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Phosphorus cycling in a Mexican tropical dry forest ecosystem

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Abstract. The study was conducted in five contiguous small watersheds (12–28 ha) gauged for long-term ecosystem research. Five 80 × 30 m plots were used for the study. We quantified inputs from the atmosphere, dissolved and particulate-bound losses, throughfall and litterfall fluxes, standing crop litter and soil available P pools. Mean P input and output for a six-year period was 0.16 and 0.06 $kg{\cdot}ha^{-1}{\cdot}yr^{-1}$, respectively. Phosphorus concentration increased as rainfall moved through the canopy. Annual P returns in litterfall (3.88 kg/ha) represented more than 90% of the total aboveground nutrient return to the forest floor. Phosphorus concentration in standing litter (0.08%) was lower than that in litterfall (0.11%). Phosphorus content in the litterfall was higher at Chamela than at other tropical dry forests. Mean residence time on the forest floor was 1.2 yr for P and 1.3 yr for organic matter. Together these results suggest that the forest at Chamela may not be limited by P availability and suggest a balance between P immobilization and uptake. Comparison of P losses in stream water with input rates from the atmosphere for the six-year period showed that inputs were higher than outputs. Balances calculated for a wet and a dry year indicated a small P accumulation in both years.

Introduction

Phosphorus is typically the most conserved nutrient in tropical forest ecosystems. Dissolved P output generally does not exceed 0.3 $kg{\cdot}ha^{-1}{\cdot}yr^{-1}$, while nitrogen, calcium, magnesium and potassium losses are between 2 to 20 $kg{\cdot}ha^{-1}{\cdot}yr^{-1}$ (Bruijnzeel 1991). The coupled P conservation by leaves (Jordan et al. 1980), roots and mycorrhizas (Stark & Jordan 1978; Cuevas & Medina 1988), microorganisms and geochemical sorption (Salcedo et al.

1991), act to retain the nutrient in the ecosystems. Evidence of nutrient cycling studies suggests that primary production in tropical forests could be limited by P availability (Vitousek 1984; Tanner et al. 1998).

Although seasonal forests represent more than 40% of the tropical forest area (Murphy & Lugo 1986) nutrient cycling processes have not been studied in them as extensively as in their humid counterparts. In areas of low rainfall with deciduous vegetation, litterfall is the major pathway of nutrient return to the soil and represents a more synchronized pulse of nutrient input to the soil than in the wet tropics. There are a small number of studies on rates of nutrient fluxes in litterfall in tropical dry forests. Jaramillo and Sanford (1995) listed three data sets and there are some others available (Singh & Singh 1991a,b, 1993; Díaz 1997). A high P- use-efficiency by plants when compared to other nutrients suggests that P could play a key role in primary production of tropical dry forests (Jaramillo & Sanford 1995).

Nutrient mass balances shed light on the relative importance of input from the atmosphere and leaching, for the nutrient economy and on long-term sustainability of the ecosystem. Although Bruijnzeel (1991) reviewed nutrient budgets in tropical forest ecosystems, none of the studies included a dry tropical forest site. Also, a review of nutrient cycling in tropical dry forest (Jaramillo & Sanford 1995) did not report nutrient budget studies, suggesting a lack of information concerning input and output of P in these ecosystems. Recently, we reported the first study on base cation input and output for a Mexican tropical dry forest (Campo et al. 2000). A long-term study on the structure and functioning of a tropical dry forest in Mexico (Sarukhán & Maass 1990) has included measurements of the rates of nutrient inputs and outputs, and of nutrient dynamics associated with organic matter.

In this paper we consider the cycle of P. A first objective of our study was to estimate P input by precipitation and output in stream water. For this input-output study we used the watershed-ecosystem method (Likens & Bormann 1995). A second objective was to determine the relative importance of throughfall, litterfall, and litter in the internal cycling of P in this tropical forest.

Study site

The study was conducted at the Chamela Biological Station, on the Pacific coast of Mexico. Details about the study site, forest ecosystem, and general procedures are described in Campo et al. (2000). Only the procedures unique to this study are given here.

Mean annual temperature is 24.9 °C, with less than a 5 °C difference between the coolest and warmest months. Mean total rainfall is 679 mm (García-Oliva et al. 1991), distributed mainly from June to October. Average

runoff is 5% of the annual rainfall, and the infiltration rate is 13.7 mm/min (Cervantes et al. 1988; López-Guerrero 1992). The landscape consists of low hills (50–100 m in elevation) with convex slopes (26° in average). The predominant lithology includes Tertiary volcanic rocks of rhyolitic and rhyodacitic composition and their associated tuffs (Campo 1995). The annual weathering rate is over 600 kg/ha and the secondary mineral in soil is authogenic kaolinite (Campo et al. 2001). The soils are young, shallow (0.5–1 m depth), and are predominantly sandy loams (Orthents). Organic matter content in the upper soil profile (20 cm) is 2.9%. Exchangeable cation concentrations are 1744 mg/kg for Ca, 163 mg/kg for K and 435 mg/kg for Mg and the pH is 6.2 (Maass 1985).

The forest is dominated by deciduous trees, 6 to 10 m in height (Lott et al. 1987). Lott (1985) reports 758 plant species from 107 families for the area, with Leguminoseae being the most important family with 15% of the species. The ecosystem is a mature and unperturbed forest, with a net ecosystem production close to zero (JM Maass, unpublished data). Aboveground biomass is 85 Mg/ha (Martínez-Yrízar et al. 1992) and belowground biomass ranges from 17 to 31 Mg/ha (Castellanos et al. 1991; Rentería 1997). With few exceptions, the species are leafless for several months each year and their phenology is driven by water availability (Bullock & Solís Magallanes 1990). Leaf area index varies between 1 m^2/m^2 and 4.5 m^2/m^2 during the year (Maass et al. 1995).

Methods

Five contiguous small watersheds (12–28 ha) were gauged for long-term ecosystem research (Sarukhán & Maass 1990; Figure 1). Even thought the watershed bedrock is not water tight, our hydrological data suggest that deep leaching in watershed is close to zero (Burgos 1999). Three permanent plots were established along an altitudinal gradient on one of the watersheds (Watershed I). The rest of the watersheds (Watershed II to V) included only one permanent plot at the middle position. Only the five middle position plots were used to study the P fluxes in litterfall and throughfall, and the standing litter (see below). Each plot was 2400 m^2 (80 $\times$ 30 m) with its long axis perpendicular to the stream channel.

Input from the atmosphere

Phosphorus bulk deposition was sampled during a 6-yr period (1990–1995). Samples were collected in 6 bulk deposition collectors maintained in cleared areas, located within the sampling area (Figure 1). The collectors were made

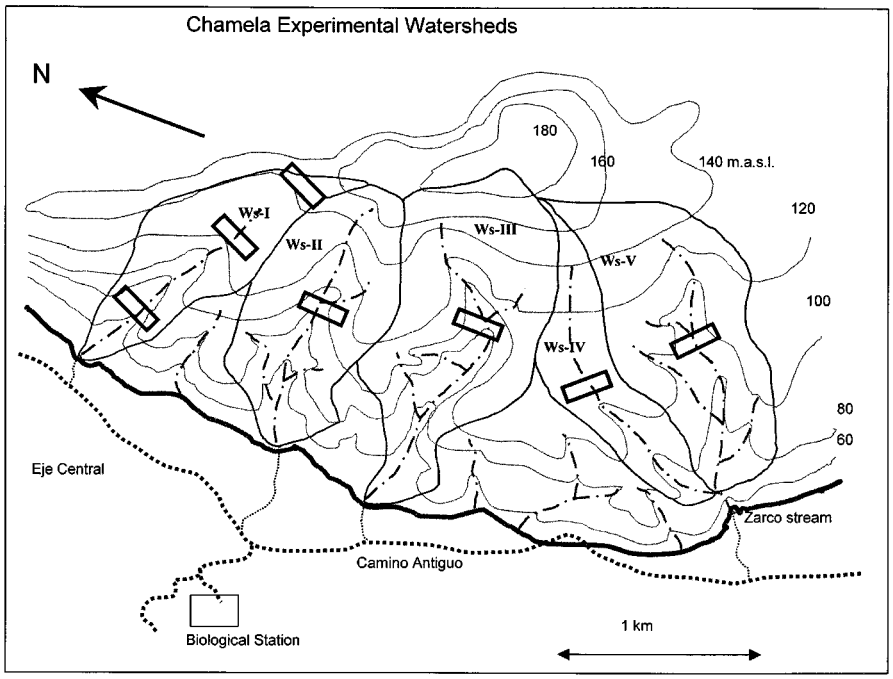

Figure 1. Map of the southfacing experimental watersheds within the Chamela Biological Station. Instrumentation of watershed-ecosystem shown is: (♦) weather station, (▼) stream gauge and stream sampling site, (□) (____) contour (m.a.s.l.), (___.___) stream channel, and (▬) watershed boundary.

with polypropylene funnels (12 cm diameter) connected to 2l polypropylene containers by tygon tubing. Containers were attached to a vapor trap and a vapor barrier formed by a loop in the tubing to prevent evaporation and gas exchange with the atmosphere. The entrance to the funnel was covered with a thin layer of glass wool to prevent contamination from insects and bird excrement. Fiberglass was rinsed with distilled water after every collection and changed each season. The container and tubing were kept from sunlight. After every storm, 0.5 ml of phenyl mercuric acetate solution (0.1 g in 15 ml dioxane, diluted to 100 ml) was added to 160 ml of collected water. Samples were stored in polypropylene containers and kept refrigerated. The collectors were cleaned after every storm with 10% HCl solution and rinsed with deionized water. The deionized water used for washing and rinsing the collectors was periodically analyzed to check cleanness and lack of contamination through washing and manipulation.

Wet and dry depositions were sampled together (with the same collector) after every rainfall event, thus a slight underestimation of nutrient input may

have occurred as a result of an infrequent sampling of dry deposition during the dry season.

Phosphorus entering the ecosystem was calculated by multiplying rainfall by nutrient concentration. Rainfall was measured with two bulk rain gauges and one recording rain gauge. All sampling devices were within a 2 km radius from the plots.

Losses from the watershed

Dissolved P exported from the ecosystem was evaluated for a 6-yr period (1990–1995), in the five small watersheds (Figure 1). Coshocton wheels were used to sample the runoff water, which was stored in polypropylene containers (50l capacity) following the same procedure as for the rain samples (see above). Drain water was collected after each storm event and analyzed accordingly. Phosphorus was determined in 160 ml aliquots of drain water from each of the five watersheds, for every runoff event. Fifty microliters of phenyl mercuric acetate solution were added to the samples that were kept refrigerated. The volumes of drainage water were gauged with one water level recorder at weir of each watershed.

Loss of particulate-bound P was estimated by collections of particulate organic material and sediments trapped at the weir. Material was collected in three 10 cm, 5 cm, and 2 cm mesh nets from water passing through the gauged weir and in a sediment trap after the net at the weir during a 2-yr period (1993 and 1994). All organic material or sediments were collected, oven-dried (80 °C) and weighed after every runoff event. Particulate organic matter was ground in a Wiley Mill. Dissolved P flux leaving the watershed was calculated as the product of nutrient concentration in runoff by the volume of water drained from the watershed. Particulate-bound P exported from the watershed was estimated as the product of nutrient concentration by the amount of organic matter or sediment output from the watershed.

Phosphorus flux in throughfall

Throughfall was collected during a 6-yr period (1990–1995) from six collectors at the plot on Watershed I. Each collector consisted of a polyvinyl chloride (PVC) channel of 0.1 $\times$ 2.0 m, drained by a tygon tubing into a polypropylene container (22.5 l capacity). The PVC channel was covered with a thin plastic mesh 1 $\times$ 1 mm, and glass wool was placed at the mouth of the drainage tubing to prevent contamination from litterfall and litter debris. The container and tubing were kept from sunlight to avoid algae growth. Water samples were treated as described for the rainfall samples. Collectors were cleaned after every sample collection with a 10% HCl solution, rinsing

with deionized water. The deionized water used for washing and rinsing the collectors was periodically analyzed to check cleanness and lack of contamination through washing and manipulation. Phosphorus flux in throughfall was determined by multiplying throughfall amount by its nutrient concentration. Net P throughfall was calculated by subtracting element mass in the bulk deposition.

Phosphorus flux in litterfall

Flux was calculated multiplying litterfall production by its P concentration. Production data for a 5-yr period (1987 to 1991) were obtained from a current long-term litterfall monitoring study initiated in 1981 (Martínez-Yrízar & Sarukhán 1990), in which 24 litter traps (50 cm diameter) were collected monthly in each of the five plots previously described. Litterfall P concentrations for the 1987–1990 period were obtained from Díaz (1997) and an additional year (1991) was included for this study (see below). Phosphorus concentrations were measured monthly.

Phosphorus pool in litter

The P pool was calculated by multiplying the mass of standing crop litter by its nutrient concentration. Forest standing crop litter was sampled in Watershed I and IV in January, May, September and November 1991 by use a circular plot (20 cm in diameter). On each of two slopes of the watersheds, twelve surface litter samples were collected on each sampling date. The samples were regularly collected along a 40 m transect perpendicular to the stream channel. The litter samples consisted of all dead plant material lying on the forest floor, including the freshly fallen litter and the more finely decomposed litter fraction. The samples were oven-dried at 80 °C during 48 hs and ground in a Wiley Mill.

Phosphorus pools in soil

Phosphorus pools were determined for resin and bicarbonate extracts. Anion exchanges resins remove solution P-inorganic, the most plant available P-inorganic form in soil. Bicarbonate extractable P represent easily solubilized P-inorganic adsorbed to soil surface and readily mineralized P-organic (Cross & Schlesinger 1995).

Soil was sampled in Watershed I during May 1993. Eight samples were collected; four from the 0–5 cm depth and four from 5–20 cm. The upper 20 cm of the soil profile in this tropical dry forest concentrates microbial biomass and soil organic matter (V.J. Jaramillo, unpublished data), root

biomass (Castellanos et al. 1991), nutrients (García-Oliva 1992) and mineral dissolution process (Campo et al. 2001). Soil was air-dried and sieved through a 2-mm mesh.

Soil resin- and bicarbonate-P were determined with a sequential extraction procedure (Hedley et al. 1982). Duplicate 0.5 g soil samples were placed in 50 cc centrifuge tubes. Thirty ml of deionized water and a 50 × 10 mm strip resin-membrane (Ion Exchange Membrane BIO-RAD AG 1-X8, in carbonate form) were added to all tubes, shaken for 16 h, and centrifuged at 10,000 rpm at 0 °C for 10 min. The strip was removed, placed in a clean centrifuge tube, shaken with 30 ml of 0.5 N HCl for 1 h and centrifuged. The supernatant was filtered to obtain the available P. The soil remaining in the tubes was shaken with 30 ml of 0.5 N $NaHCO_3$ for 16 h and centrifuged. The supernant was analyzed for bicarbonate-P.

Chemical analysis

Right after collected, rainfall, throughfall, and runoff samples were filtered to remove the suspended material. Sediment samples from weirs were air-dried and ground to pass a 2 mm sieve. Phosphorus in litterfall, litter, particulate organic matter and sediments were determined after digestion (Technichon Autoanalyzer II, 1978). A 0.5 g of vegetal material was digested with 7 ml of concentrate H_2SO_4, 1.1 g of digest mixture (K_2SO_4 and Cu_2SO_4, in 9:1 relation), and 3 ml of H_2O_2. Three grams of sediment were digested with 15 ml of H_2SO_4, 2.0 g of digest mixture (K_2SO_4 and Cu_2SO_4, relation 9:1), and 5 ml of H_2O_2. The labile P content in soil samples was determined after digestion with sulfuric acid and ammonium-persulfate (APHA 1992).

Total P in water, plant, sediment and soil bicarbonate fraction was determined by the molibdate method after ascorbic acid reduction (Murphy & Riley 1962). Resin-P concentration in soil was determined with the malachite green colorimetric reaction (Ohno & Zibilske 1991).

All chemical determinations were duplicated, rejecting those with more than 10% difference between them. Blanks were run though the analysis to detect any source of contamination.

Statistical analysis

Differences in P concentrations between bulk deposition and runoff water were determined by a one-way analysis of variance (ANOVA). Annual variation of P fluxes in litterfall and throughfall and spatial variation in P pools in the forest soil were analyzed by ANOVA. The Honest Significant Difference (HSD) test was used when statistical differences ($P < 0.05$) were observed.

Table 1. Annual input and output phosphorus in the Chamela tropical dry forest, Mexico. Values are average with standard errors in parenthesis.

Year	Rainfall (mm)	Storms per year	Runoff (mm)	Bulk deposition input		Stream water output		Net gain or loss (kg/ha)*
				(mg/l)	(kg/ha)	(mg/l)	(kg/ha)	
1990	560	28	17	0.03 (0.01)	0.130	0.06 (0.03)	0.005 (0.001)	0.125
1991	710	59	1	0.03 <(0.01)	0.167	0.09 (0.02)	<0.001 <(0.001)	0.166
1992	1090	63	216	0.02 (0.01)	0.113	0.04 (0.01)	0.102 (0.023)	0.011
1993	960	59	119	0.03 (0.01)	0.226	0.09 (0.02)	0.121 (0.022)	0.105
1994	435	52	2	0.02 (0.01)	0.069	0.12 (0.01)	0.002 <(0.001)	0.067
1995	757	42	163	0.03 <(0.01)	0.228	0.12 (0.02)	0.154 (0.020)	0.074
Mean	752 (109)	51 (6)	86 (41)	0.03 <(0.01)	0.156 (0.028)	0.09 (0.01)	0.064 (0.031)	0.092 (0.024)

*Phosphorus balance estimated as input from the atmosphere minus output by stream flow.

Results

Phosphorus inputs and outputs

Inputs from the atmosphere

Annual mean rainfall and total number of storms during 1990 to 1995 were 752 mm and 51 storms per year, respectively (F. García-Oliva pers. com.; Table 1). Phosphorus concentration from bulk deposition samplers was 0.03 $\pm$ < 0.01 mg/l (mean and S.E.). Annual means concentrations showed a low range of variation. Average monthly concentrations in bulk deposition peaked in June and again in October (Figure 2(b)).

Annual P concentration in rainfall decreased with increased amounts of rainfall, although the relationship was not significant, consequently annual P deposition did not increase with rainfall, even though annual rainfall

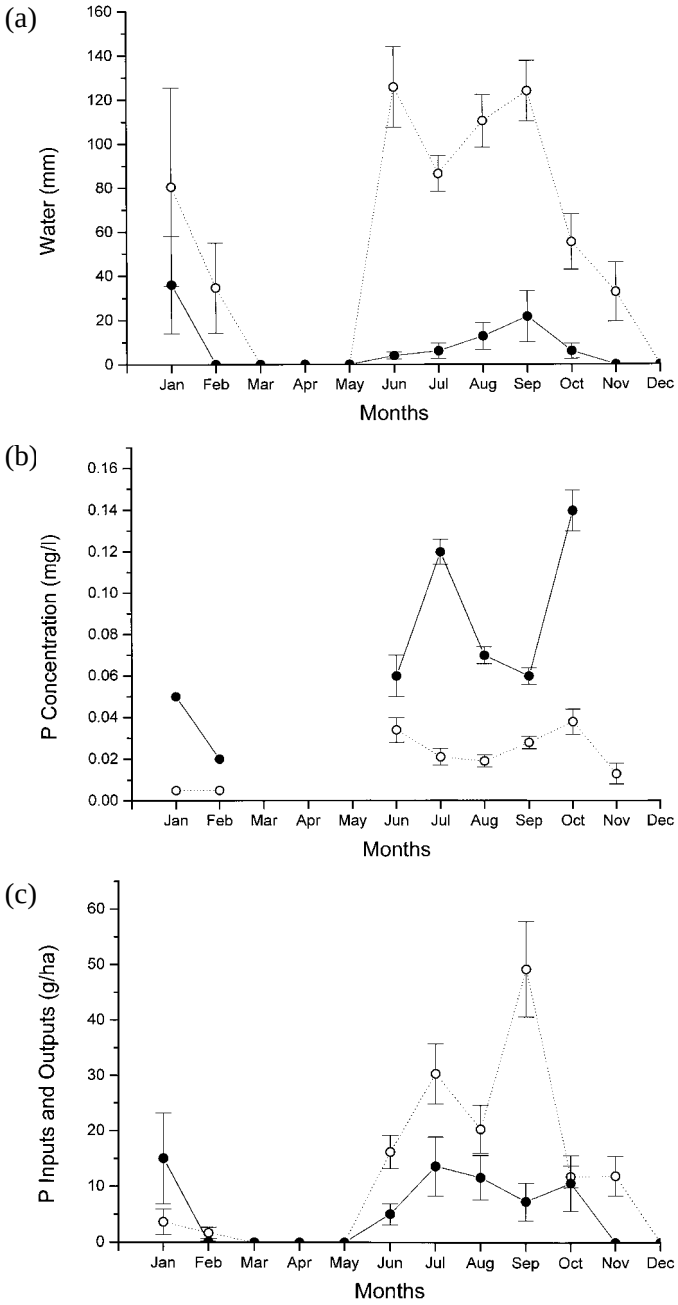

Figure 2. Monthly amounts of rainfall (–○–) and runoff water (–●–) for five watersheds in the Chamela tropical dry forest during 1990–1995 (a). Monthly concentration of P in the bulk deposition (–○–) and runoff water (–●–) in the Chamela tropical dry forest (b). Monthly inputs of P in the bulk deposition (–○–) and outputs in runoff water (–●–) in the Chamela tropical dry forest (c).

Table 2. Particulate losses of phosphorus in stream water in the Chamela tropical dry forest, Mexico. All values are the average of five watersheds with standard errors in parentheses.

Year	Organic particulate			Inorganic particulate		
	Dry weight	P		Dry weight	P	
	($kg \cdot ha^{-1} \cdot yr^{-1}$)	(%)	($kg \cdot ha^{-1} \cdot yr^{-1}$)	($kg \cdot ha^{-1} \cdot yr^{-1}$)	($\mu g/g$)	($kg \cdot ha^{-1} \cdot yr^{-1}$)
1993	4.33	0.07	0.003	19.31	196	0.002
	(0.46)	<(0.01)	<(0.001)	(1.44)	(14)	<(0.001)
1994	1.26	0.17	0.002	1.22	297	0.001
	(0.36)	(0.03)	<(0.001)	(0.74)	(13)	<(0.001)

varied by a factor of about 2 during the study period (Table 1). The inputs showed temporal trends with high values occurring during September and comprised ≈31% of the annual P inputs (Figure 2(c)). This high P input during September was primarily due to greater amounts of rainfall and not to any detectable difference in the nutrient concentration (Figures 2(a) and 2(b)).

Losses of phosphorus from the watershed

The annual mean stream runoff was 86 mm and represented 11.4% of total rainfall (Table 1). Dissolved P concentrations in stream water ranged from a low of 0.04 mg/l in 1992 to a high 0.12 mg/l in 1994 and 1995. Mean monthly concentrations peaked in October when the leaves start to fall (Figure 2(b)). Annual mean losses of dissolved P in runoff varied more than 3 times between years (Table 1) and showed a direct and significant relationship with the amounts of runoff water ($P < 0.001$).

In contrast to most years, in which dissolved P output occurred between June and November, more than 98% of the total loss in 1992 occurred between January and February. This was the result of an extraordinary rainfall event of 644 mm in January.

Phosphorus losses from the ecosystem as particulate organic and inorganic matter were lower than 5 $g \cdot ha^{-1} \cdot yr^{-1}$ (Table 2). Particulate matter represented a minor fraction of total P output (≈4%) during the wet year (1993). However, its contribution to P output in a dry year (1994) increased to 60%.

Table 3. Throughfall and its phosphorus flux in the Chamela tropical dry forest, Mexico. Values are means with standard errors in parentheses.

Year	Throughfall	P	
	(mm/yr)	(mg/l)	($kg \cdot ha^{-1} \cdot yr^{-1}$)
1990	386	0.09	0.24
	(112)	(0.02)	(0.05)
1991	520	0.12	0.37
	(118)	(0.01)	(0.07)
1992	894	0.11	0.54
	(285)	(0.03)	(0.08)
1993	735	0.10	0.23
	(180)	(0.02)	(0.06)
1994	322	0.13	0.35
	(88)	(0.04)	(0.05)
1995	686	0.12	0.38
	(190)	(0.04)	(0.07)
Mean	591	0.11	0.35
	(98)	<(0.01)	(0.05)

Intrasystem cycling

Phosphorus cycling in throughfall and litterfall

The proportion of the rainfall that reached the forest floor as throughfall between 1990 and 1995 was 78.6 ± 4.1% (S.E.). Concentration and P flux increased markedly during the passage of rainfall through the canopy. The annual mean P concentration in throughfall was 0.11 ± < 0.01 mg/l (S.E.) and its flux was 0.35 ± 0.05 kg/ha (S.E.) (Table 3). Annual means concentrations did not show significant changes among years. However, P flux was higher in the wettest year (1992).

The annual mean P concentration in litterfall was 0.11 ± < 0.01% (S.E.) and annual P return was 3.88 ± 0.16 kg/ha (Table 4). Litterfall production from 1987 to 1991 (3.39 ± 0.87 $Mg \cdot ha^{-1} \cdot yr^{-1}$) did not differ significantly from long-term litterfall production at the study site (Martínez-Yrízar & Sarukhán 1990; Martínez-Yrízar 1995).

Table 4. Litterfall production and its phosphorus flux in the Chamela tropical dry forest, Mexico. All values are averages with standard errors in parentheses.

Year	Dry weight	P	
	($Mg \cdot ha^{-1} \cdot yr^{-1}$)	(%)	($kg \cdot ha^{-1} \cdot yr^{-1}$)
1987	3.112	0.10	3.40
	(0.169)	<(0.01)	(0.27)
1988	3.568	0.13	4.89
	(0.175)	(0.01)	(0.48)
1989	2.826	0.12	3.47
	(0.171)	<(0.01)	(0.36)
1990	3.559	0.12	4.30
	(0.189)	<(0.01)	(0.40)
1991	3.752	0.09	3.45
	(0.219)	<(0.01)	(0.29)
Mean	3.388	0.11	3.88
	(0.087)	<(0.01)	(0.16)

Pools in standing litter

Phosphorus concentration in the standing litter was $0.08 \pm < 0.01\%$ (S.E.). Concentrations ranged from a low of 0.06% in the middle of the rainy season (September) to a high of 0.11% in the dry season (Table 5). These differences among sampling dates were significant ($F = 5.34$; $P < 0.005$).

The mean P pool in the litter layer was 4.07 ± 0.30 kg/ha (S.E.) and fluctuated through the year with a peak in the dry season ($F = 7.61$, $P < 0.0005$; Table 5). The difference between seasons largely reflected both changes in the standing crop litter and in P concentrations.

Pools in soil

Soil resin-P concentration was higher in the upper (0–5 cm) than in the deeper (5–20 cm) soil (3.21 ± 0.71 and 1.24 ± 0.30 μg/g, respectively). The pools were 1.22 ± 0.27 and 1.75 ± 0.46 kg/ha, for the upper and deeper soil, respectively. Upper soil bicarbonate-P concentration and pool were 12.12 ± 2.30 μg/g and 4.62 ± 0.86 kg/ha, respectively. Unfortunately, samples of bicarbonate-P from the deeper soil were lost.

Table 5. Litter standing crop and P concentrations and pools in the Chamela tropical dry forest, Mexico, in 1991. All values are averages with standard errors in parentheses.

Month	Dry weight	P	
	(Mg/ha)	(%)	(kg/ha)
January	5.652	0.11	6.26
	(0.489)	(0.01)	(0.89)
May	5.802	0.06	3.55
	(0.413)	<(0.01)	(0.26)
September	4.316	0.06	2.72
	(0.341)	<(0.01)	(0.24)
November	4.680	0.09	3.77
	(0.319)	(0.01)	(0.58)
Annual	5.113	0.08	4.07
	(0.203)	(0.01)	(0.30)

Discussion

Phosphorus input and output

The input of P from the atmosphere differed from year to year; its minimum value was observed in the driest year (1994). The mean P input is closer to lower end of the global range (0.07–1.7 $kg \cdot ha^{-1} \cdot yr^{-1}$; Newman 1995) and is similar to inputs reported for five tropical moist forests (Bruijnzeel 1991). The high concentration of P in bulk deposition in June is probably related to dust deposition during the rainless period. The peak concentration in October is unexplained, but it corresponds to the high abundance of pollen at that time (Bullock & Solís Magallanes 1990). Input values at Chamela are much lower than the internal cycling rates of litterfall and throughfall (Tables 3 and 4). Thus, bulk deposition may not play an important role in the P economy of this ecosystem, at least in the short term.

Phosphorus concentration in the runoff water was higher than that reported for tropical moist forests in the Amazon Basin on older soils (≈0.01 mg/l; Lewis 1986; Lesack 1993). The relatively high P concentrations measured in streams that drain younger parent materials at Chamela could be explained by (i) their higher P content compared to older tropical soils, and (ii) their

lower stream runoff volumes than their humid counterpart. Despite this high P concentration in runoff, amounts of dissolved P exported from the ecosystem (Table 1) represent less than 2% of available-P pools in the ecosystem (≈2% of the resin-P and <1% of the resin plus bicarbonate-P pools in the soil profile). These small losses suggest high P retention in the tropical dry forest of Chamela. This finding should be corroborated with a larger soil-sampling design. Annual average of P output at Chamela (0.064 kg/ha) is in the lower bound of the values reported by Bruijnzeel (1991) for lowland and montane tropical forests in several countries and different soil types.

Minor net P losses occurred as particulate material (Table 2). Values were lower than those from a nutrient-poor tropical moist forest (0.23 $kg \cdot ha^{-1} \cdot yr^{-1}$; Lewis 1986). This difference may be a consequence of higher mechanical erosion and humidity in tropical moist forests (Johnson et al. 1994). Particulate matter P losses at Chamela represented less than 2% of total P losses from the ecosystem during a wet year (1993). Although particulate-bound P was the main P output from the ecosystem during a dry year (1994), its amount was insignificant to ecosystem nutrient cycling.

A comparison of P outputs from the ecosystem with input rates from the atmosphere showed that input from the atmosphere was consistently higher than loss through soil leaching (Table 1). Even after including particulate P losses from the watersheds for both, rainy (1993) and dry years (1994), the results indicated that input from the atmosphere was greater than output (Tables 1 and 2). A possible P source of atmospheric P may result from slash-and-burn of surrounding dry forest in the area (Gutiérrez 1993; González-Flores 1992). Burning of tropical dry forest release substantial amounts of P into the atmosphere (Kauffman et al. 1993). We cannot say whether the forest in Chamela retains this P that seems to persist in the ecosystem. In view of the maturity of the forest major aggradation seems unlikely.

These measurements and balances represent a mature, ‘steady state’ condition. The possible impacts of fires and other disturbances could increase the P losses. Thus, given that the P stored in litter is 4.07 kg/ha (Table 5) and the annual P accumulation is 0.09 $kg \cdot ha^{-1} \cdot yr^{-1}$, one litter fire per 45 years could potentially remove the net accumulation of P. However, we have not found evidences of natural fires in the study site (e.g. charcoal in the soil) neither registered a single natural fire event in the region, in more than 30 years of the Biological Station presence.

Intrasystem cycling

Resin- and bicarbonate-P concentrations in Chamela soils were lower than those reported for a tropical dry forest in Brazil on Entisols (61 μg/g and 53 μg/g, respectively, Agbenin & Tiessen 1994). Both P pools could be

Table 6. Dry mass and P content of litterfall in tropical dry forests.

Site	Rainfall (mm/yr)	Mass ($Mg \cdot ha^{-1} \cdot yr^{-1}$)	P (%)	P ($kg \cdot ha^{-1} \cdot yr^{-1}$)	Reference
Mexico (Chamela)	752	3.39	0.11	3.88	(1)
India	821				
Leaf		3.96	0.07	2.77	(2)
Fine		1.82	0.06	1.09	
Mexico	826				
(Chamela) Leaf		2.31	0.11	2.50	(3)
Fine		2.58	0.13	3.40	
Puerto Rico	860	4.80	0.02	0.79	(4)
Belize	1030	12.60	0.07	9.20	(5)
Mexico (Puerto Morelos)	1100	6.47	0.05	3.20	(6)

(1) This study; (2) Singh & Singh 1991a,b; (3) Jaramillo & Sanford 1995; (4) Lugo & Murphy 1986; (5) Lambert et al. 1980; (6) Whigham et al. 1991.

further reduced during the rainy season by plant uptake. Campo et al. (1998) reported that labile P was ≈30% lower in the rainy season (September) than at the end of the dry season (May). Considering that total P concentration in the upper soil (0–5 cm depth) in Watershed I in Chamela is 291 ± 43 μg/g (F. García-Oliva pers. comm.), short term available P (resin-P according to Hedley et al. 1982) represents only ≈1% of the total P in this soil profile.

The magnitude of P fluxes and pools in the forest soil indicate that internal cycling processes control P dynamics in the tropical dry forest at Chamela on this time scale. The aboveground P return from vegetation to the soil is dominated by litterfall; it represents more than 90% of the total flux (litterfall plus throughfall). The amount of P in litterfall at Chamela (this study; Jaramillo & Sanford 1995) was higher than in a tropical dry forest in an infertile site in Puerto Rico (Table 6), despite similar annual litterfall production in both sites. Belowground P fluxes associated to root turnover was not estimated. However, the high proportion of biomass in the belowground system (Kummerow et al. 1990; Rentería 1997) and the high turnover of fine roots (Castellanos 1998) in this ecosystem, suggest that root P fluxes could be high.

Comparison of P concentration in the litterfall between forest sites (Table 6), showed that Chamela to have the highest value among several trop-

ical dry forests. This high P concentration is consistent with values previously reported by Jaramillo and Sanford (1995) for Chamela for a different study period. Mean residence time (MRT; Waring & Running 1998) for P (1.2 yr) and organic matter (1.3 yr) suggest a slight prevalence of plant P uptake over P immobilization. Although this observation is based on data for one-year period, Jaramillo and Sanford (1995) had reached similar conclusions based on MRT's for P and organic matter in a previous study. Both, the high concentration of P in the litterfall and the MRT's in this study support their argument that the forest in Chamela may not be limited by P availability.

Why would the P content of litterfall at Chamela be high when nutrient availability measures would suggest it could be a scarce resource? A high P concentration in the litterfall could be compensated by fast nutrient uptake. The high proportion of fine roots in the upper soil profile (Castellanos et al. 1991), where nutrient concentration is greater (García-Oliva 1992), suggests a high nutrient acquisition by plants at Chamela. At the onset of the rainy season, soluble P pools in the upper 5 cm of soil and mineralized P in litter generate a large available P pool, sufficient to compensate annual P losses from the canopy (Campo et al. 1998).

The apparent P retention, the low available pools, and the dominant intrasystem P fluxes suggest that biological process control P cycling in the Chamela tropical dry forest on short time scale.

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