:1 clays such as kaolinite, these soils have a high affinity for adsorbing mineral P, reducing its availability for plants (Sposito, 1989).

The large standing forest biomass (Gourlet-Fleury et al., 2004) seriously complicates detection of plant uptake of added nutrients against the large and highly variable background nutrient stocks, and the very high species richness in these forests restricts comparison of fertilization effects to the few species occurring in multiple plots. Instead of directly assessing trees, we therefore focussed on soil nutrient dynamics in presence and absence of the root system. To this end, we used a root exclusion cylinder (REC) technique (Huang and Schoenau 1997). RECs were PVC collars inserted 20 cm into the soil to sever all near-surface roots and mycorrhizal hyphae, and were installed in every plot prior to the first nutrient addition in 2016. To follow changes in soil N and P availability we used commercially available PRS™ probes (Western Ag Global, Saskatoon, SK, Canada), which provide proxies for plant available ions in soil solution, including inorganic N (N_i) and inorganic P (P_i), over the soil insertion period (Qian and Schoenau, 2002). To measure changes in soil N_i and P_i availabilities over time, probes were inserted in the soil four times in 2017; one month before fertilization, and four days, four weeks and finally eight weeks after fertilization. Inserting PRS probes both inside and outside the RECs allowed us to assess the differences in N_i and P_i availabilities between identical soils including and excluding roots following fertilization. With this setup, we were able to account for occlusion of added fertilizer unto the sesquioxides in the soil, which has been shown to occur rapidly after fertilization (e.g. Olander and Vitousek 2004; Buehler et al., 2002). Details of the methods and statistics are presented in the supplementary text.

After fertilisation, the plots receiving additional N, P or NP exhibited significant increases in N_i or P_i availabilities, respectively (Fig 1.), with initial peaks declining over the following two months. Additionally, in the absence of roots, P_i availabilities increased more than 10-fold following P addition and 3-fold following NP addition (Fig 1B). Root removal can also cause changes in for example aluminium reactivity (Barra et al., 2018) or microbial biomass (Minz et al., 2013), which may impact P_i availability. However, these changes alone are unlikely to explain the large differences in post fertilization P_i availability observed between root inclusion and exclusion treatments. If they were of substantial influence, these effects would most likely also be reflected in the control or +N treatment. The difference in P_i availability between the P and NP treatments may be related to greater microbial P uptake and growth in the NP treatment (Fanin et al., 2016), but this was beyond the scope of the study. Importantly, in the presence of roots the increases in P_i availability in response to P and NP addition were significantly smaller (Fig 1A) than in the absence of roots, while for N_i the presence or absence of the root system did not affect its availability (Fig 1 C and D). Combining these results, the contrasting responses for N and P suggest that the root system rapidly assimilated the added P while the added N remained in soil solution even in the presence of roots. This indicates fast and effective plant uptake of added P and most likely implies that the plants in this ecosystem are also very effective in taking up the P that continuously cycles through the forest (Reed et al., 2011). Such effective P uptake could avoid plants running into P limitation, even when soil available P is low, potentially clarifying the lack of growth response to P addition in several tropical P addition experiments (see e.g. Wright et al., 2019). Our study further demonstrates that combining a root exclusion technique with a nutrient availability proxy (first demonstrated by Huang and Schoeneau, 1997) can provide new insights into the (rapid) uptake of added nutrients by the root system over time in nutrient addition experiments, and to identify which elements are in greatest demand. This is particularly valuable in tall-statured and highly diverse ecosystems where identifying biomass stock changes is a major challenge.

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Tables and Figures

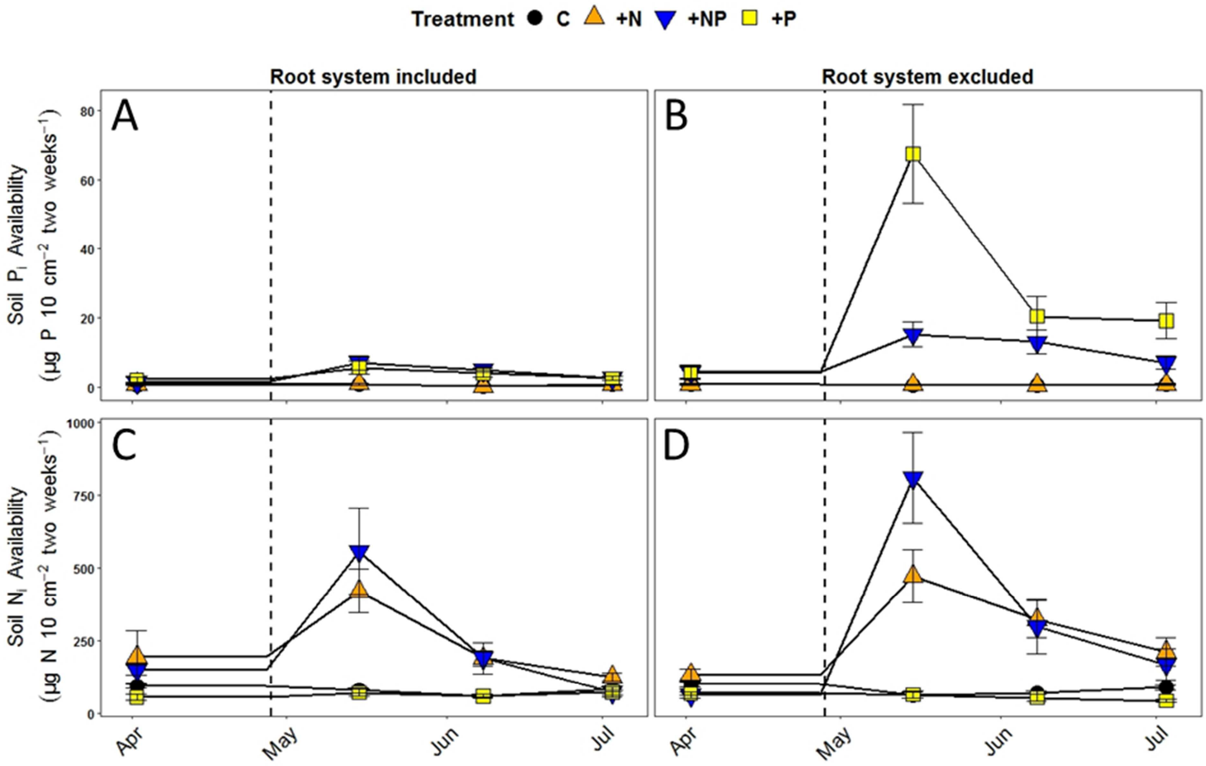

Figure 1 Inorganic P (top) and N (bottom) availabilities in the soil in the control treatment (black circle) and before and after in situ fertilization (vertical dashed line) with +N (red triangle), +NP (blue triangle) or +P (green square) fertilizer. Nutrient availabilities were measured four times; one month before fertilization, and four days, four weeks and eight weeks after fertilization. Each measurement of N_i or P_i availability was obtained with PRS probes that were inserted in the soil during 14 days, thus the unit provides the amount of N or P in µg that was accumulated on the 10 cm² ion exchange membrane inside the probe over a 14 days period. Both the availability of P_i and N_i after fertilization in the presence of the root system (top left and bottom left, respectively) and in the absence of the root system (top right and bottom right, respectively) are depicted. Error bars depict standard errors. Twelve plots divided into three blocks each receiving a control, +N, +NP or +P treatment were sampled and within a single plot, *N* = 3 for each combination of root exclusion treatment and sampling time.

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Highlights

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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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