Nitrogen and phosphorus additions negatively affect tree species diversity in tropical forest regrowth trajectories

Ilyas Siddique[1]*, Ima C.G. Vieira[2], Susanne Schmidt[1], David Lamb[1], Cláudio J.R. Carvalho[3], Ricardo de O. Figueiredo[3], Simon Blomberg[1], Eric A. Davidson[4]

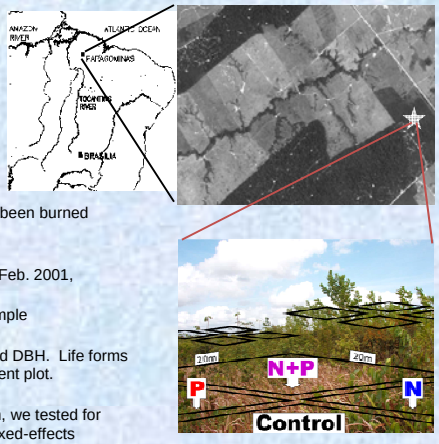
[1] The University of Queensland, School of Biological Sciences, Brisbane, Australia; [2] Museu Paraense Emílio Goeldi, Belém, PA, Brazil
[3] EMBRAPA Amazônia Oriental, Belém, PA, Brazil; [4] The Woods Hole Research Center, Falmouth, MA, USA * *ilysid@gmail.com*

ABSTRACT

Nutrient enrichment is increasingly occurring in many tropical ecosystems, but there is little information on how tropical tree diversity is affected. We re-measured trees annually before and for six years after additions of nitrogen (N) and phosphorus (P) in abandoned Amazonian cattle pastures. Nitrogen and P each stimulated growth of the dominant pioneer, *Rollinia exsucca* (Annonaceae), while N also stimulated growth of two other species. Overall, N or P addition reduced tree assemblage evenness and delayed tree species accrual over time, likely due to competitive monopolization of resources by the few species responding to nutrient enrichment. Surprisingly, N+P effects on tree biomass and species diversity were weaker than N-only and P-only effects, because remnant pasture grass biomass increased dramatically in response to N+P addition, preventing an expected positive N+P synergy for the trees. In conclusion, N or P enrichment may reduce the diversity of coexisting tree species and delay species accrual during structurally and functionally complex tropical rainforest secondary succession.

OBJECTIVES

- To investigate how N and P addition affects rates of biomass accumulation and changes in species composition in young successional Amazonian forests.
- This study was not intended to simulate atmospheric deposition. Such studies are rare for tropical ecosystems, and this one will not fill that void. However, although motivated by other research objectives, these results may be relevant to understanding expected impacts of increasing atmospheric deposition of nitrogen.



METHODS

- Study conducted in abandoned cattle pasture near Paragominas, Brazil, which had been burned repeatedly -- last burn 6 years prior to this study.
- 4 treatments x 3 block replications = 12 plots; each plot 20m x 20m
- Fertilizer applied by hand at the beginning of the rainy seasons in Jan. 2000 and in Feb. 2001, according to the following 4 treatments:
  (1) control without fertilization; (2) 100 kg N ha^{-1} as urea; (3) 50 kg P ha^{-1} as simple superphosphate; (4) N + P at these same rates.
- All individuals >2cm DBH identified by species, tagged, and measured for height and DBH. Life forms with DBH<2cm measured destructively in two 2m x 1m miniplots within each treatment plot. Aboveground woody biomass estimated by allometry.
- To account for spatial variation among plots and blocks before treatment application, we tested for effects of nutrient addition on rates of change (i.e. slopes) over time, using linear mixed-effects regression models.

Fig. 1: Photo of a control plot (left) and an N+P plot (right). Note proliferation of remnant pasture grass with N+P.

SHORT-TERM RESULTS ON BIOMASS

- Tree biomass increased significantly relative to controls after N and N+P addition (but no NxP synergistic effect). See Fig. 2.
- The apparent P response was not statistically significant, perhaps due to high spatial variation among the plots receiving P.
- Remnant grass biomass increased significantly with P and N+P. See Figs. 1 and 2.

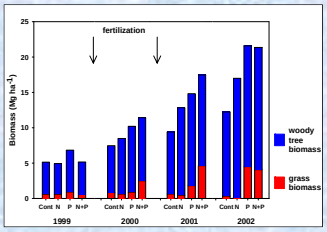


Fig. 2. First 3 years' response of tree and remnant grass biomass to fertilization.

LONGER-TERM RESULTS ON BIOMASS AND TREE SPECIES DIVERSITY

- In the 4th through 6th years after fertilization, the effect of N fertilization on tree biomass dissipated (Fig 3a, b) and grass biomass crashed in P and N+P plots. To ease readability, only fixed effects of mixed models (treatment means) are presented in Figs. 3-5 (i.e. Best Linear Unbiased Predictors).
- Across all treatments tree species richness increased as secondary succession progressed during the observation period. Nitrogen or phosphorus alone delayed tree species accumulation and reduced tree assemblage evenness (Fig. 4).
- Two common pioneers and one mid-successional tree species benefited most from the nutrient amendments (Fig. 5a-c). These species' presence in secondary succession was prolonged by nutrient amendment, perhaps because the added nutrients permitted them to compete for other resources, such as light and water. Their prolonged dominance accounts for slower accrual rates of other species (Fig. 5d)

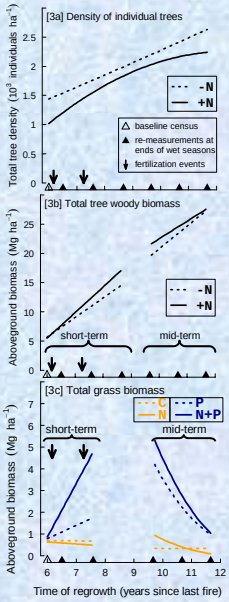


Fig. 3 (left). Trajectories of density of individuals (a), tree biomass (b), and grass biomass (c).

a) The slope of increasing tree density was steeper in the +N plots for the first 3 years, but then declined in the last 3 years.

b) The slope of increasing tree biomass was steeper in the +N plots for the first 3 years, but then declined in the last 3 years.

c) Remnant pasture grass (mostly *Panicum maximum*) biomass increased sharply in P and N+P plots during fertilization years and then crashed during the last 3 years of observation.

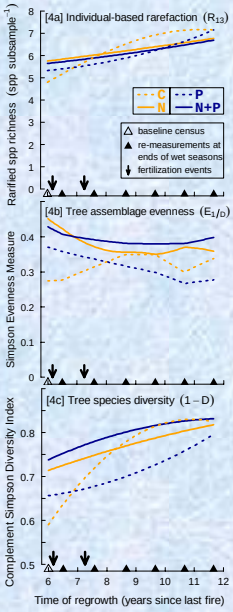


Fig. 4 (left). Trajectories of tree species diversity.

a) Tree species richness in random subsample of 13 individual trees (R_{13}) for each plot-by-census combination: 2nd-order polynomial fit (covariate: initial R_{13}). Nutrient addition depressed the rate of increase of species richness.

b) Simpson Evenness Measure ($E_{1/D}$): 2nd-order polynomial fit (covariate: density of individual trees). Evenness declined in nutrient amended plots.

c) Complement Simpson Diversity Index (1–D): 2nd-order polynomial fit (covariate: initial 1–D). Although diversity was on average initially higher (by chance) in plots randomly selected for nutrient addition, they accumulated species diversity less rapidly than the control plots.

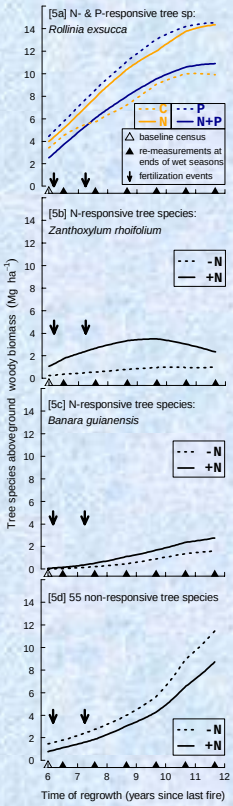


Fig. 5 (left). Trajectories of aboveground woody biomass of single tree species (2nd-order polynomial fit; covariate: density of individuals).

a) The dominant tree species, *Rollinia exsucca* (Annonaceae), accounted for 64% of initial total woody biomass, and was the only species to respond significantly to both N and P additions, but with diminishing effect sizes over time. Overall, *R. exsucca* reached a biomass plateau by 12 years, which was prolonged by nutrient addition.

b and c) Co-dominant *Zanthoxylum rhoifolium* (Rutaceae) and initially rare *Banara guianensis* (Flacourtiaceae) contributed 12% and 0.8% of total initial woody biomass, respectively. Both species responded positively to N addition, but also showed diminishing N responses over time.

d) All other 55 tree species either showed no significant nutrient response, or had too low abundances to permit parametric fits without violating model assumptions. The most abundant non-responsive species was *Vismia guianensis* (Clusiaceae).

CONCLUSIONS

- N-only addition enhanced biomass growth of three common tree species, P-only enhanced one of these species, while dozens of other tree species did not respond to nutrient enrichment.
- This differential stimulation of few common tree species coincided with reductions in tree assemblage evenness and delayed species accrual over time, likely due to competitive monopolization of other resources by few responsive species.
- Consistent negative N×P interactions on tree biomass growth and species diversity contrast with reported N+P synergies and were attributed to a positive N×P interaction in remnant pasture grass growth.
- While growth rates were elevated for only 2 years post-nutrient addition, shifts in relative species growth and reduced assemblage evenness persisted for >3 years post-nutrient addition, favoring nutrient-responsive pioneer and early-secondary species.
- N or P enrichment may reduce the diversity of coexisting species and delay species accrual during structurally and functionally complex tropical rainforest secondary succession.

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