Article Published in Pedobiologia (2010) 53:327-335

Title: Earthworm impacts on soil organic matter and fertilizer dynamics in tropical hillside agroecosystems of Honduras.

Running Title: Earthworm impacts on SOM and fertilizer dynamics

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Summary

Earthworms are important processors of soil organic matter (SOM) and nutrient turnover in terrestrial ecosystems. In agroecosystems, they are often seen as beneficial organisms to crop growth and are actively promoted by farmers and extension agents, yet their contribution to agroecosystem services is uncertain and depends largely on management. The Quesungual slash-and-mulch agroforestry system (QSMAS) of western Honduras has been proposed as a viable alternative to traditional slash-and-burn (SB) practices and has been shown to increase earthworm populations, yet the effect of earthworms on soil fertility and SOM in QSMAS is poorly understood. This study examined the role of *Pontoscolex corethrurus* in QSMAS by comparing their influence on aggregate-associated SOM and fertilizer dynamics with their effects under SB and secondary forest in a replicated field trial. Both the fertilized QSMAS and SB treatments had plots receiving additions of inorganic ^{15}N and P, as well as plots with no inorganic N additions. Earthworm populations were manipulated in field microcosms at the beginning of the rainy season within each management treatment via additions of *P. corethrurus* or complete removal of existing earthworm populations. Microcosms were destructively sampled at harvest of *Zea mays* and soils were wet-sieved (using 53, 250 and 2000 µm mesh sizes) to isolate different aggregate size fractions, which were analyzed for total C, N and ^{15}N. The effects of management system were smaller than expected, likely due to disturbance associated with the microcosm installation. Contrary to our hypothesis that earthworms would stabilize organic matter in soil aggregates, *P. corethrurus* decreased total soil C by 3% in the surface layer (0-15 cm), predominantly through a decrease in the C concentration of macroaggregates (> 250 µm) and a corresponding depletion of C in coarse particulate organic matter occluded within macroaggregates. Earthworms also decreased bulk density by over 4%, but had no effect on aggregate size distribution. Within the two fertilized treatments, the QSMAS appeared to retain slightly more fertilizer derived N in smaller aggregate fractions (<250 µm) than did SB, while earthworms greatly reduced the recovery of fertilizer N (34% decrease) in both systems. Although management system did not appear to influence the impact of *P. corethrurus* on SOM or nutrient dynamics, we suggest the lack of differences may be due to artificially low inputs of fresh residue C to microcosms within all management treatments. Our findings highlight the potential for *P. corethrurus* to have deleterious impacts on soil C and fertilizer N dynamics, and emphasize the need to fully consider the activities of soil fauna when evaluating agroecosystem management options.

Keywords: nitrogen; *Pontoscolex corethrurus*; Quesungual agroforestry system; residue inputs; soil aggregates; soil organic matter

Introduction

The maintenance of productive soils is a critical concern for agricultural systems around the globe (Sanchez, 2002; Stocking, 2003). Hillside agroecosystems of the tropics warrant particular attention, as they are often dominated by soils which are low in fertility and highly susceptible to erosion, yet provide the principal source of sustenance to local communities. Although many of the hillside systems have been managed under shifting cultivation for generations, increased demand for food production in many rural areas has resulted in the shortening of fallow periods, ultimately rendering these practices unsustainable (Szott et al., 1999; Barrios et al., 2005). The Quesungual slash-and-mulch agroforestry system (QSMAS) of western Honduras has emerged as a promising alternative to traditional practices (Hellin et al., 1999; Welchez et al., 2008). In place of slashing and burning the forest, this system relies on selective thinning and the retention of native trees to help stabilize soils and provide a source of residue inputs. The retained trees are pruned regularly to allow adequate light for crops, while leaves and small branches are not burned, but rather left on the soil surface as mulch. The mulch layer improves soil moisture retention, provides supplemental nutrients for crop growth, promotes soil biological activity and contributes to soil organic matter (SOM) stabilization (Oritz-Ceballos and Fragoso, 2004; Mulumba and Lal, 2008).

As a key determinant of soil fertility and ecosystem productivity, SOM depletion associated with agricultural disturbance is of great concern (Fernandes et al., 1997). In addition to its beneficial effect on numerous soil properties (Craswell and Lefroy, 2001), SOM represents a vast pool of terrestrial C with far reaching implications for global climate change (Lal, 2004). Research aimed at understanding how management practices affect SOM have focused to a large extent on soil structure and the physical protection of SOM within soil aggregates (Paustian et al., 1997; Six et al., 2002; Bronick and Lal, 2005). Microaggregates (53-250 µm) represent an important pool of physically protected SOM, as these structures are relatively stable, resistant to disturbance and turn over slowly (Oades, 1984; Angers et al., 1997; Six et al., 2000). Macroaggregates (> 250 µm), on the other hand, are generally more susceptible to breakage and turn over more rapidly (Oades, 1984). However, macroaggregates are also comparatively enriched in carbon and play a key role in the formation of microaggregates and thus the stabilization of SOM (Tisdall and Oades, 1982; Six et al., 2000). Thus, assessment of C contained in microaggregates within macroaggregates has been put forth as a means to measure recently stabilized C and provides a valuable tool for studying management impacts on SOM dynamics (Six et al., 2000; Six et al., 2002; Denef et al., 2007).

Earthworms are key processors of SOM turnover and soil structure in many terrestrial ecosystems. In feeding, earthworms comminute and intimately mix organic residues with mineral soil, thus facilitating their decay (Lavelle, 1988). They further influence SOM dynamics via alterations to soil water infiltration, aeration, pH, and decomposer communities (Brown et al., 2000). At the same time, earthworms can have important impacts on soil structure (Blanchart et al., 1999; Shipitalo and Le Bayon, 2004). Improved soil aggregation, in particular, may have important consequences for SOM stabilization. Several studies have shown earthworms to facilitate the incorporation of fresh residue C into microaggregates within their casts (Bossuyt et al., 2004; Fonte et al., 2007) and that this C is effectively protected against decay (Pulleman and Marinissen, 2004; Bossuyt et al., 2005). In addition to effects on SOM, earthworms can also impact nutrient dynamics in agroecosystems. Nitrogen in particular tends to become more available in the presence of earthworms (Subler et al., 1998; Araujo et al., 2004; Fonte and Six, 2010), but the ultimate fate of N may depend on agroecosystem management and the form of N being applied (Bohlen et al., 1999; Fonte et al., 2007). Thus, it seems that the influence of earthworms on SOM and nutrient dynamics may depend on a number of factors including the time frame in question (Lavelle et al., 2004), inherent soil properties (Marhan and Scheu, 2005), the level of disturbance associated with an ecosystem (Villenave et al., 1999; Brown et al., 2000), as well as the form of management in place (Pulleman et al., 2005; Fonte et al., 2007; Fonte and Six, 2010).

Recent studies have suggested that earthworms benefit from the ready supply of organic residues and the lack of burning under QSMAS management (Pauli, 2008; Pauli et al., 2009; Fonte et al., 2010), and may contribute significantly to nutrient cycling and SOM dynamics within this system and in part explain its success. Within this context, we sought to evaluate the role of earthworms on SOM stabilization and nutrient dynamics in the Quesungual system via comparisons of earthworm effects under QSMAS, tradition slash-and-burn agriculture and secondary forest. We hypothesized that earthworms would stabilize SOM and fertilizer N in soil aggregates, and more specifically in microaggregates within macroaggregates (earthworm casts). Additionally, we postulated that earthworm influence would differ with agroecosystem management, such that earthworms would increase C storage in soils under QSMAS and secondary forest, but decrease C stabilization under slash-and-burn agriculture where organic inputs are limited.

Methods

Site Description

This study was conducted in the Lempira Department of western Honduras, near the border with El Salvador (N 14°4’, W 88°34’). This rural and mountainous region is dominated by hill slope farms intermixed with pasture and patches of sub-humid tropical forest. At roughly 400 m in elevation, rainfall in this region averages 1400 mm yr^{-1}, with nearly all precipitation occurring between May and November. At the field site, mean monthly temperature varies between 22 and 27 °C year round. Given the steep terrain in this region, soils are generally shallow and rocky and dominated by Entisols (Hellin et al., 1999), with a sandy clay loam texture (47% sand, 33% silt, and 20 % clay) at the field site.

Experimental design

The on-farm experiment was carried out in research plots (10 x 10 m) established in 2005 on three replicate farms each containing five management treatments: Quesungual slash-and-mulch agroforestry system with inorganic fertilizer (QSMAS +F), Quesungual slash-and-mulch agroforestry system with no fertilizer added (QSMAS –F), traditional slash-and-burn agriculture with fertilizer (SB +F), unfertilized slash-and-burn (SB –F) and secondary forest (SF) to serve as a reference. Both QSMAS and SB plots had been converted from forest on each farm. In the QSMAS treatment, the forest was selectively thinned and pruned, while large woody debris was removed from the plots. Small branches and leaves were left as mulch on the soil surface. In the SB plots, the forest was slashed and burned, with the soil left bare at planting. Typical of surrounding farms in the region, the two cropping systems were planted with a maize (*Zea Mays*; L.) at the beginning of each wet season in May and followed by beans (*Phaseolus vulgaris*; L.), one month prior to maize harvest (in August or September). Pruning and residue management (burning or mulching) were conducted on an annual basis for the QSMAS and SB plots several weeks prior to the planting of maize.

In early May of 2007, before the onset of the rainy season, four microcosms were installed within each plot of the five treatments on all replicate farms. Microcosms consisted of a 35 cm long section of PVC tubing with an inside diameter of 20.9 cm and capped with 1 mm plastic mesh on both ends. A single large pit (50 x 50 cm) in each plot was excavated to a depth of 35 cm and a layer of sand (5 cm) was added to the base of each pit to ensure adequate drainage from the microcosms. Field moist soil removed from each pit was immediately passed through a 12 mm mesh to remove large rocks and debris and then thoroughly mixed. Four microcosms were placed in each pit, adjacent to each other and then filled to a depth of 30 cm with the homogenized soil. Litter additions to each microcosm were representative of inputs to the whole plots for each treatment (see Table 1). Microcosms under QSMAS management received a mix of maize residues from the previous growing season and green leaves from three common tree species found in the system. Microcosms in SB plots received no residue inputs, as organic materials under SB management are typically gathered and burned prior to planting. Less maize residue was applied to microcosms in the QSMAS -F plots to account for the lower productivity in these plots, while the microcosms under SF received a more diverse mix litter from 6 tree species with no inputs of maize residue (Table 1). Litter was applied to the microcosms in QSMAS and SF prior to planting in the main plots in late May. Inorganic fertilizer was applied to the +F microcosms on two dates, according to standard practices in the region, 50 kg N ha^{-1}and 55 kg P ha^{-1} shortly after planting and 100 kg N ha^{-1} one month later. N was applied as ^{15}N labeled ammonium nitrate (9.9 atom % ^{15}N), while P was added as triple super phosphate. Nutrients were dissolved in water and applied in solution evenly across the soil surface in each microcosm. Fertilizer application was followed by a thorough watering to move nutrients to deeper layers and minimize gaseous losses of N. Since fertilizer is normally buried and is not in intimate contact with plant residues, the added plant residues were removed prior to each fertilizer application and replaced immediately afterwards. Maize was planted adjacent to the microcosms, but not within them.

In late-June of 2007, once soil moisture was adequately high for earthworm populations to become active, two earthworm treatments, with (+W) and without (–W) worms, were established in the microcosms. Prior to earthworm additions, all microcosms were voided of preexisting earthworm populations using electro-shocking. Four stainless steel probes were inserted vertically (30 cm deep) around the inside edge of each microcosm and a portable generator was used to run a current (~2 Amps) through the soil in perpendicular directions by alternating the flow between opposite probe pairs for a total of 8 minutes per microcosm. Earthworms were then collected from soils adjacent to the study site by excavation and hand-sorting and returned to the lab for weighing and identification. Four mature *Pontoscolex corethrurus* individuals, the most common species at the field site (Fonte et al., 2010), were added to each of the +W treatments (totaling 2.61 g fresh biomass per microcosm), while the –W microcosms were electro-shocked at monthly intervals until the end of the experiment. This was done to minimize the effects of small juveniles that may have entered through the 1mm mesh, while producing minimal impacts on soil microbial communities (Staddon et al., 2003).

Field sampling

In Sept 2007 (at the time of maize harvest), microcosms were removed from the plots and returned to the lab for destructive sampling. Surface soils in each microcosm (0-15 cm) were sampled for aggregate fractionation by taking a single core (9.25 cm dia.). These cores were weighed and a subsample was dried for bulk density determination. Field moist soils were then immediately passed through an 8 mm sieve by gently breaking soil clods along natural planes of weakness and air-dried for subsequent analyses. A subsample was taken for moisture determination to be used for calculating bulk density. Deeper soils below 15-30 cm were sampled by taking a representative subsample from the entire soil volume below 15 cm. Soils from the entire microcosm were hand-sorted to assess earthworm growth and survival.

Aggregate fractionation

Surface soils were fractionated by wet-sieving according to Elliott (1986) to look at C and N distribution among four aggregate fractions: large macroaggregates (>2000 µm), small macroaggregates (250-2000 µm), microaggregates (53-250 µm) and silt and clay (<53 µm). These fractions were isolated by placing 50 g of the air-dried 8 mm sieved soil on top of a 2000 µm sieve and submerging it in deionized water for slaking. After 5 min, the sieve was swayed up and down in an oscillating motion for 50 cycles over a 2 min period. Soil remaining on the sieve (large macroaggregates) was rinsed into a pre-weighed aluminum pan and placed in an oven at 60 °C until dry. Material passing through the 2000 µm sieve was transferred to a 250 µm sieve and sieved for another 2 min in the same manner to isolate small macroaggregates. Material passing through the 250 µm sieve was then transferred to a 53 µm sieve and the process repeated once more to separate microaggregates from the silt and clay fraction. All fractions were dried separately at 60 °C, weighed to determine the proportion of soil in each and then ground for subsequent elemental and isotopic analyses. Aggregate stability of each soil was then calculated following van Bavel (1950) by summing the weighted proportions of each aggregate size class to determine mean weight diameter (MWD).

Macroaggregates were further separated following methods outlined by Six et al. (2000). A sub-sample (6 g) of the oven-dried macroaggregates (a representative mixture of large and small) were slaked in deionized water for 20 min then placed on top of a modified 250 µm sieve along with fifty stainless steel ball bearings (4 mm dia.). The soil and ball bearings were kept submerged and shaken on reciprocal shaker until all of the macroaggregates had broken apart (5-10 min). A continuous flow of water ensured that microaggregates and other materials released from the broken macroaggregates quickly passed through the 250 µm mesh screen to avoid further disruption. Soil passing through the 250 µm sieve was then transferred to a 53 µm sieve and sieved for 2 min as described above, yielding a total of three fractions isolated from macroaggregates: coarse sand and particulate organic matter (>250 µm; cPOM), microaggregates within macroaggregates (53-250 µm; mM) and macroaggregate occluded silt and clay (<53 µm, Msc). These fractions were dried at 60 °C, weighed to determine the contribution of each to large and small macroaggregates, and then ground for subsequent analysis.

Soil nutrient and litter quality analyses

Ground subsamples from the bulk soil (surface and below 15 cm) and aggregate fractions were analyzed for total C and N, as well as ^{15}N using a PDZ Europa Integra C–N isotope ratio mass spectrometer (Integra, Germany). Litter quality analyses were conducted at the Agriculture and Natural Resources (ANR) Analytical Laboratory (http://groups.ucanr.org/danranlab/) at the University of California, Davis. Total C and N in residues were measured through combustion of materials and subsequent measurement using gas chromatograph and a thermal conductivity detection system (AOAC, 1997a), while ash free lignin was determined by the reflux method (AOAC, 1997b).

The proportion of fertilizer-derived N, *f*, in the soil fractions from the +F treatments was calculated as follows:

$$f = (^{15}\text{N atom\%}_{\text{sample}} - {}^{15}\text{N atom\%}_{\text{n.a.}}) / (^{15}\text{N atom\%}_{\text{source}} - {}^{15}\text{N atom\%}_{\text{n.a.}})$$

where ^{15}N atom% $_{\text{sample}}$ is the ^{15}N atom% of the sampled material, ^{15}N atom% $_{\text{n.a.}}$ is the natural abundance of ^{15}N (determined prior to isotope additions) and ^{15}N atom% $_{\text{source}}$ is the ^{15}N atom% of the applied inorganic N.

The percent of added ^{15}N recovered in the bulk soil and soil fractions was also determined in the following manner:

$$^{15}\text{N \% recovery} = 100 \times (\text{soil mass} \times [\text{N}] \times f) / \text{N}_{\text{fert}}$$

where soil mass refers to the mass (g) of the soil fraction in question, [N] refers to the concentration of N in that fraction, *f* is the proportion of total N in the fraction that is derived from fertilizer (defined above) and N_{fert} is the total amount (g) of ^{15}N labeled fertilizer applied to each microcosm.

Statistical analyses

Soil values from the microcosms were analyzed with ANOVA using a mixed model approach to a randomized split-plot block design with five management treatments representing the main effects and earthworm treatment considered sub-plot factors. The model also included the earthworm x management interaction, while block (farm) and the field plot were treated as random variables. Due to the unbalanced design of management plots in this experiment (i.e., no fertilization treatments for SF), orthogonal contrasts were for the direct comparison of the most meaningful management treatment combinations (SF vs. cropping systems, +F vs. –F, and QSMAS vs. SB). Natural log transformations were applied as needed to meet the assumptions of ANOVA. All analyses were conducted using JMP 8.0 software (SAS Institute, 2008).

Results

Earthworm survival and treatment effectiveness

Earthworm manipulations proved to be largely effective with 77% survival of added earthworms and an average of 1.97 g fresh biomass (79% of original) recovered from the +W microcosms. Earthworm biomass recovery in the +W microcosms tended to be higher under SF relative to the two cropping systems, but this difference was not significant (Table 2). Although small juveniles were recovered from several of the –W microcosms, their biomass was low (average 0.11 g per microcosm), indicating that earthworms were effectively excluded in this treatment.

Effects on aggregation, C and N storage and soil properties

The influences of the earthworm and management treatments on aggregation in surface soils (0-15 cm) observed in this study were small and largely insignificant. Orthogonal contrasts revealed that the proportion of whole soil represented by large macroaggregates was significantly higher under SF (11.8%) as compared to the cropping systems (average of 4.2%). Microaggregates displayed the opposite trend, with 26.1% of the whole soil in this fraction under SF versus 33.1% in the cropping systems (Table 3). Corresponding to these changes in aggregate distribution, aggregate stability (MWD) was higher under SF than in the cropping systems (P = 0.037; Fig. 1). There were no other significant influences of management on soil structure observed in this study. Additionally, no significant influence of earthworms was found on the proportion of whole soil found in any of the aggregate fractions. Despite this apparent lack of an earthworm influence on soil structure, earthworms did reduce the soil bulk density from 1.06 to 1.01 g cm^{-3} (Table 3). Neither earthworms nor management influenced soil moisture content at the time sampling (data not shown).

In contrast to the results for soil structure, our study revealed a clear impact of earthworms on SOM. This was evidenced by a decrease in the concentration of total C and N in surface soils (0-15 cm) of roughly 3%, from 1.34 to 1.30 % C, with the addition of earthworms (P = 0.012 and P = 0.049; for C and N respectively; Fig. 2). The loss of SOM appeared to be driven by a reduction of the C concentration in macroaggregates, which represented approximately 60% of the total soil mass. The concentration of C in the combined macroaggregate fraction (large and small) was reduced by 2.6% in the presence of earthworms across all management systems (Table 4), while large macroaggregates displayed the greatest impact of earthworms with an 8% reduction in C concentration in the presence of *P. corethrurus* (P = 0.027). The earthworm induced loss of macroaggregate C was also observed in all macroaggregate components (Table 4), with C concentration decreased by nearly 15% in the cPOM fraction and smaller reductions for the mM and Msc fractions (Table 4). Earthworm effects on N (data not shown) in the various aggregate fractions largely mirrored the differences observed for C, as the cycling of these two elements are closely linked in the soil. There was no influence of management system on C or N concentration or content in any of the aggregate fractions or bulk soil and no significant management x earthworm interactions.

Dynamics of fertilizer N

Within the management treatments receiving fertilizer application (QSMAS +F and SB +F), recovery of added inorganic N was low (< 25%). Although recovery of ^{15}N under SB tended to be lower than for QSMAS (Fig. 3), this difference was significant only for microaggregates ($P = 0.022$) and the silt and clay fraction ($P = 0.017$). The effect of earthworms was more dramatic. Earthworms decreased the recovery of ^{15}N in the microcosms by over a third ($P < 0.001$), from 16.8% to 11.1% of total N added. This was mainly driven by differences in the surface 15 cm of soil ($P < 0.001$; Fig. 3) and a corresponding decrease for the incorporation of fertilizer N into all soil fractions ($P < 0.05$). The recovery of fertilizer N below 15 cm (data not shown) was not significantly influenced by earthworms or management.

Discussion

Management influences on soil structure

The influences of management in this study were relatively small and limited to minor effects on soil aggregation (Fig. 1). Of greatest relevance, the lower proportion of large macroaggregates in the two cropping systems relative to SF suggests that conversion of forest to agriculture negatively impacts aggregate stability (Fig. 1; Table 3), with potential long-term implications for SOM stabilization and storage (Paustian et al., 1997; Six et al., 2002). However, the relatively minor differences observed between management systems raise some questions. In examining soil structure and aggregate-associated SOM dynamics in these same plots (outside of the microcosms), Fonte et al. (2010) found similar, albeit much larger differences between SF and the two cropping systems. They found the conversion of forest to the cropping systems to reduce aggregate stability (MWD) by as much as 80% and decreased C and N storage in aggregate fractions, particularly large macroaggregates. We suspect that the less dramatic decrease associated with forest conversion observed in this study is related to an overall reduction in aggregation, resulting both from the disturbance associated with experiment installation (soil excavation and homogenization) as well as the absence of growing roots in the microcosms. For example, in undisturbed soil under SF, Fonte et al. (2010) found large macroaggregates to comprise over 43% of the total soil mass during the rainy season, whereas large macroaggregates in this study (also in the wet season) contributed less than 12% to the whole soil in microcosms under SF management. This same trend holds true across other management treatments and suggests that microcosm studies may be more appropriate for evaluating the influence of earthworms than for determining direct management effects on aggregate-associated SOM.

Earthworm impacts on SOM

Results from this study did not support our hypothesis that earthworms stabilize SOM within soil aggregates. Furthermore, their influence does not appear to depend on the management system in place. Alternatively, *P. corethrurus* appeared to facilitate the loss of SOM more or less uniformly across all management treatments (Fig. 2). Although a number of studies have demonstrated that earthworms can incorporate organic matter into macroaggregate fractions (Bossuyt et al., 2004; Fonte et al., 2007; Fonte and Six, 2010), others have indicated a decline in soil C similar to what we observed in this study (Desjardins et al., 2003; Marhan and Scheu, 2005; Coq et al., 2007). A number of factors may explain these apparently contradictory results. For example, soil texture may play an important role, as sandier soils are thought to facilitate the comminution of residues during gut passage and lead to in increased C loss from casts (Marhan and Scheu, 2005). The type of ecosystem and level of disturbance may be important too, as Villenave et al. (1999) found earthworms to stabilize C only in soils under highly disturbed conditions. The earthworm species in question is likely to play a role, since earthworms vary widely in food source and burrowing habits (Lavelle, 1988). Of particular relevance, the exotic *P. corethrurus* used in this study has been associated with negative impacts on soil structure and SOM (Chauvel et al., 1999; Barrios et al., 2005), suggesting that our findings may not be entirely applicable to other earthworm species. Additionally, the influence of earthworms on SOM may depend on the time scale under consideration, such that earthworms accelerate C mineralization initially, but slow SOM decay in the long term (Martin, 1991; Brown et al., 2000; Lavelle et al., 2004). Although this study specifically addressed the role of management, the agroecosystem types examined here did not appear to influence the impact of earthworms on SOM dynamics. We suggest however, that management differences, particularly within the microcosms, were not as different as intended and this may at least partly explain the lack of a management effect on earthworms.

Contrary to our expectations, *P. corethrurus* had no significant effect on aggregate stability (Fig. 1.) and were found to deplete C within macroaggregates leading to a loss in SOM (Fig. 2). Meanwhile, in a similar study conducted near this field site, Fonte and Six (2010) found *P. corethrurus* to both improve aggregation and the incorporation of SOM into large macroaggregates, with no reduction in soil C. This effect, however, was only observed with the addition of plant litter to the soil surface indicating that fresh residue inputs are key for earthworms to stabilize SOM at this site (Fonte and Six, 2010). Although leaf litter was added to the QSMAS and SF treatments, we suggest that residues inputs in this study were insufficient to support the earthworm populations present in our microcosms. In addition to greater quantities of added surface litter (roughly double) applied by Fonte and Six (2010), earthworms also received considerable belowground C inputs (e.g., roots) from maize plants growing in the mesocosms of their study, which can serve as an important food source for soil fauna (Pollierer et al., 2007). Furthermore, the soils they used contained higher background levels of SOM (2.3% C vs. 1.3% C in this study) leading to greater overall availability of C to support earthworm populations. Higher availability of C is corroborated by a general decline in earthworm biomass observed in this study across all microcosms (Table 2), whereas earthworm growth was reported by Fonte and Six (2010). We therefore speculate that a general deficiency in fresh C inputs led *P. corethrurus* to rely more heavily upon preexisting, older SOM pools, thus resulting in the loss of soil C observed here.

Changes to SOM storage within the different aggregate fractions further indicate that earthworms were deficient in organic resources, particularly fresh residue inputs. For example, losses in SOM were driven predominantly by a decrease in macroaggregate-associated C (Table 4). A large proportion of this fraction (large macroaggregates in particular) likely consists of earthworm casts, which we would expect to become depleted in C as earthworms were forced to consume soil that was increasingly deficient in organic resources. The disproportionate loss of macroaggregate-associated SOM from the cPOM fraction further corroborates the idea that fresh residues were in short supply, as this fraction is largely composed of relatively unprocessed, labile organic matter and is highly dependent on fresh C inputs for renewal. The comparatively high loss of cPOM-C from the +W microcosms agrees with past research suggesting that this fraction is important for earthworm nutrition (Fonte et al., 2009). Given that fresh residue C has been shown to play a vital role in stabilizing earthworm casts (Guggenberger et al., 1996;

Haynes and Fraser, 1998), the failure of earthworms to improve aggregation is also consistent with a general deficiency of available C in the soil. In agreement with the ideas we present here, Pulleman et al. (2005) suggested that earthworms could only effectively stabilize C with given sufficient availability of organic resources. These findings suggest that earthworms might effectively stabilize SOM given proper management, but could destabilize SOM in the absence of sufficient C inputs.

The observed decrease in bulk density by earthworms in this study is likely related to the loss in SOM in the +W microcosms. Earthworm additions in this study appeared to correspond with improved water infiltration (personal observation) and likely impacted a number of other associated soil properties. Improved aeration, in particular, could have facilitated the decomposition of SOM (Paul and Clark, 1996). Additionally, the presence of earthworms may have altered the activity and diversity of other soil decomposer organisms (Brown, 1995), indirectly impacting the decay of SOM. Although earthworms may have impacted SOM indirectly via effects on bulk density and soil structure, it is perhaps more plausible that earthworm induced decreases in SOM led to decreases in bulk density. Corroborating this idea, earthworm burrowing activity has been suggested to increase when food resources are limited, since earthworms must explore a larger soil volume to meet nutritional requirements (Marhan and Scheu, 2005).

Influences on fertilizer N

Recovery of fertilizer N was very low in both cropping systems and suggests that in the absence of plant roots to take up fertilizer N, this labile N pool is quickly lost. Despite the low retention of ^{15}N in these microcosms, important impacts of cropping system were revealed, as was indicated by higher ^{15}N recovery in the microaggregate as well as silt and clay fractions under QSMAS management. Although these differences appear small (Fig. 3), they are potentially important because they occur despite higher (albeit non-significant) soil C under SB vs. QSMAS management (Fig. 2). This suggests that the small amount of fresh residue C that was added to the microcosms under QSMAS may have been more effective in immobilizing fertilizer N than the comparatively large pool of soil C found in the microcosms under SB. We might expect differences in retention between QSMAS and SB management to increase when the actions of roots are considered, since root density is likely higher under QSMAS due to the inclusion of trees in the system.

Of greater consequence for N dynamics in this study was the impact of earthworms. *P. corethrurus* drastically reduced the recovery of fertilizer N under both cropping systems and overwhelmed the influence of agricultural practice (Fig. 3). Given that QSMAS has been shown to promote earthworm populations to a much greater extent than SB (Fonte et al., 2010), this effect may negate the slight increase in retention observed under QSMAS and emphasizes the need to fully consider soil faunal activities when evaluating overall agroecosystem performance. A number of studies have shown earthworms to facilitate N loss via leaching (Subler et al., 1997; Dominguez et al., 2004), but this appears to depend to a large extent on the form of N added. For example, earthworms have been shown to facilitate the loss of inorganic N additions, but not N added in organic forms (Bohlen et al., 1999; Fonte et al., 2007). The earthworm induced N losses observed in this study may also have resulted from gaseous losses of N, as earthworm casts have been suggested to be ideal microsites for denitrification due to high moisture content, anaerobic conditions, and high concentrations of labile C and N (Parkin and Berry 1999, Rizhiya et al. 2007). It should be noted that N losses could be counteracted by the presence of plants, as earthworms have been shown to increase plant uptake of labile N (Baker et al., 2002). The findings of Fonte and Six (2010) further corroborate this idea, as *P. corethrurus* in their study decreased fertilizer N recovery in the soil, but increased recovery in plants by a similar magnitude. Despite the clear effect of earthworms in the present study and ample evidence demonstrating that some earthworms can facilitate loss of N, we suggest that the effect of earthworms on N dynamics is more complex and likely depends on the ecological context.

Although not directly concluded from the results of this study alone, ample evidence exists to suggest that the findings presented here were influenced in part by the use of simplified microcosms (i.e., no active plant roots) to manipulate earthworm populations. In spite of this, the research presented here provides valuable information about the potential influence of *P. corethrurus* on SOM and nutrient dynamics, but urges careful consideration in the interpretation of studies employing a similar research approach.

Conclusion

This study emphasizes the potential importance of soil fauna in governing soil C and N dynamics in small holder farms in the tropics. In this study, the exotic earthworm *P. corethrurus* appeared to negatively affect several key ecosystem services by instigating a loss of soil C and reducing fertilizer N retention in surface soils. Despite the apparent deleterious impacts of earthworms on nutrient cycling reported here, there is strong evidence to suggest that these findings may result from a lack of plant influence in the microcosms. This emphasizes caution in the interpretation of findings where earthworms are manipulated in highly simplified settings (i.e., field microcosms, incubation studies). We suggest that large inputs of fresh residue C (from roots and litter) may be important for earthworms to have a beneficial effect on SOM stabilization and nutrient dynamics. In light of this research we suggest that the Quesungual system may offer key advantages for small farmers in this region given that high levels of organic matter inputs can be maintained. Findings of our study emphasize the need to fully evaluate the impacts of soil fauna for any management option that may encourage their populations.

Acknowledgements

This research would not have been possible without the support of many people. In Honduras we thank Edwin Garcia of the TSBF Institute of CIAT as well as Dr. Miguel Ayarza and the staff at the CIAT office in Tegucigalpa for providing logistical support. We appreciate the help of Hector Vásquez and many others for their assistance in the field. We also thank the farmers in Candelaria, Lempira who participated in this research and allowed this research to be conducted on their farms. In the lab at UC Davis we greatly appreciate the help of Angelie Do and Kwun Luen Lai. This project was funded in part by a Fulbright student grant from the International Institute of Education. Additional support was also provided by the Challenge Program on Water and Food of the CGIAR (PN-15).

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Table 1: Litter and nutrient additions to microcosms within different management systems (SF = secondary forest; QSMAS = Quesungual slash-and-mulch agroforestry system; SB = slash-and-burn agriculture; +F = inorganic fertilizer added; -F no inorganic fertilizer).

Treatment	**Biomass Added**		**Litter Types Applied**[a]	**Litter Quality Indicators**				**Fertilizer Additions**[b]	
	Maize Residues	**Litter Inputs**		**N**	**P**	**Lignin**	**C:N**	**N**	**P**
	g m^{-2}			**%**				**g m^{-2}**	
SF	0	82.0	Ba, Ca, Dr, Lo, Mi, Pg	2.95	0.19	12.9	17.6	0	0
QSMAS +F	205.0	41.0	Ca, Dr, Pg	1.89	0.26	5.9	23.1	15.1	5.5
QSMAS -F	102.5	41.0	Ca, Dr, Pg	2.09	0.26	6.6	23.5	0	0
SB +F	0	0	-	-	-	-	-	15.1	5.5
SB -F	0	0	-	-	-	-	-	0	0

[a] Tree species used in litter additions: Ba - *Bauhinia sp.* (sub-family Caesalpinoideae, family Leguminosae); Ca - *Cordia alliodora* (Boraginaceae) ; Dr - *Diphysa robinioides* (sub-family Papilionoideae, family Leguminosae); Lo - *Lonchocarpus sp.* (sub-family Papilionoideae, family Leguminosae); Mi - *Miconia sp.* (Melastomataceae); Pg - *Psidium guajava* (Myrtaceae)

[b] N was applied as ammonium nitrate and P as triple super phosphate

Table 2: Survival and biomass recovery of the earthworm *Pontoscolex corethrurus* in field microcosms under different management treatments (SF = secondary forest; QSMAS = Quesungual slash-and-mulch agroforestry system; SB = slash-and-burn agriculture; +F = inorganic fertilizer added; -F no inorganic fertilizer) sampled in September 2007 in western Honduras. Standard errors are presented in italics to the right of each treatment average.

Treatment	**Survival**[a]		**Biomass Recovery**[b]	
	%		**g**	
SF	81.3	*7.7*	2.45	*0.38*
QSMAS +F	70.8	*10.0*	1.88	*0.38*
QSMAS -F	68.8	*12.0*	1.56	*0.34*
SB +F	79.2	*10.0*	1.80	*0.25*
SB -F	83.3	*8.3*	2.14	*0.20*

[a] Survival of mature *P. corethrurus* added to each microcosm

[b] Fresh biomass - includes mature earthworms, juveniles and cocoons; out of 2.61 g added

Table 3: Aggregation and bulk density in field microcosms under different earthworm and management treatments (SF = secondary forest; QSMAS = Quesungual slash-and-mulch agroforestry system; SB = slash-and-burn agriculture; +F = inorganic fertilizer added; -F no inorganic fertilizer; +W = earthworms added; -W = earthworms excluded) sampled in September 2007 in western Honduras. P-values for management and earthworm effects are reported below each column. No significant earthworm x management interaction was found.

Treatment		**Bulk Density**	**Aggregate Fractions**[a]				**Macroaggregate Components**[b]		
		$g\ cm^{-3}$	**Large Macros**	**Small Macros**	**Micros**	**Silt & Clay**	**cPOM**	**mM**	**Msc**
Management	**Earthworm**		**——— % of Whole Soil ———**				**— % of Macros —**		
SF	+W	1.01	11.5	53.9	26.4	8.1	31.8	47.9	20.3
SF	-W	1.04	12.2	53.9	25.8	8.1	31.4	48.2	20.4
QSMAS +F	+W	0.99	4.2	54.4	33.5	7.9	38.9	45.1	16.0
QSMAS +F	-W	1.05	3.9	54.7	33.4	8.0	36.6	45.5	17.9
QSMAS -F	+W	1.04	4.5	50.2	35.1	10.3	40.6	41.5	17.8
QSMAS -F	-W	1.09	2.8	50.4	35.9	10.9	39.5	42.6	18.0
SB +F	+W	0.99	3.8	57.6	31.9	6.8	31.4	52.3	16.3
SB +F	-W	1.05	3.3	55.9	33.2	7.6	31.6	52.5	15.9
SB -F	+W	1.04	5.4	54.3	30.1	10.2	33.0	47.1	19.9
SB -F	-W	1.06	6.1	53.6	31.7	8.6	34.6	46.8	18.6
Management Effect[c]		ns	0.034	ns	0.029	ns	ns	ns	ns
Earthworm Effect[d]		< 0.001	ns	ns	ns	ns	ns	ns	ns

[a] Large Macros = macroaggregates (> 2000 µm); Small Macros = macroaggregates (250-2000 µm); Micros = microaggregates (53-250 µm); Silt & Clay = combined silt and clay fraction (< 53 µm)

[b] Components within combined large and small macroaggregate fraction; cPOM = coarse sand and particulate organic; matter; mM = microaggregates within macroaggregates; Msc = macroaggregate occluded silt and clay

[c] P-value for orthogonal contrasts comparing SF with agricultural systems; ns = P > 0.05

[d] P-value for earthworm effect across all management treatments based on ANOVA; ns = P > 0.05

Table 4: Concentration of C in soil aggregate fractions in field microcosms under different earthworm and management treatments (SF = secondary forest; QSMAS = Quesungual slash-and-mulch agroforestry system; SB = slash-and-burn agriculture; +F = inorganic fertilizer added; -F no inorganic fertilizer; +W = earthworms added; -W = earthworms excluded) sampled in September 2007 in western Honduras. P-values for earthworm effects are reported below each column. No significant earthworm x management interaction was found.

Treatment		**Aggregate Fractions**[a]			**Macroaggregate Components**[b]		
		Macros	**Micros**	**Silt & Clay**	**cPOM**	**mM**	**Msc**
Management	**Earthworm**	**% C**			**% C**		
SF	+W	1.31	1.10	1.36	0.78	1.62	1.97
SF	-W	1.36	1.09	1.44	1.03	1.66	1.93
QSMAS +F	+W	1.19	1.08	1.44	0.66	1.60	1.87
QSMAS +F	-W	1.27	1.07	1.46	0.83	1.64	2.04
QSMAS -F	+W	0.97	0.95	1.28	0.45	1.32	1.79
QSMAS -F	-W	0.99	0.97	1.35	0.54	1.42	1.95
SB +F	+W	1.51	1.39	1.98	0.75	1.81	2.32
SB +F	-W	1.53	1.39	1.89	0.72	1.82	2.40
SB -F	+W	1.41	1.32	1.62	0.68	1.73	2.13
SB -F	-W	1.44	1.34	1.67	0.77	1.79	2.27
Earthworm Effect[c]		0.014	ns	ns	< 0.001	0.022	0.031

[a] Macros = macroaggregates (250-2000 μm); Micros = microaggregates (53-250 μm); Silt & Clay = combined silt and clay fraction (< 53 μm)

[b] Components within combined large and small macroaggregate fraction; cPOM = coarse sand and particulate organic; matter; mM = microaggregates within macroaggregates; Msc = macroaggregate occluded silt and clay

[c] P-value for earthworm effect across all management treatments based on ANOVA; ns = P > 0.05

Figure Captions

Figure 1: Aggregate stability of surface soil (0-15 cm) in field microcosms under different earthworm and management treatments (SF = secondary forest; QSMAS = Quesungual slash-and-mulch agroforestry system; SB = slash-and-burn agriculture; +F = inorganic fertilizer added; -F no inorganic fertilizer; + Worm = earthworms added, - Worm = earthworms excluded) sampled in September 2007 in western Honduras. Error bars represent the standard error around each treatment mean.

Figure 2: Total C in surface soils (0-15 cm) in field microcosms under different earthworm and management treatments (SF = secondary forest; QSMAS = Quesungual slash-and-mulch agroforestry system; SB = slash-and-burn agriculture; +F = inorganic fertilizer added; -F no inorganic fertilizer; + Worm = earthworms added, - Worm = earthworms excluded) sampled in September 2007 in western Honduras. Error bars represent the standard error around each treatment mean.

Figure 3: Recovery of fertilizer-derived nitrogen in aggregate fractions isolated from the surface soil (0-15 cm) within field microcosms under different earthworm and management treatments (QSMAS = Quesungual slash-and-mulch agroforestry system; SB = slash-and-burn agriculture; + Worm = earthworms added, - Worm = earthworms excluded) sampled in September 2007 in western Honduras. Error bars represent the standard error around each treatment mean.

Figure 1

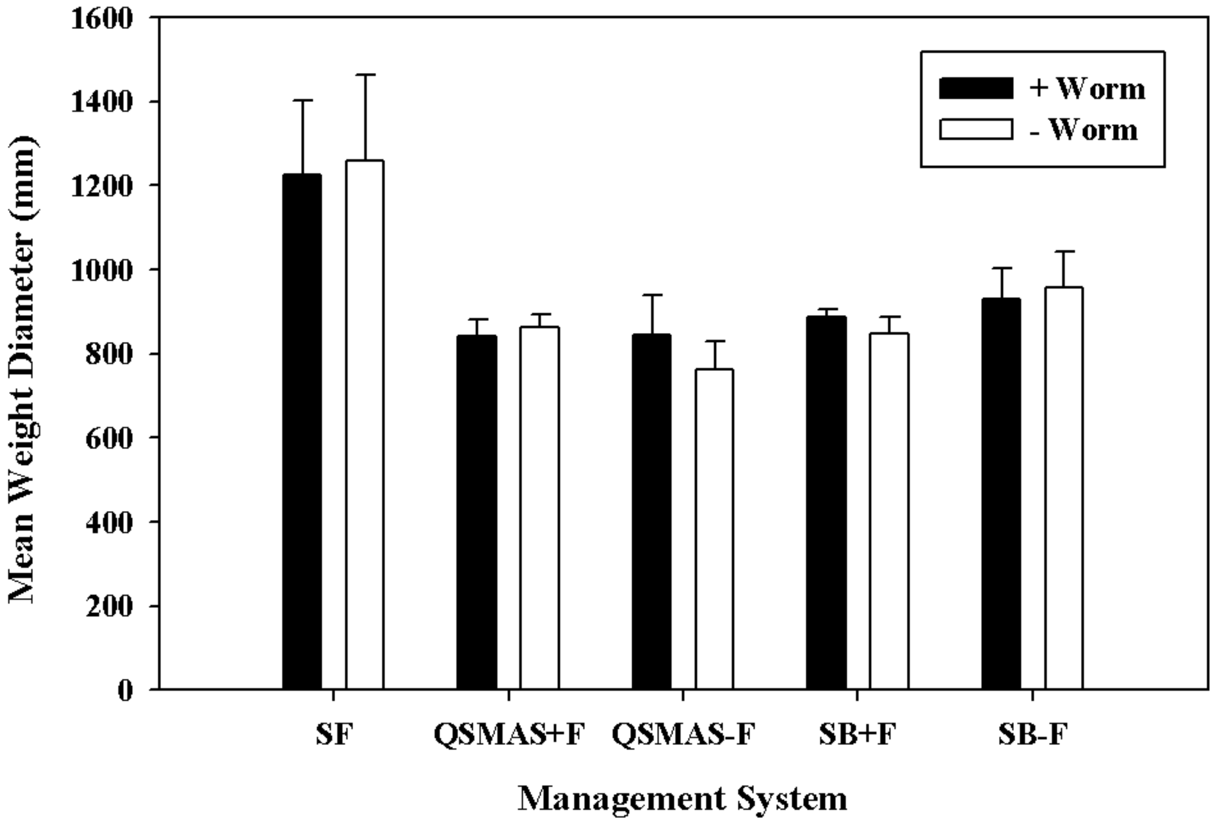
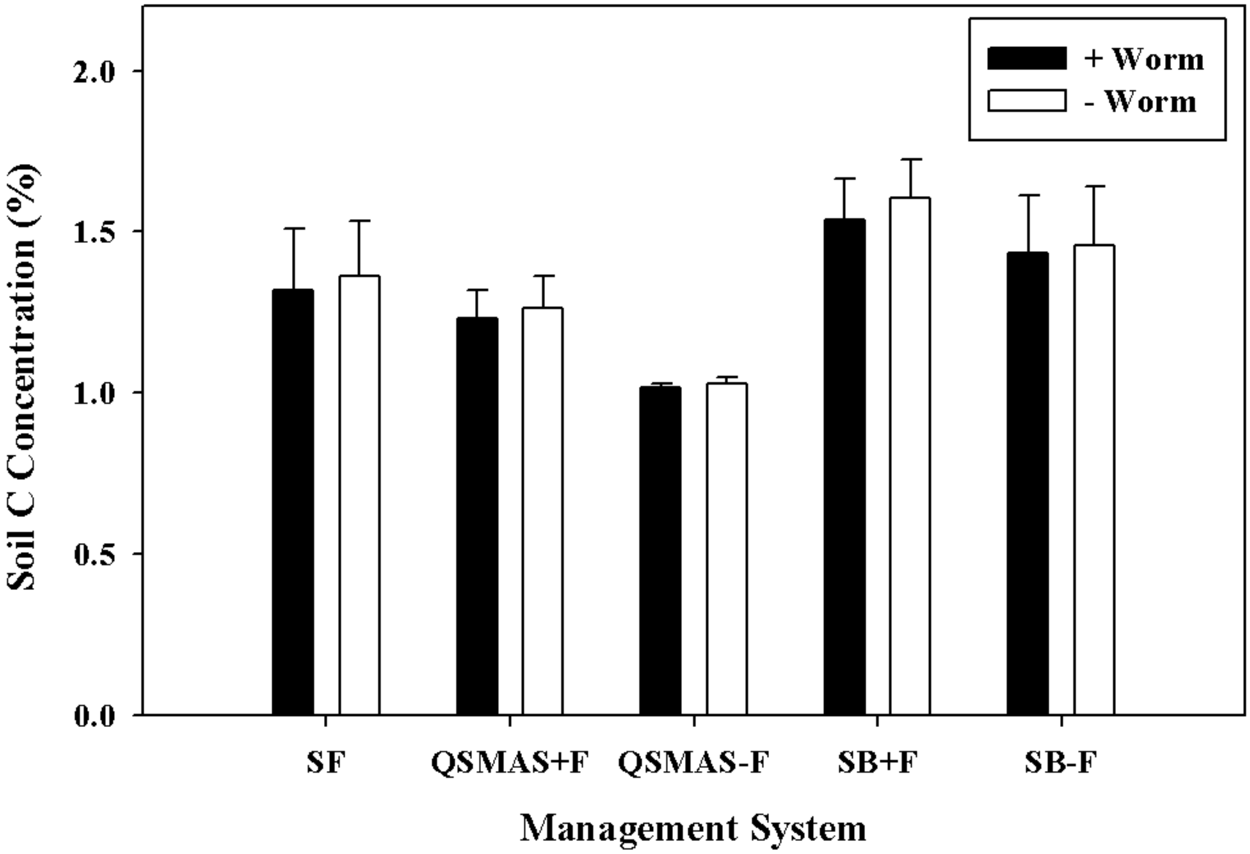
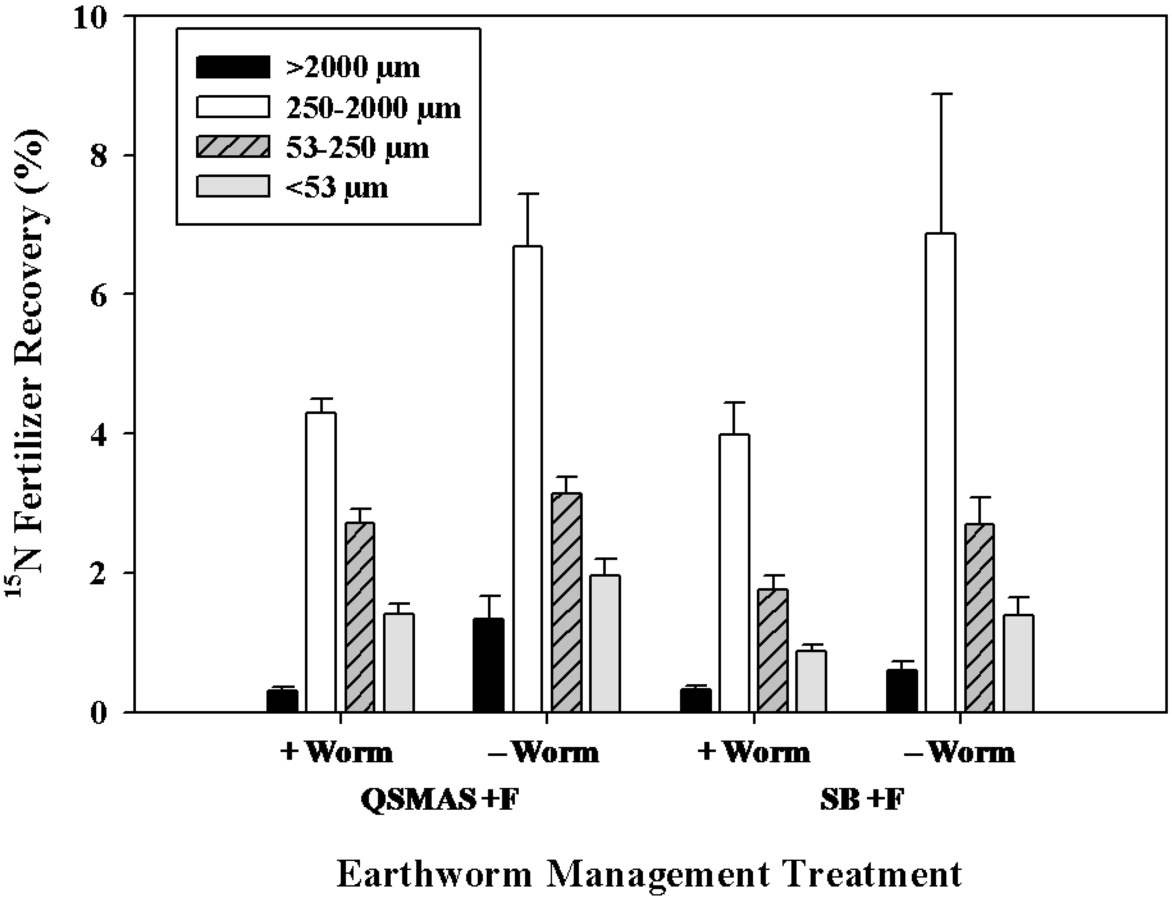

1600
1400
1200
1000
800
600
400
200
0
Mean Weight Diameter (mm)
+ Worm
- Worm
SF
QSMAS+F
QSMAS-F
SB+F
SB-F
Management System

Figure 2



+ Worm
- Worm
Soil C Concentration (%)
2.0
1.5
1.0
0.5
0.0
SF
QSMAS+F
QSMAS-F
SB+F
SB-F
Management System

Figure 3



>2000 µm
250-2000 µm
53-250 µm
<53 µm
^{15}N Fertilizer Recovery (%)
0
2
4
6
8
10
+ Worm
– Worm
+ Worm
– Worm
QSMAS +F
SB +F
Earthworm Management Treatment