



Is Biological Nitrogen Fixation Important in Tropical Successional Forests?

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Nitrogen (N) used by pasture grasses and secondary forests following land use change may be supplied by the mineralization of soil organic matter, but the possible contribution from biological N fixation (BNF) has been widely debated. Because secondary forests cover about 30% of the tropical forest biome, we need improved understanding of the legacies of previous land use and the recovery of nutrient cycling processes and biomass accumulation in successional forests. Although mature tropical lowland forests often exhibit phosphorus (P) limitation and not N limitation, N losses during land-use change can severely reduce N availability in the pasture and secondary forest ecosystems that follow. Here we present multiple lines of evidence from experimental studies and modeling in a degraded cattle pasture of the eastern Amazon region that indicate an important role for BNF to support the growth of early successional forests.

These pasture soils have large total N and P stocks, but very low levels of Mehlich-III P and inorganic-N. Nutrient amendment experiments demonstrated growth responses of grasses but not native tree species to P addition and responses of some early successional tree species to N addition. In a replicated experimental study using mass balance and a ^{15}N tracer in lined soil pits of (1) plant-free control plots; (2) planted *Brachiaria brizantha* pasture grass, and (3) regrowth of early successional secondary forest species, accumulation of N in grass biomass slightly exceeded estimates of net N mineralization from the plant-free control plots, but was within the margin of error, so inputs of BNF may not have been needed. In contrast, the secondary forest vegetation accumulated about three times as much biomass-N annually as the net N mineralization estimate. Based on isotopic and mass measurements of N-fixing species, BNF was estimated to contribute at least $27 \pm 3\%$ of mean annual plant uptake in the secondary forest regrowth plots.

These experimental results are consistent with results of a quantitative stoichiometric model linking measurements of aboveground and belowground stocks during each phase of land-use change. The model demonstrates that, whereas P is conservatively cycled, N pyrolyzation during pasture formation and management depletes available-N pools, reduces nitric oxide and nitrous oxide emissions, and limits potential rates of secondary forest regrowth. Nutrient limitation is also largely controlled by the N:P stoichiometry of the dominant vegetation in each land use. *Brachiaria brizantha* grass has a low N:P ratio of 14, whereas mature and secondary forest foliage is three times as N-rich. Consequently, the model shows the likely need for a period of significant biological N fixation for early-to-mid-successional forest regrowth. While plant demand stoichiometry changes abruptly with land-use change, the N:P ratio of mineralization changes more slowly due to the buffering capacity of large stocks of soil pools that mineralize gradually. Although BNF is probably important for recuperation of tropical secondary forests following land-use change, the majority of the N taken up by both grasses and secondary forest regrowth arises from mineralization of the stocks of soil N.