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

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Abstract

Tree growth on weathered soils in lowland tropical forests is limited by low phosphorus (P) availability. However, nutrient manipulation experiments do not always increase the P content in these trees, suggesting that they have strategies to acquire P from their environment. In French Guianese lowland rainforest, we measured changes in nitrogen (N) and P availability before and up to two months after N and P fertilizer addition, in soils with intact root systems and in soils where roots and mycorrhizal fungi were excluded by 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 in soils with an intact root system. Soil N dynamics were unaffected by root presence/absence. These results are evidence of rapid P uptake, but not N uptake, by tree roots, suggesting a very effective P acquisition process in these lowland rainforests.

Keywords

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

1   A long-standing paradigm in terrestrial ecology is that tropical forest productivity is limited by

2   phosphorus (P) availability (Vitousek, 1984; Vitousek and Sanford, 1986) because the strongly

3   weathered soils of the tropics are depleted in P (Walker and Syers, 1976; Wardle et al., 2004). There is

4   a wealth of indirect evidence for P limitation in tropical forests, including high N:P ratios in leaves and

5   correlations between forest productivity and soil P stocks at continental scale (Quesada et al., 2012;

6   ter Steege et al., 2006). Nutrient addition experiments confirm that soil microbial communities

7   experience P limitation in tropical forests (Camenzind et al., 2018), but these experiments do not

8   always confirm a P limitation in trees (Cleveland et al., 2011; Wright, 2019). The lack of a clear growth

9   response to P addition in tropical forests on P-poor soils has been taken to suggest that these trees are

10 strongly adapted to the low P conditions (Turner et al., 2018). Still, it is not known whether the added

11 P is quickly occluded in the soil mineral fraction or assimilated by microbes (Olander and Vitousek,

12 2004), making it unavailable trees, or if trees are very effective in acquiring P (e.g. from dead organic

13 matter) and hence are not experiencing P limitation as suggested by Gill and Finzi (2016).

14 We used a NxP fertilization experiment in the lowland rainforests of French Guiana to explore the

15 effectiveness of added P uptake by plants. To this end, we assessed the fate of added P fertilizer and

16 compared this to the fate of added N, a nutrient that is usually in ample supply in tropical rainforests

17 (Hedin et al., 2009). We hypothesized that the trees, adapted to low P availability soils, are much more

18 effective in the assimilation of added P than in the assimilation of added N, which is more abundant in

19 this forest (Van Langenhove et al., 2019). The fertilization experiment started in 2016 at the Paracou

20 research station in French Guiana and consisted of twelve plots that received a +N, +P, +NP or no

21 treatment (control). Soils are highly weathered and have typical characteristics associated with low

22 fertility, such as low cation exchange capacity, high acidity and very low total and available P

23 concentrations (Sabatier et al., 1997; Gourlet-Fleury et al., 2004; Grau et al., 2017; see supplementary

24 text). Due to a sesquioxide dominated mineral fraction and the presence of 1:1 clays such as kaolinite,

25 these soils have a high capacity to adsorb mineral P, reducing its availability to plants (Sposito, 1989).

26 The large standing forest biomass in the French Guianese lowland rainforest (Gourlet-Fleury et al.,

27 2004) seriously complicates detection of plant nutrient uptake, considering the large and highly

28 variable nutrient stocks in the plant community. In addition, the very high species richness in these

29 forests makes it difficult to replicate the plant community from one plot to the next, so fertilization

30 effects can only be compared among a few common species that are found in multiple plots. Instead

31 of assessing trees directly, we chose to focus on soil nutrient dynamics in presence and absence of the

32 root system. Therefore, we used a root exclusion cylinder (REC) technique (Huang and Schoenau 1997).

33 RECs were PVC collars inserted 20 cm into the soil to sever all near-surface roots and mycorrhizal

34 hyphae, and were installed in every plot prior to the first nutrient addition in 2016. To follow changes

35   in soil N and P availability we used commercially available PRS^{TM} probes (Western Ag Global, Saskatoon,

36   SK, Canada), which provide proxies for plant available ions in soil solution, including inorganic N (N_i)

37   and inorganic P (P_i), while they are in contact with soil (Qian and Schoenau, 2002). To measure changes

38   in soil N_i and P_i availabilities over time, probes were inserted in the soil four times in 2017; one month

39   before fertilization, and four days, four weeks and finally eight weeks after fertilization. Inserting PRS

40   probes both inside and outside the RECs allowed us to assess the differences in N_i and P_i availabilities

41   with time in the same soil mass, which either included or excluded roots, following fertilization. With

42   this setup, we were able to account for occlusion of added fertilizer into sesquioxides, occurs rapidly

43   after fertilization (e.g. Olander and Vitousek 2004; Buehler et al., 2002). Details of the methods and

44   statistics are presented in the supplementary text.

45   After fertilization, the plots receiving additional N, P or NP exhibited significant increases in N_i or P_i

46   availabilities, respectively, with initial peaks declining over the following two months (Fig 1.).

47   Additionally, in the absence of roots, P_i availabilities increased more than 10-fold following P addition

48   and 3-fold following NP addition (Fig 1B). Root removal can also cause changes in aluminum reactivity

49   (Barra et al., 2018) or microbial biomass (Minz et al., 2013), which may impact P_i availability. However,

50   these changes alone are unlikely to explain the large differences in post fertilization P_i availability

51   observed between root inclusion and exclusion treatments. If they had a substantial influence, these

52   effects would most likely also be reflected in the control or +N treatment. The difference in P_i

53   availability between the P and NP treatments may be related to greater microbial P uptake and growth

54   in the NP treatment (Fanin et al., 2016), but this was beyond the scope of the study. Importantly, in

55   the presence of roots the increases in P_i availability in response to P and NP addition were significantly

56   smaller (Fig 1A) than in the absence of roots, while for N_i the presence or absence of the root system

57   did not affect its availability (Fig 1 C and D). The contrasting dynamics of soil N and P suggest that the

58   root system rapidly assimilated the added P while the added N remained in soil solution even in the

59   presence of roots. This indicates fast and effective plant uptake of added P and most likely implies that

60   the plants in this ecosystem are also very effective in taking up the P that continuously cycles through

61   the forest (Reed et al., 2011). Such effective P uptake could avoid plants running into P limitation, even

62   when soil available P is low, potentially clarifying the lack of growth response to P addition in several

63   tropical P addition experiments (see e.g. Wright et al., 2019). Our study further demonstrates that

64   combining a root exclusion technique with a nutrient availability proxy (first demonstrated by Huang

65   and Schoeneau, 1997) can provide new insights into the (rapid) uptake of added nutrients by the root

66   system over time in nutrient addition experiments, and to identify which elements are in greatest

67   demand. This method is particularly valuable in highly diverse, tree-based ecosystems where

68   identifying biomass and nutrient stock changes is a major challenge.

Acknowledgements

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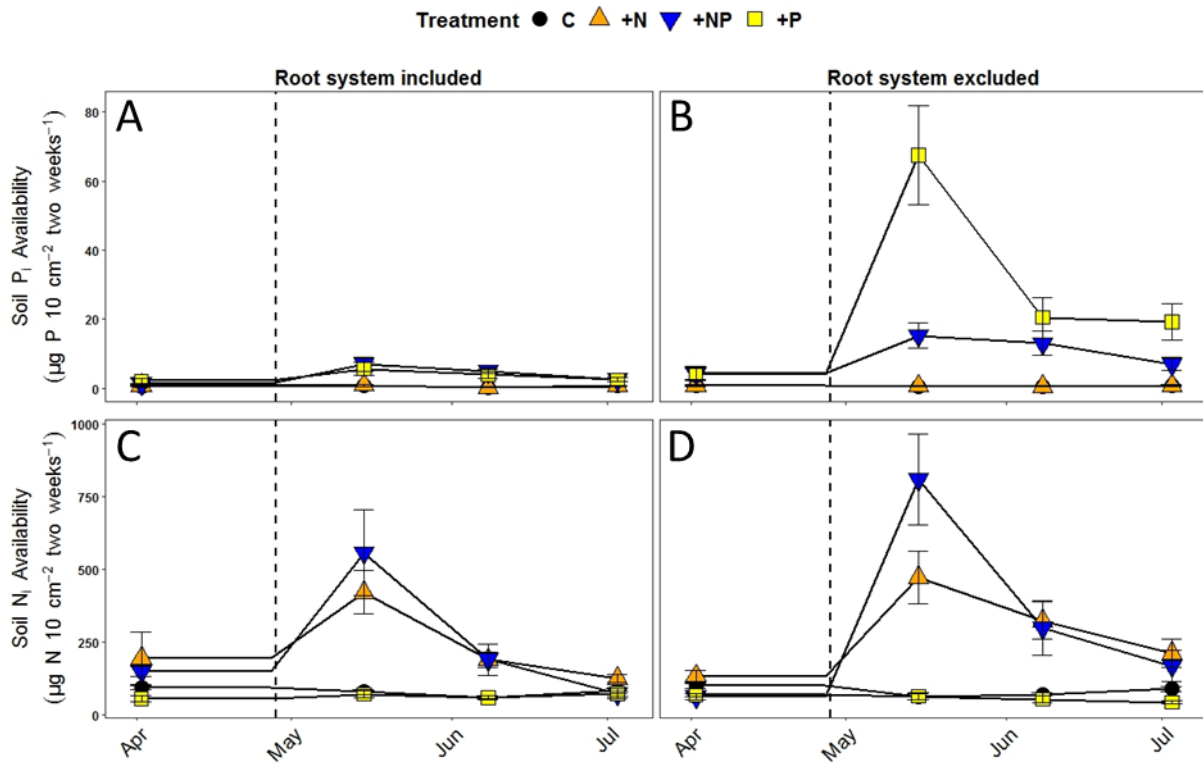
Tables and Figures

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.