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Population dynamics of earthworm communities in corn agroecosystems receiving organic or inorganic fertilizer amendments

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Abstract The dynamics of earthworm populations were investigated in continuously-cropped, conventional disk-tilled corn agroecosystems which had received annual long-term (6 years) amendments of either manure or inorganic fertilizer. Earthworm populations were sampled at approximately monthly intervals during the autumn of 1994 and spring and autumn of 1995 and 1996. The dominant earthworm species were Lumbricus terrestris L. and Aporrectodea tuberculata (Eisen), which comprised 50-60% and 8-13%, respectively, of the total annual earthworm biomass. Lumbricus rubel-(Hoffmeister) and Aporrectodea trapezoides (Dugés) were much less abundant and contributed a small fraction of total earthworm biomass. Earthworm numbers and biomass were significantly greater in manure-amended plots compared to inorganic fertilizertreated plots during the majority of the study period. Seasonal fluctuations in earthworm numbers and biomass were attributed to changes in soil temperature and moisture, and cultivation. Unfavorable climatic conditions in the summer and autumn of 1995 caused earthworm abundance and biomass to decline significantly. Mature L. terrestris, L. rubellus and A. tuberculata were most abundant in May and June of 1995 and 1996, and cocoon production was greatest in June and July 1995 and June 1996. Recruitment of juveniles of Lumbricus spp. and Aporrectodea spp. into earthworm communities occurred primarily in the autumn. Longterm amendments of manure or inorganic fertilizer did not change the species composition of earthworm communities in these agroecosystems. The earthworm populations in both manure and inorganic fertilizer plots have declined significantly after 5 years of continuously-cropped corn.

Key words Earthworms · Biomass · Abundance · Manure · Inorganic fertilizer · Agroecosystems

Introduction

One of the greatest challenges in agriculture today is the need to adopt practices which protect environmental and ecological resources, minimize economic costs, and promote social stability while sustaining relatively high crop yields (Poincelot 1990; Edwards 1992). In North America, there is increasing interest in reducing inputs of agrochemicals and using organic fertilizers rather than inorganic fertilizers to supply nutrients for crop production. It is well known that earthworms influence nutrient cycling processes in terrestrial ecosystems significantly (Lee 1985; Blair et al. 1995; Edwards and Bohlen 1996), and as farm managers continue to move towards reduced input agriculture, earthworms could become even more important in affecting soil productivity and fertility in agroecosystems.

It is widely believed that organic fertilizers support higher earthworm populations by providing a nutrient-rich substrate for earthworm populations, whether they feed directly upon the organic matter or upon the microorganisms which colonize the organic materials. Inorganic fertilizers may also contribute indirectly to an increase in earthworm populations by increasing the quantity of crop residues returned to the soils (Edwards et al. 1995), although the long-term use of inorganic nitrogen fertilizers may sometimes cause a decrease in earthworm abundance and biomass, particularly if it is ammonia-based (Ma et al. 1990).

Despite the potential importance of earthworms in organic-based agriculture, there have been few studies which have examined how long-term organic and inorganic fertilizer applications affect earthworm popula-

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tions. Werner and Dindal (1989) reported that manure amendments supported higher earthworm densities and biomass than inorganic fertilizers after 5 years of soybean-corn-legume rotations. Edwards and Lofty (1982) stated that in long-term continuous cereal production, earthworm abundance and biomass was greatest in plots receiving a combination of manure and inorganic fertilizer. Earthworm biomass in plowed fallow plots of a former pineapple orchard was found to be three times greater in plots receiving manure than in inorganically fertilized plots, while a combination of manure and inorganic fertilizer supported the greatest earthworm biomass (Tiwari 1993).

While earthworm numbers and biomass are influenced primarily by soil temperature and moisture, the influence of fertilizer amendments on population dynamics in earthworm communities in conventionally tilled agroecosystems is poorly understood. Cultivation and fertilizer amendments can influence the temperature and water-holding capacity of soils and their ability to support earthworm communities. Tilled soils are typically warmer and drier than untilled soils; however it has been suggested that the addition of organic amendments and retention of crop residues may increase earthworm populations, by conserving soil moisture as well as by providing a food resource for earthworms (Werner and Dindal 1989). Seasonal patterns of recruitment, survivorship, growth, and reproduction in earthworm populations have not been described for conventionally tilled agroecosystems receiving organic or inorganic fertilizer amendments. Gerard (1967) reported that in permanent pasture, the greatest number of juveniles of Aporrectodea caliginosa (Savigny) and Aporrectodea chlorotica (Savigny) were recruited in late spring, while the greatest proportion of the overwintering populations were adults. A similar seasonal pattern has been reported for Aporrectodea rosea (Savigny) and Aporrectodea trapezoides in soils under cereal, lucerne and pasture production, although no seasonal trends were observed for Octolasion cyaneum (Savigny) (Baker et al. 1993; Garnsey 1994).

The objectives of this investigation were: (1) to examine the abundance and biomass of the species in earthworm communities over a 2 year period, in a conventional disk-tillage agroecosystem, (2) to determine whether longer-term amendments of inorganic or organic fertilizers can significantly influence earthworm communities in continuously cropped corn agroecosystems, and (3) to assess seasonal changes in the recruitment of juveniles into earthworm communities in these agroecosystems.

Materials and methods

Study site

This investigation was conducted at the Ohio Agricultural Research and Development Center in Wooster, Ohio, USA. Mean monthly temperatures ranged from −4.8 °C in January to 21.2 °C

in July and the mean annual precipitation was 1010 mm. The experimental site is a relatively flat area on a fine, mixed, mesic Fraguidalf soil of the Canfield series (Luvisol), a major agricultural soil type in the region. The soil texture is silt loam (13.5% sand, 73.7% silt, 12.8% clay) with a mean organic matter content of 3.7%. The pH of this soil was 6.3, and the cation exchange capacity was $10 \text{ mEq} 100 \text{ g}^{-1}$ soil.

The site was planted with corn (*Zea mays*) from 1984 to 1987 and with alfalfa (*Medicago sativa*) from 1987 to 1991. Since 1992, the site has been used for continuous corn production under a conventional disk tillage system. The earthworm species found at this site include *Lumbricus terrestris* L., *L. rubellus* (Hoffmeister), *Aporrectodea tuberculata* (Eisen), and *A. trapezoides* (Dugés).

Experimental design

In the spring of 1991, 12 field plots (20 m \times 30 m) were established in a randomized complete block design with four replicates of each of three agroecosystem nutrient treatments: (1) NH₄NO₃ fertilizer (inorganic), (2) legume/rye (Vicia villosa/Secale cereale) cover crop (legume), and (3) straw-packed dairy cow manure (manure). The plots were planted with soybeans in the spring of 1991 and no nutrients were applied. Beginning in 1992, amendments were applied in spring at a rate of approximately 150 kg N ha⁻¹ year⁻¹ and disk-incorporated to 10 cm depth in late May or early June. About 10 Mg dry matter ha⁻¹ year⁻¹ was added in the manure-amended plots. Due to poor cover-crop establishment, the legume/rye treatment was supplemented with 5 Mg dry matter ha -1 of alfalfa hay to supply an equivalent amount of nitrogen as the manure and inorganic fertilizer treatments. The herbicides cyanazinde, alachlor, and paraquat were used for weed control in all treatments. After harvest, corn residues were left on the plots and incorporated by disking the following spring. The quantity of organic matter in above-ground corn residues incorporated into each plot was approximately 6.5 Mg dry matter ha year -1.

Earthworm sampling

The earthworm populations were sampled in the manure and inorganic plots at approximately monthly intervals during the spring/early summer and autumn, when temperature and moisture conditions were most conducive to earthworm activity. Due to time constraints, earthworm populations were sampled in the legume plots only at the first sampling date in the spring and autumn of each year. Results from the legume plots are not reported here. In the autumn of 1994, earthworm populations were sampled on 29 September, 3 November, and 6 December. During 1995, they were sampled on 20 April, 16 May, 16 June 13 July, 10 October, and 27 November. In 1996, they were sampled on 18 April, 14 May, 20 June, 18 September, and 24 October. Earthworms were collected from four randomly selected locations in each of the nitrogen-amended plots by first hand-sorting 38 cm × 38 cm quadrats to a depth of 15 cm. Dilute formalin (0.25%) was then poured onto the bottom of each quadrat to collect the deeper-dwelling L. terrestris. The sampling locations were chosen to include both soil in which corn was planted and soil between rows. The earthworms were collected and stored in a 5% formalin solution until species identification could be made.

Earthworms were separated into age classes on the basis of clitellum development and were categorized as fragments (incomplete earthworm fragments), juveniles, pre-clitellate adults (clitellum present but not fully developed), and clitellate adults (fully developed clitellum). Sexually mature specimens were identified to the species level using the Schwert key (Dindal 1990). Juveniles could not be identified easily to the species level and were classified as either *Lumbricus* spp. or *Aporrectodea* spp. Larger (>6 cm) *Lumbricus* juveniles were designated as *L. terrestris* juveniles since these sexual features are apparent in *L. rubellus* once they have reached this size. Earthworm abundance was

based on a head count of intact specimens and fragments that contained an identifiable head. On each sampling date, two $10.5~\rm cm$ (diameter) $\times 15~\rm cm$ (deep) cores were taken adjacent to three of the four earthworm quadrats in each plot for assessment of cocoon abundance. One core was taken immediately adjacent to the row and one core was taken from the middle of the corn row. The cores were wet sieved through stacked screens (top screen mesh size = $2.38~\rm mm$, bottom screen mesh size = $0.79~\rm mm$) in the laboratory to collect earthworm cocoons and measure cocoon biomass. Earthworms and cocoons were oven-dried (60 °C for 48 h) and then ashed at $500~\rm C$ for 4 h to determine ash-free dry weight (AFDW).

Meterological data

Meterological data were obtained from the Ohio Agricultural Research and Development Center weather station, which reports daily mean air and soil temperatures, precipitation, wind, and solar radiation. Monthly precipitation and mean monthly soil temperatures measured at a 10 cm depth at the study site from 1994 to 1996 are summarized in Fig. 1.

Statistical analyses

The abundance and biomass of earthworm populations were analyzed statistically using a repeated-measures ANOVA procedure (SAS Institute 1990). Treatment effects on mean monthly earthworm abundance and biomass, at a given sampling date, as well as seasonal fluctuations in mean monthly earthworm abundance and biomass for each fertilizer treatment were determined by multiple ANOVAs using a GLM model. Significant differences were determined using a Tukey (HSD) means comparison test at the 95% confidence level.

Results

Abundance and biomass of earthworm communities

The numbers and biomass of the total earthworm communities in corn agroecosystems were affected significantly (P<0.05) by the fertilizer treatments during the study (Fig. 2). Plots amended with manure supported significantly greater (P<0.05, HSD) earthworm numbers than inorganically fertilized plots in October to December 1994, from May to July 1995 and in September and October 1996 (Fig. 2A). Total earthworm biomass was also significantly greater (P<0.05, HSD) in the manure-amended plots, compared to inorganic fertilizer-treated plots, in November and December 1994, from May to July 1995, and in September and October 1996 (Fig. 2B).

In addition, there were significant (P < 0.05) seasonal fluctuations in earthworm populations and biomass during the study (Fig. 2). The total number and biomass of earthworm populations declined significantly (P < 0.05, HSD) in July 1995 compared to that on previous sampling dates. Following the decline of earthworm numbers and biomass in July 1995, earthworm populations did not recover and remained significantly lower through the remainder of the study in both manure-amended and inorganic fertilizer-treated plots.

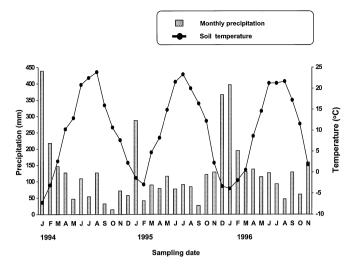
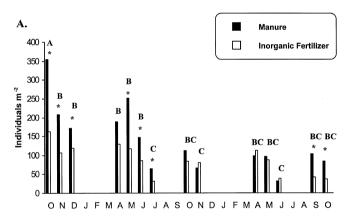


Fig. 1 Monthly precipitation and mean monthly soil temperature at 10 cm depth in corn agroecosystems in Wooster, Ohio from 1994 to 1996



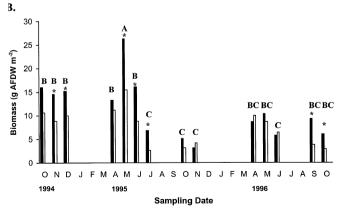


Fig. 2 Seasonal fluctuations in mean monthly (A) total earthworm community abundance and (B) total earthworm community biomass in corn agroecosystems receiving different fertilizer amendments from 1994 to 1996. Significant differences (P < 0.05, HSD) in earthworm biomass and abundance between fertilizer treatments at a given sampling date are indicated by an asterisk. Differences between sampling dates for both treatments (pooled) are indicated by capital letters where bars with the same letter are not statistically significantly different at P < 0.05 (HSD)

The earthworm communities were dominated numerically by juveniles of *Lumbricus* spp. and *Aporrectodea* spp., which comprised 29–39% and 30–53%, respectively, of the community (Table 1). Large juveniles, pre-clitellate and adult *L. terrestris* constituted 10–19% of the community, while pre-clitellate and adult *A. tuberculata* comprised 7–14%. Mature (pre-clitellate and adult) *L. rubellus* and *A. trapezoides* were a relatively small component of total earthworm community and constituted less than 6% and 2%, respectively. Interestingly, although the fertilizer amendments influenced total earthworm numbers significantly (Fig. 2), little difference was observed in the species composition of earthworm communities in plots receiving manure or inorganic fertilizer amendments (Table 1).

While mature L. terrestris constituted less than 19% of the earthworm community based on earthworm numbers, it represented as much as 60% of the annual total biomass of the earthworm community (Table 1). Juvenile Lumbricus spp. and Aporrectodea spp. biomass represented a relatively small proportion of total earthworm biomass (8–10% and 6–20%, respectively) in contrast to their numerical abundance. However, juvenile Aporrectodea spp. biomass was about 20% of the total earthworm biomass in 1994 (Table 1). Mature A. tuberculata biomass was between 8% and 13% of the total biomass, and A. trapezoides biomass was less than 2% of the total earthworm community biomass during this study. The biomass of mature L. rubellus ranged from 1% to 6% of the total earthworm community biomass during the study. Between 2% and 7% of the annual total earthworm community biomass was based on

incomplete specimens (fragments) that were identified as belonging to either *Lumbricus* spp. or *Aporrectodea* spp. and so are an artifact of the sampling procedure (Table 1). Less than 1% of the total annual biomass was contributed by earthworm cocoons (Table 1).

Abundance and biomass of Lumbricus spp.

The numbers of all (juvenile and mature) *Lumbricus* spp. were significantly greater in the manure-amended plots compared to the inorganic fertilizer-treated plots in November and December 1994, April and May 1995, and October 1996 (Fig. 3A, B). *Lumbricus* spp. numbers were lowest in July 1995 and June 1996 in the manure-amended plots, while in the inorganic fertilizer-treated plots *Lumbricus* spp. numbers were lowest in July 1995 (Fig. 3A, B).

The biomass of juvenile and mature *Lumbricus* spp. was significantly greater (P<0.05, HSD) in the manure-amended plots compared to the inorganic fertilizer-treated plots and followed similar trends to the abundance data for *Lumbricus* spp. (data not shown). The biomass of juvenile *Lumbricus* spp. ranged from 1.32 g to 6.89 g AFDW m⁻² in manure-amended plots and from 0.88 g to 4.02 g AFDW m⁻² in inorganic fertilizer treated plots. Mature *L. terrestris* biomass was between 1.05 g and 8.21 g and between 0.81 g and 5.91 g AFDW m⁻² in the manure-amended and inorganic fertilizer-treated plots, respectively. Mature *L. rubellus* biomass ranged from 0 g to 0.57 g AFDW m⁻² in the manure-amended plots and from 0 g to 0.78 g AFDW m⁻² in the inorganic fertilizer-treated plots.

Table 1 Percentage of total annual earthworm population and biomass contributed by the earthworm species in corn agroecosystems receiving annual manure and inorganic fertilizer amendments

Species	Abundance						Biomass					
	1994		1995		1996		1994		1995		1996	
	Manure (%)	Inorganic (%)										
Lumbricus terrestris Lumbricus	10.2	12.3	15.2	14.0	14.5	18.6	51.7	50.7	55.7	51.3	51.7	60.6
rubellus Aporrectodea	0.8	0.6	1.6	5.4	3.9	2.6	1.0	0.5	1.7	6.2	4.8	2.2
tuberculata Aporrectodea	6.6	9.6	12.3	13.6	13.7	13.8	8.5	10.6	12.0	10.7	13.0	9.4
trapezoides Lumbricus	0	0.3	0.7	0.3	1.1	0.1	0	0.4	0.8	0.9	1.7	0.3
spp. juve- niles	29.2	32.3	38.6	36.3	35.5	33.5	9.5	7.6	9.5	9.2	9.1	7.7
Aporrectodea spp. juve-niles Lumbricus	53.2	44.9	31.5	30.4	31.2	31.4	20.0	18.7	9.5	9.6	7.7	6.2
spp. fragment		_	-	-	_	-	1.9	4.4	3.4	4.3	4.4	7.3
spp. fragment		_	_	_	_	_	7.1	7.3	7.1	7.4	7.4	6.1
Cocoons	-	_	-	_	-	_	0.1	0.01	0.3	0.4	0.3	0.4

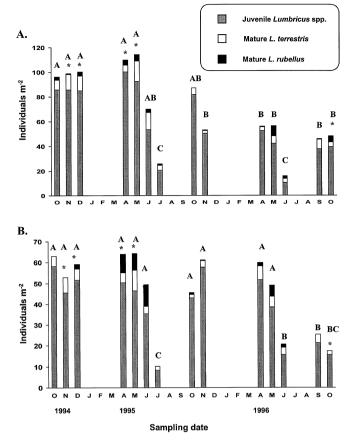


Fig. 3 Mean monthly abundance and community structure of Lumbricus spp. in plots receiving (A) manure or (B) inorganic fertilizer from 1994 to 1996. Significant differences (P < 0.05, HSD) between fertilizer treatments for total (juvenile and mature) Lumbricus spp. abundance at each sampling date are indicated by asterisks, and significant differences in total Lumbricus spp. abundance between sampling dates within each fertilizer treatment are denoted by capital letters. Bars with the same letter are not statistically significantly different at P < 0.05 (HSD)

Abundance and biomass of *Aporrectodea* spp.

Total Aporrectodea spp. abundance was significantly greater (P < 0.05, HSD) in the manure-amended plots than in the inorganic fertilizer-treated plots during October and November 1994, May and June 1995, and September 1996 (Fig. 4A, B). Aporrectodea spp. populations were greatest during October 1994 in both fertilizer treatments, and there was a significant (P < 0.05, HSD) decrease in *Aportectodea* spp. populations from October 1994 to October 1996 (Fig. 4A, B). There was a sevenfold decrease in Aporrectodea spp. numbers in the manure-amended plots from 258.5 m⁻² in October 1994 to 35.9 m⁻² in October 1996, and a five-fold decline in Aporrectodea spp. numbers in the inorganic fertilizer-treated plots from 98.5 m⁻² to 19.9 m⁻² during this period. In the manure-amended plots, Aporrectodea spp. abundance declined to very low levels by November 1995 and did not increase significantly by the end of the investigation (Fig. 4A). A similar trend was

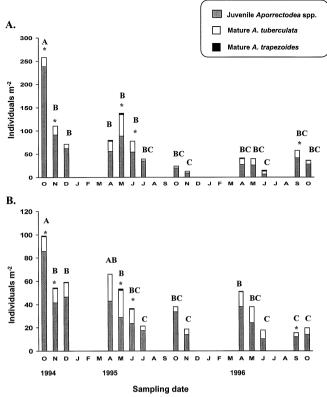
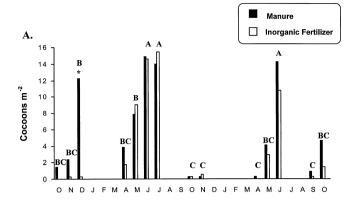


Fig. 4 Mean monthly abundance and community structure of *Aporrectodea* spp. in plots receiving (A) manure or (B) inorganic fertilizer from 1994 to 1996. Significant differences (P < 0.05, HSD) between fertilizer treatments for total (juvenile and mature) *Aporrectodea* spp. abundance at each sampling date are indicated by *asterisks*, and significant differences in total *Aporrectodea* spp. abundance between sampling dates within each fertilizer treatment are denoted by *capital letters*. *Bars* with the same letter are not statistically significantly different at P < 0.05 (HSD)

noted in the inorganic fertilizer-treated plots, where total *Aporrectodea* spp. populations declined significantly by July 1995, and, except for April 1996, did not change significantly during the remainder of the study (Fig. 4B).

The total biomass of *Aporrectodea* spp. was significantly greater (P < 0.05, HSD) in the manure-amended plots than in the inorganic fertilizer-treated plots and followed a similar trend to the *Aporrectodea* spp. abundance results (data not shown). The biomass of juvenile Aporrectodea spp. ranged from 0.11 to 4.68 g AFDW m⁻² in manure-amended plots and from 0.11 g to 2.63 g AFDW m⁻² in inorganic fertilizer treated plots. Mature A. tuberculata biomass was between 0.14 and 4.14 and between 0.21 and 1.70 g AFDW m⁻² in the manure-amended and inorganic fertilizer-treated plots, respectively. Only a few individuals of mature A. trapezoides were present at any sampling date, and mature A. trapezoides biomass ranged from 0 g to 0.28 g AFDW m⁻² in the manure-amended plots and from 0 g to 0.25 g AFDW m⁻² in the inorganic fertilizertreated plots.



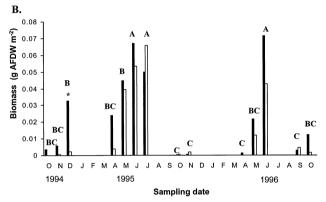


Fig. 5 Mean monthly (A) abundance and (B) biomass of earthworm cocoons in corn agroecosystems receiving manure or inorganic fertilizer amendments from 1994 to 1996. Significant differences (P < 0.05, HSD) in cocoon biomass and abundance between fertilizer treatments at a given sampling date are indicated by an asterisk (*). Differences between sampling dates for both treatments (pooled) are indicated by capital letters where bars with the same letter are not statistically significantly different at P < 0.05 (HSD)

Reproduction of earthworms in corn agroecosystems

Periods of earthworm reproduction coincided with the sampling dates at which the number of mature L. terrestris and A. tuberculata were greatest. The number and biomass of earthworm cocoons were significantly higher (P < 0.05, HSD) in June and July 1995 and June 1996 (Fig. 5A, B). Cocoon numbers and biomass were significantly (P < 0.05, HSD) greater in manureamended plots compared to inorganic fertilizer-treated plots in December 1994; however, there was no difference in the effects of fertilizer amendments on cocoon numbers or biomass on any other sampling date (Fig. 5A, B).

Discussion

Long-term cultivation of corn has proven detrimental to the survival of earthworm communities in these tilled, continuously-cropped agroecosystems. We observed an overall decline in the numbers and biomass of the earthworm community in manure-amended and inorganic fertilizer-treated corn agroecosystems from 1992 to 1996. At the beginning of the investigation in April 1992, Bohlen (1994) reported 195 individuals m⁻² of *Lumbricu* spp in the manure plots and 136 m⁻² in the inorganic fertilizer plots. The numbers of *Aporrectodea* spp. in the manure plots were 322 m⁻², while in the inorganic fertilizer plots, there were 260 individuals m⁻². The earthworm numbers in the manure and inorganic fertilizer plots were not statistically significantly different in 1992. From April 1992 to April 1996, there was a decline of 56–71% in *Lumbricus* spp. numbers, while *Aporrectodea* spp. numbers declined by 78–89% in the corn agroecosystems.

Although there was a long-term decline under continuous corn with both fertilizer types, the numbers and biomass of earthworms were greater in the manure plots than in the inorganic fertilizer plots on most sampling dates. Earthworm populations ranged from 31 to 355 individuals m⁻² in the manure plots, and from 32 to 162 m⁻² in the inorganic fertilizer plots, while earthworm biomass was between 3.2 g and 26.3 g AFDW m^{-2} and between 2.6 g and 15.5 g AFDW m^{-2} in the manure and inorganic fertilizer plots, respectively. Edwards and Lofty (1982) reported that in long-term cultivated cereal plots, the earthworm population was 90 m⁻² in plots receiving farm-yard manure, compared to 21 m⁻² in plots receiving an equivalent amount of nitrogen in inorganic fertilizer. Earthworm biomass in their agroecosystem was 43.6 g dry weight m⁻² in the manure plots and 6.2 g dry weight m⁻² in the inorganically fertilized plots. In a tropical orchard, Tiwari (1993) stated that earthworm populations and biomass were 60 m⁻² and 28.4 g dry weight m⁻², respectively, in plots treated with manure compared to 24 m⁻² and 14.3 g dry weight m⁻² in inorganically fertilized plots.

It is likely that the total earthworm populations and biomass were much lower in the inorganic fertilizer plots than in the manure plots because the earthworm populations in the inorganic fertilizer plots were limited by the availability of organic substrates. Organic matter inputs in the inorganic fertilizer plots consisted only of corn residues and litter from dead weed biomass which totaled about 6.5 Mg dry matter ha⁻¹ year⁻¹. Although earthworms are capable of processing substantial quantities of corn residues (Mackay and Kladivko 1985), Shipitalo et al. (1988) reported that corn leaves were a poorer quality organic resource than alfalfa or red clover leaves for L. terrestris and L. rubellus. Corn residues and dead weed biomass were also retained in the manure plots, and 8–10 Mg dry matter ha⁻¹ were added each year in straw-packed cow manure prior to cultivation, providing these plots with a much larger quantity of organic matter than the inorganic fertilizer plots. The quality of the organic resource in the manure plots was improved by the annual addition of organic nitrogen, and there was a C:N ratio of 30 in surface residues in the manure-amended plots, while organic residues in the inorganic fertilizer plots had a C:N ratio of 40 (Bohlen et al. 1997). It has been found that earthworms remove organic materials with a lower C:N ratio preferentially (Bohlen et al. 1997; Ketterings et al. 1997). The quality of organic substrates may be particularly important for *L. terrestris*, which consumes primarily plant litter and organic residues on the soil surface, and for *L. rubellus*, which inhabits the top layer of soil and surface litter. We have shown that *L. terrestris* numbers and biomass were significantly greater in the manure plots compared to the inorganic fertilizer plots. However, there was no effect of the fertilizer treatment on *L. rubellus* during this study, which was likely due to its low numbers and relatively small contribution to earthworm community biomass.

It is well-documented that earthworm populations and biomass are significantly influenced by soil temperature and moisture, and in temperate agroecosystems, earthworms are usually most active during spring and autumn (Parmelee and Crossley 1988; Baker et al. 1993; Curry et al. 1995). Earthworm populations and biomass were greatest during autumn 1994 and spring 1995 when the soil temperatures were between 4 and 18°C and monthly rainfall was 14.7–115.3 mm. High soil temperatures during the summer of 1995 followed by the early onset of winter may have been partially responsible for the very low earthworm numbers and biomass in both manure and inorganic fertilizer plots during the latter part of 1995. Earthworm numbers and biomass remained lower through the rest of the investigation in both agroecosystems until September and October 1996, when earthworm numbers and biomass were significantly greater in the manure plots than the inorganic fertilizer plots. Werner and Dindal (1989) hypothesized that organic fertilizers might protect earthworm populations by improving the soil moisture retention and providing a more favorable habitat for earthworms than soils receiving inorganic fertilizers. No evidence was found to support this hypothesis in this investigation since the earthworm populations in both manure and inorganic plots were affected adversely by unfavorable climatic conditions during 1995.

Interestingly, there was relatively little difference in the proportion of each species present in the earthworm communities in either the manure or inorganic fertilizer plots on an annual basis. A similar trend was reported in long-term cereal production where the contribution of Apporrectodea longa and A. caliginosa to earthworm populations and biomass were virtually identical in farmyard manure-amended and inorganic fertilizer-treated plots (Edwards and Lofty 1982). However, in the same study, the proportion of L. terrestris in earthworm communities was lower in the inorganic fertilizer-treated plots compared with the farmyard manure-amended plots, while A. chlorotica was higher. Since the earthworm communities were only sampled once in Edwards and Lofty's (1982) study, it is not clear whether these differences represented a real change in the earthworm communities in long-term manure and inorganically fertilized plots. Our results indicate that longterm additions of manure and inorganic fertilizers have not altered the composition of the earthworm communities in corn agroecosystems significantly.

Cultivation is another factor that is known to significantly influence earthworm populations. Fraser et al. (1996) stated that continuous arable production resulted in a decline in earthworm populations and biomass from $400 \,\mathrm{m}^{-2}$ and $9 \,\mathrm{g}$ dry weight m^{-2} after 3 years to less than 100 m⁻² and 2 g dry weight m⁻² after 9 years of arable production, and Boström (1995) reported that earthworm biomass was reduced by 61-68% after rotary cultivation. Disk cultivation appears to have less impact on earthworm populations than rotary cultivations, and Berry and Karlen (1993) reported that populations of Aporrectodea spp. were unchanged or increased in disk-tilled agroecosystems compared to no-till agroecosystems. However, populations of L. terrestris were 42–74% lower in disk-tilled agroecosystems than in no-till agroecosystems. In our investigation, earthworm numbers and biomass were lower in July 1995 and June 1996 after cultivation than before, and it appeared that both Lumbricus spp. and Aporrectodea spp. were affected negatively by cultivation. It is likely that the lower earthworm populations and biomass of L. terrestris and A. tuberculata observed in July 1995 and June 1996 were at least partially a result of disktillage cultivation prior to these sampling dates.

Mature Lumbricus spp. and Aporrectodea spp. were most numerous during May and June of 1995 and 1996. Since the greatest number of cocoons were collected from soil samples taken during June and July of 1995 and 1996, it is likely that most earthworm reproduction occurred during this period, with the possibility of additional reproduction occurring during late autumn; this occurred in December 1994 when climatic conditions were favorable. Cocoon production has been found to be much higher in the spring than in the autumn for both Aporrectodea spp. and L. terrestris (Christensen and Mather 1990), and Boström and Lofs (1996) noted that the greatest cocoon production by A. caliginosa, in a meadow fescue ley, occurred in June. It was not possible to distinguish between L. rubellus and A. tuberculata cocoons, since they are roughly the same size, and our method of sampling cocoons may underestimate L. terrestris reproduction, if their cocoons were deposited at depths greater than 15 cm. The recruitment of juveniles into the earthworm community occurred primarily in the autumn for both Lumbricus spp. and Aporrectodea spp.

It seems clear that the development of sustainable agroecosystems that substitute organic fertilizers for inorganic fertilizers will have the capacity to support much greater earthworm populations and biomass. The earthworm communities in agroecosystems that receive organic fertilizers will probably be relatively much more important in maintaining soil fertility and crop productivity, through their roles in organic matter decomposition and nutrient cycling. There is growing evidence that earthworms can accelerate nutrient cycling

processes significantly (Edwards and Bohlen 1996) and are responsible for the turnover of large quantities of nitrogen (Parmelee and Crossley 1988; Curry et al. 1995). Further research is needed to quantify the ecosystem level effects of earthworms on the soil chemical, physical, and biological properties of agroecosystems and their contribution to long-term agricultural sustainability.

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