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Shift from ecosystem P to N limitation at precipitation gradient in tropical dry forests at Yucatan, Mexico

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E-mail: jcampo@ecologia.unam.mx**Keywords:** litter, litterfall, Mexico, plant–climate–soil interactions, nutrient limitation**Abstract**

The effect of precipitation regime on N and P cycles in tropical forests is poorly understood, despite global climate models project total precipitation reductions during the 21st Century. I investigated the influence of variation in annual precipitation (1240–642 mm yr⁻¹) on N and P intra-system cycling along a precipitation regime gradient at Yucatan including 12 mature, tropical dry forests (TDFs) growing under otherwise similar conditions (similar annual temperature, rainfall seasonality and geological substrate). I analyzed N and P storage and turnover in the forest floor and mineral soil and explored the dependence of these processes and pools on precipitation level. The study findings indicate that with decreasing precipitation the litterfall decreases slightly (10%), while nutrient use efficiency increases by 20% for N, and by 40% for P. Decomposition rate and nutrient release was smallest in the dry extremity of precipitation regime. The difference between N and P turnover times in the forest floor and in organic matter indicates that different nutrients control the ecosystem function across the precipitation gradient. The data from this study reveals a pattern of limitation shifting from P towards N with decreasing annual precipitation. I suggest that the long-term consequences of the expected decrease in precipitation in many tropical dry regions would changes N and P supply could have long-term negative effects on primary productivity and future carbon storage in TDFs.

1. Introduction

Tropical forests play a dominant role in global biogeochemical cycles and Earth's climate (Bonan 2008). Because of their high rate of carbon (C) exchange with the atmosphere every year, tropical forests account for a large proportion of global terrestrial cycling and storage of this bioelement (Pan *et al* 2011). Different Earth-system models have shown that these C fluxes in tropical forests will become increasingly vulnerable during the twenty-first century, since reduced mean annual precipitation (MAP) is predicted for large areas of the tropics (Neelin *et al* 2006, IPCC 2013). Several data syntheses from nutrient manipulation experiments have indicated that C cycling in tropical forests is commonly limited by nitrogen (N) and/or phosphorus (P) (Elser *et al* 2007, LeBauer and Treseder 2008, Bejarano-Castillo *et al* 2015, Powers *et al* 2015) and it is expected that such limitations will increase in the future

(Vitousek *et al* 2010, Wieder *et al* 2015). Although climate and nutrient availability regulate aspects of all terrestrial ecosystem function, the nature and extent of such controls in the tropical forest biome remain poorly understood (Cleveland *et al* 2011).

Tropical forest biomes are home to mosaics of different vegetation entities; this is the case in lowlands, rain forests and tropical dry forests (TDFs). TDFs are forests with a MAP range from 250 to 2000 mm, an annual ratio of precipitation to potential evapotranspiration of less than 1.0, and 4 to 7 dry months (Dirzo *et al* 2011); all these characteristics contribute to shaping the control of biogeochemical cycles (Campo *et al* 2001a, Gei and Powers 2014, Verduzco *et al* 2015). Although TDFs occupy around 40% of global tropical forest surface area (Miles *et al* 2006), and consequently their effect on the interactions between land surface and atmosphere may be substantial (Ahlström *et al* 2015), the potential effect of rainfall variability on biogeochemical processes in these

water-stressed ecosystems has not been studied as extensively as it has in their tropical wet forest counterparts. The lack of information on the relationship between precipitation regime and ecosystem function in TDFs limits our understanding of the potential effects of predicted increases in the frequency and duration of droughts and long-term reduction in MAP for many regions with TDFs (Meir and Pennington 2011). Although the usual perception is that the positive effect of lower rainfall on soil fertility and productivity observed in wet-to-mesic climates may be applicable across a broad range of tropical forests (Schuur and Matson 2001, Schuur 2003, Luyssaert *et al* 2007, Posada and Schuur 2011), it is not clear that rainfall decrease has the same effect in species-rich TDFs, where water availability in the highest rainfall areas is nonetheless relatively low (Vicente-Serrano *et al* 2013). Such uncertainty limits our capacity to elucidate the effects of future changes in precipitation regime on tropical forest function, and could produce biases in analyses of future global atmospheric CO₂ concentration.

To better understand the complex interactions between precipitation and nutrient cycling, I analyzed the influence of a large reduction in annual rainfall on litter N and P content and fluxes along a precipitation regime gradient (1240 to 642 mm). Such litter nutrients may be especially critical in TDF function, where seasonal variations of nutrients in litterfall constitute one of the most important aspects of the entire nutrient cycle (Campo *et al* 2001a). The gradient contains 12 mature TDFs located in subhumid, intermediate and semiarid climates in the Yucatan Peninsula, Mexico, where previous work at intermediate climate indicates that forest function is primarily driven by seasonal drought, and limited by P (Campo and Vázquez-Yanes 2004). Nutrient limitation in TDFs is related to water limitation because dry conditions prevent plant uptake of available nutrients from soil, and affect the release and mineralization of nutrients by slowing decomposition (Campo *et al* 1998, Saynes *et al* 2005, Bejarano *et al* 2014). On the other hand, TDFs may be limited by P because its adsorption to calcium in carbonate-rich soils such those of the Yucatan Peninsula (Lugo and Murphy 1986, Read and Lawrence 2003, Krasilnikov *et al* 2013).

For this investigation I compiled (i) data on litterfall, litter-layer masses and, their N and P contents, and, using a mass balance approach, estimated the residence time of organic matter and of each nutrient in the forest floor, and (ii) measurements of N and P concentration in mineral soils in the three climates. Using the combination of these data sets, I sought to answer the following major question: How does precipitation regime impact on nutrient cycling through litterfall and decomposition? The first hypothesis is that higher MAP has a positive effect on nutrient fluxes by litterfall. Second, a decrease in MAP would create a possible nutrient restriction in the ecosystem

by a decrease in nutrient availability due to slower mineralization rates. Regional spatial precipitation gradients in the Yucatan have the advantage that most site conditions can be assumed to be relatively similar across the gradient (e.g., temperature, seasonal precipitation pattern, topography, elevation, soil parent material, soil types, and vegetation). This provides an opportunity to examine the effects of alterations in amount of precipitation on nutrient cycling in tropical forest ecosystems, in a region where climate models project an increase in the frequency and severity of drought due to higher temperatures and changes in precipitation in the North American Monsoon System (Christensen *et al* 2013).

2. Materials and methods

2.1. Study sites and climate

The study was carried out at three sites on the Yucatan Peninsula, situated along a strong south-to-north gradient in MAP from south/wettest to north/driest sites (figure 1 and table 1). The study sites are located between 50 and 120 km apart. Within each of the three study sites, four mature TDF stands were selected to provide forest ecosystem variability at each precipitation regime condition. Specific locations were selected because they had not been subjected to human intervention, such as slash-and-burn agriculture or other interventions, for at least 60 years.

Long-term climate data from National Weather Service shows that all sites are characterized by a distinct period of low precipitation (five to seven months with precipitation below 100 mm month⁻¹; table 1). The three sites differ strongly in annual ratio of potential evapotranspiration to precipitation, and in mean monthly precipitation during the dry season, which modulates plant water use throughout the year (Eamus *et al* 2001). Across the sites, variation in mean annual temperature is less than a 1 °C, and the climate, subhumid to semiarid, would support either tropical dry or very dry forest in the Holdridge Life Zone System (Holdridge *et al* 1971).

The sites are on consistently flat terrain, with less than 50 m of altitudinal variation among them (table 1). The soils of the Yucatan Peninsula are formed on Tertiary limestone in a typical karstic landscape of flat rock outcrops and shallow depressions (Bautista *et al* 2011), and generally fall into two groups: shallow black soils (*Lithic usthorrens*) surrounding rock outcrops and deeper red soils with poor differentiation of horizon (*Lithic haplustolls*) at slightly lower relief (table 2). Soils at the wet extreme of the gradient are mainly red soils, comprising only approximately 78% of the landscape area; with increase MAP, the cover area of black soils also increase, making them the main soils at the driest site (covering 83% of the landscape) (Campo, *unpublished data*). Organic debris and limestone fragments make up a large portion of the soil

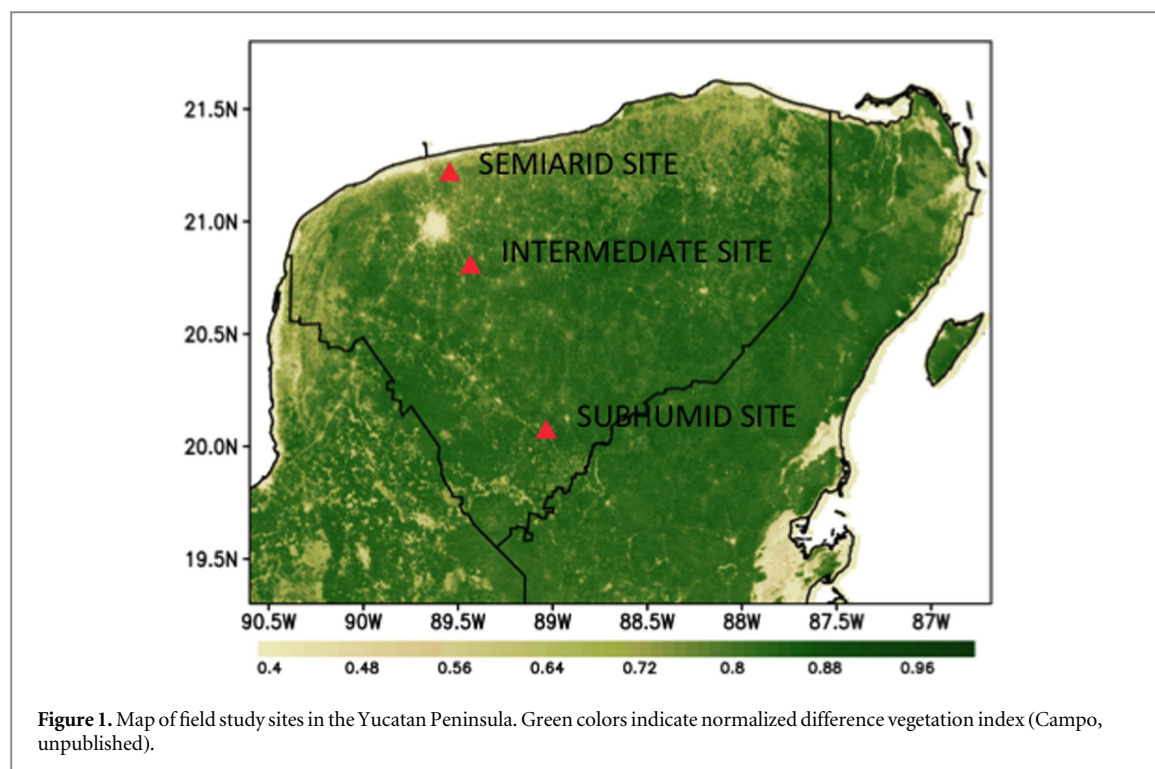


Table 1. Characteristics of the forest sites.

	Semi-arid	Intermediate	Subhumid
Coordinates	21° 12' N, 89° 36' W	20° 48' N, 89° 26' W	20° 04' N, 88° 02' W
Altitude (m asl)	6	11	36
Climate ^a	BS1	Aw0	Aw1
Mean annual temperature (°C) ^b	25.4	25.9	25.5
Mean annual precipitation (mm yr ⁻¹) ^b	642	995	1240
Potential evapotranspiration (mm yr ⁻¹) ^b	1713	1677	1719
Annual ratio of precipitation to potential evapotranspiration (mm mm ⁻¹)	0.37	0.59	0.72
Dry season months	November–May	December–May	December–April
Mean monthly precipitation in the dry season (mm month ⁻¹)*	30.2	38.6	42.6

^a García (2004).

^b National Weather Service—CONAGUA.

Table 2. Mean \pm SE of some soil properties in the study sites.

	Semi-arid		Intermediate		Subhumid	
	Red soils	Black soils	Red soils	Black soils	Red soils	Black soils
Clay (%)	28 \pm 2.1	26 \pm 1.0	30 \pm 1.1	24 \pm 1.4	64 \pm 1.7	46 \pm 2.4
Bulk density (g cm ⁻³)	0.71 \pm 0.02	0.61 \pm 0.02	0.78 \pm 0.02	0.64 \pm 0.03	0.84 \pm 0.024	0.68 \pm 0.01
pH	8.1 \pm 0.06	8.1 \pm 0.05	7.9 \pm 0.05	8.0 \pm 0.04	7.5 \pm 0.07	7.6 \pm 0.06
Organic C (mg C g ⁻¹)	154.5 \pm 6.3	221.8 \pm 13.4	120.5 \pm 7.5	200.7 \pm 11.2	59.4 \pm 2.1	84.3 \pm 2.9

matrix in black soils. They also contain amorphous metal oxides and more stable secondary minerals, as well as some 2:1 layer minerals such as illites, talc and chlorite, inherited from impurities in the weathered calcite and dolomite (Shang and Tiessen 2003). Thick, red, and clayey soils have a dominance of kaolinite in a pigmented red iron oxides matrix, with Fe content (Cabada-Báez *et al* 2010). At the semi-arid and

intermediate sites, the pH of the soils is higher, and the soils are less dense due to greater amount of soil organic matter (Campo and Merino 2016), than those at the subhumid site (table 2). Soil water retention increases with rainfall, from 33% to 45% to of field capacity from the semi-arid to the intermediate sites, and to 66% of field capacity at the subhumid site (Roa-Fuentes *et al* 2012), reflecting changes in soil clay

content, a paramount factor in controlling water retention (table 2). These variations in the physical and chemical properties of the soil across the Yucatan Peninsula tend to correlate with variations in both local microtopography and the regional age of parent material (Krasilnikov *et al* 2013). Specifically, red soils are generally deeper and usually contain fine material. On the other hand, the more fertile black soils are generally associated with lower levels of pedogenesis.

The predominant vegetation at the three studied sites is TDF. Mean canopy height is small due to hurricanes are an important part of the natural disturbance regime of the Yucatan Peninsula (Boose *et al* 2003, Mascorro *et al* 2016), and they often cause extensive disturbance to forest structure (Vandecar *et al* 2011, McGroddy *et al* 2013), and decreases from 5.4 m at the subhumid site to 3.3 m at the semiarid site (Roa-Fuentes *et al* 2012). Data from four stands at each site indicates that the intermediate site has more trees (diameter at breast height, dbh ≥ 2.5 cm) (mean ± 1 SE = 7210 ± 391 trees per hectare) than semiarid and subhumid sites (2600 ± 300 and 3900 ± 305 trees per hectare, respectively) (Roa-Fuentes *et al* 2012). Floristically, *Fabaceae* are the most important family at all forest sites (Roa-Fuentes *et al* 2012). I did not enumerate the species composition in this study, but it is known that the predominant vegetation along of the Yucatan Peninsula is the tropical deciduous forest (Miranda 1958) with floristic composition similar to that found on limestone substrates throughout the dry tropics of the Caribbean and Middle America (White and Hood 2004). Floristically, *Fabaceae* is the most important family in the three studied forests and the most important species reported at each study region are: in the semiarid site, *Acacia gauderi* S.F. Blake, *Bursera simaruba* (L.) Sarg., *Caesalpinia gauderi* Greenm., *Gymnopodium floribundum* Rolfe, *Leucaena leucocephala* (Lam.) de Wit, *Lysiloma latisiliquum* (L.) Benth., *Piscidia piscipula* (L.) Sarg., *Thouinia paucidentata* Radlk. (González-Iturbe *et al* 2002); in the intermediate site, *A. gauderi*, *Bunchosia glandulosa* (Cav.) DC., *B. simaruba*, *C. gauderi*, *Cordia alliodora* (Ruiz & Pav.) Cham., *G. floribundum*, *Lonchocarpus yucatanensis* Pittier, *L. latisiliquum*, *P. piscipula* (Ceccon *et al* 2002); and in the subhumid site, *B. simaruba*, *C. gauderi*, *Eugenia axillaris* Vell., *G. floribundum*, *L. yucatanensis*, *P. piscipula*, *Vitex gauderi* Greenm. (White and Hood 2004). The common species along the three sites are *A. gauderi*, *B. simaruba*, *C. gauderi*, *G. floribundum*, *L. yucatanensis*, *L. latisiliquum* and *P. piscipula*.

2.2. Soil samples

At each site (i.e., semiarid, intermediate and subhumid), four mature forest stands were selected between one and five km apart. For mineral soil sampling, four plots (12×12 m) were set up in each of forest stand in 2010. In each of these plots, 36 mineral soil samples

(obtained by excavation of 7 cm diameter from the upper 20 cm of the soil profile or to lithic contact) were collected regularly in March (dry season) within the 10×10 m central area of each plot. Both black and red soils appear in each plot; samples were composited to build four composite samples by soil type for each forest stand ($n = 4$ for black and red, respectively). All soil samples were stored at 4°C for up to 48 h until processing. Soil samples were not dried nor ground.

2.3. Litterfall and litter samples

In one forest stand from each site, others twelve 12×12 m plots were also established in 2010, for a total of 16 plots. At each of these 16 plots studied, five randomly located litter traps (50 cm diameter) were installed within the 10×10 m central area. Litterfall was collected monthly for one year (from June 2010 to May 2011). The dry mass of the litter in each trap was measured, average monthly litterfall per plot was estimated, and mean annual litterfall in each selected forest stand was calculated ($n = 16$).

Forest standing crop litter in each selected forest stand at each site was sampled using circular plots (20 cm in diameter). Four samples were collected regularly within the 10×10 m central area of each plot in June, September, December, and March for one year (June 2010 to March 2011). The litter samples consisted of all dead plant material lying on the forest floor, including freshly fallen litter and a more finely decomposed litter fraction. Mean litter standing crop was calculated for each forest ($n = 16$).

All plant material (i.e., litterfall and litter) was oven-dried at 60°C and weighed to determine dry masses. The mean of litterfall dry masses was calculated for each plot, and these means were summed to obtain yearly totals per stand. The mean litter mass was estimated for each plot, and these means were used to calculate the yearly averages per stand. Finally, the mean residence time (MRT) of the organic matter on the forest floor was estimated using a mass balance approach between litter and litterfall masses (Chapin *et al* 2011).

2.4. Laboratory procedures

Mineral soils were air-dried and passed through a 2 mm sieve prior to analysis; fine roots (<4 mm in diameter) were removed.

Inorganic N concentrations ($\text{NO}_3\text{-N}$ plus $\text{NH}_4\text{-N}$) were measured by extracting a 15 g sub-sample of each composite sample soil in 100 ml 2 M KCl (Robertson *et al* 1999). The soil KCl solution was shaken for 1 h and allowed to settle overnight. A 20 ml aliquot supernatant was transferred into sample vials and frozen for later analysis (inorganic N concentrations).

Phosphorus was extracted using a modified sequential Hedley fractionation. A 2 g sample was placed in a 50 ml polypropylene centrifuge tube with 30 ml of 0.5 M NaHCO_3 (pH 8.5) (bicarbonate-

Table 3. Mean \pm SE of nitrogen and phosphorus concentrations in soils.

	Semiarid		Intermediate		Subhumid	
	Red soils	Black soils	Red soils	Black soils	Red soils	Black soils
Total N (mg N g^{-1})	11.9 ± 0.9	16.5 ± 0.9	8.7 ± 0.8	13.9 ± 0.9	3.4 ± 0.1	6.4 ± 0.3
NO_3 ($\mu\text{g N g}^{-1}$)	12.9 ± 1.3	24.5 ± 3.4	17.8 ± 2.2	25.8 ± 2.8	12.6 ± 1.3	17.8 ± 1.4
NH_4 ($\mu\text{g N g}^{-1}$)	14.1 ± 1.3	23.1 ± 3.2	10.8 ± 0.9	19.5 ± 2.3	20.2 ± 1.4	17.7 ± 1.3
$\text{NO}_3:\text{NH}_4$ ratio	0.90 ± 0.08	1.13 ± 0.11	1.75 ± 0.25	1.69 ± 0.35	0.63 ± 0.05	1.19 ± 0.22
Total P ($\mu\text{g P g}^{-1}$)	731 ± 45	816 ± 56	608 ± 61	711 ± 41	422 ± 22	581 ± 42
Bicarbonate P total ($\mu\text{g P g}^{-1}$)	15.8 ± 2.1	20.4 ± 1.6	6.9 ± 0.7	7.1 ± 0.4	10.6 ± 1.8	17.6 ± 1.5
Hydroxide P total ($\mu\text{g P g}^{-1}$)	90.6 ± 6.5	86.0 ± 6.1	61.6 ± 4.7	51.7 ± 7.4	27.6 ± 3.4	34.7 ± 4.7

Note. Nutrient concentrations to 20 cm deep mineral soil or until lithic contact.

extractable P). Samples were shaken for 16 h at 25 °C, and centrifuged for 10 min at 10 000 rpm. The extract was filtered through 0.45 μm Millipore filter. Subsequently, the remaining soil sample was extracted with 30 ml of 0.1 M NaOH (hydroxide-extractable P). The NaHCO_3 and NaOH extracts were digested with $\text{H}_2\text{SO}_4\text{--H}_2\text{O}_2$ in order to determine the total P. All extracts were analyzed for orthophosphate with the total P procedure following colorimetry (Lajtha *et al* 1999).

The bicarbonate-P extracts included both readily exchangeable inorganic P and P that is easily dissolved from solid phases in the soils. Organic P derives from organic compounds that are readily mineralized by microbes. Bicarbonate-extractable P is considered to be plant- and microbe-available in the short term. The hydroxide-P extract is thought to remove P that is associated with the surface of amorphous and some crystalline minerals and is probably available in the intermediate term, and more stable P that is involved in the intermediate-term P transformations in soils. The remaining P in the soil (difference between total P in the soil and the sum of total P in bicarbonate and hydroxide extracts) represents P that is available over long time periods (Cross and Schlesinger 1995).

All plant material (i.e., litterfall and litter) was oven-dried at 80 °C, weighed, and ground in a Wiley Mill. The concentrations of total N and total P in soil, litterfall and litter were determined from acid digestion in concentrated H_2SO_4 using an NP elemental analyzer (Technicon Autoanalyzer II).

2.5. Calculations

The concentrations of total and inorganic N and available P in the soil were transformed into area units (grams per square meter) according to the bulk density, depth, and rock content of each soil (i.e., red and black soils) in each plot from each forest.

Monthly N and P fluxes in litterfall were calculated by multiplying litterfall production by its nutrient concentrations. The means of litterfall N and P masses per month calculated for each plot were summed to obtain yearly totals per plot. These annual nutrient

input values to soil were used to calculate within-site nutrient use efficiency, defined as kilograms of dry litter mass per kilograms of nutrient litter content (*sensu* Vitousek 1982, 1984). I chose this index to assess stand nutrient cycle due to it may serve as an appropriate reference for the whole forest nutrient cycle (Vitousek 1984, Silver 1994). Mean N and P pools in litter for each plot in each sampling period were calculated by multiplying standing litter mass by each nutrient concentration. These means were used for calculating yearly averages. Rates of nutrient release in the forest floor at each site were calculated as the ratio of litter N or P pools to the annual litterfall N or P flux.

2.6. Statistical analysis

Mean soil data (the concentration of mineral N, available and hydroxide P and, total N and P) per stand were calculated, and these values were used for statistical analysis with $n = 4$ stands per site. Mean litterfall and litter data (the concentration of N and P, and the N and P masses) per plot of the selected stand were calculated, and these values were used for statistical analysis with $n = 16$ per site. Statistical analyses were based on one-way or two-way analysis of variance with Tukey's honest significant difference (HSD) post hoc tests. In cases in which ANOVA assumptions were violated by untransformed data, as detected by non-normal distribution or non-homogeneous variances, the response variable was transformed logarithmically before analysis. The main factors tested in the analysis of data set from forest soils were sampling site and/or soil type; there was no significant interaction ($P < 0.05$) site per soil for any of the soil variables. N and P concentrations and masses in litterfall and litter, as well as nutrient release in the forest floor, were examined using analysis of variance to elucidate the effects of site. Mean residence time for organic matter, N and P were compared using one-way analysis of variance separately for each site. All analyses of variance were processed using the statistical package STATISTICA.

Table 4. Mean \pm SE of amounts of nutrients in litterfall and litter.

	Semiarid	Intermediate	Subhumid
<i>Litterfall</i>			
Dry mass ($\text{kg m}^{-2} \text{yr}^{-1}$)	0.61b \pm 0.01	0.65a \pm 0.03	0.66a \pm 0.01
N ($\text{g N m}^{-2} \text{yr}^{-1}$)	8.6b \pm 0.9	11.5a \pm 1.9	11.8a \pm 1.0
P ($\text{g P m}^{-2} \text{yr}^{-1}$)	0.506b \pm 0.111	0.627b \pm 0.108	0.917a \pm 0.067
N:P ratio	17a \pm 1.8	18a \pm 2.1	13b \pm 0.9
<i>Litter</i>			
Dry mass (kg m^{-2})	1.09a \pm 0.07	0.89b \pm 0.08	0.53c \pm 0.02
N (g N m^{-2})	19.2a \pm 1.5	16.6a \pm 1.1	9.1b \pm 0.5
P (g P m^{-2})	0.933a \pm 0.078	1.148a \pm 0.101	0.744b \pm 0.049
N:P ratio	21a \pm 1.9	14b \pm 2.3	11b \pm 0.9

Note. Different letters within a line indicate significant differences ($P < 0.05$) across sites.

3. Results

3.1. N and P concentrations in soils

Across all sites and forest soil types, total N concentration varied significantly with MAP (table 3). Semiarid and intermediate sites had the highest total soil N concentration (reflecting the high organic matter content in the soil; table 2), whereas subhumid site had soils with the lowest concentration ($P < 0.001$). On the other hand, soil total N concentrations differed considerably between red and black soils (by 39%–88%; $P < 0.001$). Differences in total soil N concentrations between red and black soils decreased with decreasing MAP.

NO_3 concentrations varied significantly among sites, but changes were not consistently related to precipitation regime (table 3). NO_3 concentrations were lowest at the wettest forest site, and highest at the intermediate site ($P = 0.047$). In contrast, precipitation regime did not affect the concentration of soil NH_4 ($P = 0.169$). There were significant differences in these concentrations between soils. Concentrations of inorganic N (i.e., NO_3 and NH_4) were greater in black soils than in red ones ($P < 0.001$, for NO_3 ; $P < 0.01$ for NH_4).

Soil $\text{NO}_3:\text{NH}_4$ ratio differed among sites by a factor of almost 1.7, largely reflecting differences in NO_3 concentrations between soils from the intermediate site and soils from other sites (table 3; $P < 0.001$). In contrast, differences in the $\text{NO}_3:\text{NH}_4$ ratio in red and black soils were low and non-significant ($P = 0.246$).

Hydroxide-P and total P concentrations in soils varied considerably among the three sites as a function of MAP (table 3). An increasing gradient of hydroxide-P and total P concentrations in the direction of subhumid < intermediate < semiarid was found. The corresponding ANOVA indicated that this gradient is highly significant ($P < 0.001$ for both, hydroxide- and total P concentrations), and paired comparisons using the Tukey–Kramer HSD test showed that soils from the subhumid site consistently sustained lower levels of P concentrations ($P < 0.05$ in both cases), while soils from the semiarid site were the most P-rich.

Bicarbonate-P concentrations also varied significantly among sites, but changes were not consistently related to MAP ($P < 0.001$) (table 3). Soils from the semiarid site had the highest concentration of bicarbonate-P, whereas soils from the intermediate site had the lowest concentration. Soils from the subhumid site constituted an intermediate group. Bicarbonate- and total P concentrations were higher in black soils than in red ones ($P < 0.05$, for bicarbonate and total P). In contrast, concentrations of hydroxide P were very consistent between soils within each of the sampling sites. An analysis of the variance of hydroxide P concentrations between the two soils indicated that inter-soil variation was non-significant ($P = 0.567$).

3.2. Rates of N and P release in the forest floor

Annual litterfall was highest at the wettest site (table 4) ($P < 0.01$). Although variation in litterfall across sites was less than 10%, N and P fluxes in litterfall differed considerably among sites (by $\approx 40\%$ in the case of N, and by $\approx 80\%$ in the case of P), reflecting large differences in nutrient concentrations across sites (17.9, 17.7 and 14.1 mg N g^{-1} , for the subhumid, intermediate and semiarid site, respectively; 1.39 mg P g^{-1} for the subhumid site, 0.96 mg P g^{-1} for the intermediate site, and 0.82 mg P g^{-1} for the semiarid site). For both nutrients, the semiarid site showed the lowest flux to the soil ($P < 0.05$ for both nutrients). Nitrogen fluxes were very consistent between the intermediate and subhumid sites. The range of variation between both wetter sites (i.e., intermediate and subhumid sites) was only 2.5%. In contrast, P-fluxes in litterfall at the intermediate site were lower than those at the subhumid site. The forests at the subhumid site showed significantly lower N:P ratios than forests at the intermediate and semiarid sites ($P < 0.01$).

An increasing gradient of litter standing crop in the direction of subhumid < intermediate < semiarid was found (table 4) ($P < 0.001$). Although N concentrations in litter were consistent across sites (17.2, 17.6 and 17.6 mg N g^{-1} for subhumid, intermediate, and semiarid sites, respectively), fluxes of N in litter differed considerably among sites (by a factor of 2),

Table 5. Mean \pm SE of residence time for organic matter and nutrients in the forest floor.

	Semiarid	Intermediate	Subhumid
Organic matter (yr)	1.79aB \pm 0.15	1.37bB \pm 0.10	0.80cA \pm 0.05
N (yr)	2.23 aA \pm 0.17	1.45bB \pm 0.09	0.77cA \pm 0.06
P (yr)	1.84aB \pm 0.11	1.83 aA \pm 0.15	0.81cA \pm 0.07

Note. Different lower case letters within a line indicate significant differences ($P < 0.05$) across sites.

Different upper case letters within a column indicate significant differences ($P < 0.05$) among the residence time of organic matter, N and P for a forest site.

reflecting differences in litter masses ($P < 0.001$). In contrast, the P pool in litter was greatest at the intermediate site ($P < 0.05$), reflecting a combined effect of litter masses and P concentrations (1.29 mg P g^{-1} at the intermediate site versus 0.86 mg P g^{-1} at the semiarid, and 1.40 mg P g^{-1} at the subhumid site). The N:P ratio in litter varied with MAP across forest sites; paired comparisons using the Tukey–Kramer HSD test showed that the forest floor at the semiarid site consistently sustained higher ratios, while forest floors at the subhumid site showed the lowest N:P ratios ($P < 0.01$).

A mass balance approach between litter standing crop and litterfall masses indicated that the MRT of the organic matter in the forest floor consistently increased with decrease in MAP (table 5) ($P < 0.001$). In addition, the rates of N release decreased (as indicated by its MRT on the forest floor) with decreasing MAP ($P < 0.001$). Although the rate of P release in the forest floor was highest at the wettest site ($P < 0.001$), differences between the MRTs of P at the intermediate and semiarid sites did not vary significantly ($P > 0.05$).

The residence times for organic matter and nutrients were very consistent within the subhumid site ($P > 0.05$). At that site, the ranges of variation of MRTs among nutrients and organic matter was only 5% between N and P, and less than 4% in cases of N or P and organic matter. In contrast, the same comparison of MRTs at sites with less than 1000 mm yr^{-1} of MAP yielded different results: analyses showed P immobilization at the intermediate site and N immobilization at semiarid site.

4. Discussion

A major research priority in the study of TDFs is to understand the effects of climate change, since many regions that are home to these forests are predicted to experience more frequent droughts and decreased MAP (Meir and Pennington 2011, IPCC 2013).

4.1. Relatively moderate variation in litterfall and a more subtle change in nutrient use efficiency may reflect adaptations of TDF plants to decrease in MAP

My objective was to test the prediction that low precipitation regimes would be related with lower productivity and an increase in N and P use in TDFs. Consistent with this, I found a slightly decrease in litterfall with decreasing MAP, a pattern that has been observed in other TDFs (Martínez-Yrizar and Sarukhán 1990, Read and Lawrence 2003). This observed slight responses, is consistent with the findings of a low sensitivity of litterfall to precipitation regime in TDFs (Meir and Pennington 2011). Although this low sensitivity of litterfall to changes in precipitation regime across these tropical forests cannot be interpreted as a lack of aboveground productivity responses to changes in water availability, considering that plants adjust to increases in water shortage by altering allocation to trunk growth (Doughty *et al* 2014), it is comparable with the low variation observed in NDVI data for these TDFs across the precipitation gradient (figure 1; Campo, unpublished data).

In contrast to these moderate site effects on litterfall, an important increase in plant nutrient use efficiency was found with reduced MAP, rather than changes in litterfall. Nutrient use efficiency suggests that N and P are cycled more efficiently with greater water deficit (N use efficiency increases from 56 at the subhumid site to 71 at the semiarid site, and P use efficiency increases from 720 at the subhumid site to 1205 at the semiarid site; estimated from table 4). On the other hand, the data also indicates a relatively more straightforward climate influence on plant nutrient use than on litterfall in this TDF biome. The strong sensitivity of nutrient use to MAP provides insight into a potential P and/or N limitation of plant productivity in response to changes in precipitation regimen, and supports the prediction that many tropical forests are limited by P and/or N (Vitousek 1984, McGroddy *et al* 2004). Moreover, the very large increases in P use efficiency (an increase of 40%) than on N-use efficiency (an increase of 21%) with decrease in MAP, shows that the dry season extent and/or intensity may have created P limitation in these ecosystems (Campo and Vázquez-Yanes 2004). In karstic landscape of the Yucatan Peninsula where soil pH is more than neutral, P may be chemically bound to calcium (Gamboa *et al* 2010, Cuevas *et al* 2013). Phosphorus availability in TDFs may be further reduced because dry conditions prevent dissolution and plant uptake of P bound to the soil (Lugo and Murphy 1986, Campo *et al* 2001b). This condition would be pronounced in drier sites, where shallow soils and slow P release create bad P conditions, producing the regional patterns in P use efficiency and litter N:P ratio that I found.

Table 6. Mean \pm SE of nitrogen and phosphorus pools in soils.

	Semiarid	Intermediate	Subhumid
Total N (g N m^{-2})	463b \pm 21.0	896a \pm 94.0	538b \pm 39.4
Inorganic N ^a (g N m^{-2})	1.32c \pm 0.09	2.94b \pm 0.47	4.74a \pm 0.27
Bicarbonate total P (g P m^{-2})	0.575b \pm 0.040	0.656b \pm 0.071	1.637a \pm 0.091

Different letters within a line indicate significant differences ($P < 0.05$) across sites.

Nutrient pools were calculated to 20 cm deep mineral soil or until lithic contact.

^a Inorganic N = $\text{NO}_3 + \text{NH}_4$.

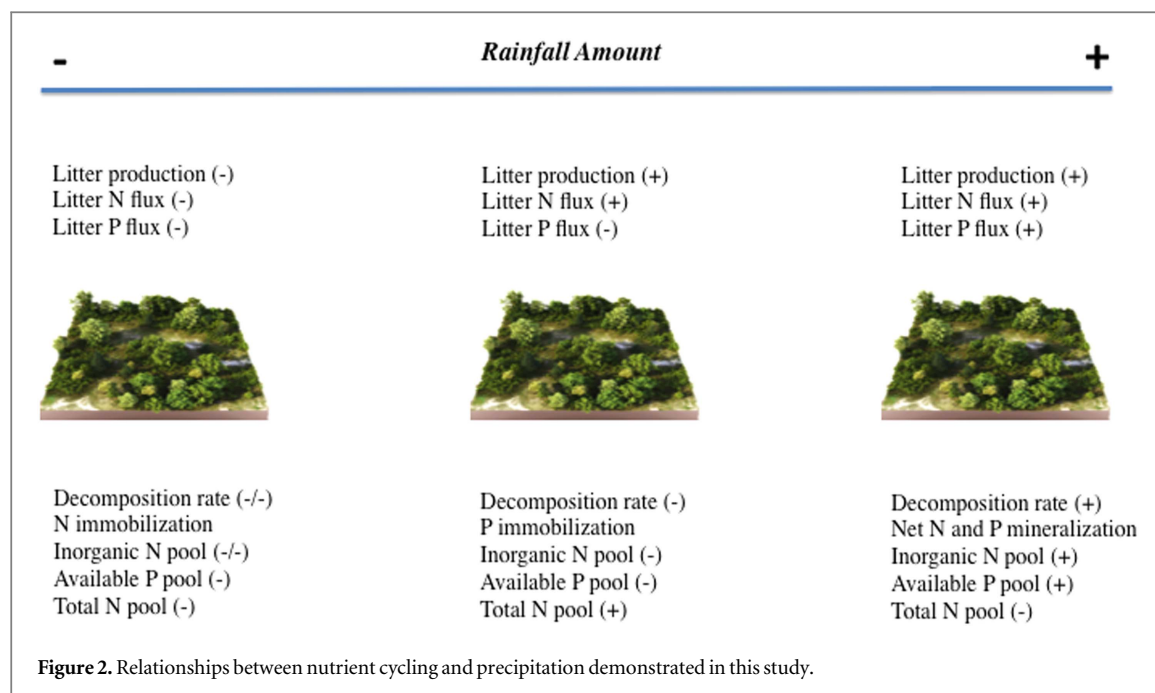
4.2. A hypothesis: limitation patterns shift from phosphorus towards nitrogen with decreasing precipitation

The strong decrease in precipitation amount from subhumid to semiarid climates limits aspects of ecosystem function on the Yucatan Peninsula (Bejarano *et al* 2014, Campo and Merino 2016). This, in turn, fosters an increase in biomass investments below- *versus* above-ground (Roa-Fuentes *et al* 2013). Despite the importance of water limitation for ecosystem processes in the Yucatan Peninsula, other resources, such as essential nutrients, also place constraints on aspects of ecosystem function. Although long-term field fertilization experiments are often considered the best approach for assessing nutrient limitation (Chapin *et al* 1986), logistical difficulties in the field create the need for more tractable proxies for potential limitation status (Condit *et al* 2013); comparisons of nutrient concentrations in litter and litterfall, as well as comparisons of MRT for nutrients to MRT for organic matter in the forest floor, may also offer predictive insight into nutrient limitation (Vogt *et al* 1986). The results of both these types of comparison in the present study (greater nutrient concentration in litter than in litterfall, and greater MRT for nutrients than for organic matter) indicate the prevalence of nutrient immobilization, and support the notion of nutrient limitation for TDFs. Here, both comparisons (i.e., element concentrations and MRTs) reveal that the subhumid site had neither N nor P limitation, while ecosystem function at the intermediate site appeared to be regulated by P limitation, and at the semiarid site it appeared to be regulated by N limitation.

Although large quantities of P are cycling at the study sites, and P inputs are associated with long-distance dust transport on the Yucatan Peninsula (Das *et al* 2013), data indicates an unequivocal relationship between the size of the P-available pool in the soil (table 6) and the possible existence of P limitation at the intermediate site. However, P-available concentrations in soils are also low, as expected in a P-limited ecosystem. These results agree with experimental fertilization studies within the same intermediate climate area, which indicate P-limitation (Campo and Vázquez-Yanes 2004) and could be linked to the high nutrient requirement of deciduous species (Givnish 2002). The lack of nutrient limitation with

increased rainfall at the subhumid site is probably related to the accumulation of a thicker horizon and lower rock content than at both drier sites (i.e., intermediate and semiarid sites). In addition, increased MAP promotes a more active microbial community, and this is reflected by the higher rate of P release in the forest floor of the subhumid site (around 55% faster than at either the intermediate or the semiarid site), which could be sufficient to support the nutrient demands of plants and soil microbes.

In this study, high concentrations of inorganic N were found to accumulate in the soils of the driest, semiarid, site on the precipitation gradient. One factor that may be an important determinant of this N accumulation at the semiarid site relative to the wetter sites is the reduced leaching and release of large amounts of nutrients immobilized in organic and mineral soil under intense drought conditions (Singh *et al* 1989, Campo *et al* 1998). However, when soil nutrient pools are considered, the data indicates that inorganic N pool in the soil decreased with reduced precipitation due to the shallowness of soils. Moreover, the comparison of MRTs for N and organic matter, and the comparison of N concentration in litter and litterfall, signal N immobilization in the forest floor of the semiarid site, and suggest that ecosystem function at the driest extreme of the precipitation gradient is N-limited. Although there is a lack of nutrient fertilization experiments to support the hypothesis of N-limitation at the semiarid site, the mass balance approach between N pool in litter and N flux in litterfall indicates that N release in the forest floor declined by 35% from the intermediate site to the semiarid site, and by 65% from the subhumid site to the semiarid site. These findings regarding N-limitation in the semiarid forest agree with results from other sites on the Yucatan Peninsula (outside the current study's sites) that indicated N limitation in TDFs (Campo and Vázquez-Yanes 2004). Also, Roa-Fuentes *et al* (2015) have previously shown that levels of ^{15}N in leaves and soils increase with dry season length across this climate gradient, suggesting that the forest at the semiarid site might experience relatively high rates of gaseous N loss compared to the rates of N losses at both wetter sites (i.e., intermediate and subhumid sites), as well as an increased openness of N cycling due to increased water limitation. Different factors could promote N losses in the drier end of the gradient, such as a lower plant N demand due to



low gross primary productivity or pulsed rain events which decouple plant N demand and supply lead N to be less tightly conserved. This interpretation is mainly supported by observation that semiarid site is characterized by episodic pulsed rain events that are known to promote microbial activity (Campo *et al* 1998) and fractionating denitrification losses (Austin *et al* 2004, Fang *et al* 2015), favored by the high soil nitrate levels in Yucatan that provide a substrate pool for rapid denitrification upon soil wetting. This increased openness of N cycling with increased duration of the dry season could promote a limitation by N availability, as has been suggested by Hedin *et al* (2009), and is also suggested by the balance studies.

5. Conclusions

The future productivity and terrestrial C storage capacity of tropical forests is uncertain, and feedbacks among decreased precipitation, net primary productivity and nutrient availability are complex (Townsend *et al* 2007, Asner *et al* 2015). Tropical forests are generally expected to be limited by the availability of P (Vitousek 1984) but N limitation is also common (Bejarano-Castillo *et al* 2015), and these nutrient limitations could be exacerbated by changes in forest biogeochemistry in response to less rainfall (Schlesinger *et al* 2016). Although water limitation is widespread in TDFs, including at these study's sites on the Yucatan Peninsula, the data from this study reveals a pattern of limitation shifting from P towards N with decreasing annual precipitation (figure 2).

The climate relationships observed on the Yucatan Peninsula add to our conceptual understanding on the effects of precipitation regime on tropical forest biogeochemistry (Cleveland *et al* 2011), and reveal

the consequences of changes in water shortage on forest function under subhumid to semiarid climates. My findings suggest that the predicted decrease in precipitation (of up to 30 mm per decade) in southern and southeastern Mexico and other tropical areas (e.g. Conde *et al* 2011) would have profound consequences on the N and P cycles in TDFs through changes in litterfall production, quality, decomposition rates and nutrient availability (figure 2). Ultimately, changes in the rate of nutrient supply could have long-term negative effects on net primary production and the future carbon storage in these ecosystems. Further studies would be necessary to confirm the mechanistic links suggested by the study findings, particularly by doing experimental manipulations of nutrient availability and rainfall exclusion in wetter forests.

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