Leaf and soil nitrogen and phosphorus availability in a neotropical rain forest of nutrient-rich soil

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Abstract. The nitrogen and phosphorus supply in a lowland rain forest with a nutrient-rich soil was investigated by means of the leaf N/P quotient. It was hypothesised a high N and P supply to the forest ecosystem with a N and P rich soil. Total N and extractable P were determined in the surface (10 cm) soil of three plots of the forest. Total N was analysed by the Kjeldahl method, and P was extracted with HCl and NH_4F. The leaf N/P quotient was evaluated from the senesced leaves of 11 dominant tree species from the mature forest. Samples of 5 g of freshly fallen leaves were collected from three trees of each species. Nitrogen was analysed by microkjeldahl digestion with sulphuric acid and distilled with boric acid, and phosphorus was analysed by digestion with nitric acid and perchloric acid, and determined by photometry. Concentrations of total N (0.50%, n = 30) and extractable P (4.11 µg g^{-1}, n = 30) in the soil were high. As expected, P supply was sufficient, but contrary to expected, N supply was low (N/P = 11.8, n = 11). Rev. Biol. Trop. 54(2): 357-361. Epub 2006 Jun 01.

Key words: Los Tuxtlas, lowland forest, Mexico, N/P ratio, senescent leaves.

Nitrogen (N) and phosphorus (P) have been recognised as the essential nutrient elements for productivity in the natural ecosystems (Vitousek 1984, Koeuselman and Meuleman 1996, Aidar *et al*. 2003, Martínez-Sánchez 2005). Foliar nutrient concentrations provide an alternative means of characterizing nutrient availability in tropical forests (Grubb 1977). The leaf N/P quotient indicates the nutrient availability in the plant tissue and hence in the soil (Koeuselman and Meuleman 1996). Other forms of estimating nutrient supply to the plants like the nutrient use efficiency (dry aboveground mass/nutrient mass), have been used. However Grubb (1989) has pointed out the inconveniences of this method.

The aim of this paper was to analyse the nitrogen and phosphorus supply to the forest in a nutrient-rich soil, by means of the leaf N/P quotient. It was hypothesised that N and P supply to the forest ecosystem in a nutrient-rich soil, would be high.

The study site was located in the undisturbed forest reserve “Estación de Biología Los Tuxtlas” on the east coast of Mexico (18°34’ - 18º36’ N, 95º04’ - 95º09’ W), belonging to the Universidad Nacional Autónoma de Mexico. Los Tuxtlas is the northernmost extension of the lowland evergreen tropical rain-forest formation in the neotropics. Most of the forest reserve lies over basaltic rocks of about 800 000 yr old (Nelson and González-Caver 1992). However, soil development and fertility may have been influenced by relatively recent (in 1664 and 1793) volcanic activity with significant quantities of ash and a small volume of lava flows, as well as by climate (Nelson and González-Caver 1992, Friedlaender and Sander 1923 as cited in Martin-Del Pozzo 1997). Soils in the region are classified as well-drained, coarse-textured, vitric Andosols mixed with volcanic ash (Anonymous 1975). Surface (0-10 cm) soil in the undisturbed forest is relatively nutrient-rich. It has a clay to clay/loamy texture, a pH_{H20} of 6.9, 0.63 $cmol_c$ kg^{-1} of K^+, 0.55 of Na^+, 14.2 of Ca^{2+}, 8.6 of Mg^{2+}, 0.3 of H^+, 0.14 of Al^{3+}, and 24.3 $cmol_c$ kg^{-1} of CEC (Martínez-Sánchez 2003). Mean annual temperature at the forest reserve (110 m altitude, ≈ 2 100 d of data from 1988 to 1997) is 25.1 ºC. Mean annual rainfall from 1972 to 1997 (data missing for three complete years) was 4 487 mm; 48% spans August to November. Evaporation at Sontecomapan (*c*. 10 km SE from the reserve) from 1976 to 1997, measured as the amount (mm) of water evaporated in a sink in 24-h terms, had an annual mean of 1 390 mm.

Three 50 x 50-m plots were placed in the mature forest of the reserve. Total basal areas of the plots were 8.0, 8.1, and 8.8 m^2 (Martínez-Sánchez 1999). During May and October 1996 ten soil samples (0-10 cm deep) in each plot were collected for chemical analyses, in a stratified random way with an 8-cm-diameter soil corer. The samples were immediately air-dried and passed through a 1.2-mm mesh. Samples were kept in polythene bags at 20ºC until the laboratory analyses. Soil analyses were conducted in the Instituto de Geología of the Universidad Nacional Autónoma de México. Analyses were all made in duplicate and checked with international standards. Total N was analysed by the Kjeldahl method, and P was extracted by 0.025 M HCl and 0.03 M NH_4F (Black 1965).

Estimation of ultimate leaf nutrient concentrations on senesced leaves are preferred over estimation on fresh leaves which have the problem of spatial and temporal variation in nutrient concentrations (Killingbeck 1996). During September 1997 (rainy season) freshly fallen leaves of 11 tree species (Table 1) were collected for nutrient-element analysis, in about 10 ha of the east side of the reserve including two of the soil plots. Species accounted for 48% of the plots basal area and for 44% of the total leaf litterfall (Martínez-Sánchez 1999). Three trees (≥ 10 cm dbh) of each species were randomly selected. Forest canopy structure around the selected trees ranged from small gap to mature phase. Samples of 5 g of freshly (<3 d) fallen leaves were collected from the ground below each tree. All leaves were dried at *c*. 40ºC for 3 d.

Nutrient analyses of leaf material were done in the Laboratorio de Edafología, Colegio de Postgraduados at Montecillos, Mexico. All material was oven-dried at 105ºC. Nitrogen was analysed by microkjeldahl digestion with sulphuric acid and distillation with boric acid (Bremmer 1975, Chapman and Pratt 1979). Phosphorus was analysed by digestion with nitric acid and perchloric acid (2:1) for a minimum of 12 h, and determined in 7.5 ml of vanadomolybdenum-phosphorus complex by photometry at 470 nm.

The leaf N/P ratio for the 11 species was calculated and had a mean value of 11.8 (Table 1). The forest soil was rich in total N and extractable P (Table 2).

Extrapolating from aquatic ecology and agricultural sciences where the low N/P ratio indicates a nutrient deficiency in the ecosystems, Koeuselman and Meuleman (1996) proposed that the N/P ratio in the plant tissue in terrestrial ecosystems can be a good predictor of limitation of these nutrients in the soil. They proposed that a N/P ratio <14 indicates N limitation, a ratio >16 indicates P limitation, and a ratio between 14 and 16 indicates N and P limitation. Based on this assumption, the mean leaf-litter N/P ratio at Los Tuxtlas (11.8) indicates a N-deficiency in the soil. As expected, P availability in the ecosystem does not seem to be limited, but contrary to expected, N availability seems to be limited. It is noteworthy that this index never leads to a non-limited condition of soil nutrients however.

Concentrations of total N in the soil from a range of lowland rain forests around the world were 0.02-1.0% (Proctor 1983). Total N availability in the soil at Los Tuxtlas is high (0.50%), however the low N/P ratio points out that there is a low N supply to the vegetation. A possible explanation is that some critical forms of N are limited in the soil at Los

TABLE 1

Mean nitrogen and phosphorus concentrations (%) in senesced leaves and N/P quotient

Species	Senesced % N	leaves % P	N/P quotient
Cecropia obtusifolia Bertol. Cecropiaceae	1.19 (1.03-1.33)	0.17 (0.10-0.23)	7.8 (5.2-10.3)
Heliocarpus appendiculatus Turcz. Tiliaceae	1.03 (0.92-1.17)	***0.23*** (0.16-0.30)	***4.8*** (3.1-6.2)
Trichospermum galeottii (Turcz.) Kosterm. Tiliaceae	***0.71*** (0.60-0.89)	***0.04*** (0.03-0.06)	***17.1*** (15.0-21.3)
Ficus tecolutensis (Liebm.) Miq. Moraceae	0.86 (0.71-1.12)	0.08 (0.07-0.09)	10.4 (7.9-12.4)
F. yoponensis Desv. Moraceae	0.99 (0.79-1.12)	0.08 (0.01-0.09)	11.9 (11.2-13.2)
Nectandra ambigens (S.F. Blake) C.K. Allen. Lauraceae	1.01 (0.83-1.19)	0.13 (0.12-0.20)	6.4 (5.9-6.9)
Pseudolmedia oxyphyllaria Donn. Sm. Moraceae	1.28 (1.20-1.33)	0.08 (0.07-0.09)	16.7 (16.2-17.1)
Spondias radlkoferi Donn. Sm. Anacardiaceae	1.04 (0.93-1.11)	0.09 (0.08-0.10)	11.2 (10.8-11.6)
Faramea occidentalis (L.) A. Rich. Rubiaceae	1.25 (1.13-1.36)	0.08 (0.07-0.09)	15.8 (12.5-19.4)
Orthion oblanceolatum Lundell. Violaceae	***2.26*** (2.21-2.32)	0.17 (0.16-0.23)	12.0 (10.1-14.2)
Rheedia edulis (Seem.) Triana & Planch. Clusiaceae	0.79 (0.76-0.83)	0.05 (0.04-0.06)	16.1 (13.8-19.0)
Mean	1.13	0.109	11.83
C.V. (%) among species	36.8	54.1	36.1

The highest and the lowest values are shown in bold (n = 3, range in parenthesis).

TABLE 2

Mean, S.D., and overall percentage of coefficient of variation (% CV) of soil N and P from forest plots at Los Tuxtlas, México. n = 10

	Plot 1		Plot 2		Plot 3		Overall	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	% CV
N total (%)	0.41	0.13	0.56	0.29	0.55	0.15	0.50	40.8
P Bray ($\mu g\ g^{-1}$)	7.47	3.36	2.55	1.09	2.32	0.64	4.11	76.2

Tuxtlas. Nitrogen in its ion form is the most useful form to plant growth, and soil total N could be mostly organic N. Nitrogen is lost in the ecosystems by denitrification and NH_3 volatilization. Unlike mineral-N in the ammonium form, nitrate is extremely mobile through leaching and readily available to denitrifiers for conversion to nitrogen gases (Robertson 1984). In a Costa Rican tropical rain forest at 1 000 m altitude, Marrs *et al*. (1988) found that denitrification may be a limiting factor for mineral-N availability. Very wet soils (moisture content of 80%) with low aeration may increase denitrification and may limit N-mineralisation (Marrs *et al*. 1988). N-mineralisation rates in tropical forests varies widely, and a volcanic soil in Costa Rica are towards the high end of the spectrum of tropical soils (Robertson 1984). N-supply at Los Tuxtlas has to be experimentally assessed. Some stages of the N-pathway like mineralisation, nitrification, denitrification and direct ammonium assimilation, may be interesting topics to investigate in this forest.

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RESUMEN

A través del cociente foliar N/P, se investigó la disponibilidad de nitrógeno y fósforo en una selva húmeda tropical con suelo fértil. Como hipótesis se esperaba encontrar una alta disponibilidad de N y P en el ecosistema debido a un suelo rico en N y P. Se determinó el N total y el P extraible en el suelo superficial (10 cm) en tres sitios de la selva. El N total se analizó por el método Kjeldahl y el P por extracción con HCl y NH_4F. El cociente foliar N/P se evaluó a partir de hojas seniles de 11 especies arbóreas dominantes de la selva madura. Se recolectaron muestras de 5 g de hojas recién caídas de tres árboles de cada especie. El nitrógeno se analizó por digestión microkjeldahl con ácido sulfúrico y destilación con ácido bórico, y el fósforo por digestión con ácido nítrico y ácido perclórico, y determinación con fotometría. Las concetraciones de N total (0.50%, n = 30) y P extraible (4.11 $\mu g\ g^{-1}$, n = 30) en el suelo fueron altas. Tal como se esperaba, la disponibilidad de P fue suficiente, pero contrariamente a lo esperado, la disponibilidad de N fue baja (N/P = 11.8, n = 11).

Palabras clave: cociente N/P, hojas seniles, Los Tuxtlas, México, selva húmeda tropical.

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