

# Soil and Leaf Micronutrient Composition in Contrasting Habitats in Podzolized Sands of the Amazon Region

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## ABSTRACT

Plant macronutrient distribution in podzolized sands of the Amazon caatinga has received attention in several studies; however, the distribution of micronutrients has not been assessed. Soil micronutrient availability has been hypothesized to reflect contrasting habitat characteristics as well as fundamental differences in substrate, and leaf micronutrient composition may reflect the macronutrient content needed to maintain balance for leaf cell functions. In this study, soil and leaf samples were obtained in a toposequence (valley, slope, and mound). Available soil micro- and macronutrients as well as total leaf content were measured by inductively coupled plasma-atomic emission spectrometer and mass spectroscopy. Soil Zn ( $<1.41 \text{ mg}\cdot\text{kg}^{-1}$ ) and B ( $<0.31 \text{ mg}\cdot\text{kg}^{-1}$ ) as well as Cu ( $<1.33 \text{ mg}\cdot\text{kg}^{-1}$ ) levels were very low. Soil Mn was low in the valleys and slopes ( $0.62 - 0.87 \text{ mg}\cdot\text{kg}^{-1}$ ), but higher in the mound ( $6.59 \text{ mg}\cdot\text{kg}^{-1}$ ). Soil Fe ( $11.48 - 21.13 \text{ mg}\cdot\text{kg}^{-1}$ ) was well above the critical level in all of the habitats. Leaf micronutrients Cu, B, Zn, and Fe were below the critical levels for tropical crops of 3 - 7, 20 - 70, 15 - 20, and  $72 \text{ mg}\cdot\text{kg}^{-1}$ , respectively. Leaf Mn ( $<188 \text{ mg}\cdot\text{kg}^{-1}$ ) and Al ( $<50 \text{ mg}\cdot\text{kg}^{-1}$ ) were below the accumulators level. A strong relationship between leaf micro- and macronutrients suggests the maintenance of a homeostatic elemental composition, which may favour photosynthetic function. Therefore, the local distribution of species may be shaped by their abilities to maintain a balance of micronutrient collected through roots under critically low levels of available Zn, B, and Cu whilst excluding potentially deleterious ions of Mn, Fe, and Al.

**Keywords:** Acid Soils; Amazon Caatinga; Ionome; Leaf Nutrient Homeostasis; Micronutrients; Toxic Elements

## 1. Introduction

Micronutrient availability and cycles in tropical areas are poorly understood, even though such information is imperative for a thorough understanding of the complexities of major element cycles in these habitats [1]. Very low micronutrient levels have been found in tropical natural areas that have severely impoverished macronutrient levels as well [2,3]. The micronutrient distribution is particularly relevant in a situation of deficiency, when alternative plant developmental processes and biochemical pathways may be prioritized as a function of growth, development, metabolic status, and environment [4]. Thus, the interactions among elements within plant cells tend to reflect the regulatory network involved in the homeostasis of the ionome [5,6]. These interactions and the balance of ions in plant tissue may have an ecophysiological significance as well, which requires further investigation in order to gain insight into these processes.

The upper Rio Negro in the Amazon basin experiences high yearly rainfall levels, as well as differential soil types and topographical conditions. Consequently a mosaic of vegetation types is featured. The Amazon caatinga complex is located on lowland areas with infertile, bleached, sandy podzols surrounded by low rolling hills containing oxisol soils [7]. A clear toposequence (valley-slopes-domes) with gradual changes is found within the caatinga, which forms a complex community continuum [8]. The macronutrient concentration and fluxes in soil organic matter as well as the organic matter turnover rates have paramount importance for the maintenance of fertility across the caatinga habitats [9,10]. Historically, plant macronutrient distribution has received most attention for this vegetation type [9,11,12], and the distribution of micronutrients has not been assessed previously. In this study, it was hypothesized that soil micronutrient availability may reflect contrasting habitat characteristics,

and that the leaf micronutrient composition of species thriving in different habitats may reflect the macronutrient content at particular sites in order to maintain the ion balance for leaf cell functions. In this study, the micronutrient composition of soils and leaves of dominant tree species within the toposequence of the caatinga vegetation was assessed. In particular, differences in the dominant species thriving in each of these contrasting sites were determined.

## 2. Material and Methods

### 2.1. Study Site and Species

The study site is located near the confluence of the Rio Negro and the Casiquiare River in southern Venezuela near the village of San Carlos de Rio Negro (1°54'N, 67°3'W, 119 m ASL). The area features a mean annual temperature of 26°C and mean annual rainfall of 3600 mm. Podzol soils of the caatinga have developed probably from Precambrian sandstone, and the top soil contains medium-textured sand mixed with humus [7]. In the valleys, soils are water saturated and dominated by *Eperua leucantha* Benth (Caesalpiniaceae; “yaguacana” forest). The slopes (ecotone) are dominated by *Micranda sprucei* (Müll.Arg.) R. E. Schultes (Euphorbiaceae; “cunuri” forest), which maintain a relatively stable water table, and the slightly higher sandy mounds suffer droughts during short rainless periods [7,8]. The species selected for this study were *E. leucantha* and *M. sprucei* from the close, high stature forests (18 - 25 m; valley and slopes). The less fertile and drought-prone tops of the sandy mounds contain tree species of low stature and open arrangement (“bana” forest; 5 - 7 m). At this site, *Pachira sordida* (R.E. Schult.) W.S. Alverson (syn. *Rodognaphalopsis discolor* A. Robyns), (Malvaceae) and *Remijia morilloi* Steyerl (Rubiaceae) are the dominant species. The use of dominant species has proven to be ecological indicators of typical habitats within the upper Rio Negro vegetation [13]. From the valley towards the slopes and sandy mounds, leaves become more scleromorphic, and those on sandy mounds are relatively more drought-resistant [14,15].

### 2.2. Leaf and Soil Sampling

For each species, three mature trees with a fully exposed top canopy were selected and tagged for soil and plant collection during August 2010 [13]. Four soil samples consisting of sand and humus were collected from 0 - 5 cm depth under each tree (*E. leucantha* and *M. sprucei*) or under a pair of trees (*P. sordida* and *R. morilloi*). The four samples were pooled in the field after all visible plant pieces were removed by hand. Each sample consisting of sand and humus was dehydrated at room temperature, ground, homogenized, and sieved through 2

mm mesh. A total of three pooled soil samples were analyzed in each of the three habitats. Three top canopy branches were detached in each tagged tree and adult leaves with a healthy appearance were collected and pooled. Leaf blade samples, excluding major veins, were oven dried to a constant weight at 60°C and ground prior to performing the analysis. A total of three pooled leaf blade samples were analyzed for each plant species.

### 2.3. Soil Analysis

Soil subsamples were used for the following analyses: soil pH was measured in a slurry of 5 g soil in distilled water at a ratio of 1:1. Buffer pH or acidity was estimated in subsamples of 5 g by using Mehlich 3 as a buffer solution to estimate the acidity. Organic content (OM) was determined by weight loss on ignition in subsamples of approximately 5 - 7 g. Soil exchangeable micronutrients (Fe, Mn, Zn, B, and Cu) and macronutrients (P, Ca, K, and Mg) as well as Al were measured by using an Inductively Coupled Plasma-Atomic Emission Spectrometer (ICP-AES, Varian, Model 730-ES, Palo Alto, California, USA). The Mehlich 3 soil test extract was used in subsamples for element extraction, except for B, which was extracted in hot water. Soil subsamples weighing 10 g were used for B extraction and a subsample measuring 2.5 cm<sup>3</sup> was used for the other elements. Soil cation exchange capacity (CEC) was estimated from the sum of soil acidity (see above) and the Ca, Mg, and K content and expressed as meq/100 g. The percentage of base saturation (BS) was calculated as the percentage of soil CEC occupied by Ca, Mg, and K. Detailed soil analysis procedures have been previously described [16]. The soil N and C composition analysis was performed at the Stable Isotope Research Facility for Ecological Research (SIRFER), University of Utah (Salt Lake City, USA).

### 2.4. Leaf Analysis

Leaf samples were analyzed for the same elements measured in the soils using the ICP-AES as well. A total of 0.2 g per leaf sample was muffled and ashed, dissolved in 2 ml of 5 N HCL, and heated at 200°C for 2 min. Subsequently, the samples were brought to a 10 ml volume with de-ionized water and centrifuged at 2000 rpm for 4 minutes to precipitate carbon rests prior to performing ICP measurements. The procedure followed is described elsewhere [17]. The leaf N and C compositions of these species have been previously reported [14,18].

### 2.5. Statistical Analysis

Measurements were performed on independent replicates taken randomly, and data are presented as mean ± standard error. The normality of distributions was assessed

using the Kolmogorov-Smirnov test and equality of variance using Levene's test. When the data were normally distributed with equal variance, one-way analysis of variance (ANOVA) was used and multiple comparisons were made with the Holm-Sidak test. Conversely, if data normality and/or equal variance tests failed, then an ANOVA-on-ranks test was used and statistical differences were determined with the Tukey test. Pearson correlation coefficients were used to quantify the relationships between micro- and macro-nutrients. Significance level was set at  $P < 0.05$  and the analyses were performed using SigmaStats 3.1 software for Windows (Systat Software, Inc., Chicago, USA).

### 3. Results

#### 3.1. Soil Analysis

The results of soils analysis are shown in **Table 1**. Soil pH was significantly different across sites, with the lowest ( $3.33 \pm 0.06$ ) and highest ( $4.22 \pm 0.03$ ) values found in the waterlogged valley bottoms and sandy mounds, respectively ( $p < 0.05$ ). The pH was negatively related to OM ( $r = -0.88$ ;  $P < 0.001$ ) and CEC ( $r = -0.87$ ;  $P < 0.001$ ). Additionally, pH was also negatively related to

Al ( $r = -0.91$ ;  $P < 0.001$ ), C ( $r = -0.92$ ;  $P < 0.001$ ), N ( $r = -0.92$ ;  $P < 0.001$ ), and the N/P ratio ( $r = -0.94$ ,  $P < 0.001$ ). In contrast, pH was positively correlated with Mn ( $r = 0.60$ ;  $P < 0.05$ ) as well as with Mg ( $r = 0.73$ ;  $P < 0.05$ ), Ca ( $r = 0.77$ ;  $P < 0.01$ ), and consequently to BS ( $r = 0.71$ ;  $P < 0.05$ ).

Soil K values were statistically indistinguishable among sites, ranging from  $88.5$  to  $107 \text{ mg}\cdot\text{kg}^{-1}$ . The slopes of the toposequence had mineral concentrations (in  $\text{mg}\cdot\text{kg}^{-1}$ ) that was statistically indistinguishable to that in the valleys: (Mn:  $0.62 \pm 0.14$  vs.  $0.87 \pm 0.08$ ; Cu:  $1.33 \pm 0.01$  vs.  $1.24 \pm 0.06$ ), macronutrients (P:  $30 \pm 3.8$  vs.  $29.5 \pm 3.7$ ; Ca:  $77.1 \pm 0.4$  vs.  $55.7 \pm 2.9$ ), and Al ( $159 \pm 24$  vs.  $290 \pm 43$ ), respectively. Slopes and domes had statistically comparable C content ( $49 \pm 5$  vs.  $35 \pm 14 \text{ g}\cdot\text{kg}^{-1}$ ) but lowest of that in the valley ( $139 \pm 32 \text{ g}\cdot\text{kg}^{-1}$ ), respectively. Mounds had the statistically lowest concentration of Cu ( $1.03 \pm 0.01 \text{ mg}\cdot\text{kg}^{-1}$ ) and Al ( $62 \pm 2 \text{ mg}\cdot\text{kg}^{-1}$ ), and the highest Mn ( $6.59 \pm 1.83$  vs.  $0.62 \pm 0.14$  and  $0.87 \pm 0.08 \text{ mg}\cdot\text{kg}^{-1}$ ) compared to slopes and valley, respectively. Similarly, mound had the lowest concentrations of the macronutrients N ( $1.08 \pm 0.04$  vs.  $1.92 \pm 0.02$  and  $5.21 \pm 1.3 \text{ g}\cdot\text{kg}^{-1}$ ) and P ( $18.2 \pm 2.3$  vs.  $29.5 \pm 3.7$  and  $30 \pm 3.8 \text{ mg}\cdot\text{kg}^{-1}$ ) as well as the highest C/N ratio ( $32.4 \pm 1.4$  vs.  $25.5 \pm 0.4$  and  $27.0 \pm 0.5 \text{ kg}\cdot\text{kg}^{-1}$ ) as compared to those in slopes and valley, respectively.

**Table 1. Soil characteristics and nutrient composition.**

	Toposequence sites		
	Valley	Slope	Mound
pH	$3.33 \pm 0.06$ c	$4.01 \pm 0.04$ b	$4.22 \pm 0.03$ a
OM (%)	$19.2 \pm 4.4$ a	$7.5 \pm 0.7$ b	$6.6 \pm 1.2$ b
CEC (meq/100 g)	$20.6 \pm 0.1$ a	$17.9 \pm 0.4$ b	$14.4 \pm 0.8$ c
BS (%)	$2.4 \pm 0.2$ b	$2.9 \pm 0.1$ b	$11.9 \pm 0.3$ a
Fe ( $\text{mg}\cdot\text{kg}^{-1}$ )	$14.36 \pm 0.06$ b	$11.48 \pm 0.79$ b	$21.13 \pm 0.58$ a
Mn ( $\text{mg}\cdot\text{kg}^{-1}$ )	$0.87 \pm 0.08$ b	$0.62 \pm 0.14$ b	$6.59 \pm 1.83$ a
Zn ( $\text{mg}\cdot\text{kg}^{-1}$ )	$1.41 \pm 0.03$ a	$0.99 \pm 0.07$ b	$1.35 \pm 0.14$ ab
B ( $\text{mg}\cdot\text{kg}^{-1}$ )	$0.20 \pm 0.05$	$0.31 \pm 0.05$	$0.17 \pm 0.04$
Cu ( $\text{mg}\cdot\text{kg}^{-1}$ )	$1.24 \pm 0.06$ a	$1.33 \pm 0.01$ a	$1.03 \pm 0.01$ b
Al ( $\text{mg}\cdot\text{kg}^{-1}$ )	$290 \pm 43$ a	$159 \pm 24$ a	$62 \pm 4$ b
C ( $\text{g}\cdot\text{kg}^{-1}$ )	$139 \pm 32$ a	$49 \pm 5$ b	$35 \pm 14$ b
N ( $\text{g}\cdot\text{kg}^{-1}$ )	$5.21 \pm 1.30$ a	$1.92 \pm 0.02$ b	$1.08 \pm 0.04$ c
K ( $\text{mg}\cdot\text{kg}^{-1}$ )	$107 \pm 8.7$	$88.5 \pm 6.1$	$107 \pm 1.1$
Ca ( $\text{mg}\cdot\text{kg}^{-1}$ )	$55.7 \pm 2.9$ b	$77.1 \pm 0.4$ b	$185 \pm 12$ a
Mg ( $\text{mg}\cdot\text{kg}^{-1}$ )	$33.0 \pm 2.9$ b	$44.0 \pm 4.0$ ab	$63 \pm 9.2$ a
P ( $\text{mg}\cdot\text{kg}^{-1}$ )	$29.5 \pm 3.7$ a	$30.0 \pm 3.8$ a	$18.1 \pm 2.3$ b
C/N ( $\text{kg}\cdot\text{kg}^{-1}$ )	$27.2 \pm 0.5$ b	$25.5 \pm 0.4$ b	$32.4 \pm 1.4$ a
N/P ( $\text{kg}\cdot\text{kg}^{-1}$ )	$171 \pm 23$ b	$66.1 \pm 6$ a	$63.6 \pm 11$ a

Values are mean  $\pm$  SE of soil pH in water, organic matter (OM), cation exchange capacity (CEC), base saturation (BS), micronutrients, and macronutrients as well as C/N and N/P. Means followed by different letters are statistically different at  $P < 0.05$ .

#### 3.2. Plant Analysis

Plant analysis results are shown in **Table 2**. The values of Fe ( $20.6 - 39.5 \text{ mg}\cdot\text{kg}^{-1}$ ) and Zn ( $6.5 - 14.3 \text{ mg}\cdot\text{kg}^{-1}$ ) tended to decline significantly in species from the mounds (*P. sordida* and *R. morilloi*) as compared to that of the valley (*E. leucantha*). Values of Cu ( $1 - 2.5 \text{ mg}\cdot\text{kg}^{-1}$ ) were species specific. Values of B were slightly higher in *E. leucantha* ( $17.4 \pm 1.2 \text{ mg}\cdot\text{kg}^{-1}$ ) from the valley and *M. sprucei* ( $15.3 \pm 0.5 \text{ mg}\cdot\text{kg}^{-1}$ ) from the slope, as compared to *P. sordida* ( $11.2 \pm 1.0 \text{ mg}\cdot\text{kg}^{-1}$ ) and *R. morilloi* ( $10.6 \pm 0.3 \text{ mg}\cdot\text{kg}^{-1}$ ) from the mound. In contrast, Mn ( $43.6 - 188 \text{ mg}\cdot\text{kg}^{-1}$ ) was relatively high in all species except *P. sordida* (mound;  $12.8 \pm 3.8 \text{ mg}\cdot\text{kg}^{-1}$ ). Differences in leaf Al concentrations ( $4.6 - 49.4 \text{ mg}\cdot\text{kg}^{-1}$ ) were species specific across habitats. Regarding the macronutrients, the trend of leaf N and P was to decline from the valley towards the mounds. By contrast, leaf N/P, Ca, Mg, and K were species specific and did not show a clear trend along the toposequence.

Statistically significant correlations were found between micro- and macronutrients (**Table 3**). Thus, Fe is correlated with N ( $r = 0.92$ ;  $P < 0.001$ ) and P ( $r = 0.62$ ;  $P < 0.05$ ), Zn with N ( $r = 0.94$ ;  $P < 0.001$ ) and P ( $r = 0.68$ ;  $P < 0.01$ ) and B with N ( $r = 0.77$ ;  $P < 0.01$ ) and P ( $r = 0.59$ ;  $P < 0.05$ ). Similarly, Mn was correlated with Ca ( $r = 0.56$ ;  $P < 0.05$ ) and Mg ( $r = 0.63$ ;  $P < 0.05$ ). The set of

**Table 2. Leaf nutrient composition of the dominant species.**

	Toposequence sites			
	Valley	Slope	Mound	
	<i>E. leucantha</i>	<i>M. sprucei</i>	<i>P. sordida</i>	<i>R. morilloi</i>
Fe	39.5 ± 1.0 a	26.9 ± 1.6 b	20.6 ± 1.6 c	22.9 ± 0.3 c
Mn	88.5 ± 11.1 b	188 ± 43 a	12.8 ± 3.8 d	43.6 ± 6.1 c
Zn	14.3 ± 1.1 a	7.4 ± 0.4 b	6.9 ± 0.5 b	6.5 ± 0.4 b
B	17.4 ± 1.2 a	15.3 ± 0.5 a	11.2 ± 1.0 b	10.6 ± 0.3 b
Cu	2.5 ± 0.1 a	1.0 ± 0.1 b	2.9 ± 0.2 a	2.2 ± 0.2 a
Al	14.9 ± 1.9 b	4.6 ± 0.6 c	5.8 ± 1.1 c	49.4 ± 5.6 a
N	16.7 ± 0.3 a	9.3 ± 0.3b	9.1 ± 0.5 b	7.4 ± 0.4 c
K	3.89 ± 0.39 c	6.42 ± 0.39 b	10.0 ± 0.69 a	3.20 ± 0.29 c
Ca	1.57 ± 0.08 b	0.93 ± 0.14 b	3.68 ± 0.89 a	1.64 ± 0.26 b
Mg	1.41 ± 0.03 b	1.28 ± 0.06 b	3.05 ± 0.89 a	1.62 ± 0.09 b
P	1.15 ± 0.03 a	0.84 ± 0.01 b	0.96 ± 0.08 b	0.45 ± 0.01 c
N/P	14.6 ± 1.4 a	11.1 ± 0.5 ab	9.6 ± 0.5 b	16.4 ± 1.9 a

The values are in mg·kg<sup>-1</sup>, except that of N, K, Ca, Mg and P (g·kg<sup>-1</sup>) and N/P (kg·kg<sup>-1</sup>). Values are mean ± SE. Means followed by different letters are statistically different at P < 0.05.

**Table 3. Correlation coefficients between leaf micro- and macronutrients across species.**

	Fe	Mn	Zn	B	Cu
N	<b>0.92***</b>	0.11	<b>0.94***</b>	<b>0.77**</b>	0.16
K	0.48	0.18	0.41	0.19	0.15
Ca	-0.39	<b>0.56*</b>	0.25	0.34	<b>0.59*</b>
Mg	<b>-0.58*</b>	<b>0.63*</b>	0.35	<b>0.57*</b>	<b>0.70**</b>
P	<b>0.62*</b>	0.11	<b>0.68**</b>	<b>0.59*</b>	0.20

Significant correlations are in bold and P < 0.05 (\*), P < 0.01 (\*\*), and P < 0.001 (\*\*\*).

Fe, Zn, and B as well as the set of Mn, Ca, and Mg are involved in leaf chloroplast and mitochondrial function. A negative correlation between Fe and Mg (r = -0.58; P < 0.05) was consistent with its antagonistic role in plants.

#### 4. Discussion

Soil critical values for tropical crops of Fe (2.5 - 5.8 mg·kg<sup>-1</sup>), Mn (1 - 4 mg·kg<sup>-1</sup>), Zn (3.3 mg·kg<sup>-1</sup>), B (1 - 2.4 mg·kg<sup>-1</sup>), and Cu (1 - 2 mg·kg<sup>-1</sup>) were previously compiled by Oyendola and Chude [3]. Consistent with these ranges, the Zn and B levels were low at all of the sites, Cu was very low but above the critical value of 1 mg·kg<sup>-1</sup>, Mn was limited in the valleys and slopes but higher in the mounds, and Fe was well above the critical level in all of the habitats. Values of Zn (0.99 - 1.41 mg·kg<sup>-1</sup>) B (0.17 - 0.31 mg·kg<sup>-1</sup>) and Cu (1.03 - 1.33 mg·kg<sup>-1</sup>) were comparable to those found in other nutrient poor environments [19,20]. However, in more fertile soils the levels of Zn (2 - 4 mg·kg<sup>-1</sup>), B (5 - 8 mg·kg<sup>-1</sup>)

and Cu (12 - 20 mg·kg<sup>-1</sup>) are considerable higher [21-23]. Micronutrient shortages greatly affect soil fertility and consequently constrain plant productivity, inhibit growth, and exacerbate leaf senescence [19,24]. Additionally, litter decomposition rates are also lower under limiting micronutrient availability, given that the process is dependent on metallomic enzymes [25,26]. In leached and strongly acid tropical soils, the pool of soluble Fe, Mn, and Al are high, which may be potentially toxic for plants [20,27,28]. Decreasing levels of soil N in the Amazon caatinga habitats, from the valleys towards mounds, was corroborated by the values of total N, available P, and N/P ratio [9,10,14].

Mineral nutrient composition of leaves did not follow the same pattern of availability found in the soils (Tables 1 and 2). The total level of micronutrients in the soil is determined by the original geological substrate and subsequent geological and pedogenic regimes [21], but the accumulation of a given element within plants is controlled by complex processes regulated by a network of gene products critical for uptake, binding, transportation, and sequestration [5]. The concentrations of leaf micronutrients: Fe, Zn, B, and Cu were below the sufficiency levels 72, 15 - 20, 20 - 70, 3 - 7 mg·kg<sup>-1</sup>, respectively, as defined by Marschner [29]. Furthermore, values of Fe, Zn, and Cu were at the lower end of the range previously reported in tropical acid soils: 10 - 2467, 8 - 139, and 1 - 53 mg·kg<sup>-1</sup>, respectively [2,20,30]. Values of B in *E. leucantha* (valley) and *M. sprucei* (slopes) were within a range of marginal sufficiency (14 - 18 mg·kg<sup>-1</sup>) [31]. Conversely, species from the mounds had the lowest B. In contrast, Mn was above the sufficiency level (10-20 mg·kg<sup>-1</sup>) in all species except *P. sordida*, but below the accumulator levels of 1000 mg·kg<sup>-1</sup> [32]. Similarly, despite across species differences in leaf Al concentrations; values were much lower than 2300 - 3900 mg·kg<sup>-1</sup>, which is typical for Al accumulator species in tropical habitats [33]. The species with the higher Al (49.4 mg·kg<sup>-1</sup>) was *R. morilloi* of the Rubiaceae family. This family has a large number of Al accumulator species in tropical environments [27]. Leaf macronutrient composition showed a pattern similar to that previously found in the same species [11,12]. In addition, the N/P ratio was comparable across all sites and was less than 16.4 kg·kg<sup>-1</sup>, which confirmed the notion that N limitation overrides that of P in the three zones of the Amazon caatinga toposequence following the criteria outlined by Lambers [34].

Although the close relationships between macro- and micronutrients were found in this study, they are not fully understood, Fe, Mn, Zn, N, P, and Mg all have essential roles in photosynthetic leaf function. We found positive and statistically significant correlations between these micro- and macro-nutrients (Fe-P; Fe-N; Mn-Mg; Zn-N; Zn-P). Consequently, the maintenance of a balanced ac-

cumulation of these micro- and macronutrients in leaves may have an adaptive value for growth in habitats with limited availability. Indeed, some interrelationships have been previously identified between micro- and macronutrients. For example, a nucleic acid-protein set has been correlated with concentrations of P, N, Cu, S, and Fe, and structural, photosynthetic, and enzymatic sets have also been correlated with concentrations of Mn, Mg, Ca, and K [35]. However, further studies including a wide variety of habitats and species are required for a complete understanding of this issue.

## 5. Conclusions

Based on the results of the present study, the following conclusions were drawn:

1. The soil Zn, B, and Cu levels were very low in all of the habitats of the Amazon caatinga toposequence.
2. The soil levels of Fe would be potentially toxic in all habitats, Mn levels may be toxic in the mounds, and Al may be toxic in valleys and slopes.
3. In all of the habitats, the leaf concentrations of Cu, B, Zn, and Fe were below sufficiency levels, and concentrations of Mn and Al were within normal range found in non-accumulators.
4. A strong relationship between leaf micro- and macronutrients suggested the maintenance of a homeostatic nutrient composition, which would favor photosynthetic function at the leaf level. Therefore, the local distribution of species may be shaped for their abilities to maintain a balanced collection of micronutrients through roots under critical levels of available Zn, B, and Cu as well as the ability to exclude Mn, Fe, and Al.

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