

Plant functional constraints on foliar N:P ratios in a tropical forest landscape

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Abstract

Although large scale analyses of foliar N:P ratios suggest an overall pattern of P limitation in tropical forests, analyses within the biome are less indicative of a consistent pattern of nutrient limitation. High tree species diversity and soil heterogeneity are important factors driving the variability of foliar chemistry in the tropics; however, this variability could be reduced at the level of the functional characteristics of the species present at a site. In this study it is hypothesized that foliar N:P ratios would be more constrained when the species are grouped according to functional characteristics, and would reveal patterns of nutrient limitation. The study was conducted in a tropical forest landscape of the Porce region in Colombia, which consists of patches of primary and secondary forests of different ages. The functional groupings revealed consistent patterns of conservative N cycling in species present at young secondary sites, as well as conservative P cycling of the species present later in succession and in primary forests. Although the observed data have limitations in terms of capturing the overall variability for each functional group, the classification used here provided support for the proposed hypotheses. It is concluded that functional composition, rather than taxonomic composition, can potentially improve our understanding of nutrient cycling in tropical forests.

1 Introduction

Large scale analyses of foliar element concentrations suggest well constrained C:N:P ratios at a global level, as well as broad patterns of P limitation in tropical plants and forests (Hedin 2004, McGroddy et al. 2004, Reich and Oleksyn 2004). This pattern of P limitation is conceptually supported on the Walker & Syers model of soil development, which has been elegantly tested on a long-term chronosequence in the Hawaiian islands (Crews et al. 1995, Vitousek 2004). However, the Hawaiian ecosystems are characterized by a low level of biological and biogeochemical diversity and it could be argued that this broad pattern of P limitation may not apply everywhere in the tropics. A recently published compilation of foliar N:P ratios revealed a significant level of variability in tropical plants that challenges

the hypothesis of overall P limitation in the tropics (Townsend et al. 2007). In addition, this database showed that plant element ratios may not be as well constrained as previously believed (e.g. Hedin 2004, McGroddy et al. 2004).

In addition to natural variability of biological species and environmental conditions, patterns of land use also add an important level of variation to the biogeochemistry of the tropical biome. As anthropogenic activities increase in the tropics, secondary forests play an increasing role. Recent work suggests that young secondary forests exhibit N-cycling properties similar to temperate forests on young soils, but as forest ages this pattern switches to P limitation as in mature ecosystems (Davidson et al. 2007). Consequently, forests in the tropical biome may exhibit different levels of N and P limitation depending on their successional status. Co-limitation of both P and N is also an alternative possibility that has been recently suggested (Davidson and Howarth 2007, Elser et al. 2007); however, there is no clear evidence based on foliar analysis that indicates overall patterns of nutrient limitation in the tropics.

The sequence of processes during forest succession, as well as changes in general aspects of structure, are quite predictable (Peet 1992, Guariguata and Ostertag 2001, Rees et al. 2001, Franklin et al. 2002). After the abandonment of agricultural lands in the tropics, light demanding species such as herbs, grasses and ferns are the first colonizers persisting for the first one to five years. Short-lived pioneers, commonly N-fixing legumes, replace the initial colonizers. After 5-20 years the short-lived pioneers are gradually replaced by long-lived pioneers and shade-tolerant tree species (Guariguata and Ostertag 2001). These different functional groups of species may have important differences in chemical composition that can influence the overall biogeochemical status at the ecosystem level.

If young tropical forests exhibit a conservative N cycle (Davidson et al. 2007), it can be hypothesized that foliar N:P ratios of the first colonizers are relatively low compared to species in later stages in successional development. In addition, species in a closed-canopy forests may present higher foliar N:P ratios indicative of a conservative P cycle.

Based on this set of ideas we evaluated foliar N and P concentrations of plants in a tropical forest landscape composed by patches of primary and secondary forests. First, we hypothesized that foliar N:P ratios would present important differences among different functional groups along the successional gradient. Second, foliar N:P ratios would be lower early in succession and higher in later stages of stand development, exhibiting a switch from a conservative N cycle in young secondary forests to a conservative P cycle in mature systems.

2 Methods

Foliage samples were collected from primary and secondary forests of the Porce region, Colombia (6° 45' 37" N, 75° 06' 28" W). Mean annual precipitation is 2078 mm, and mean annual temperature at 975 m a.s.l. is 22.7 °C. This area is a fragmented landscape

with secondary forests of different ages (5-30 years) intermixed with patches of remnant primary forests (Sierra et al. 2007). Soils are derived from granitic rocks, mainly Entisols and Inceptisol, with Ustoxic Dystropept, Typic Tropaquent, and Typic Tropopsamment as the main subgroups. Steep slopes dominate the topography of this region, where rates of erosion may exceed rates of soil formation in some sites.

At each forest type, *a priori* tree functional groups were defined according to their role in C and N cycling. This functional classification was based on previous groups proposed by Denslow (1996) and Ashton et al. (2001) for tropical forest trees (Table 1). Samples of foliage were collected from the canopy using a telescopic pole pruner. Foliage samples were classified and mixed according to their functional group, air-dried, and then oven-dried before nutrient analysis. Composite samples of approximately 20 g containing a random mix of species by each group were ground to pass a 0.2 mm mesh in a Wiley mill. Three replicates per functional group were analyzed for C, N and P at the Central Analytical Laboratory, Oregon State University. For C and N, a Leco CNS-2000 Macro Analyzer was used to determine element concentrations, and for P a Perkin Elmer Optima 3000DV plasma optical emission spectrometer.

3 Results

All element ratios are reported here on a mass basis (Annex 1). The average foliar N:P ratio found for all species groups was 20.73 ± 8.01 (\pm SD), and ranged from a minimum of 8.25 in secondary forests to a maximum of 33.54 in primary forest (Figure 1). On average, species groups in secondary forests had a foliar N:P ratio of 17.28 ± 8.45 , and of 24.17 ± 6.07 in primary forests. A two sample Welch *t*-test performed on the data provided evidence for differences between the means between both forest types (p -value = 0.033).

The lowest N:P ratios were found for pioneer species in the stages of stand initiation and exclusion. Species in later stages of forest development had higher foliar N:P ratios as well as legume species in secondary forests. In primary forests, legume species had a lower average N:P ratio than species of this family in secondary forests. The highest values of foliar N:P were found for species in the upper canopy of primary forests and for regenerating trees in canopy gaps.

4 Discussion

Foliage chemistry in the forest landscape of the Porce region of Colombia showed a high level of diversity; however, some well constrained patterns emerged as different levels of heterogeneity were distributed among different levels of observation, *i.e.*, forest type and functional groups (Figures 1 and 2). These results provide supportive evidence for the hypotheses previously stated. First, well constrained N:P ratios were found for the different species groups and forest types analyzed (Figure 1 and 2). Second, lower foliar N:P ratios

Table 1. *A priori* defined functional groups for primary and secondary forest plants. Modified from groups proposed by Denslow (1996) and Ashton et al. (2001).

Group	Characteristics	Effects on C and nutrient dynamics	Some species common in study area
<i>Primary forests</i>			
Legumes	Often dominant plant family. High N concentrations in litter.	High litter production and decomposition rates.	<i>Enterolobium schomburgkii</i> , <i>Inga</i> spp., <i>Pithecellobium jupumba</i> , <i>Acacia</i> spp.
Palms	Voluminous, high lignin content in litter.	High C:N ratios, slow decomposition rates.	<i>Oenocarpus bataua</i> , <i>Euterpe precatoria</i> , <i>Bactris</i> sp.
Upper canopy	Dominant plant form. Shade tolerant, long-lived but may be fast growing.	High litter production, high longevity, diverse litter quality.	<i>Cedrela odorata</i> , <i>Cordia bicolor</i> , <i>Xilopia sericea</i> , <i>Alchornea megaphylla</i> , <i>Anacardium excelsum</i> , <i>Nectandra</i> sp., <i>Ocotea guianensis</i> , <i>Pachira</i> sp.
Gap colonizers	Colonize small gaps. Shade intolerant, short lived, fast growing.	High turnover, low quality litter.	<i>Didymopanax morotoni</i> , <i>Byrsonima arthropoda</i> , <i>Pouruma</i> sp.
<i>Secondary forests</i>			
Pioneers of initiation	Can colonize mineral soils, high abundance, shade intolerant, short lived, fast growing.	High growth rates and turnover, low litter quality.	<i>Piper</i> spp., <i>Heliocharpus americanus</i> , <i>Myrsine</i> spp., <i>Vismia</i> spp.
Pioneers of exclusion	High light demanding, medium-lived, fast growing.	High litter production and growth. Low quality litter	<i>Vochysia ferruginea</i> , <i>Vismia</i> sp., <i>Jacaranda copia</i> .
Legumes	High N concentration in tissues.	High litter production and decomposition rates.	<i>Pithecellobium jupumba</i> , <i>Inga</i> spp., <i>Acacia</i> sp.
Late successional	Shade tolerant, resprouters, long-lived but may be fast growing.	High litter production. Medium litter quality.	<i>Cedrela odorata</i> , <i>Cordia bicolor</i> , <i>Xilopia sericea</i> .

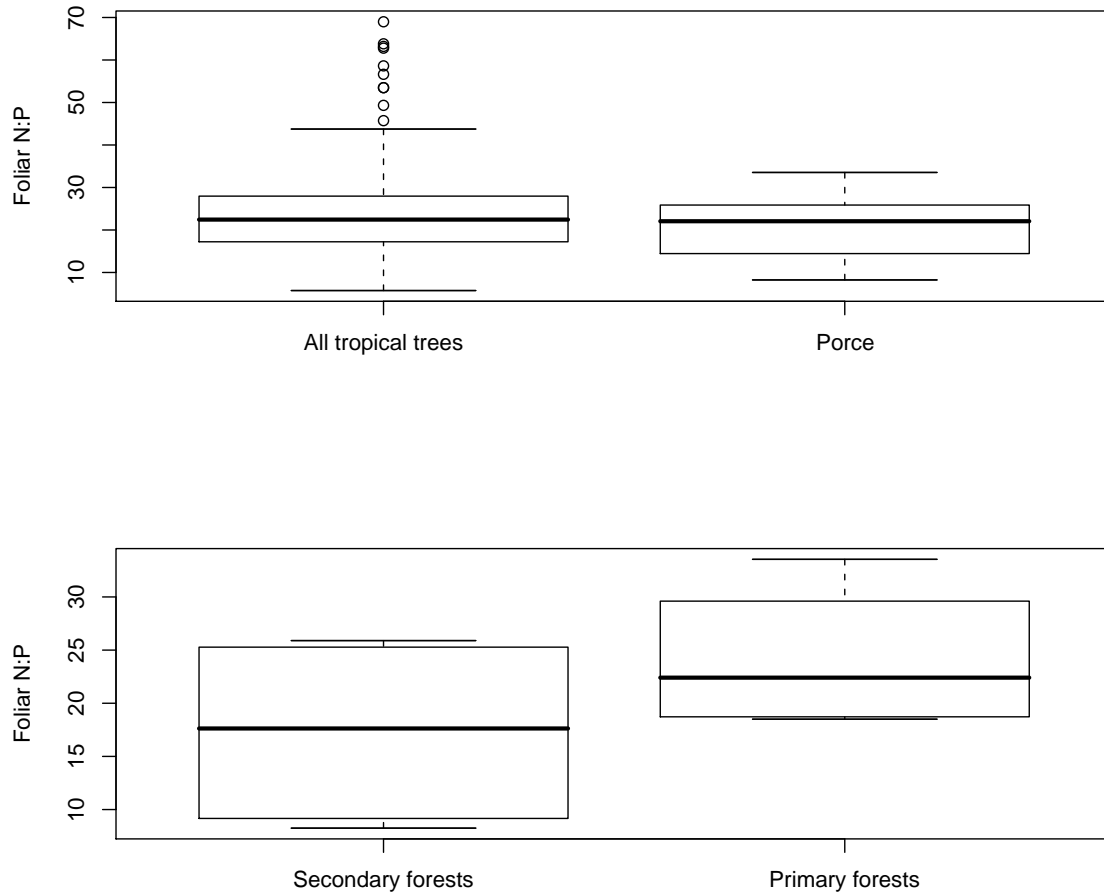


Figure 1: Boxplots of foliar N:P ratios for species in the Porce region, Colombia, compared to N:P ratios of tropical trees compiled by Townsend et al. (2007) (Upper panel). Comparison of foliar N:P ratios of species in primary and secondary forests of the Porce region (lower panel); a comparison of means suggest significant differences (Welch t -test, p -value = 0.03).

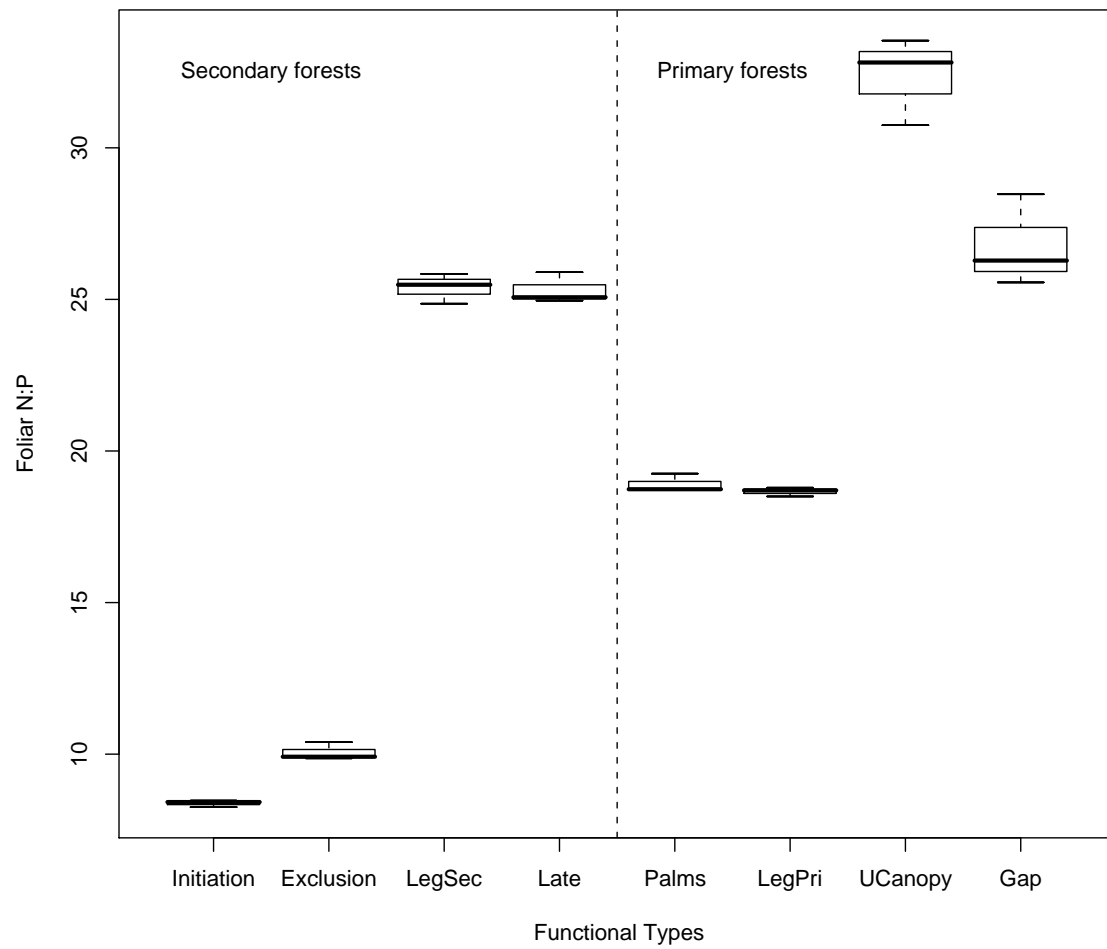


Figure 2: Foliar N:P ratios for the functional groups: pioneers of initiation, pioneers of stand exclusion, legumes, and late successional in secondary forests. In primary forests the groups are palms, legumes, upper canopy, and pioneers in canopy gaps.

were also found in species growing on secondary forests, which supports the hypothesis of a conservative N-cycle in these seral communities. Given that previous land use altered the nutrient status of these soils, these young forests are likely to be under conditions of N limitation (Davidson et al. 2007). Forests without any indication of previous disturbance, *i.e.* primary forests, are more likely under conditions of a conservative P cycle, and perhaps under P limitation (Townsend et al. 2007). Foliar N:P ratios in primary forests were relatively high compared to secondary forests, particularly for the dominant species in the upper canopy. Small disturbances caused by episodic mortality events do not seem to drastically alter the nutrient status, because species regenerating in these gaps do not exhibit low N:P ratios and are more similar to the ratios of species in the upper canopy.

In secondary forests, N:P ratios were more indicative of N limitation for the species groups that are more abundant in the first stages of secondary succession, while species groups more abundant in later stages showed higher concentrations of P relative to N. Legume species, which are common in all stages of succession, seem to play a significant role fixing N into the system that allows for the success of late successional species. Interestingly, N:P ratios of legumes in primary forests were relatively low and almost similar to the ratio for palms, however total N concentrations were still high (Figure 3). Palms, which represent only 5.9% of the aboveground biomass in primary forests (Sierra et al. 2007) had the lowest N and P concentrations, but N:P ratios were higher than the groups present early in succession.

4.1 Limitations and opportunities

Given the sampling methodology used in this study it was not possible to appropriately calculate the variability of foliar chemistry within the functional groups. The measures of variability provided here represent instrumentation error rather than true variability due to the different species within groups. However, the composite samples used for the chemical analyses aggregate this variability and provide a general indication of the overall foliar chemistry for each functional group. Although the comparisons provided may not represent within group variability, they still suggest patterns that are supported by theory. The value of this analysis lays on suggesting the hypothesis that foliar N:P ratios could be constrained by functional characteristics of the species present at a site.

Taxonomic diversity of trees is associated with chemical diversity in forest canopies (Townsend et al. 2008), which could complicate biogeochemical analysis in tropical ecosystems. However, predictable ranges of biogeochemical variation emerge when taxonomic groups are pulled together according to their functional characteristics. In fact, the functional grouping used in this analysis support recent developments in the understanding of nutrient cycling (Davidson et al. 2007, Davidson and Howarth 2007). However, certain broad functional groups used for global scale modelling may not be appropriate for analyzing foliar chemistry as suggested by Hättenschwiler et al. (2008). If the results of this study are confirmed with larger datasets and different sites, significant progress can be

achieved in the understanding of the global patterns of nutrient limitation.

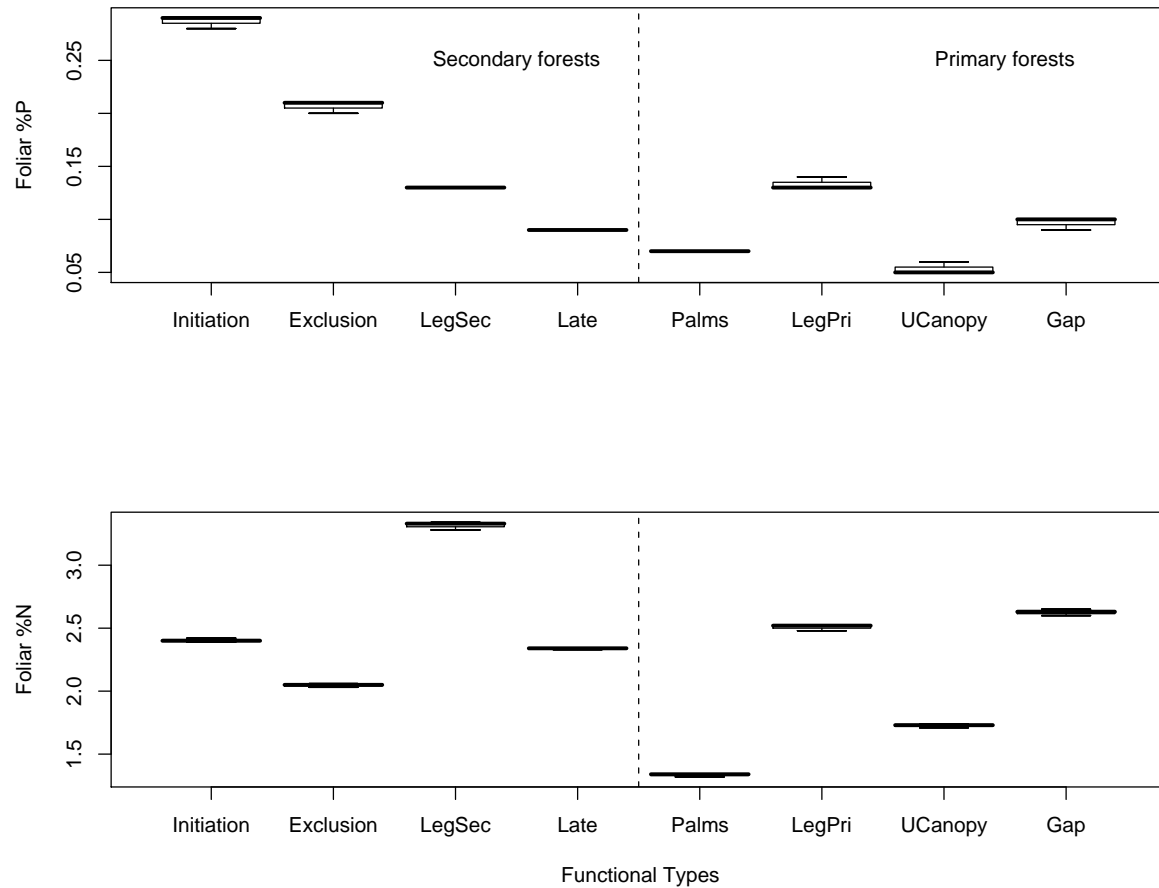


Figure 3: Foliar P and N concentrations on a mass basis for the functional groups present in primary and secondary forests.

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Appendix 1. groups present	Average nutrient concentrations in primary and secondary forests				concentrations in foliage of the different region, Colombia.									
	% P	%K	%S	%Ca	%Mg	Mn (ppm)	Cu (ppm)	B (ppm)	Zn (ppm)	Fe (ppm)	Al (ppm)	%C	%S	%N
<i>Primary forest</i>														
Palm	0.07	0.92	0.06	0.13	0.13	229.25	55.64	6.70	9.20	50.98	54.55	48.03	0.12	1.33
Leg prim	0.13	1.37	0.07	1.35	0.28	121.27	109.28	27.85	20.56	69.73	109.94	44.22	0.12	2.51
Up Canopy	0.05	0.74	0.04	1.41	0.30	405.82	24.59	26.52	13.29	41.15	7729.93	41.59	0.11	1.72
Gap	0.10	1.17	0.14	1.83	0.76	494.12	44.48	30.12	39.49	91.96	308.21	45.00	0.21	2.63
<i>Secondary forest</i>														
Initiation	0.29	2.52	0.10	1.55	0.29	158.02	18.67	63.97	41.11	150.36	834.48	41.32	0.16	2.40
Exclusion	0.20	1.82	0.10	2.01	0.30	109.67	30.17	44.14	38.67	171.01	1203.36	43.03	0.13	2.05
Leg sec	0.13	1.81	0.09	0.97	0.53	204.90	24.46	26.62	20.42	203.24	71.27	45.67	0.20	3.32
Late	0.09	1.14	0.10	1.21	0.33	286.47	19.34	24.11	16.87	89.24	2731.24	44.66	0.17	2.34