

Multiple nutrients constrain fine root functioning in a lowland tropical rainforest: initial responses from a large-scale nutrient manipulation experiment in Central Amazonia

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Abstract

Phosphorus (P) is hypothesised to be the main nutrient limiting forest productivity in tropical forests, but more recent evidence suggests that multiple nutrients could regulate forest functioning. Root functional trait expression represents a trade-off between maximising the acquisition of limiting resources and minimising root tissue construction and maintenance. Therefore, if the limiting soil nutrient supply is increased, plant investment in root biomass and nutrient uptake strategies should decrease. To test this hypothesis we investigated how fine root traits associated with nutrient acquisition responded to large-scale nutrient additions of nitrogen, phosphorus and cations in a slow-growing mature tropical forest established on low fertility soils in the Central Amazon. To evaluate short-term responses to nutrient addition 6 months after fertilisation commenced, we sampled young fine roots (<2mm diameter), measuring root biomass and productivity, root morphological traits (root diameter, specific root length, specific root area and root tissue density) and root phosphatase enzyme activity. We hypothesised that if tropical forests are P limited, responses to P addition would be strongest, resulting in i) a decrease in root production; ii) a shift in root morphology from acquisitive to more conservative traits by increased root diameter and decreased specific length and area and iii) decrease in the investment in phosphatase enzyme. As expected, root phosphatase activity decreased by ~13% with P addition. Among the root morphological traits, root diameter increased, mainly for the 0-10 cm soil layer, with the addition of cations and P, but there were no significant effects on other root morphological traits. Contrary to expectations, root productivity was >50% higher in plots where cations were added, with no effects of P addition. Although we found support for the hypothesis that P limits some aspects of plant functioning in this Central Amazon forest, the results also suggest that cations could play an important role in controlling the expression of root traits. We conclude that multiple nutrients may limit belowground process in Central Amazon forests and that even slow-growing tropical forest can respond very rapidly to changes in soil nutrient availability.

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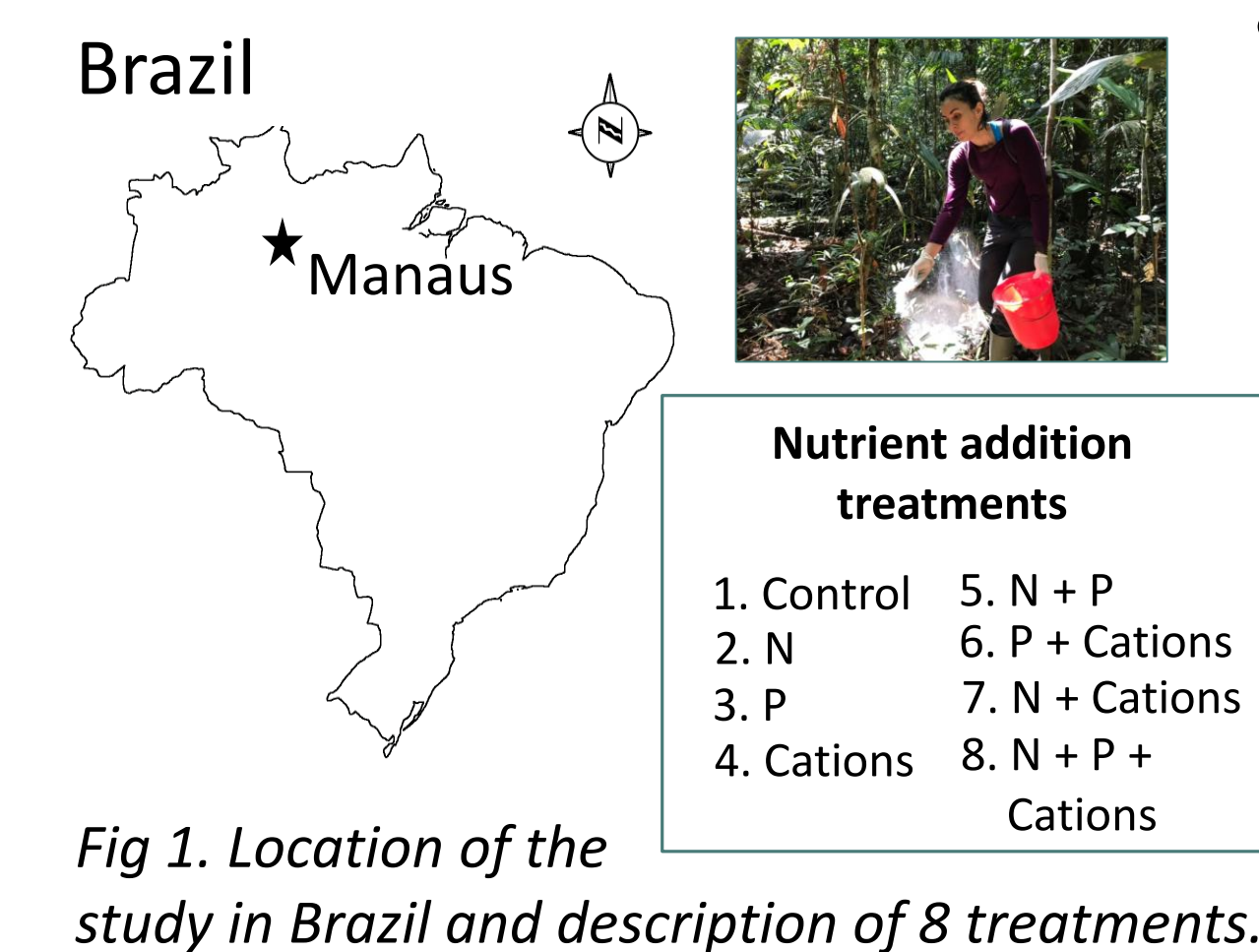
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1. Introduction

- Phosphorus (P) is considered the main nutrient limiting productivity in tropical forests¹
- 60% of Amazon forests grow in low-fertility soils²
- Root traits expression represents a trade-off between maximising the acquisition of resources and minimising root construction and maintenance costs³
- Plant investment in root biomass and nutrient uptake strategies should decrease with alleviation of nutrient limitation

How do fine root traits respond to nutrient addition in a slow-growing tropical forest in central Amazon?

2. Methods



- AFEX (Amazon Fertilisation Experiment)**, located in low-fertility soils in a lowland *terra firme* forests near Manaus, Brazil
- 32 plots (50 x 50 m) where **N**, **P** and **cations** (Ca, Mg, K) were added

- Fine roots (<2mm diameter) sampled using **ingrowth cores** (IGC)⁴ down to 30 cm (Fig 2a)
- Total **productivity** was calculated and subsamples were scanned for **morphological traits**⁵ (Fig 2b)
- Arbuscular mycorrhizal** (AM)⁵ (Fig 2c) colonisation and **root phosphatase activity**⁶ were also determined



Fig 2. a) Details of the IGC in the field; b) image of roots scanned to determine morphological traits; c) root stained to account for AM colonisation.

3. Results

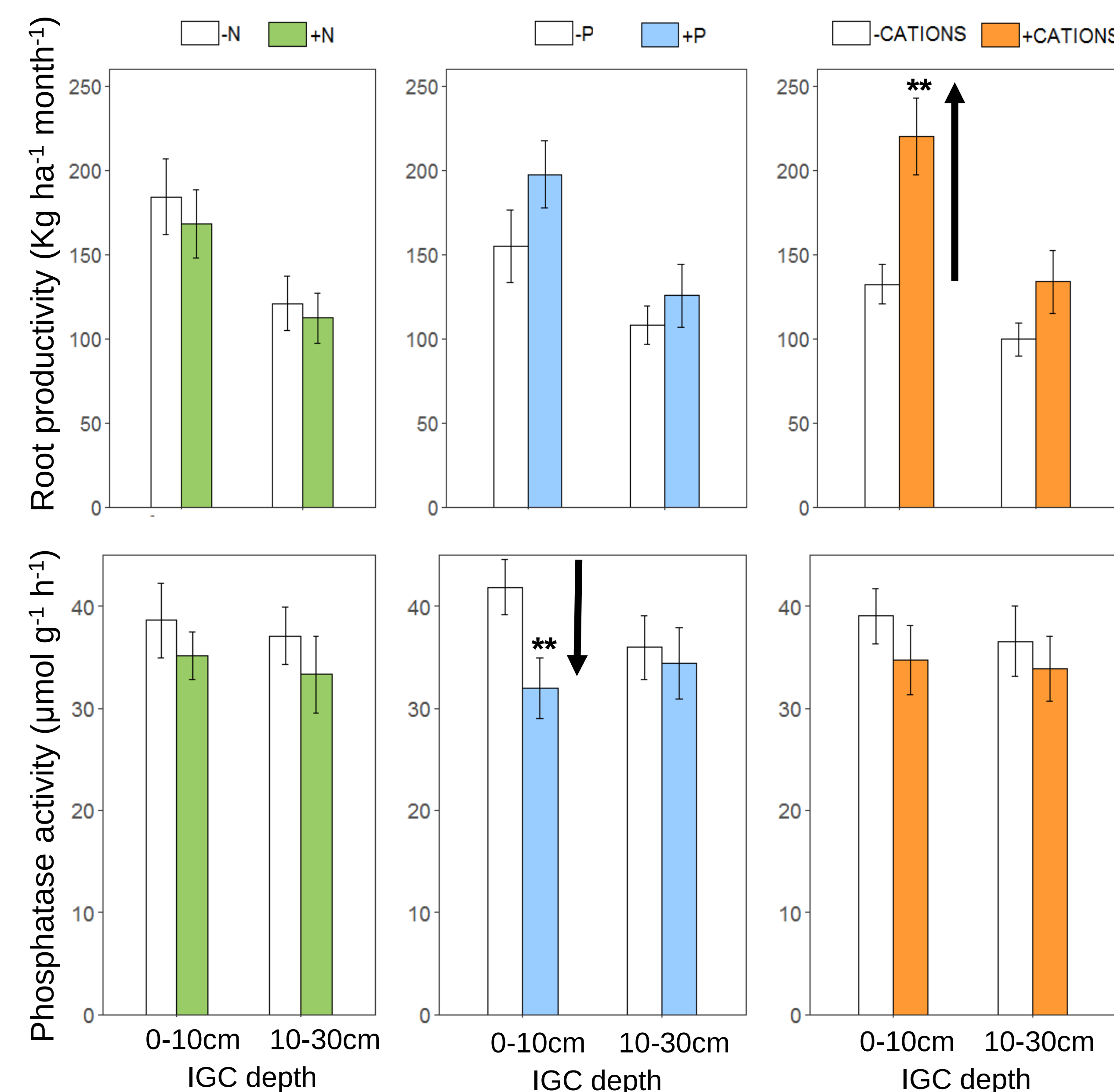


Fig 3. Responses of root productivity and root phosphatase activity after nutrient addition in two different soil depths. White bars are plots without the addition of a specific nutrient (n=16). Coloured bars are plots with the addition of nutrients (n=16).

- Increased root diameter with **P addition** (0-10cm) and **cations addition** (0-30cm)
- No effects of nutrient addition on root specific length, area or tissue density

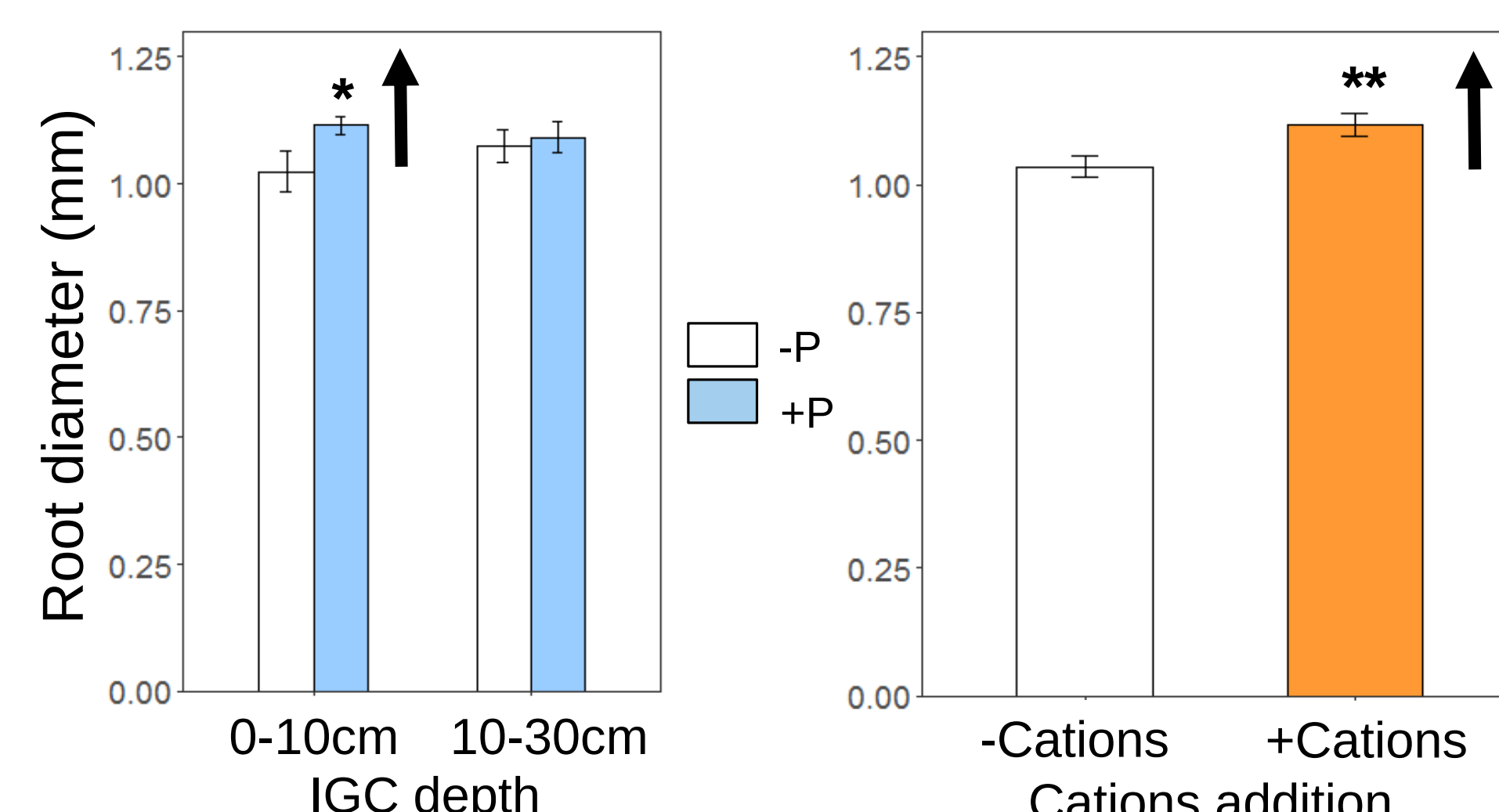


Fig 4. Responses of root diameter to P addition (blue bars; 0-10 and 10-30 cm) and cations addition (orange bars; mean 0-30 cm).

- Root productivity increased **~52% with cations** addition only
- No effects of N and P addition
- Root phosphatase activity decreased **~23% with P addition** (0-10 cm soil depth only)
- No effects of N and cations
- Total root colonisation by **AM increased ~53% with P addition** (although not significantly; n=4)

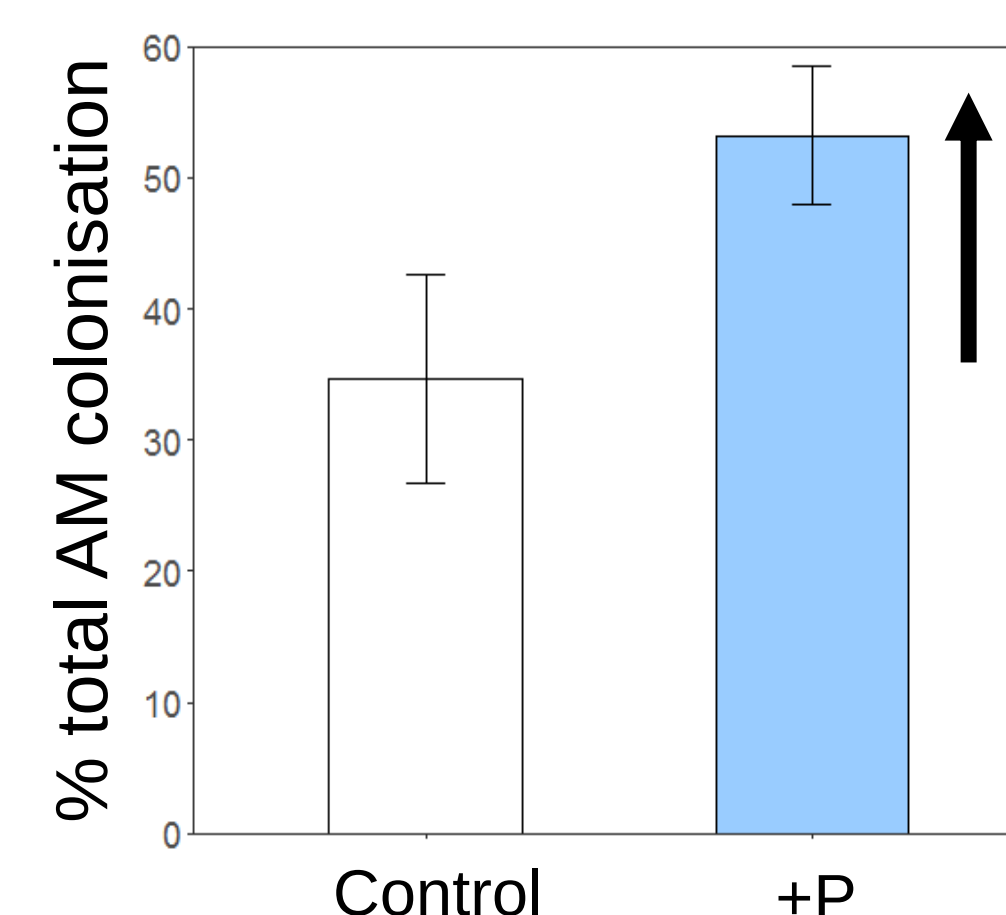
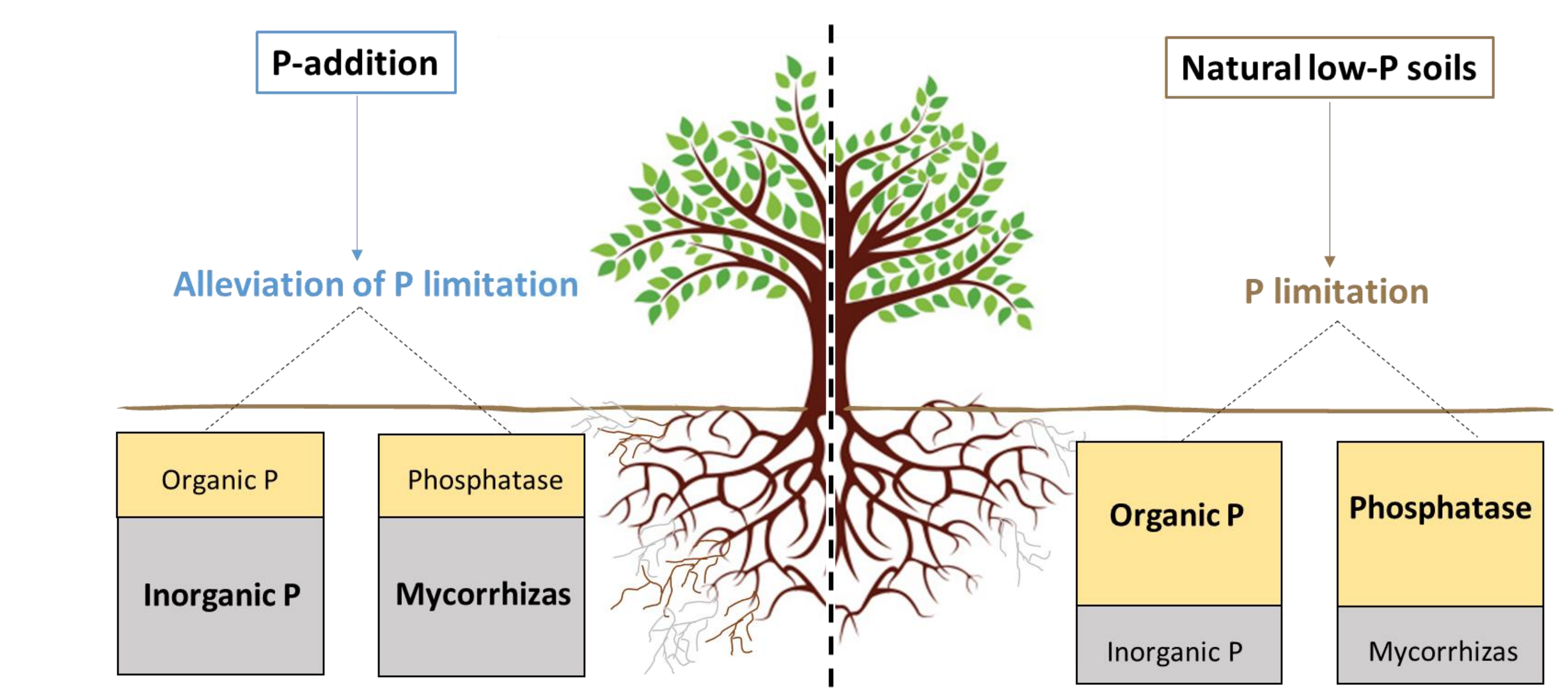


Fig 5. Responses of root AM colonisation to the addition of P (only control and +P plots in the 0-10 cm soil layer).

4. Discussion

- Higher **root productivity** with cations addition:
 - Sign of root limitation by **cations**?
 - Short-term response
- Increase, rather than decrease in **root diameter** with P and cations addition:
 - Increased mechanical protection against pathogens⁷
 - Increased number of root cortical cells that could associate with mycorrhizas**⁸
- Decrease in phosphatase exudation & increase in mycorrhizal colonisation with P addition:
 - Alleviation of P limitation**
 - Shift from **P-mining** (phosphatase) to **foraging strategies** (mycorrhizas) with increased P availability⁹



5. Conclusions

- Root traits, even in slow-growing Amazon forests can respond very rapidly to changes in soil nutrient availability
- Multiple nutrients may limit belowground processes in central Amazon forests:
 - Direct and clear evidence for **P limitation**
 - Direct or indirect **role of cations** limiting plants
 - No effect of **N** addition on fine roots
- Shift in allocation between **P-uptake strategies** with alleviation of P limitation