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Temporal and spatial dynamics of earthworm surface casting in a temperate soybean agroecosystem

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ABSTRACT

Earthworm activity is expected to have a beneficial effect on soil structure and plant growth in agroecosystems, but active populations are temporally dynamic and spatially heterogeneous under field conditions. The objective of this research was to evaluate the temporal and spatial variation in surface casting by earthworms at the row-interrow scale in a temperate soybean agroecosystem. Earthworm populations were manipulated in 2.9 m^2 field enclosures by applying carbaryl pesticide to reduce the naturally occurring earthworm population before juveniles and adults of *Aporrectodea caliginosa* (Sav.) and *Lumbricus terrestris* L. were added. Surface casting was measured weekly during a 14-week period. There was very little surface casting during the first 6 weeks of the study, possibly due to insufficient food resources and shade at the soil surface. We collected nearly 3400 casts from weeks 7 to 14, and surface casting rates during this period ranged from 0.95 to 2.51 g dry weight m^{-2} day^{-1}. More casts were deposited within 30 cm of the soybean row than at distances up to 50 cm from the row, indicating that the planted row was a zone with greater earthworm activity than the inter-row. Better understanding of the timing and small-scale variation in earthworm activities will aid our understanding of how earthworms contribute to plant growth.

1. Introduction

As ecosystem engineers, earthworms generate important physical changes in the soil environment. Since many of these changes are seen as beneficial, earthworms are considered valuable soil organisms for soil rehabilitation and as indicators of biological soil quality (Langmaack et al., 2002; Dunger and Voigtländer, 2005). Earthworm casting activity improves soil physical characteristics because casts function like stable soil aggregates (McKenzie and Dexter, 1987; Scullion and Ramshaw, 1988; Schrader and Zhang, 1997). Thus, casts may help protect the soil from erosive and compacting forces, facilitate water infiltration and gas exchange, and ease root penetration. Fresh casts also contain more organic carbon and plant-available N, P, K and Mg than the bulk soil, which has led some authors to suggest that casts could positively influence plant growth (Sharpley and Syers, 1976; McKenzie and Dexter, 1987; Tomati et al., 1994; Schrader and Zhang, 1997; Chaoui et al., 2003). In addition, casts may act as seed banks that aid in the regeneration of plant communities (Jiménez and Decaëns, 2004).

The patchy nature of earthworm populations, however, limits our understanding of how casting activity may affect plant growth in natural and managed ecosystems (Hendrix, 1995; Whalen, 2004). Generally, the spatial distribution of earthworm assemblages is not related to the plant species present in large plots (50 m × 50 m or larger), suggesting that earthworms are not necessarily associated with specific types

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of vegetation or land use (Jiménez et al., 2001; Margerie et al., 2001; Maestre and Cortina, 2002). Yet, earthworms may be associated with plants at smaller spatial scales. Boettcher and Kalisz (1991) found that the number and species of earthworms present in eastern Kentucky forests were controlled by plants at the scale of an individual tree, or an individual tree and its associated understory vegetation. Similarly, Babel et al. (1992) found more earthworms under clumps (at least 40 cm diameter) of *Rumex obtusifolius* than grasses in a temperate meadow in southwestern Germany, possibly because litter and other organic substrates in the vicinity of *R. obtrusifolius* were more palatable. In temperate maize agroecosystems, more earthworms were generally found in the planted rows than in the inter-row space, and the planted row had lower bulk density and about nine times more macropores than the inter-rows (Binet et al., 1997). In non-compacted soils, earthworms deposited twice as many surface casts in the maize row than in the inter-row (Binet and Le Bayon, 1999). If soil in the vicinity of plant roots is a favorable microenvironment for earthworms, and if earthworms are most active in the rooting zone during periods when plants are rapidly growing, then mutually beneficial plant–earthworm relationships may occur in the field. Better understanding of the timing and location of earthworm activities in agroecosystems is therefore important. We hypothesize that the strength of plant–earthworm relationships depends on the earthworm species or functional groups present, but this remains to be determined.

A field experiment was designed to determine the temporal fluctuations and spatial variation in surface casting by earthworm functional groups (endogeic and anecic), separately and together, at the row-interrow scale in a temperate soybean agroecosystem. The earthworms *Aporrectodea caliginosa* and *Lumbricus terrestris* were used as model species for the endogeic and anecic groups, respectively. We have previously found that the endogeic earthworm *A. caliginosa* deposits casts on the soil surface (Whalen et al., 2004), so the activity of both anecic and endogeic earthworms can be assessed by measuring surface cast production.

2. Materials and methods

2.1. Site description

The study site was located on the Macdonald Campus Research Farm of McGill University, Ste. Anne de Bellevue, Québec, Canada (45°28′N, 73°45′W). The site was cultivated for soybean and corn production in the 2 years prior to this study, and before that was a mowed grass soccer field for more than a decade. Soil at the site was a mixed, frigid Typic Endoaquent (Chicot sandy-loam) that contained 580 g kg^{-1} of sand, 300 g kg^{-1} of silt and 120 g kg^{-1} of clay with 24.5 g C kg^{-1}, 1.98 g N kg^{-1} and pH (H_2O) 5.9. A survey of a 30 m × 30 m area at the study site on 18 June 2003 found an earthworm population dominated numerically by *A. caliginosa* and *L. terrestris* with a few individuals of *A. longa* (<1 individuals m^{-2}, on average). Earthworm populations ranged from 28 to 161 individuals m^{-2} (mean = 66 m^{-2}, mean biomass = 40.34 g fresh weight m^{-2}), with approximately 50 individuals m^{-2} of *A. caliginosa* and 15 individuals m^{-2} of *L. terrestris*.

2.2. Field enclosures

In April 2004, field enclosures were installed at the study site to permit manipulation of earthworm populations and functional groups (Eriksen-Hamel and Whalen, 2007). These rectangular enclosures measured 2.44 m long × 1.2 m wide (2.9 m^2), with the longest side along the east–west axis. They were constructed from stainless steel sheets (0.1 cm thick) buried to a depth of 0.30–0.40 m. The top edges of the sheets, which protruded about 0.2–0.3 m above the soil surface, were bent at right angles and fitted tightly at the corners to minimize the chance of earthworm escape from enclosures.

To reduce the populations of naturally occurring earthworms within enclosures, the soil surface was sprayed five times from 28 April to 21 May 2004 with Sevin XLR Plus (Bayer Group), delivering a total of 0.02 kg a.i. m^{-2} of carbaryl. This is about four times greater than the amount of carbaryl applied to turfgrass by Potter et al. (1990), which reduced naturally occurring earthworm populations by 90%. The last carbaryl application occurred 10 days before any earthworms were added to the enclosures. On 28 May 2004, a single row of 100 soybean seeds (*Glycine max* (L.) Merr. cv. OAC Champion) was planted by hand in a row (5 cm deep) along the east–west axis in the center of each enclosure (equivalent to 350,000 seeds ha^{-1}). No fertilizers or pesticides were applied during the growing season, and weeds growing in the enclosures were removed by hand every 7–14 days.

2.3. Experimental design

The experiment was a randomized complete block design with seven earthworm treatments, replicated four times. Briefly, these included: *A. caliginosa* alone (A), *L. terrestris* alone (L) and a combination of *A. caliginosa* and *L. terrestris* (AL), at the background population level (1×) and double the background population level (2×). There were also control (C) enclosures where no earthworms were added. The earthworms added to the enclosures came from arable fields surrounding the study site. They were collected from 1 to 4 weeks before this experiment began by handsorting and formalin extraction (Raw, 1959), sorted by species and age class, and kept in the laboratory (20 °C) in 37 L plastic containers containing moist soil from the study site plus a small quantity of composted cattle manure. On an overcast day, 1 June 2004, earthworms were introduced into the enclosures and covered with straw to minimize predation and desiccation. The number and biomass of juveniles and adults added to each treatment are provided in Table 1. Three days later (4 June), we removed the straw cover.

2.4. Surface cast collection

Each enclosure was divided in twenty 0.1 m × 1 m transects along the north–south axis, which was perpendicular to the soybean row. Surface casts were collected from one randomly selected transect every 7–8 days starting on 21 June 2004, for a total of 14 collection dates. No transect was sampled twice during the study. One week before collecting surface casts, we removed all casts and aggregates present in the transect by scraping the surface with a small hand rake. The spatial variation in casting activity was assessed by dividing the

Table 1 – Earthworm populations and biomass added to field enclosures in June 2004 and average numbers and biomasses collected after soybean harvest (October 2004)

Earthworm treatment	Earthworm population (individuals m^{-2})		Biomass (g fresh weight m^{-2})	
	June 2004	October 2004	June 2004	October 2004
C	0	77 ± 12[a]	0	25 ± 7.5[a]
A1×	50	190 ± 56	21	56 ± 15
A2×	100	330 ± 87	42	86 ± 22
L1×	15	170 ± 24	34	55 ± 9.2
L2×	30	220 ± 46	67	77 ± 12
AL1×	65	180 ± 62	55	86 ± 25
AL2×	130	380 ± 47	109	92 ± 8.7
Background[b]		123 ± 30		59 ± 4.5

Earthworm treatments included: *A. caliginosa* alone (A), *L. terrestris* alone (L) and a combination of *A. caliginosa* and *L. terrestris* (AL) at the background population level (1×) and double the background population level (2×). No earthworms were added to the control (C) enclosures in June 2004.

[a] Values are the mean (±standard error) of four replicates.

[b] Background earthworm populations and biomass at two sampling locations adjacent to the field enclosures.

transect into five intercepts (0.2 m each) along the north–south axis. Intercept 1 (starting −0.5 m from the planted row) corresponded to the southern most section of the transect, the soybean plants were rooted in intercept 3 (encompassing −0.1 to +0.1 m from the planted row) and intercept 5 (ending +0.5 m from the planted row) was at the northern most part of the transect. We measured the number and mass of surface casts (oven-dry basis, 60 °C for 48 h) deposited in each intercept (0.1 m × 0.2 m), which summed to give us the number and mass of surface casts generated in transect (0.1 m^2 area) during 1 week. Then, we calculated the cumulative number (casts m^{-2}) and mass (g dry weight (dw) m^{-2}) of surface casts deposited in the intercepts and the transects during the 14-week study.

Every week, soil temperature was measured in every enclosure ($n = 28$) at a 10 cm depth using a hand-held model HH21 microprocessor thermometer (Omega Technologies, Stamford, CT). Soil moisture was determined by oven drying (60 °C for 48 h) soil samples (0–10 cm depth) collected from two randomly selected enclosures. Soil moisture was converted to water-filled pore space (WFPS, in %) using the equation:

$$\mathrm{WFPS} = 100\left(\frac{w(\rho_b/\rho_w)}{1-(\rho_b/\rho_s)}\right) \quad (1)$$

where w is the gravimetric moisture content (%), ρ_w the density of water (1 g cm^{-3}), ρ_b the soil bulk density, on average 1.08 g cm^{-3} in the 0–10 cm layer of the enclosures and ρ_s is the soil particle density (2.65 g cm^{-3}). From 21 June to 21 September 2004, the duration of our study, the average daily air temperature was 18.7 °C and the mean precipitation was 0.42 mm day^{-1} (Environment Canada, 2004).

2.5. *Cast and bulk soil analysis*

We conducted a detailed analysis of surface casts and bulk soil (0–10 cm depth) collected from the replicate A2× and L2× enclosures on weeks 8 and 12 of the study. We assumed that surface casts (generally <1 mm diameter) in the A2× enclosure were deposited by *A. caliginosa* and large surface casts (>1 mm diameter) from the L2× enclosure were deposited by *L. terrestris*. Bulk soil ($n = 16$) and surface casts ($n = 8$ in A2× enclosures, and $n = 8$ in L2× enclosures) were analyzed for total carbon and nitrogen using a NC soil analyzer (Flash EA 1112 Series, Thermo-Finnigan Carlo Erba). Mineral N (NH_4–N and NO_3–N) was determined in 0.5 M K_2SO_4 soil extracts (1:5 soil:extractant) and analyzed colorimetrically using the cadmium reduction-diazotization and salicylate methods with a Lachat Quick-Chem AE flow injection autoanalyzer (Lachat Instruments, Milwaukee, WI). Dissolved organic N was the difference between the NO_3–N concentration in persulfate digests and the mineral N (NH_4–N, NO_3–N) concentration in undigested solutions (Cabrera and Beare, 1993). Microbial biomass N (MBN) was determined using the chloroform fumigation direct extraction procedure followed by persulfate digestion and calculated as: [(total extractable N after fumigation − total extractable N before fumigation)/K_{EN}], where K_{EN} value of 0.54 was used to correct for extraction efficiency (Joergensen and Mueller, 1996). The dissolved organic C (DOC) and microbial biomass C (MBC) concentrations in unfumigated and fumigated soil K_2SO_4 extracts was measured by wet combustion with a Shimadzu TOC-V carbon analyzer (Shimadzu Corporation, Kyoto, Japan). The MBC concentration was adjusted using the K_{EC} factor of 0.45 to correct for extraction efficiency (Joergensen, 1996). Results are presented as the mean (±standard error) nutrient concentrations in surface casts and bulk soil.

2.6. *Sampling earthworm populations*

Five days after soybean harvest (4 October 2004), earthworm populations were sampled from a soil pit (50 cm × 30 cm, to a depth of 20 cm) dug in the middle of the enclosure. Soil removed from the pit was handsorted to collect surface-dwelling earthworms, while earthworms at deeper depths were collected by formalin extraction (Raw, 1959). The number, biomass and age classes of individuals were determined and sexually mature individuals were identified using the key of Reynolds (1977).

2.7. *Statistical analysis*

The effects of earthworm treatment and sampling intercept on the cumulative number and mass of casts collected from

Table 2 – Mean number (individuals m^{-2}) and proportion (%) of earthworms in each species and age class collected from enclosures in October 2004

Earthworm treatment	*A. caliginosa*		*L. terrestris*		*A. longa*		Adults (m^{-2})	Juveniles (m^{-2})
	m^{-2}	%	m^{-2}	%	m^{-2}	%		
C	63	84	5	7	8	9	17	50
A1×	153	80	23	16	12	5	50	132
A2×	273	82	24	9	33	10	100	198
L1×	136	81	20	10	18	9	42	111
L2×	167	77	33	15	22	8	65	147
AL1×	133	76	30	16	17	8	45	122
AL2×	287	78	33	10	37	12	72	253
Background[a]	90	73	17	14	17	14	37	87

Earthworm treatments are described in Table 1. Proportions may not sum to 100% because some earthworm fragments could not be classified.
[a] Background earthworm populations at two sampling locations adjacent to the field enclosures.

field enclosures were evaluated with a split-plot analysis of variance using the PROC GLM function of SAS (Version 8.2, SAS Institute Inc., Cary, NC). The main plot (earthworm treatment) and split-plot (sampling intercept) effects were significant ($P < 0.05$), permitting us to compare the means with a Student–Newman–Keuls test at the 95% confidence level. The relationship between weekly cast weight and soil conditions (temperature, water-filled pore space) was evaluated with the PROC STEPWISE procedure of SAS, but only temperature met the criteria ($P < 0.15$) for entry into the model. The linear regression equation between cast weight and temperature was fitted with the PROC REG function of SAS.

3. Results

Earthworms added to field enclosures appeared to survive, grow and reproduce, since we collected more individuals in October 2004, following soybean harvest, than we added (Table 1). Carbaryl applications reduced the naturally occurring earthworm population within enclosures, and there were fewer earthworms in the control enclosures than at locations adjacent to the enclosures (background population) or in enclosures with added earthworms (Table 1). Yet, the earthworms recovered in October 2004 were mostly *A. caliginosa* (76–84% of the population), with a few *L. terrestris* and *A. longa* (Table 2).

We collected 3528 surface casts from field enclosures during this 14-week study, but most of them were collected in weeks 7–14 of the study (Fig. 1). During the first 6 weeks, only 240 surface casts were collected and the weekly mass ranged from 0.4 to 5.8 g dw m^{-2} (Fig. 1). Although the weight of surface casts was 31–40% lower in week 11 than weeks 10 and 12, following the measurement of 11% water-filled pore space in week 10, there was generally no relationship between cast production and soil moisture (Fig. 1). In contrast, surface casting declined significantly ($P < 0.05$) as the soil temperature increased (Fig. 2).

The control enclosure contained fewer casts than the other enclosures (Table 3). More surface casts were collected from the A2× treatment than the other enclosures with added earthworms, but there were few differences in cast weight among enclosures with added earthworms (Table 3). Daily surface casting ranged from 0.31 g dw m^{-2} day^{-1} in the control to 0.84 g dw m^{-2} day^{-1} in the L2× treatment, but daily surface casting rates increase to 0.95 g dw m^{-2} day^{-1} in the control and 2.51 g dw m^{-2} day^{-1} in the L2× treatment if data from weeks 1 to 6 was not included (Table 3). Surface casting was greater in the intercept ending 0.3 m south of the crop row than in the intercepts furthest from the crop row (–0.5 m south and +0.5 m north) and there was no difference in the weight of casts deposited in the area within 30 cm of the soybean row (Fig. 3).

We assumed that casts <1 mm diameter in the A2× enclosures were deposited by *A. caliginosa* and larger surface casts in the L2× enclosures were from *L. terrestris*, but population assessment in October 2004 revealed that both species (plus a few *A. longa*) were found in all enclosures (Table 2). Therefore, the only relevant comparison was between surface casts and bulk soil. Surface casts from the A2× and L2× field enclosures contained similar total and extractable C and N concentrations as bulk soil, although the NO_3–N concentration was about two-fold greater in casts than bulk soil (Table 4).

4. Discussion

We were not able to eliminate earthworms within enclosures by applying carbaryl, although it did reduce the naturally

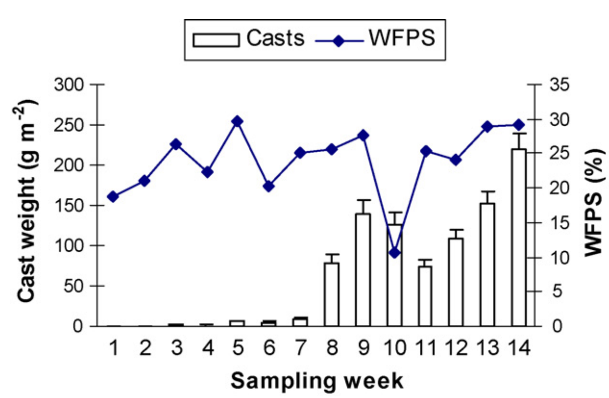

Fig. 1 – Temporal variation in surface casting (g dw m^{-2}) by earthworms in field enclosures and the water-filled pore space (WFPS) during the 14-week study (21 June–21 September 2004). Bars represent the mean cast weight (with standard error bars) in 28 enclosures each week.

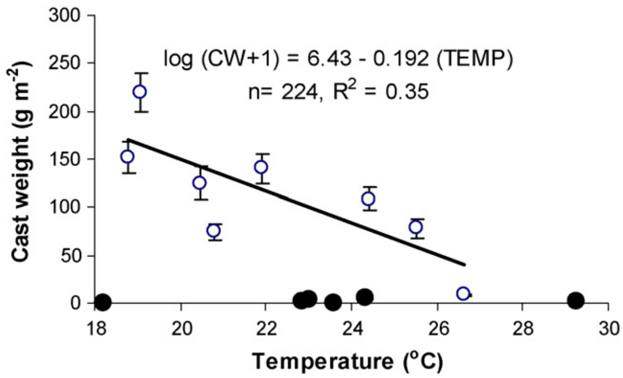

Fig. 2 – Relationship between soil temperature (TEMP) and the mean cast weight (CW, g dw m^{-2}) with standard error bars in 28 enclosures each week. Data from weeks 1 to 6 (filled circles, ●) were considered to be outliers, hence the equation fits values from weeks 7 to 14 (clear circles, ○) only.

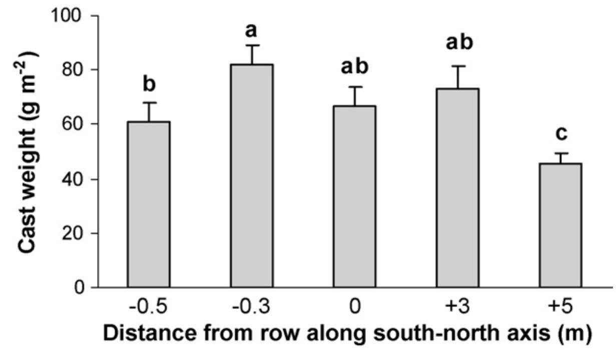

Fig. 3 – Mean weight (g dw m^{-2}) of surface casts collected from field enclosures during a 14-week period, as influenced by the distance from the soybean row. Negative values (−0.5 and −0.3 m) were south of the soybean row while positive values (+0.3 and +0.5 m) were north of the row. Standard errors of the mean are indicated, and bars with different letters represent locations with a significantly ($P < 0.05$, Student–Newman–Kuels test) different mass of surface casts.

occurring earthworm populations. Carbaryl has a short half-life ($t_{1/2}$ = 2–9 days) in well-aerated soils and is also photo-degraded when it remains on the soil surface (Thapar et al., 1995; Nkedi-Kizza and Brown, 1998; Bondarenko and Gan, 2004). We suggest that surface casting in the control enclosures was from earthworms that did not come into contact with the pesticide or were cocoons when it was applied. We assumed that surface casting in other field enclosures came from earthworms added in June 2004 plus earthworms that survived the pesticide applications.

We also found that *L. terrestris* added to the enclosures did not survive as well as the *A. caliginosa*. This may have been due to residual toxicity from the carbaryl (Nkedi-Kizza and Brown, 1998), insufficient surface litter for *L. terrestris* growth or other limiting factors (Edwards and Bohlen, 1996). Therefore, it is not possible to compare surface casting by earthworm functional groups in this study, since all enclosures contained mixed populations as well as *A. longa* that were not deliberately added. Further research on methods for controlling and manipulating earthworm functional groups in the field is warranted.

4.1. *Temporal fluctuations in surface casting*

Very few casts were collected during the first 42 days of this study. This is consistent with a report by Le Bayon et al. (2002), who collected very few surface casts in the first 45 days after maize was planted. They attributed this to earthworm mortality following spring ploughing, but it could not have been the case in our study since the site was not ploughed in the spring. Low surface casting rates during the first 6 weeks did not seem to be related to environmental factors, since the soil temperature (18–29 °C) and water-filled pore space (19–30%) during this period were similar to those observed during weeks 7–14 of the study (temperatures ranged from 19 to 27 °C with 11–29% water-filled pore space). Instead, we suggest that a limited quantity of food near the soil surface during the first 6 weeks restrained earthworm activities. Raking the soil surface to remove casts and aggregates led to the removal of surface litter, as did weeding, and it appears that there were insufficient organic substrates and shade to attract earthworms to the soil surface

Table 3 – Mean number (m^{-2}) and weight (g dry weight (dw) m^{-2}) of surface casts collected from field enclosures during a 14-week period

Earthworm treatment	Cumulative number (casts m^{-2})	Cumulative weight (g dw m^{-2})	Daily surface casting (g dw m^{-2} day^{-1})	
			All weeks	Weeks 7–14 only
C	53 c[a]	30.3 c	0.31 ± 0.07	0.95 ± 0.20
A1×	82 b	52.6 b	0.54 ± 0.11	1.62 ± 0.33
A2×	116 a	78.1 a	0.80 ± 0.08	2.41 ± 0.26
L1×	95 b	69.2 ab	0.71 ± 0.06	2.13 ± 0.19
L2×	97 b	82.3 a	0.84 ± 0.11	2.51 ± 0.34
AL1×	87 b	70.4 ab	0.72 ± 0.10	2.18 ± 0.31
AL2×	101 b	76.9 a	0.78 ± 0.12	2.36 ± 0.37

Daily surface casting (mean ± standard error), with and without weeks 1–6, was also calculated. Earthworm treatments are described in Table 1.

[a] Values within a column followed by the same letter were not significantly different ($P < 0.05$, Student–Newman–Kuels test).

Table 4 – Total and extractable carbon and nitrogen concentrations in bulk soil and in surface casts from A2× and L2× field enclosures under soybean production

Nutrient concentration	Bulk soil	Surface casts	
		A2×	L2×
Total N (g kg^{-1})	3.1 ± 0.2	3.7 ± 0.2	3.1 ± 0.4
Total C (g kg^{-1})	29.8 ± 1.5	34.9 ± 0.5	30.2 ± 0.57
NH_4–N (mg kg^{-1})	0.85 ± 0.09	N.D.[a]	0.14 ± 0.15
NO_3–N (mg kg^{-1})	11.4 ± 1.0	24.5 ± 1.5	25.7 ± 4.1
Microbial biomass N (mg kg^{-1})	79.7 ± 2.7	109 ± 43.2	23.5 ± 19.8
Microbial biomass C (mg kg^{-1})	143 ± 29	132 ± 18	103 ± 33

Earthworm treatments are described in Table 1.
[a] N.D.: non-detectable.

until the soybeans reached the V2–V3 growth stages (Fehr et al., 1971). The poor survival of *L. terrestris* added to the field enclosures was probably also related to a lack of suitable organic substrates at the soil surface, where it usually feeds, during the first 6 weeks of this study.

Some authors have found that surface casting increases as soil moisture content increases (Sharpley and Syers, 1976; Hindell et al., 1994), and that peaks in cast production tend to appear within 1–3 days after measurable rainfall events (Binet and Le Bayon, 1999). Surface cast production was not related to soil moisture content, but declined as the soil temperature increased during this study. Our findings are consistent with the general observation that earthworms activity declines when field soil temperature is greater than 20 °C (Edwards and Bohlen, 1996).

4.2. *Cumulative surface cast production and daily surface casting*

The 3528 surface casts collected from field enclosures during this 14-week study weighed 2574 g dw, which represents about 90 surface casts m^{-2} weighing roughly 65.7 g dw m^{-2} deposited in 98 days. When data from weeks 1 to 6 was not included, daily surface casting rates ranged from 0.95 to 2.51 g dw m^{-2} day^{-1}. This range is consistent with a surface casting rate of 3.6 g dw m^{-2} day^{-1} estimated from the annual minimal cast production of 1328 g dw m^{-2} $year^{-1}$ reported by Le Bayon et al. (2002), but is less than the surface cast production of 8.6 g dw m^{-2} day^{-1} reported by Binet and Le Bayon (1999). Both of these studies were conducted in temperate maize agroecosystems. Surface casting is expected to be lower in row-cropped agroecosystems than those with permanent vegetation. Chevallier et al. (2006) reported daily surface cast production ranging from 15 to 60 g dw m^{-2} day^{-1} in a grazed pasture in New Zealand.

4.3. *Spatial variations in surface casting*

It is possible that soil disturbance during the placement of the steel sheets used to construct the enclosures affected earthworm surface casting, but we did not evaluate casting within 0.1 m of the enclosure wall to avoid this confounding effect. In addition, enclosures were in place for more than 3 months before we observed significant surface casting (weeks 7–14 of this study). Our results indicate that the spatial pattern of earthworm surface casting was more strongly affected by the presence of plants than other factors. In an unfertilized maize agroecosystem, Binet et al. (1997) reported greater earthworm numbers and biomass in the planted row than inter-row spaces, while Binet and Le Bayon (1999) found more surface casting in the row than inter-row of maize agroecosystems with non-compacted soils. Earthworms appear to be more active in the planted row of row-cropped agroecosystems, perhaps because this microenvironment favors earthworm reproduction, growth and survival (Binet et al., 1997). Schmidt et al. (2003) suggested that living plants could provide the same advantages to earthworms as mulch, i.e. protection against light and predation, more organic substrates and microbial activity, and less fluctuation in temperature and moisture that prevents stress and desiccation. Soybeans can be grown in widely spaced rows (0.75 m) or solid seeded in rows spaced at least 0.2 m apart (P. Seguin, personal communication). Clearly, row spacing is an important factor to consider when evaluating the interactions between earthworms and crop plants at the agroecosystem level.

4.4. *Carbon and nitrogen concentrations in bulk soil and surface casts*

Surface casts are expected to contain more total and extractable nutrients than bulk soil (Edwards and Bohlen, 1996), but the surface cast material collected from field enclosures was not always richer in C and N than bulk soil. The total C and N content of casts is related to earthworm diet and so may be similar to or greater than the values reported for bulk soil, depending on what organic substrates are ingested by earthworms (Syers et al., 1979; Scheu, 1987). Greater NO_3–N concentrations in surface casts than bulk soil is consistent with other reports indicating that casts are a source of plant-available N (Syers et al., 1979; Curry et al., 1995). The NH_4–N and NO_3–N concentrations in casts depend on microbially mediated transformations of organic substrates as they pass through the digestive tract and after they are deposited on the soil surface, so the measured amounts are expected to vary with cast age (Decaens et al., 1999; Chevallier et al., 2006). Greater microbial biomass and activity have been generally reported in fresh earthworm casts compared with bulk soil (Tiunov and Scheu, 2000; Scullion et al., 2002; Aira et al., 2003), but our results were not consistent for surface casts coming from deposited by *A. caliginosa* and *L. terrestris*. This illustrates the dynamic nature of microbial communities associated with surface casts under field conditions.

5. Conclusions

This work highlights the challenges associated with manipulating earthworm populations in the field. We were not able to control the composition of earthworm communities and functional groups in field enclosures, but our research demonstrates a clear spatial association between earthworm surface casting and plants in a small-scale (<3 m^2) soybean agroecosystem. Although earthworms were added soon after planting the soybeans, there was a lag of about 6 weeks before much surface casting was observed. Further work into plant–earthworm relationships at the field scale should take into account the small-scale and temporally dynamic interactions between these organisms. Such efforts will ultimately help us to better understand how earthworms contribute to plant growth in natural and managed ecosystems.

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