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Phosphorus in soil and *Brachiaria decumbens* plants as affected by the geophagous earthworm *Pontoscolex corethrurus* and P fertilization

José Cinco Patrón[1,2], Prometeo Sánchez[1], George G. Brown[3], Michel Brossard[4], Isabelle Barois[3] and Cuauhtémoc Gutiérrez[5]

[1] Nutrición Vegetal Edafología, IRENAT Colegio de Postgraduados. Carretera México-Texcoco Km 35.5, Montecillos, Texcoco, Edo. de México, México, C.P. 56230
[2] Present Address: Centro de Investigaciones en Ciencias Microbiológicas, Instituto de Ciencias, Benemérita Universidad Autónoma de Puebla, A.P. 1622, Puebla, Pue., México. C.P. 72000
[3] Departamento de Biología de Suelos, Instituto de Ecología, A.C. A.P. 63, Xalapa, Veracruz, México. C.P. 91 000
[4] IRD-ORSTOM, CP 7091, Brasília D.F., 71619-970, Brasil
[5] Instituto Nacional de Investigaciones Nucleares, Km 36.5 Carr. México-Toluca, Salazar, Edo. Mex, México

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Summary. A greenhouse experiment was performed using the radioisotope ^{32}P to study the effects of earthworms (*Pontoscolex corethrurus*) and P fertilization on *Brachiaria decumbens* pasture production and P dynamics in a P-limited soil from a pasture in Veracruz, Mexico. Two fertilization levels (0 and 10 kg ha^{-1} P) were applied, while the soil P pool was labelled with 10mg ^{32}P pot^{-1} (equivalent to 1.6 kg P ha^{-1}). At harvest (51d) measurements included shoot and root biomass, total, inorganic, organic & exchangable P in the soil and earthworm castings, mycorrhizal infection in roots, and earthworm populations. Fertilization with 10 kg ha^{-1} (injected P) increased shoot biomass by almost 10 times and root biomass by three times. Earthworms were only important for biomass production and P uptake with 10 kg ha^{-1} P, where despite significant yield reductions, more ^{32}P fertilizer was imported into plants and the coefficient of ^{32}P fertilizer use was significantly higher. On the other hand, treatments with earthworms tended to have lower organic P and higher available-P contents. Both fertilization and earthworms had a significant negative effect on root infection by VAM. Total P contents of earthworms was high (0.4 %), and ^{32}P derived from the fertilizer reached from 3 to 4 % of the total at harvest. Earthworm castings were richer in total P and especially organic P, than uningested soil. By ingesting soil rich in organic P, producing large amounts of castings (P-rich microsites), and stimulating P mineralization processes in soils, *P. corethrurus* forms an important component of the soil P cycle, and further research should pay attention to their potential as priming agents within the soil, and their effects on plant growth and nutrient uptake.

Key words: P fertilization, ^{32}P, earthworms, *Brachiaria decumbens*

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[1] *Author for Correspondence, e-mail:* patron5@siu.cen.buap.mx

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Introduction

The level of phosphorus available in most tropical soils is not sufficient to satisfy the nutrient requirements of plants in modern agriculture (Handbook on phosphate fertilization 1990). Phosphate fertilization is a high input normally applied in single cultivation cycles, but generally has an efficiency of less than 20 %, particularly in soils with high P-fixation capacity (Goswani et al. 1990). The solubility of phosphorus is low, it is easily retained in the soil, little mobile (undesirable characteristics) and is concentrated in the upper layer of the edaphic profile (0–15 cm) where the microbiota and fauna are generally most active. Endogeic geophagous (soil-feeding) earthworms, such as the species *Pontoscolex corethrurus*, that develop mutualistic relationships with soil microorganisms in their guts to digest soil organic matter, can stimulate the mineralization and recycling of nutrients, particularly N (Lavelle et al. 1992) and P (López-Hernández et al. 1993) in their castings. Furthermore, earthworm activities can potentially improve the physical properties of soils, such as its water-holding capacity, or water fluxes through and into the soil (Logsdon & Linden 1992), thus indirectly affecting P movement and plant assimilation.

Brachiaria decumbens is a mycorrhizal (VAM) tropical pasture grass, known to be well adapted to acid tropical soils low in nutrients such as P (Rao et al. 1996), and is increasing in popularity in Mexico, with many thousands of hectares planted to this species since the early 1990's (Enríquez 1994). Under pastures such as these, the widespread peregrine earthworm *P. corethrurus* flourishes (Brown et al. unp. data), reaching biomasses of more than 30 g m^{-2} (Lavelle et al. 1987). In their review, Brown et al. (1999a) showed how tropical earthworms, were important modulators of plant production in several sites throughout the tropics, and that *P. corethrurus* had a high potential for increasing yields, particularly in nutrient-poor soils, and of perennial plants. Given the important role of *P. corethrurus* in affecting soil chemical properties and potentially pasture production, the present study was set up to assess the effect of this earthworm species on P dynamics in the soil and *B. decumbens* plants using a nutrient-poor soil and ^{32}P in order to better trace P throughout its forms and translocations, and differentiate from soil ^{31}P.

Materials and Methods

The experiment was performed in a greenhouse at the Instituto Nacional de Investigaciones Nucleares (ININ) (Salazar, Mexico), using 20-L plastic buckets, containing about 12 kg (air dry equivalent) of an acid (pH = 5.5) sandy loam (82 % sand, 11 % clay, 7 % silt) nutrient-poor Inceptisol (0.08 % N; 0.85 % C; CEC = 12.1 meq 100 g^{-1}) taken from the A (0–10 cm) horizon of a pasture near La Vibora, Veracruz. ^{31}P fertilizer was applied as ammonium phosphate (10 kg ha^{-1} P) injected into the soil with a 10 mL plastic syringe at 5 cm depth, near the plant root zone. The soil was labelled with ^{32}P by applying a high activity (120,250,000 Bq = 3.25 mCi) but low concentration (10 mg P $bucket^{-1}$) solution of ammonium phosphate (equivalent to 1.6 kg ha^{-1} P, and assumed to be unimportant for plant P nutrition) to the surface of each bucket. *P. corethrurus* (W) were inoculated at the rate of 6.4–7.5 g pot^{-1} (wet weight) (mean equivalent to 110 g m^{-2}), or about 9–14 individuals pot^{-1} (mean 150 ind. m^{-2}), and 15 plants of *B. decumbens* transplanted, for a total of 8 treatments: P0 & PW0, ^{32}P0 & ^{32}PW0, P10 & PW10, ^{32}P10 & ^{32}PW10. All the other essential elements for the plant were supplied to each bucket (N, K & micronutrients). At the first signs of flowering (51d after transplanting), the pots were cut open, earthworms removed, counted and weighed, shoots and roots harvested, dried at 60 °C for 48 h, weighed, ground in a mill and samples taken to establish the activity of ^{32}P (through wet digestion) and total P (colorimetric technique of Vanadium-Molibdate). ^{32}P activity (wet digestion of 2 g) and concentrations of total P (P nitrofenol, colorimetric technique) (Olsen & Sommers 1982), organic P (Bray), inorganic P (Inorganic P = Total – Organic P) and exchangeable (resin) P (anion exchange membrane) were measured in initial and final soil, as well as in earthworm castings. Total P and ^{32}P activity in earthworms was measured on tissues (guts voided previously) obtained by killing the earthworms in boiling H_2O for 3s, drying at 60 °C for 24 h and grinding in a mortar. ^{32}P activity was assessed using a liquid cyntillation counter (Packard-Tri-Carb Model 4530) at the ININ, and radioactivity (cpm, counts per minute) measured after 10 or 20 minutes. Vesicular arbuscular mycorrhizal (VAM) root colonization was estimated on fragments from treatments without ^{32}P using the technique of Phyllips and Hayman (1973). The statistical analyses (ANOVAS) were performed using the SAS (Statistical Analysis System) package (SAS Institute Inc. 1985).

Results

Temperatures in the greenhouse were extreme, on the low side reaching absolute minima of 6–7 °C on several occasions, and an average minimum of 12.4 °C. Maximum temperatures were on average 39.5 °C, with absolute maxima of 50 °C. The greatest plant shoot (4.5, 4.2 and 3.8 T ha^{-1}) and root (0.27, 0.26 and 0.23 T ha^{-1}) biomasses were obtained in the treatments $^{32}P10$, P10 and PW10, respectively. These were significantly different ($P < 0.05$) when compared with the remaining treatments 51d after transplanting (Fig. 1). These three treatments represented the highest % increases in shoot biomass compared to the total control (P0), all over 1000 %. Earthworm effects were only significant (lower) for both shoots and roots with 32P10 kg ha^{-1}, likely due to problems linked with soil H_2O (ponding on the surface was common). Soil labeling with 1.6 kg ha^{-1} applied ^{32}P led to slight but not significant increases in both shoot and root production in treatments with and without earthworms, compared with the 0 kg ha^{-1} P treatment.

Total P in *B. decumbens* shoots (Table 1A), was not highest in PW0 and lowest in P10. There were few significant differences between treatments, although the only significant (pairwise) effect was observed comparing P10 and $^{32}P10$. P uptake by the plants was highest (and significant compared with other treatments) in $^{32}P10$, PW10 and P10 (24.3, 16.0 and 14.8 mg, respectively). The amounts of ^{32}P taken up by the plants (Pf, in mg), in earthworms and soil were calculated applying the formula:

$$Pf = \frac{r}{R} * F$$

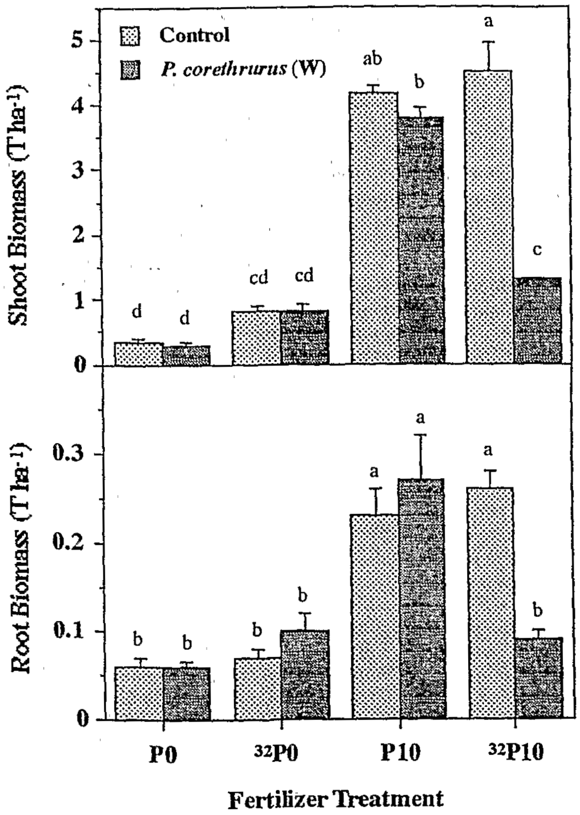

Fig. 1. Dry weight (T ha^{-1}; means + se bars) of *B. decumbens* shoots and roots 51d after transplanting into soils with 2 levels of fertilization (0 and 10 kg ha^{-1} ^{31}P) in the absence (Controls) or presence of *P. corethrurus* and soil labeling with ^{32}P (1.6 kg ha^{-1}). Different letters indicate significant differences at $P < 0.05$

Where r = the radioactivity measured (in Bq or cpm) at time t (depending on the analysis date), R = the radioactivity of the initial (Day 0) ^{32}P fertilizer solution at time t, and F = the quantity of ^{32}P (10 mg) added to each pot. Treatments ^{32}P0, ^{32}PW0 and ^{32}PW10 all had significantly higher Pf in the plants than ^{32}P10 (Table 1A). Pf in the earthworm tissue was similar in both ^{32}PW10 and ^{32}PW0 (Table 1B). Highest Pf values were observed in the soil, and these were significantly lower in ^{32}PW10 compared with the other treatments, although differences in the total amounts were small (Table 1C).

Table 1. The effect of two levels of P fertilization (0 and 10 kg ha^{-1}) with or without ^{32}P soil labelling, and the presence or absence of *Pontoscolex corethrurus* on various plant (A), earthworm (B) and soil (C) parameters after 51d of transplanting *Brachiaria decumbens* into a P-poor acid soil. Different letters within a same column indicate significant differences between treatments at $P < 0.05$

A. Plant parameters

Treatments[1]	P added *(kg ha^{-1})*	Shoot P *(mg kg^{-1})*	P uptake *(mg)*	Pf[2] *(mg)*	Ps[3] *(mg)*	Pdff[4] *(%)*	RCU[5] *(%)*	VAM root colonization *(%)*
P0	0	770 abc	1.9 c	–	–	–	–	10.8 a
PW0	0	939 a	2.2 c	–	–	–	–	4.2 b
^{32}P0	0[6]	854 ab	4.8 c	1.3 a	3.5 a	29.3 a	12.8 a	–
^{32}PW0	0[6]	712 abc	4.7 c	1.2 a	3.4 a	34.3 a	12.3 a	–
P10	10	562 c	15.6 b	–	–	–	–	2.5 b
PW10	10	671 bc	17.1 b	–	–	–	–	0 b
^{32}P10	10[7]	857 ab	25.8 a	1.0 b	24.8 b	4.2 b	10.3 b	–
^{32}PW10	10[7]	701 bc	5.7 c	1.2 a	4.5 a	21.1 a	12.0 a	–

B. Earthworm parameters

Treatments[1]	P added *(kg ha^{-1})*	Pe[8] *(mg)*	Pf[2] *(mg)*	Ps[3] *(mg)*	Pdff[4] *(%)*	RCU[5] *(%)*
^{32}P0	0[6]	22.8 a	–	–	–	–
^{32}PW0	0[6]	27.1 a	0.9 a	26.2	3.5 a	9.4 a
^{32}P10	10[7]	18.1 a	–	–	–	–
^{32}PW10	10[7]	22.0 a	1.0 a	21.0	4.5 a	9.8 a

C. Soil Parameters

Treatments[1]	P added *(kg ha^{-1})*	Pf[2] *(mg)*	Pdff[4] *(%)*	SR[9] *(cpm mg^{-1})*
^{32}P0	0[6]	2.0 a	0.42 b	12.3 b
^{32}PW0	0[6]	1.97 ab	0.44 a	13.2 a
^{32}P10	10[7]	2.0 a	0.28 c	8.0 c
^{32}PW10	10[7]	1.92 b	0.23 d	6.3 d

Notes: 1 – For description of the treatments, see text. 2 – ^{32}P uptake. 3 – Fraction of soil ^{31}P in plant or earthworm tissues. 4 – P derived from the ^{32}P fertilizer added (1.6 kg ha^{-1}). 5 – Real Coeficient of Utilization of ^{32}P added. 6 – Actual amount was 1.6 kg ha^{-1} P. 7 – Actual amount was 11.6 kg ha^{-1} P. 8 – Total P mass in earthworm tissues. 9 – Specific Radioactivity

The amount of P derived from soil (^{31}P) pools in both plants and earthworms (Ps) was calculated using the formula:

$$Ps = P_{e,p} - Pf$$

Where $P_{e,p}$ is the total mass of P (in mg) in earthworm (e) or plant (p) tissue. For plants, only the treatment with ^{32}P10 was significantly different from the others (Table 1A). In earthworms, no significant difference between Ps of both fertilizer treatments were found (Table

1B). The percentage of the total plant and earthworm and soil (s) P derived from the ^{32}P fertilizer, was thus calculated using the following formula:

$$Pdff = \frac{Pf\,(e, p, s)}{Pt\,(e, p, s)}$$

Where Pf = the total amount of ^{32}P fertilizer taken up by e or p, and Pt = the total P content (in mg) of e or p. The treatments with earthworms had a tendency towards higher absorption of the ^{32}P fertilizer, with 34 % (^{32}PW0) and 21 % (^{32}PW10), respectively, of the P derived from the applied fertilizer in plant tissues (Table 1A), although the only significant differece was observed for ^{32}P10 (lower without earthworms). In earthworm tissues, Pdff was similar between treatments, varying from 3.5–4.5 % (Table 1B). In soil, Pdff was low, ranging from 0.23–0.44 %, although significant differences between treatments were observed, with significant earthworm (higher in ^{32}PW0, lower in ^{32}PW10) and fertilizer (lower with 10 kg ha^{-1} P) effects (Table 1C). The real coefficient of ^{32}P fertilizer usage (RCU) by the plants and earthworms, expressed in percentage, was calculated using the formula:

$$RCU = \frac{Pf}{F} * 100$$

Earthworms did not increase RCU in plants with 0 kg ha^{-1}, but when 10 kg ha^{-1} were applied, RCU was significantly greater (Table 1A). Comparing fertilization levels, plant RCU was significantly lower in ^{32}P10 (10.3 %) than the other treatments (12–12.8 %). In earthworms, RCU was not significantly different between fertilization treatments, averaging around 9.6 % (Table 1B). Finally, the specific radioactivity (SR) of the P (in cpm mg^{-1} P) in earthwom castings (c) and the soil (s), was calculated as:

$$SR = \frac{(R/r \text{ of } c,\, s) * 100}{Pt}$$

Where Pt is the total P content (in mg kg^{-1}) of the soil or casts (c). Since Pt was not measured in the ^{32}P labeled soil, values of Pt from the corresponding treatments without ^{32}P application were used. SR in soil with earthworms was higher with ^{32}PW0 and lower with ^{32}PW10. There was a significant reduction in soil SR with fertilization of 10 kg ha^{-1} P. SR of *P. corethrurus* casts from the treatment with ^{32}PW10 was 6.6 cpm mg^{-1} on average, a value slightly higher but not significantly different than in bulk soil (6.3 cpm mg^{-1}; Table 1C) from the same treatment.

P analysis of the soil showed a total P concentration in the treatment PW10 of 83.2 mg kg^{-1}, and in the castings of 91.2 mg kg^{-1} (Table 2). These amounts are significantly higher than the initial total P (61.4 mg kg^{-1}). Initial soil had 16.9 mg kg^{-1} of organic P, which repre-

Table 2. Total, organic, inorganic and resin P (mg kg^{-1}) of the initial experimental soil, in casts of the earthworm *Pontoscolex corethrurus* and in soils under two fertilization regimes (0 and 10 kg ha^{-1}) in the presence and absence of earthworms. Different letters within a same column indicate significant differences between treatments at $P < 0.05$

Treatment	*Total P*	*Organic P*	*Inorganic P*	*Resin P*
Initial soil	61.4b	16.9b	43.7a	20.5abc
P. corethrurus casts	91.2a	49.8a	39.4a	30.2a
P0	40.9b	15.4b	30.8a	14.6c
PW0	38.6b	6.1b	32.4a	15.9bc
P10	61.7ab	24.7ab	55.9a	24.5ab
PW10	83.2a	4.4b	83.0a	28.5a

sents 27.5 % of total P, while earthworm castings had significantly higher organic P, at 49.8 mg kg^{-1} (40 % of total P). Inorganic P had a tendency for higher values in treatment PW10, with 82.9 mg kg^{-1}. Exchangeable (resin) P was also highest in PW10 (28.46 mg kg^{-1}) followed by P10 (24.5 mg kg^{-1} P) (Table 2). Neither inorganic nor resin-P were significantly different in castings compared with uningested soil.

The effect of fertilization on earthworm density and biomass is shown in Table 3. In general, a trend for lower density with fertilization was observed although the only significant difference was between ^{32}PW10 (lower) and PW0. No effect of fertilization on biomass was found. A high number of cocoons was produced (up to 52 in one pot), indicating adequate conditions for reproduction. No difference in the number or biomass of cocoons was observed between treatments. Total P concentration in earthworm tissues was high (3925 mg kg^{-1} or 0.4 %), up to 4 times that in plant tissue (Table 1A), although the Pf of earthworms was slightly lower than in plant tissues. The amount of P derived from the ^{32}P (Pdff) was also lower than in plant tissues, ranging from 3.5 % in ^{32}PW0 to 4.5 % in ^{32}PW10. This represents a slow assimilation of the fertilizer ^{32}P, and much of the P seems to transit right through the guts of earthworms, entering the castings.

Table 3. Earthworm population parameters in the presence and absence of P fertilizers after 51d of transplanting *Brachiaria decumbens* into a P-poor acid soil. Different letters within a same column indicate significant differences between treatments at P<0.05

Treatments	Individuals innoculated *(no. pot-1)*	Biomass inoculated *(g pot^{-1})*	Individuals recovered *(no. pot^{-1})*	Biomass recovered *(g pot^{-1})*	Cocoons recovered *(no. pot^{-1})*	Biomass cocoons *(g pot^{-1})*
PW0	10a	7.4a	11a	4.2a	26a	1.1a
^{32}PW0	10a	6.8b	8ab	5.1a	26a	1.2a
PW10	11a	7.3a	5ab	4.6a	28a	1.3a
^{32}PW10	10a	7.4a	4b	5.6a	30a	1.6a

Mycorrhizal root colonization (Table 1) was highest in treatment P0 (without fertilization), at 10.7 %, a value significantly (P<0.05) greater than in fertilized and earthworm treatments.

Discussion

Phosphorus fertilization is generally recommended throughout tropical America (Fenster & León 1979) and in Mexico (Ortiz 1977) for the establishment and maintenance of new pastures to obtain economically profitable yields in acid infertile tropical soils. When applied, P fertilizers are generally broadcast, although banding of P within the row (for the plant roots) has been shown to improve yields of *B. decumbens* and other forages, over broadcasting, particularly in P-poor soils (Fenster & León 1977). In the present experiment, the P fertilizer was injected. Injection is not a common method of P application, being used more often for anhydrous ammonia (gas) fertilization; nevertheless, the benefits of P fertilizer placement within the root growth zone (even at low doses), which could be adapted for a more general use, can be easily seen in the results of P10, PW10 and ^{32}P10, that yielded up to 10 times more than treatments with 0 kg ha^{-1} P fertilization.

When the yields from the present experiment are extrapolated to yearly production, with 5 cuts in one year and similar production levels at each harvest, the treatments with 10 kg ha^{-1} ^{31}P would have yielded on average around 20 T ha^{-1} (shoots), respectively. These yields are similar to *B. decumbens* production levels obtained in neighboring Tabasco (Pastrana 1994) with 8–24 kg ha^{-1} P applied as TSP or rock phosphate (15–22 T ha^{-1}) and higher than obtained in various CIAT (Colombia) experiments mentioned by Fenster & León (1977) with 22 kg ha^{-1} P applied (15 T ha^{-1}). This is to be expected given the confined nature of the pots (smaller soil volume) and the temperature and moisture regulated conditions of this greenhouse study.

The low value of total P in the initial soil (61.4 mg kg^{-1} P) is typical of sandy soils of the humid tropics (Frossard et al. 1995), although the results of resin-P indicate that there was enough P in the solution for plant uptake, particularly in the fertilized treatments. Nevertheless, the critical P concentration (that required to obtain 80 % of maximum yields) in *B. decumbens* shoots of about 0.1 % (Rao et al. 1996), was not reached in any of the treatments (max 0.09 % in PW0), and P uptake was conditioned by fertilizer applications. In the absence of fertilizers, plant P uptake was low, but with 10 kg ha^{-1} applied P it increased by more than 3 times (except in ^{32}PW10). The amount of ^{32}P in plant tissues derived from the fertilizer (Pdff) was variable, from around 4.2 to 34.3 %, and tended to be higher with earthworms. This is despite the very low application rates of ^{32}P (1.6 kg ha^{-1}). In all treatments, most (66–96 %) of the plant P was coming from the soil ^{31}P pool (Ps). In treatments with 10 kg ha^{-1} P fertilization, Pdff was lower (although only significant for ^{32}P10), probably due to dillution with ^{31}P fertilizer. Real coefficients of ^{32}P fertilizer use (CRU) in plants ranged from 10–13 %, and earthworms increased CRU in ^{32}PW10. However, the lower Pf, Pdff and RCU in the treatment with ^{32}P10 is probably due to higher ^{31}P uptake from the applied fertilizer (isotopic dillution) compared with remaining treatments. P recovery over a single growing season is rarely >20 % (Goswani et al. 1990), so the present results are within the range of expected values.

Earthworms can be important promoters of grassland productivity, both in the temperate region (Stockdill 1982) and the tropics (Blakemore 1997; Brown et al. 1999a), by ameliorating soil physical and chemical limitations, particularly P availabilities (Mackay et al. 1982; Syers & Springett 1984). Neither plant root nor shoot yields were positively affected by earthworm presence in this experiment, and in ^{32}PW10 significant decreases in production were observed. A smaller, but also significant decrease (–30 %) in *B. decumbens* yields with 100 kg ha^{-1} P applied was observed in the same soil by Brown et al. (1999b). Reasons for this decrease due to earthworms are still not clear, but could be related to a negative effect on mycorrhizal root colonization or increases in soil bulk density and decreases in water permeability (e.g., Barros et al. 1998). Future experiments will attempt to address this issue in more detail.

P. corethrurus, a polyhumic endogeic, is known to be active in the rhizosphere of various plant species (Brown 1999) and to feed on portions of the soil richer in clay and C (Barois et al. 1999). Thus, castings of this species collected from the same soil used in this experiment were shown to have a greater plant-available nutrient status, with a higher pH, CEC and concentrations of C, N, NO_3, NH_4, Bray-P, and the exchangable cations K and Mg (Barois et al. 1999). *P. corethrurus* castings collected in the present experiment had significantly higher total and organic-P content than in uningested soil, yet no difference was observed in plant-available forms (inorganic & resin-P), despite slightly higher values for resin-P. In contrast, treatments with earthworms (PW0 & PW10) had a trend for lower organic P and slightly higher inorganic and resin P contents (esp. PW10), which could be due to an accelerated transformation of organic P into plant-available P forms with time-exposure to earthworm activities, as well as to the absorption of organic P into earthworm tissues. These results are supported by those of Chapuis & Brossard (1995), who found lower organic P concentrations, but higher levels of inorganic and rapidly exchangable P in *P. corethrurus* casts, the latter also being found by López-Hernández et al. (1993). Given that *P. corethrurus* can process annually from 160 up to 400 T ha^{-1} soil at selected pastures in Veracruz (Lavelle et al. 1987; Patrón 1998), the estimated effect on P cycling, and increased availability to plants can be large.

Compared with the castings, earthworm biomass is a small component of the P cycle, since an annual *P. corethrurus* biomass turnover of around 30 g m^{-2} will release only about 0.1 kg ha^{-1} P. The low percentage (3.5–4.5 %) of the ^{32}P fertilizer in earthworm tissues (Pdff) reveals a slow ^{32}P accumulation in *P. corethrurus*, despite relatively higher RCU (about 9.6 %) values. P losses in earthworms, such as in excretion, are generally low (Bahl 1947), and very little is known of P assimilation by earthworms. Given the importance of earthworms to P cycling in the soil, further and more formal efforts should address earthworm P assimilation efficiencies.

In general, P fertilization is thought to positively affect earthworm populations indirectly via an increase in plant production (Edwards & Bohlen 1996). In the present experiment, a slight reduction in earthworm densities but no effect on biomass with 10 kg ha^{-1} P was found, although most differences (esp. for biomass) were not significant. Mycorrhizal-plant associations, on the other hand, are known to decrease with P fertilization (Jasper et al. 1979), which is due to a greater independence of the plant for P nutrition. In the present experiment, not only did fertilization with 10 kg ha^{-1} P reduce VAM root colonization, earthworm presence also had a negative effect. *P. corethrurus* is known to disperse VAM spores (Reddell & Spain 1991), and to enhance VAM infection in tropical tree seedlings (Ydrogo 1994), although Brown et al. (1999b) found contrasting results, with increased or decreased VAM colonization of *B. decumbens* due to earthworms, depending on the fertilizer combination used. With only P fertilizer (100 kg ha^{-1}), a decrease in VAM colonization was observed in the upper (0–10 cm) roots, and an increase in the lower (10–20 cm), due to *P. corethrurus*. When observed, the negative effect of earthworms is likely due to physical abbrasion of the VAM network (Pattinson et al. 1997), and possibly to consumption of hyphae and mycelia as well as alterations in spore germination all of which reduce VAM colonization and infection potential in the roots. The soil in the present experiment was stored for several months before use, and no VAM inoculum was added, both factors which probably explain the low VAM root colonization percentages observed (compared with Brown et al. 1999b, up to 83 %).

Soil P distribution and bioavailability is regulated by processes such as the dissolution of fertilizers and soil mineral phosphates, decomposition of organic P contained in plant, animal and microbial detritus, retention of P by inorganic soil constituents and immobilization of P by microbial biomass and plant uptake (Di et al. 1997). In the present experiment the role of plants, earthworms and soil in ^{32}P fertilizer retention has been assessed under two ^{31}P fertilization regimes. Soil retained the greater part of the applied ^{32}P, although earthworms and plants also took up small quantities. With 0 kg ha^{-1} ^{31}P applied, earthworms reduced P mobilization (larger SR), but with 10 kg ha^{-1} ^{31}P, the opposite (increased mobilization) was observed (despite lack of significant differences between soil SR and cast SR in $^{32}PW10$). Therefore since castings and earthworm-processed soils have the potential for higher P availabilities than uningested soils, we can assume that over the long term their activities are bound to be important for both plant production and P uptake. Even though in the present work earthworm effects on plant production and nutrient uptake were not as high as those observed in other experiments with this species (Brown et al. 1999a), we suggest that the results presented support an important role of *P. corethrurus* in soil P dynamics and the transfer of P into plants growing in low-P status soils.

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