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# Pulses of soil phosphorus availability in a Mexican tropical dry forest: effects of seasonality and level of wetting

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**Abstract** Intact cores from the upper soil profile and surface litter were collected at the peak of the dry season and during the rainy period in the tropical deciduous forest of the Chamela region, Jalisco, México, to (1) analyze upper soil phosphorus (P) movement and retention, (2) compare soil P dynamic pools (soluble, bicarbonate, and microbial) in dry and rainy seasons, and (3) determine the response of these P pools to wetting. Unperturbed litter-soil cores were treated in the laboratory with either 10 mm or 30 mm of simulated rain with carrier-free $^{32}P$ and compared to a control (no water addition) to determine the fate and retention of added P. $^{31}P$ concentrations and pools in most litter and soil fractions were higher in the dry than in the rainy season. Soluble P was 0.306 g/m$^2$ and microbial P was 0.923 g/m$^2$ in the dry season (litter plus soil) versus 0.041 (soluble) and 0.526 (microbial) g P/m$^2$ in the rainy season. After water addition, rainy-season cores retained 99.9 and 94% of $^{32}P$ in the 10- and 30-mm treatments, respectively. Dry-season samples retained 98.9 and 80% of inputs in the same treatments. Retention after wetting occurred mostly in soil (bicarbonate and microbial fractions). Simulated rainfall on rainy-season soils increased P immobilization. On the other hand, simulated rainfall on dry-season soils released P through mineralization. The P release represents between 46 and 99% of the annual litterfall return. Our results suggest that both soluble and microbial P constitute important sources for initiation of plant growth at the onset of the rainy season in tropical dry forest.

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## Introduction

There is strong evidence that phosphorus (P) availability limits primary production in many moist tropical forests (Vitousek 1984). The few studies on P dynamics in tropical dry forests suggest this may be true for some but not for all of them (see a review in Jaramillo and Sanford 1995). Nevertheless, phosphorus use efficiency is high, suggesting a possible key role of P in the ecosystem (Jaramillo and Sanford 1995).

Fine-root growth (Kummerow et al. 1990) and foliage expansion (Reich and Borchert 1984; Borchert 1994) occur rapidly at the onset of rains in seasonally dry tropical forests, requiring a substantial flux of nutrients. Microbial P immobilization, particularly during the dry season, has been proposed as an important nutrient conservation mechanism in tropical dry forests (Singh et al. 1989). Furthermore, nutrients released by microbial plasmoptysis in response to wetting of dry soil (Kieft et al. 1987) after the first rainfall events potentially represent an important source for plant uptake and growth (Singh et al. 1989; Raghubanshi et al. 1990). The significance of microbially mediated pulsed nutrient release in tropical moist and dry forests has been recently discussed (Lodge et al. 1994; Jaramillo and Sanford 1995).

In strongly seasonal ecosystems, such as tropical deciduous forests, a high leaching potential exists only during the rainy season. Soluble nutrients may therefore accumulate during the dry period. The presence of a reduced fine-root system at the onset of the wet period, because of root mortality during the dry season (Kummerow et al. 1990), suggests, however, that plant retention of nutrients in the early part of the growing season may be especially difficult.

The importance of microbial nutrient pools for initiation of plant growth in tropical dry forest has been proposed mostly from point comparisons of soil mi-

crobial pools between wet and dry seasons (Singh et al. 1989) and from correlations between soil moisture and microbial nutrients (Srivastava 1992). However, the potential role of soluble nutrient pools accumulated during the dry period for plant growth has not been considered. The objectives of the present study were (1) to analyze upper-soil P movement and retention, (2) to compare soil P dynamic pools (soluble, bicarbonate, and microbial) in dry and rainy seasons, and (3) to determine the response of these P pools to wetting.

## Materials and methods

### Study site and sample collection

The study was conducted with soil of the tropical deciduous forest at the Chamela Biological Station, on the Pacific coast of Mexico (19°30′ N and 105°01′ W). The forest is dominated by deciduous trees, 6–10 m in height (Lott et al. 1987). With few exceptions, the species are leafless for several months each year and their phenology is driven by water availability (Bullock and Solís-Magallanes 1990). Rainfall is strongly seasonal with 7 dry months (November to May) and 5 wet months (June to October). Mean annual rainfall is 679 mm (García-Oliva et al. 1995) and the mean annual temperature is 24.9°C (Bullock 1986). Annual litterfall is 395 g/m$^2$ per year and litter production exhibits a pronounced seasonality, with a peak near the onset of the dry season (Martínez-Yrízar and Sarukhán 1990). Leaf litter is the dominant component of the litterfall. Surface litter standing crop is 900 g/m$^2$ and the turnover rate is 2.1 years (Martínez-Yrízar and Sarukhán 1993). The soils are young sandy loams (Orthens), and they are shallow (Solís 1993). Total P concentration in the upper soil (0–10 cm) is 355 ± 24 μg/g (mean ± 1 SE, V.J. Jaramillo, unpublished data).

Forty intact cores containing litter and the upper 5 cm of soil were obtained midway through the rainy season (September 1993) and at the end of the dry season (May 1994) by carefully introducing PVC cylinders, 7.1 cm in diameter, into the soil (a total of 80 cores). The upper 5 cm of the soil profile in this tropical dry forest concentrates microbial biomass and soil organic matter (V.J. Jaramillo, unpublished data), fine roots ( < 1 mm in diameter, J. Castellanos, personal communication) and nutrients (García-Oliva 1992). A nylon mesh was placed on the bottom of the core to avoid soil loss during manipulation. September samples were collected 8 days after the previous rainfall event and May samples 5 months after the last rain of the season. The samples were taken 4 m apart in a site with a slope of 41%. Standing leaf litter in the cores was 571 ± 66 g/m$^2$ in the rainy season and 557 ± 38 g/m$^2$ in the dry period (mean ± 1 SE). Soil bulk density (1.25 g/cm$^3$) and pH (6.5) did not vary significantly among samples and seasons.

### Experimental protocol

Each set of unperturbed litter-soil cores was subjected to an independent simulated rainfall experiment. Treatments were two simulated rainfall levels (10 mm and 30 mm) and a control (no water addition). Four litter-soil cores from each season were analyzed to determine the initial size of the P pools before treatment (time zero). Simulated rain consisted of distilled water with 0.1 ml/l of carrier-free $^{32}$P-orthophosphoric acid in 0.02 M HCl (1 mCi/l; Dupont Nen Research Products). Radioactive P was used to determine the fate and movement of input P in the litter-soil system. The same solution was used for both simulated rainfall events, so the 30-mm treatment had three times the amount of $^{32}$P (0.0012 g/m$^2$) of the 10-mm event (0.0004 g/m$^2$). Rainfall intensity and amounts were selected according to a rainfall frequency analysis study for the region (García-Oliva et al. 1995). The most frequent lower and higher rainfall events during the growing season are represented by 10 and 30 mm, respectively. Simulated-rainfall intensity was 10 mm/h for all treatments in both experiments. Plastic cups were placed underneath each PVC core to collect $^{31}$P and $^{32}$P leached from the sample after wetting. A total of 36 litter-soil cores (12 per treatment) for each experiment (dry or wet season) were incubated in a growth chamber with an ambient temperature of 22.5 °C and 12 h of daylight. All cores were randomly placed in the chamber and 12 (4 per treatment) were withdrawn at each of the three incubation periods: 10 h, 5 days, and 10 days.

### Sample analysis

Leaf litter was removed after each incubation period and cut into 4–9 mm$^2$ fragments. Soil samples were sieved with a 2-mm mesh. Moisture content was determined by drying litter and soil subsamples at 70 °C for 3 days.

Soluble (water-extractable), bicarbonate, and microbial $^{31}$P and $^{32}$P contents in both litter and soil were analyzed with a modified sequential extraction procedure (Hedley et al. 1982). Undried, duplicate 0.150-g (litter) and duplicate 0.500-g (soil) samples were placed separately in 50-cm$^3$ centrifuge tubes. Thirty milliliters of deionized water were added to all tubes, shaken for 1 h, and centrifuged at 10,000 rpm at 0 °C for 10 min. The supernatant was filtered to obtain soluble P. The litter and soil remaining in the tubes were used to determine bicarbonate and microbial P. One of the soil duplicates and one of the litter duplicates was shaken with 30 ml of 0.5 N $NaHCO_3$ for 16 h, and centrifuged. The other duplicates received 1 ml of liquid chloroform ($CHCl_3$) followed by overnight evaporation of the $CHCl_3$. Then 30 ml of 0.5 N $NaHCO_3$ were added, shaken for 16 h, and centrifuged. The fumigated and non-fumigated supernatants were filtered with a 0.45-μm Millipore filter. Soluble P (above) and P content in the filtrate of fumigated and non-fumigated samples were determined after digestion with sulfuric acid and ammonium persulfate (APHA 1992). The $^{31}$P was analyzed by the molybdate method after ascorbic acid reduction (Murphy and Riley 1962). Microbial P was calculated by the difference in P release between fumigated and non-fumigated samples. Microbial P was further corrected for P fixation by measuring the recovery of a known amount of orthophosphate-P added to the sample in the $NaHCO_3$ extract (Brookes et al. 1982). Briefly, 1 ml of a solution of $KH_2PO_4$ containing 40 μg P was added to 30 ml 0.5 N $NaHCO_3$ and shaken with unfumigated sample (0.150 g litter or 0.500 g soil) under the same conditions as the fumigated and non-fumigated samples. The $^{32}$P activity was determined at the laboratory of the National Commission on Nuclear Safety of Mexico using a Beckman liquid scintillation counter. Duplicate 2-ml aliquots of the digests were placed in scintillation vials (Beckman HP), 10 ml of a scintillation cocktail was added and samples were counted for 30 min.

### Statistical analyses

Seasonal differences in P concentration for the different fractions in litter and soil were compared with *t*-tests. Treatment effects in the wetting experiment were determined with analysis of variance (ANOVA) for each time period. Means were compared with the Tukey honest significant difference (HSD) test when the ANOVA was significant ($P < 0.05$). Analyses were performed with Statistica (1993). All values are means and 1 SE.

## Results

### Seasonal comparison of $^{31}$P concentrations and pools

The initial litter and soil moisture contents were, as expected, lower during the dry season (7.3 ± 0.9%

for litter and 3.6 ± 0.3% for soil) than in the rainy season (17.6 ± 2.3% for litter and 14.9 ± 1.7% for soil).

P concentrations in all litter and soil fractions were higher in the dry than in the rainy-season samples, except for soil bicarbonate P (Table 1). Soluble and microbial P concentrations in litter were one order of magnitude higher in the dry than in the rainy period. Soil P concentrations in dry-season samples were also higher, but in the same order of magnitude, than in the wet-season samples. Concentrations in litter were much higher than in soil.

Soluble P was 0.041 ± 0.007 g/m$^2$ and microbial P was 0.526 ± 0.058 g/m$^2$ in the rainy-season cores (litter plus soils), whereas these pools were higher in the dry-season cores, with values of 0.306 ± 0.028 g P/m$^2$ (soluble) and 0.923 ± 0.047 g P/m$^2$ (microbial; see time zero values in Fig. 1). Soluble P was only 4% in wet-season cores (litter plus soil), but 19% of the total in dry-season cores.

**Table 1** Litter and soil $^{31}$P concentration (μg/g) in rainy- and dry-season cores. Values are averages of 12 replicates with standard errors in parentheses

| | | Rainy | Dry | *P* |
|---|---|---|---|---|
| Litter | Soluble | 26.37 (4.03) | 251.48 (42.35) | *** |
| | Bicarbonate | 50.81 (4.77) | 76.25 (7.67) | *** |
| | Microbial | 58.20 (6.16) | 300.00 (22.52) | *** |
| Soil | Soluble | 1.46 (0.28) | 4.31 (0.29) | *** |
| | Bicarbonate | 10.45 (0.80) | 10.29 (0.87) | NS |
| | Microbial | 12.38 (1.36) | 18.07 (0.76) | *** |

*** $P < 0.001$; *NS* not significant

**Table 2** Phosphorus retention and leaching and water loss from litter-soil cores. Values are percentages (%) of total added except for $^{31}$P, where values are percentages of the dynamic P pools (see text). Values are averages of four replicates with standard errors in parentheses

| | 10 mm rainfall | | 30 mm rainfall | |
|---|---|---|---|---|
| | Rainy season | Dry season | Rainy season | Dry season |
| $^{32}$P retained in litter | 9.40 (1.39) | 9.02 (0.89) | 10.34 (1.24) | 6.15 (0.67) |
| $^{32}$P retained in soil | 90.51 (9.56) | 89.85 (9.65) | 83.71 (7.94) | 73.92 (7.15) |
| $^{32}$P leached from core | 0.09 (< 0.01) | 1.13 (0.10) | 5.95 (0.51) | 19.93 (1.79) |
| Water loss from core | 1.01 (0.07) | 1.36 (0.10) | 40.41 (3.15) | 40.76 (2.98) |
| $^{31}$P leached from core | 0.0001 (< 0.001) | 0.18 (0.01) | 0.01 (< 0.001) | 0.72 (0.07) |

## P retention, leaching, and activity

P inputs ($^{32}$P) were retained mainly by soil (Table 2). With the 10-mm simulated rainfall, 99.9% and 98.9% of added $^{32}$P were retained in the rainy- and dry-season samples, respectively. The difference was greater with the 30-mm treatment where 94% of $^{32}$P was retained in the rainy-season cores and 80% in the dry-season cores. Of the $^{32}$P retained in litter, the percentage retained in the microbial fraction (46.0 ± 2.6%) was nearly three times greater than in the bicarbonate-extractable fraction (17.2 ± 3.4%) regardless of the season (Campo 1995), whereas in soil, these fractions retained relatively similar percentages (34.9 ± 2.8% and 40.5 ± 2.0% for the microbial and bicarbonate fractions, respectively). Native phosphorus ($^{31}$P) also leached out from the cores and the greatest percentage, albeit small, leached out from the dry-season samples with the 30-mm rain (Table 2).

## Simulated-rainfall effects on P dynamics

P pools (litter and soil) in control cores (no water added) in both seasons did not change significantly with incubation. Thus, their reference values are those indicated at time zero (Fig. 1). The order in the description of results below includes litter before soil pools for rainy- and dry-season cores.

### *Rainy-season cores*

Soluble and microbial P changed during incubation after water addition. Litter microbial P showed similar trends and values with both rainfall treatments (Fig. 1a). For example, microbial P increased at day 5 in both cases and accounted for more than 60% of analyzed litter P. In addition, mineralization occurred at day 10 and there was a concurrent increase in litter soluble P.

In contrast, only the 30-mm rainfall stimulated microbial activity in the soil (Fig. 1a). By day 5, microbial P increased to 0.763 g P/m$^2$ and represented 66% of the analyzed P pools in the soil. A fraction of this microbial P was mineralized by day 10 and a peak in soluble P was observed (Fig. 1a).

### *Dry-season cores*

Litter microbial activity was stimulated by both rainfall treatments, but the pattern was opposite to the wet season. Mineralization, instead of immobilization, was observed at day 5 and microbial P only represented 9 and 24% of litter pools in the 10- and 30-mm treatments, respectively (Fig. 1b). Five days later, 0.076 g P/m$^2$ (10 mm) and 0.143 g P/m$^2$ (30 mm) were immobilized. Only the 30-mm rainfall affected soluble litter P and this was evident 10 days after wetting (Fig. 1b).

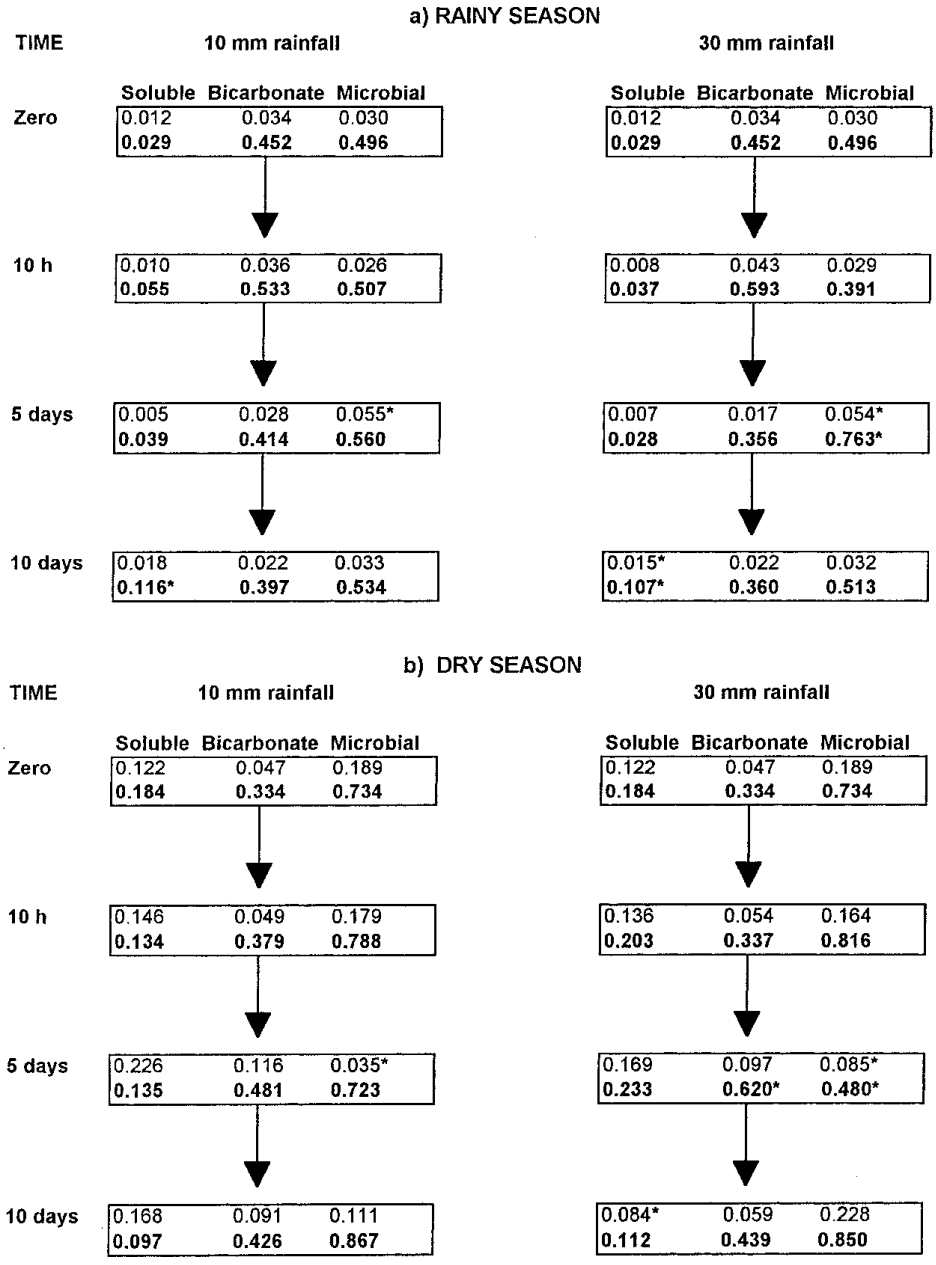


**Fig. 1** Changes in native phosphorus ($^{31}P$) pools in the litter and the upper 5 cm of soil during the experiment with rainy-season samples (**a**) and the experiment with dry-season samples (**b**). Litter P and soil P pools are in *light* and *bold*, respectively. All values are in g/$m^2$ and are the average of four replicates collected at each of the periods shown (*$P < 0.05$ for difference with time)

Similar to rainy season samples, soil microbial P did not respond to a 10-mm rainfall, but was stimulated by the 30-mm treatment (Fig. 1b). The trend was the opposite to that observed in wet-season samples. P mineralization occurred at day 5 and bicarbonate P increased. At day 10, immobilization occurred and the microbial P pool did not differ significantly from controls (Fig. 1b).

## Discussion

Our results, comparing soil collected during the rainy and the peak of the dry seasons in the tropical deciduous forest of Chamela, support the findings of Singh et al. (1989) and Srivastava (1992) for tropical dry forest in India. That is, microbial P was greater in soil during the dry period. Moreover, our data showed that microbial P pools in both litter and soil during the dry season were nearly twice those recorded during the wet season. Elevated immobilization during the dry period in tropical seasonal forests may occur because microbes are active when plants and microbial grazers are not (Singh 1969; Singh et al. 1989). When soil moisture decreases in seasonally dry ecosystems, protozoa, fungivorous microarthopods, and nematode populations also decrease (Ingham et al. 1986).

The extended dry season with reduced leaching and plant uptake may also promote the accretion of soluble nutrient forms in litter and topsoil and result in higher P

pools. At this time most of the trees are leafless and fine roots are mostly dead (Kummerow et al. 1990). Thus, soluble P accumulates in the forest soil.

Massive uptake of nutrients by vegetation from soil during the growing season lowers the soil P pool in the wet period. Our data showed that soluble P pools in litter and topsoil in the rainy season were lower than in the dry period (0.041 and 0.306 g $P/m^2$, respectively). When the soil becomes wet at the beginning of the rainy season, P mobility is no longer restricted and soluble P becomes available for microbial growth and plant uptake. Vitousek and Matson (1985) showed that in intact forest soils, relatively rapid biological uptake of available N is one of the reasons for the meager size of the available N pools. In Chamela, the annual P return from the vegetation to the soil is 0.43 $g/m^2$, with 0.36 $g/m^2$ as litterfall and 0.07 $g/m^2$ in throughfall (Campo 1995). Therefore, soluble P in dry-season litter and upper soil represents as much as 70% of the aboveground P return.

The higher soluble P pools in the dry-season soil in Chamela are consistent with the strong seasonal patterns in soil nutrient concentration that characterize tropical dry forest (Davidson et al. 1993; Roy and Singh 1995). These patterns contrast markedly with results from a tropical moist forest in Panama, with a reduced dry season (3 months, rainfall $\approx$ 80 mm), that lack seasonal trends in the size of inorganic P and N (Yavitt and Wright 1996). This suggests that the length and severity of the dry season plays a critical role in soil nutrient cycling in tropical seasonal ecosystems.

The simulated rainfall experiment with the dry-season soil showed that P mineralization may occur soon after the start of the wet season. With a 30-mm precipitation event, litter and soil mineralization released 0.358 g $P/m^2$ ($\Delta$P microbial = microbial P in litter plus soil at time zero minus microbial P in litter plus soil at day 5). This flux represents 83% of the annual aboveground P return. However, the released P was immobilized 5 days later, possibly because of the absence of plant uptake in the experimental design. Irrigation during the dry season in a semideciduous lowland forest was also followed by large microbial activity (Wieder and Wright 1995). Water addition to rainy-season samples also stimulated microbial activity. Interestingly, and in contrast to the dry season, litter and soil P were immobilized in response to the 30-mm rainfall event which may prevent nutrient loss through leaching. These results with dry- and wet-season samples suggest that litter and soil moisture contents prior to a rainfall event may determine the pattern of microbially mediated nutrient fluxes.

## Implications

The root system of tropical dry forest ecosystems responds rapidly and opportunistically to soil wetting after an extended dry period (Kavanagh and Kellman 1992). In Chamela, fine roots ($< 1$ mm in diameter) are concentrated in the upper soil (top 5 cm) and profuse new root tip production occurs 3 days after the first rain of the season (Kummerow et al. 1990; Castellanos et al. 1991). Plants may thus take up soluble and mineralized P at the onset of the rainy season to support tree growth. Although the methods did not allow us to measure soil P inputs through leaching from litter, its importance has been documented elsewhere (Tietema and Wessel 1994; Yavitt and Wright 1996) and represents another potential source of nutrients for plant growth.

The fine-root systems of tropical dry forests are reduced after the extensive dry periods they experience (Kummerow et al. 1990; J. Castellanos, personal communication). Thus, in spite of the rapid response they show to the first rainfall events, the start of the wet season should also bring about a high nutrient leaching potential. Our data showed higher $^{32}P$ loss in the dry-season samples. This suggests that P retention mechanisms are less efficient during the dry season and likely during the first rainfall events, possibly as a result of the presence of inactive, dead, and slow-responding microbes (Anderson and Domsh 1985; Paul and Clark 1989). Nevertheless, total leached native P (in both dry- and rainy-season samples) from the first 5 cm of the soil profile represented less than 1% of the dynamic pools (soluble, bicarbonate, and microbial). A strong pulse of available P as a result of nutrients mineralized during the dry season and nutrients released after the first rains may occur early in the rainy season in tropical dry forest.

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