

## Title of project or data set

Data and code associated with Wong, M., et al. Trees adjust nutrient acquisition strategies across tropical forest secondary succession.

## Dataset version and citation

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## Abstract

Nutrient limitation may constrain the ability of recovering and mature tropical forests to serve as a carbon sink. However, it is unclear to what extent trees can utilize nutrient acquisition strategies – especially root phosphatase enzymes and mycorrhizal symbioses – to overcome low nutrient availability during succession. We use a large-scale, full factorial nitrogen and phosphorus fertilization experiment of 76 replicate plots along a tropical forest secondary succession gradient in Panama to test the extent to which trees adjust nutrient acquisition strategies. We show that tropical forests are highly dynamic in adjusting strategies – particularly root phosphatase – during forest recovery, reflecting a shift from strong nitrogen to weak phosphorus limitation over succession. We contextualize these results within a broader meta-analysis, where tree strategies also dynamically respond to nutrients and forest age. Together, our findings indicate that high functional diversity characterizes nutrient strategies in tropical forests, likely critical for alleviating nutrient limitation on the carbon sink.

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## Keywords

Nutrient limitation, root phosphatase, mycorrhizal fungi, nitrogen, phosphorus, tropical carbon sink, tropical forests, biodiversity, meta-analysis

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### Timeframe

- Begin date: November 2019
- End date: September 2023
- Data collection ongoing/completed? Completed

### Geographic location

Agua Salud Project (9°13'59" N, 79°41'59" W)

Gigante Peninsula (9°06'31" N, 79°50'37"W)

## Methods

### Field study site

We conducted the study at the Agua Salud Project, a 15 km<sup>2</sup> area near Soberania National Park, and the Gigante peninsula in the Barro Colorado Nature Monument, both located within the Republic of Panama. The study spans nitrogen and phosphorus factorial fertilization for 0.16-ha plots across three forest ages in early secondary succession within the Agua Salud Project and for 0.16-ha plots in mature forest at Gigante. The nitrogen and phosphorus factorial experiment within the Agua Salud Project (9°13'59" N, 79°41'59" W) was conducted on plots in forests recovering from pasture at three different age class groupings: forests that were directly recovering from cleaned pasture (0 years), and forests at 10 (approximately between 8-12) and 30 (approximately between 26-30) years of recovery (Van Breugel *et al.* 2013), and had been fertilized for four years at the time of sampling (note that at the time of sampling, the 0-year-old forest now was 4-year-old forest). Each treatment was replicated five times, for a total of 60 plots. For the mature forest age class (>600 years since human disturbance), the nitrogen and phosphorus factorial fertilization plots (9°06'31" N, 79°50'37" W) were replicated four times, for a total of 16 plots, which had been fertilized for 22 years at the time of sampling. Across all sites, fertilizer was applied by hand four times a year at rates of 125 kg N ha<sup>-1</sup> yr<sup>-1</sup> as urea and 50 kg P ha<sup>-1</sup> yr<sup>-1</sup> as triple superphosphate. The mean annual temperature was 26°C, with a mean annual precipitation of 2700 mm and 2600 mm at Agua Salud and Gigante, respectively, with a distinct dry season between January and April. Soil types at Agua Salud are closely related Oxisols (Inceptic Hapludox) while, at Gigante, the soils are Oxisols derived from a Miocene basalt.

### Root collection

We randomly collected five soil cores (0-10 cm depth) within each of the 76 plots during the end of the wet season of 2019. The wet season typically represents periods of higher belowground activity (Turner *et al.* 2013; Turner & Wright 2014). In the laboratory, we sampled the soils for fine roots (0-1 mm) and kept roots in the refrigerator (4°C) for no more than two days before assaying roots for root phosphatase activity. The 0-1 mm size class has been found to represent first to third-order roots (Wurzburger & Wright 2015) that most actively exchange nutrients. A second smaller subsample was preserved in 95% ethanol and refrigerated at 4°C for subsequent analysis for arbuscular mycorrhizal colonization. To scale phosphatase activity rates per gram of root to the forest scale, we collected fine root biomass for 64 of the 76 plots (four replicates of each treatment per age class) in the middle of the rainy season (early August to middle September) of 2019 (Tang 2022). Briefly, five soil cores (6 cm in diameter to 10 cm depth) per plot were sampled and homogenized, and live fine roots (<2 mm) were collected, dried, and weighed.

### Root phosphatase activity

To quantify root phosphatase activity, we used a method adapted from Turner *et al.* (2001), using para-nitrophenyl (pNPP) and bis para-nitrophenyl (bis-pNPP) as analogue substrates for phosphomonoesterase and phosphodiesterase, respectively. Phosphomonoesterase is the dominant root phosphatase enzyme that hydrolyzes simple phosphate monoesters to release a phosphate ion for plant uptake, while phosphodiesterase hydrolyzes nucleic acids and phospholipids to release a

monoester phosphorus group (Browman & Tabatabai 1978; Tabatabai 1994). The monoester group further requires phosphomonoesterase to produce a phosphate ion for plant uptake, thus phosphodiesterase represents more plant investment in acquiring phosphorus from less labile sources (Turner 2008).

For each plot, we collected three subsamples of fine roots for measuring phosphomonoesterase activity, three subsamples for phosphodiesterase activity, and one for measuring color production without substrate added. Briefly, between 200-500 mg of fresh root were added to a glass vial with 9 mL of 50 mM sodium acetate-acetic acid buffer (pH 5.0) and shaken in a water bath at 26°C for five minutes to simulate surface soil temperatures. To initiate the reaction, we added 1.0 mL of 50 mM pNPP or 10 mM bis-pNPP (5.0 mM and 1.0 mM final concentration, respectively). The reaction was terminated by mixing 0.5 mL of buffer/substrate solution with 4.5 mL of 0.11 M NaOH, which was then vortexed and measured for absorbance at 405 nm against paranitrophenol (pNP) standards on a spectrophotometer. Two sodium acetate-acetic acid buffer and substrate blanks were run for every assay. Roots were removed from the vials and dried at 60°C for 3 days to express the activity as  $\mu\text{mol pNP g}^{-1}$  dry mass roots  $\text{h}^{-1}$ .

### Arbuscular mycorrhizal colonization

We focused on arbuscular mycorrhizal fungi as 75% of the trees in our plots are identified as arbuscular mycorrhizal (23% of trees did not have a known mycorrhizal association) based on associations derived from Steidinger *et al.* (2019). We cleared preserved root samples in 5% KOH between 60 and 70°C for up to seven hours, neutralized for 15 minutes in 2% HCl, and stained with 0.05% trypan blue in a 1:1:1 mixture of lactic acid, glycerol, and deionized water for 15 min at 70°C following Wurzburger & Wright (2015). Roots were destained in a 1:1 lactic acid glycerol solution for a minimum of 12 hours prior to observation. We studied roots under a compound microscope and quantified the number of mycorrhizal structures (arbuscules, vesicles, and hyphae) using a random-intercept method (McGonigle *et al.* 1990). Mycorrhizal colonization was calculated as the percentage of fine-root length colonized by either arbuscules, vesicles, or hyphae (Supporting Information). If intracellular coils were identified, they were categorized with arbuscules.

### Meta-analysis study selection

To search for mycorrhizal colonization rates across secondary forest age, we searched Web of Science using terms “tropic\* AND forest AND (secondary OR succession) AND mycorrhiza\* AND colonization” which resulted in 49 studies on March 22, 2021. We also searched the terms ((mycorrhiz\* OR fine root\* OR phosphatase OR fixation) AND forest AND (tropic\* OR Borne\* OR Amazon\* OR Africa\* OR Panama OR “Costa Rica” OR Belize OR Brazil OR Peru OR Ecuador OR Colombia OR Venezuela OR “French Guiana” OR Guyana OR Surinam OR Bolivia OR Jamaica OR “Puerto Rico” OR Hawaii OR Cameroon OR Nigeria OR Gabon OR “Central African Republic” OR Malaysia OR Indonesia OR Thailand OR “New Guinea” OR Australia) AND (addition\* OR fertiliz\*)) AND (nutrient OR nitrogen OR phosphorus OR calcium OR potassium)), which resulted in 544 studies on March 22, 2021. To search for responses of root phosphatase and mycorrhizal colonization, we used the terms “forest AND (tropic\* OR Borne\* OR Amazon\* OR Africa\* OR Panama OR “Costa Rica” OR Belize OR Brazil OR Peru OR Ecuador OR Colombia

OR Venezuela OR “French Guiana” OR Guyana OR Surinam OR Bolivia OR Jamaica OR “Puerto Rico” OR Hawaii OR Cameroon OR Nigeria OR Gabon OR “Central African Republic” OR Malaysia OR Indonesia OR Thailand OR “New Guinea” OR Australia) AND “mycorrhiza colonization” AND (secondary OR succession)) which resulted in 61 studies on March 22, 2021. We based these search terms from Wright (2019).

### Meta-analysis data

We focused our meta-analysis on mycorrhizal colonization as a percentage of root length colonized and root phosphomonoesterase activity, the dominant phosphatase enzyme. For each case study, we recorded site locations (latitude and longitude), climatic variables (mean annual precipitation [MAP] and temperature [MAT]). If data were not presented, site latitude and longitude were extracted from Google Maps (<https://www.google.com/maps>) based on the approximate location reported in the publication, and we extracted MAT and MAP from the WorldClim database (<https://www.worldclim.org/>) (Fick & Hijmans 2017). When results were presented graphically, we used DataThief to digitize the data (Tummers 2006).

### Meta-analysis data analysis

To evaluate the effects of fertilization on root phosphatase activity and mycorrhizal colonization, we used the natural log of the response ratio (Hedges *et al.* 1999).

$$\ln RR = \ln\left(\frac{X_{N,P,or NP}}{X_{control}}\right)$$

The variance ( $v$ ) of  $\ln RR$  is calculated as:

$$v = \frac{S_{N,P,NP}^2}{N_{N,P,NP} * X_{N,P,NP}^2} + \frac{S_{control}^2}{N_{control} * X_{control}^2}$$

We calculated the percent change of nutrient acquisition strategies in response to nutrient addition, as  $(e^{R^+} - 1) \times 100$ , where  $R^+$  is the weighted mean effect size. All meta analyses were performed in the “metafor” package in R (Viechtbauer 2010).

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## Location of field samples or specimens

Samples were destructively analyzed. Some duplicate root samples are stored in the Batterman Lab at the Cary Institute of Ecosystem Studies

## Data Table

**Table name(s):** AS\_fertilization\_root\_data

**Table description(s):** Data for mycorrhizal colonization and root phosphatase activity in response to nitrogen and phosphorus fertilization across four forest age classes in Panama

Column name	Description	Unit	Code explanation or date format	Empty value code
trait	Traits include: phosphomonesterase, phosphodiesterase, phosphomonesterase_scaled mycorrhizal colonization, arbuscules, hyphae, vesicles	Described in “unit” column	categorical	
sample	Unique numerical identifier for sample		numerical	
replicate	Numerical analytical replicate if more than one sample was taken per plot		numerical	



<b>value</b>	Numerical value		numerical	
<b>units</b>	The units “uM_pNP_per_g_hr” represents $\mu\text{M}$ (micromoles) of pNP (substrate) per dry gram of root per hour; “mol_pNP_per_ha_hr” represented moles of pNP (substrate) per hectare per hour, which is enzyme activity scaled to fine root biomass on an areal basis; and "percent" ranges from 0-100 for percent colonized of root		categorical	
<b>n_intersections_mycorrhizae</b>	Unique column for mycorrhizal data (number of intersections measured per root). Usually ten but if segments were unclear, these were removed from the dataset prior to analysis		numerical 1-10	blank
<b>plot_number</b>	Unique numerical identifier for plot number		numerical	
<b>site</b>	Numerical grouping of block-design experiment		numerical	
<b>treatment</b>	Treatments include: “C” for control, “N” for nitrogen, “P” for phosphorus, and “NP” for nitrogen and phosphorus		categorical	
<b>location</b>	Locations of plots include: Arnulfo, Gate, Alfagia, Plantation, Gigante		categorical	
<b>forest_age</b>	Forest age groupings include: 4, 14, 30, and >600-year-old forests	years	years	
<b>years_fertilized</b>	Number of years fertilized when data was collected. Groupings include: 4,22	years	years	
<b>N</b>	Nitrogen treatment, whereby 1 represents if nitrogen was added, and 0 represents if nitrogen was not added	0, 1	0, 1	
<b>P</b>	Phosphorus treatment, whereby 1 represents if phosphorus was added, and 0 represents if phosphorus was not added	0, 1	0, 1	

Table name(s): AS\_secondary\_forest\_mycorrhizal\_colonization\_literature\_review

Table description(s): Data for literature review on mycorrhizal colonization rates across secondary succession in tropical forests

Column name	Description	Unit	Code explanation or date format	Empty value code
<b>Citation</b>	Citation abbreviated		categorical	
<b>Reference</b>	Full citation where data was extracted from		categorical	
<b>Location</b>	Location of study		categorical	
<b>lat</b>	Latitude of study location	degrees	numerical	
<b>long</b>	Longitude of study location	degrees	numerical	
<b>MAT</b>	Mean annual temperature	C	numerical	
<b>MAP</b>	Mean annual temperature	mm	numerical	
<b>AM_EM</b>	AM: arbuscular mycorrhizal; EM: ectomycorrhizal		AM: arbuscular mycorrhizal; EM: ectomycorrhizal	
<b>Site</b>	Site or plot name		categorical	blank
<b>Forest_age_years_classification</b>	Forest age of plot (mature forests without a reported age were grouped as "100")	Years	numerical	
<b>Forest_age_years_actual</b>	Forest age of plot known	Years	numerical	
<b>Age_confirmed</b>	Whether or not the forest age was confirmed		Confirmed or unconfirmed	
<b>N</b>	Number of observations within a forest age grouping		numerical	blank
<b>Percent_colonization</b>	Percent root length colonized by mycorrhizal fungi	Percentage (1-100)	numerical	
<b>Standard_error</b>	Standard error of percent root length colonized by mycorrhizal fungi per forest age grouping	Percentage (1-100)	numerical	Blank

<b>Standard_deviation</b>	Standard deviation of percent root length colonized by mycorrhizal fungi per forest age grouping	Percentage (1-100)	numerical	Blank
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Table name(s): AS\_plasticity\_phosphatase\_mycorrhizae

Table description(s): Data for meta-analysis of root phosphatase and mycorrhizal colonization responses to nitrogen and phosphorus additions in tropical forests

Column name	Description	Unit	Code explanation or date format	Empty value code
<b>Citation</b>	Citation abbreviated		categorical	
<b>Reference</b>	Full citation where data was extracted from		categorical	
<b>Ecosystem_stage</b>	Category of study, whether seedling or field study (primary or secondary forest)		categorical	
<b>Study_type</b>	Category of study, whether seedling or field study		categorical	
<b>Fertilization_length_years</b>	Length of fertilization experiment	years	numerical	
<b>Fertilization_rate_kg_N_ha</b>	Annual fertilization rate of nitrogen	kg N /ha	numerical	
<b>Fertilization_rate_kg_P_ha</b>	Annual fertilization rate of phosphorus	kg P /ha	numerical	
<b>Seedling_study_length_days</b>	Length of seedling experiment	days	numerical	
<b>Fertilization_mg_N_pot</b>	Fertilization rate of nitrogen per plant for length of experiment	milligrams per plant	numerical	
<b>Fertilization_mg_P_pot</b>	Fertilization rate of phosphorus per plant for length of experiment	milligrams per plant	numerical	
<b>lat</b>	Latitude of study location	degrees	numerical	
<b>long</b>	Longitude of study location	degrees	numerical	
<b>MAT</b>	Mean annual temperature	C	numerical	

<b>MAP</b>	Mean annual temperature	mm	numerical	
<b>Category</b>	Root phosphatase or mycorrhizal colonization		categorical	
<b>Site</b>	Site or plot name			
<b>Unit</b>	“umol PNPP g root-1 hr-1”, “% colonization”, “m colonized root g-1 plant-1”		categorical	
<b>Control_mean</b>	Mean of control values	Units in “unit” column	numerical	
<b>Control_N</b>	Number of observations within control group		numerical	
<b>Control_se</b>	Standard error of mean of control values	Units in “unit” column	numerical	blank
<b>Control_sd</b>	Standard deviation of mean of control values	Units in “unit” column	numerical	blank
<b>Treatment</b>	“Nitrogen”, “Phosphorus”, or “Nitrogen + Phosphorus”		categorical	
<b>Treatment_mean</b>	Mean of treatment values	Units in “unit” column	numerical	
<b>Treatment_N</b>	Number of observations within treatment		numerical	
<b>Treatment_se</b>	Standard error of mean of treatment values	Units in “unit” column	numerical	blank
<b>Treatment_sd</b>	Standard deviation of mean of treatment values	Units in “unit” column	numerical	blank
<b>ln_response_ratio</b>	Natural log of response ratio (treatment/control), explained in the methods above		numerical	
<b>variance</b>	Variance of log response ratio, explained in the methods above		numerical	blank

### **File Inventory:**

AS\_roots\_README\_04222024.pdf

AS\_code.R

AS\_fertilization\_root\_data.csv

AS\_Plasticity\_phosphatase\_mycorrhizae.csv

AS\_secondary\_forest\_mycorrhizal\_colonization\_literature\_review.csv