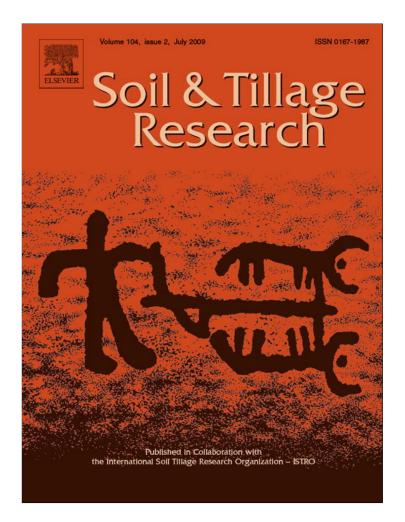
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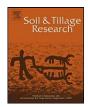
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Earthworm populations and growth rates related to long-term crop residue and tillage management

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ABSTRACT

Conventional tillage creates soil physical conditions that may restrict earthworm movement and accelerate crop residue decomposition, thus reducing the food supply for earthworms. These negative impacts may be alleviated by retaining crop residues in agroecosystems. The objective of this study was to determine the effects of various tillage and crop residue management practices on earthworm populations in the field and earthworm growth under controlled conditions. Population assessments were conducted at two long-term (15+ years) experimental sites in Québec, Canada with three tillage systems: moldboard plow/disk harrow (CT), chisel plow or disk harrow (RT) and no tillage (NT), as well as two levels of crop residue inputs (high and low). Earthworm growth was assessed in intact soil cores from both sites. In the field, earthworm populations and biomass were greater with long-term NT than CT and RT practices, but not affected by crop residue management. Laboratory growth rates of Aporrectodea turgida (Eisen) in intact soil cores were affected by tillage and residue inputs, and were positively correlated with the soil organic C pool, suggesting that tillage and residue management practices that increase the soil organic C pool provide more organic substrates for earthworm growth. The highest earthworm growth rates were in soils from RT plots with high residue input, which differed from the response of earthworm populations to tillage and residue management treatments in the field. Our results suggest that tillage-induced disturbance probably has a greater impact than food availability on earthworm populations in cool, humid agroecosystems.

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1. Introduction

Soil cultivation is often reported to be detrimental to earthworms, but this depends on the frequency of tillage, plow depth, and amount of crop residue returned to soils. Frequent tillage causes physical harm and exposes earthworms to predators, while deep tillage damages earthworm burrows, causing earthworms to expend energy on rebuilding burrows in unstructured soils rather than on reproduction (Edwards and Lofty, 1982; Clapperton et al., 1997; Chan, 2001). Populations of epigeic earthworms such as *Lumbricus rubellus* (Hoff.), whose habitat is disrupted when the litter layer is chopped and incorporated, and anecic earthworms like *L. terrestris* L. that travel through vertical burrows to feed and reproduce at the soil surface, are expected to be negatively affected by tillage (Kladivko, 2001). Yet, tillage operations that alleviate soil compaction or incorporate crop residues serving as a food source for earthworms can maintain or enhance earthworm populations (Wuest et al., 2005; Metzke et al., 2007). Boström (1995) reported that rotary cultivation and plowing reduced earthworm populations by 73–77%, but one year later, there were five times more large adult earthworms and earthworm biomass was similar to pre-tillage levels. The incorporation by tillage of alfalfa and meadow fescue residues, which are readily decomposed and consumed by the dominant endogeic earthworm *Allolobophora caliginosa* (Savigny), was considered to be a major factor in earthworm population recovery.

In NT systems, crop residues left on the surface keep the soil cool and moist, improve the soil structure and serve as a food resource for earthworms (House and Parmelee, 1985; Wardle, 1995; Chan, 2001). Thus, long-term NT should create favorable conditions for earthworms by improving soil physical properties such as soil moisture content, porosity and bulk density, and by increasing food availability (Kladivko, 2001). The addition of crop residues to tilled soils could alleviate some of the negative impacts of tillage, thus improving earthworm growth and maintaining more stable earthworm populations. However, the response of

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earthworm populations to crop residue inputs depends on residue characteristics. Alfalfa and meadow fescue residues are readily eaten, but barley straw must be chopped into small pieces or partially decomposed before it is consumed by earthworms (Boström and Lofs-Holmin, 1986). Besides food availability, other factors controlling earthworm populations under field conditions include environmental conditions (especially soil temperature and moisture), soil texture and hydrology, agrochemical inputs and biotic interactions like competition, synergism and predation (Haukka, 1988; Nuutinen, 1992; Kladivko et al., 1997; Curry, 1998; Virto et al., 2007).

The objectives of this study were (1) to evaluate the effect of long-term crop residue and tillage management systems on earthworm populations in Québec, Canada and (2) to determine the growth rates of *A. turgida* in intact soil cores from various long-term crop residue and tillage management systems under controlled laboratory conditions.

2. Methods

2.1. Study sites

Earthworm populations were studied at two agricultural field sites in the northeastern region of the Mixed Wood Plain ecozone of Canada (Ecological Stratification Working Group, 1996). This ecozone is characterized by a cool humid climate, with temperature as low as -12 °C in January, warm summers (from 18 to 22 °C in July) and 720–1000 mm of precipitation annually.

The first site was located on the Macdonald Research Farm of McGill University in Ste-Anne-de-Bellevue, Québec (45°30'N, 73°35′W). Average temperature ranges from -10.2 °C in January to 20.9 °C in July, with mean annual precipitation of 979 mm (Environment Canada, 2009). The soil was a mixed, frigid Typic Endoaquent (Dystric Gleysol) belonging to the St-Amable and Courval series. This sandy-loam soil contained an average of 815 g kg⁻¹ sand, 89 g kg⁻¹ silt, and 96 g kg⁻¹ clay in the top 20 cm, with 19.9 g organic C kg⁻¹ and pH 5.2–5.8 when the study was initiated. The long-term experimental plots were established in the spring of 1991, after plowing down an alfalfa (Medicago sativa L.) crop and incorporating about 7 Mg ha⁻¹ of agricultural lime. The experiment had a factorial design with three types of tillage (CT, RT and NT) and two types of residue management (low residue input and high residue input), for a total of 6 factorial treatments. The factorial plots were $18.5 \text{ m} \times 80 \text{ m}$, arranged in a randomized complete block design with three blocks, giving 18 experimental plots.

After initial site preparation, no additional tillage operations were undertaken in the NT plots. The CT plots were cultivated with a moldboard plow (about 20 cm depth) each fall after harvest and with a tandem disk harrow (10 cm depth) each spring before seeding. The RT plots were tilled to about 10 cm with an offset disk harrow in the fall and a tandem disk harrow (10 cm depth) in the spring before planting. All plots were seeded with the same corn (Zea mays L.) hybrid each year using John Deere 7100 Max Emerge seeder. Corn nutrient requirements were met by banding inorganic fertilizers (starter and sidedress applications). Further information about the site, including planting dates, hybrids used from 1991 to 2002, fertilizers and weed control were reported by Burgess et al. (1996) and Dam et al. (2005). Corn hybrids were Mycogen 2610 in 2003 and Mycogen 2K350 from 2004 to 2006, and there was no change in site management. Each year, silage corn was harvested from the low residue treatment using a silage harvester, leaving only 0.15 m of intact stalk stubble and roots as crop residue. In the high residue treatment, the grain was removed with a combine harvester each year, leaving above-ground residues (cobs, leaves and stems) plus roots in the plots. Above-ground residues remained on the surface of NT plots, were partially incorporated in RT plots and completely mixed in the cultivated layer of CT plots.

The second site was located at the Agriculture and Agri-Food Canada Experimental Farm at La Pocatière, QC, Canada (47°21'N, 70°2′W). Average temperatures range from -11.7 °C in January to 18.9 °C in July, with mean annual precipitation of 962 mm (Environment Canada, 2009). The soil was a Kamouraska clay classified as a mixed, frigid Typic Humaquet (Orthic Humic Gleysol), containing about 100 g kg^{-1} sand, 300 g kg^{-1} silt, and 600 g kg⁻¹ clay in the top 20 cm, with 31 g organic C kg⁻¹ and pH 5.6-6.1 when the study was initiated. The long-term experimental plots were established in fall 1987 after plowing down a rye (Secale cereale L.) green manure crop. The experimental design was a splitplot with three crop rotations as main-plot treatments and three tillage practices (CT, RT and NT) as subplot treatments. For this study, a subset of these experimental treatments was selected. The main plot treatments were a barley (Hordeum vulgare L.) monoculture and a crop rotation consisting of barley underseeded with red clover (Trifolium pratense L.) (1988-1998), followed by a four-year barley-canola (Brassica napus)-wheat (Triticum aestivum L).-soybean (Glycine max (L.) Merr) rotation (1999-2005). Details about site management, fertilization and weed control have been reported by Angers et al. (1993) and Légère and Samson (2004). The main plots were split into three tillage subplots (5 m \times 30 m), which were randomly assigned and replicated in four blocks, for a total of 24 experimental plots.

The CT treatment consisted of moldboard plowing (15-18 cm depth) each fall after harvest and with a rigid-tooth finishing harrow (7 cm depth) once or twice each spring before seeding. Plots with RT were tilled with a chisel plow (12-15 cm) in the fall after harvest and with a rigid-tooth finishing harrow (7 cm depth) in the spring before planting, while NT plots were not disturbed by tillage operations. Although this experiment was not designed specifically to investigate crop residue inputs, we assumed that residues would be more slowly decomposed in plots with a higher C:N ratio than a low C:N ratio. Thus, the barley monoculture constituted a high residue treatment because barley residues have a C:N ratio of about 75 (Mueller et al., 1998). Legumes in the barley-red clover and barley-canola-wheat-soybean rotations produce residues with C:N ratios between 12 and 30 (Havlin et al., 2005; Naramabuye and Haynes, 2006), so the plots with crop rotation represent a low residue treatment.

In 2006, a corn test crop was seeded across all plots to measure residual treatment effects. Glyphosate resistant 'Baxxos' corn was seeded at 74,000 plants ha⁻¹ on 1 June, 2006. Fertilization was minimal in order to allow the expression of residual treatment effects in the corn test crop. A broadcast fertilizer application was made just prior to seeding (130 kg ha⁻¹ of 14–10–10), followed by a postseeding broadcast application 10 d later (165 kg ha⁻¹ of 27–0–0+25 kg ha⁻¹ of 0–20–20). Glyphosate was applied at 900 g a.e. ha⁻¹ on 21 June, 2006 in NT plots and on 5 July, 2006 in CT and RT plots.

2.2. Earthworm populations

Prior to this study, the sandy-loam site had a 15-year history, whereas the clay site had an 18-year history of tillage and crop rotation treatments. These sites were well suited to evaluate the long-term effects of crop residue and tillage management on earthworm populations. In the cool humid ecozone, soil texture has an important influence on the timing of tillage and other agricultural operations. Sandy-loam soils tend to warm up and dry out several weeks before clay soils. A well-drained sandy-loam soil could be cultivated and seeded by early to mid-May, but a poorly drained clay soil like the one in this study could remain saturated until early June. Therefore, spring sampling of sites with

contrasting soil texture could lead to biased estimates of earthworm population. A temporary reduction in earthworm populations is expected from July to early September, based on climatic norms for this ecozone and the sensitivity of earthworms to heat and drier soil conditions. Generally, the autumn presents cool, moist soil conditions that should be favorable to earthworm populations at both sites, which is why we chose to collect earthworms and soils after harvest, but before tillage operations in October.

Earthworm populations were evaluated in October 2006 by excavating one soil pit $(0.3 \text{ m} \times 0.3 \text{ m} \times 0.2 \text{ m})$ per plot and handsorting to collect specimens. Dilute formalin solution (0.5%) formaldehyde) was poured into the bottom of the pit until saturated and deeper-dwelling earthworms were collected shortly after the solution had drained through macropores. Earthworms were preserved in 5% formalin solution until the number and biomass of intact individuals and fragments could be assessed in the laboratory. Earthworms with a fully developed clitellum were identified to the species level using the key provided by Reynolds (1977). Earthworm biomass was expressed on an ash-free dry weight (AFDW) basis, which is the earthworm dry mass (105 °C for 24 h) minus the soil mass remaining when earthworms were ashed in a muffle furnace (360 °C for 4 h).

2.3. Earthworm growth in intact soil cores

In October 2006, we collected one intact soil core from the middle of each experimental plot (n = 18 for the sandy-loam soil, n = 24 for the clay soil plus three extra cores for each site) by hammering a PVC tube (45 cm long \times 10 cm I.D.) to a depth of 30 cm and digging out the tube. Fine plastic mesh (<1.5 mm) was secured with elastic bands on both ends of the core to prevent the loss of soil and surface residues (fragments <5 cm long were retained and collected with the core). Cores were stored in a cold room at -4 °C for at least four weeks to kill any earthworms that may have been present. We also collected samples near the intact soil core to characterize soil conditions. Soil bulk density was assessed by inserting a metal tube 7.7 cm long \times 8.5 cm I.D. about 2 cm below the soil surface and determining the mass after drying (105 °C for 24 h). A composite of six samples taken with a hand auger (15 cm long, 3 cm I.D.) within 1 m of the intact soil core was used for soil chemical analysis. After drying (60 °C for 48 h) and sieving through 2 mm mesh, the soil pH was analyzed (1:2 soil:water). A subsample was finely ground to pass a 250 µm mesh and the soil organic C content was determined with a Carlo Erba NC Soils Analyzer (Milan, Italy).

Evaporative water loss from cores during storage was determined by destructively sampling the extra cores collected from each site. The soil was moistened to about 40% water-filled pore space, based on the bulk density of each treatment and the soil moisture conditions known to be favorable for earthworm growth (Eriksen-Hamel and Whalen, 2006). The earthworm used in this study was A. turgida, collected from arable fields at the Macdonald Research Farm of McGill University and reared for about four weeks at 20 °C in a sandy-loam soil in the laboratory. Juvenile A. turgida were rinsed with distilled water, placed on moistened tissue paper to void their guts for 24 h, then rinsed again, gently blotted dry and weighed (gut-free fresh weight). Three juvenile earthworms with a combined initial mass of 0.81 ± 0.01 g (standard error, n = 42) were added to the top of each core, misted with 2-3 mL of distilled water, and the fine plastic mesh was replaced to prevent earthworm escape. Cores were placed in a controlled climate incubator (20 °C) in the dark. Humidity was checked by weighing every 3-5 d and adding water when necessary. The mean water-filled pore space was $42 \pm 3\%$ in the sandy-loam soil and $44 \pm 2\%$ in the clay soil at the end of the experiment. After 28 d, the cores were destructively sampled to remove earthworms, which were placed on a moistened tissue paper to void their guts for 24 h before determining the fresh weight.

Earthworm growth during the 28-d period was determined as the instantaneous growth rate (IGR, d⁻¹), calculated as: IGR = $\ln(W_f/W_i)/\Delta t$; where W_i and W_f are initial and final earthworm mass (g), respectively, and Δt is the growth interval measured in days (Brafield and Llewellyn, 1982). We recovered 97% of the earthworms added to the cores. Two cores from each site were designated as missing values in the analysis of variance (n = 16 for the sandy-loam soil and n = 22 for the clay soil) because one earthworm was missing from each core after 28 d.

2.4. Statistical analysis

Earthworm populations and biomass were transformed with a square root function to achieve a normal distribution prior to analysis of variance. Homogeneity of variance of the transformed data was confirmed with a Shapiro-Wilk test using the PROC UNIVARIATE function of SAS statistical software (version 9.1, SAS Institute Inc., Cary, NC). Data from both field sites were analyzed as a randomized complete block, and the error associated with experimental blocks was included in the statistical model. The effects of soil texture, tillage and residue treatments on earthworm populations, biomass, growth rates and soil characteristics were evaluated by analysis of variance using the PROC GLM function of SAS software. When treatment effects were significant, mean values were compared with a post hoc Tukey–Kramer test (P < 0.05).

The Pearson correlation coefficient (r) describing the relationship between earthworm growth rates and the soil organic C pool was calculated using the PROC CORR function of SAS. To achieve homogenous variance in the pooled dataset (e.g., earthworm growth and soil organic C from two field sites, n = 42), we excluded seven cores from the RT plus high residue input treatment because of significantly greater growth rates (Table 1) and seven cores due to missing earthworms, negative growth rates and an outlier (soil organic C value). The soil organic C pool (Mg C ha⁻¹) was calculated by multiplying the soil organic C content (g kg⁻¹, to 15 cm depth) by the soil bulk density (Mg m⁻³) and expressed on a per hectare basis following Ellert and Bettany (1995). There was no difference (P > 0.05) in the bulk density due to tillage or residue treatments, thus we did not calculate the soil organic C pool for an equivalent mass of soil as suggested by Ellert and Bettany (1995). Data presented in the tables and figures were back-transformed means and standard errors.

3. Results and discussion

3.1. Earthworm populations

Most of the earthworms collected were juveniles, probably of *A. turgida* and *L. terrestris*, the dominant species at these experimental sites. We also found *A. tuberculata* (Eisen) in the sandy-loam soil, and there were a few (less than 3% of the earthworm population) *A. rosea* (Savigny), *A. longa* (Ude) and *Octolasion tyrtaeum* (Savigny) in the clay soil. At these long-term sites, earthworm populations and biomass were affected by tillage (P < 0.05), but not by residue treatments. The NT plots supported the largest earthworm populations, with up to 422 individuals m⁻² in the sandy-loam soil (Fig. 1A). This is within the range of 137–913 individuals m⁻² in NT systems reported by Chan (2001). At each site, there was more biomass in NT plots (10.2 g AFDW m⁻² in the sandy-loam soil; 24.7 g AFDW m⁻² in the clay soil) than in the other tillage treatments (Fig. 1B). Earthworm populations in the sandy-loam soil were predominantly *A. turgida* and their offspring, which does not represent much biomass (the weight of a formalin-preserved)

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Table 1

Soil characteristics from two long-term tillage experiments with high and low crop residue inputs, and instantaneous growth rates (IGRs) of three juveniles of *A. turgida* in intact cores from each treatment. Values are means ± standard errors (*n* = 3 for sandy-loam soil, *n* = 4 for clay soil).

Soil texture	Tillage system	Residue input	pH	Soil organic C $(g kg^{-1})$	IGR (×10 ⁻³ d ⁻¹)
Sandy-loam	СТ	Low	$\textbf{6.1} \pm \textbf{0.1}$	22.7 ± 4.8	6.15 ± 5.0
		High	5.7 ± 0.1	24.8 ± 2.5	10.3 ± 3.3
	RT	Low	5.7 ± 0.1	23.8 ± 4.3	8.6 ± 3.7
		High	$\textbf{6.2}\pm\textbf{0.3}$	25.3 ± 2.8	18.7 ± 0.2
	NT	Low	$\textbf{6.3} \pm \textbf{0.3}$	24.5 ± 0.9	10.7 ± 1.7
		High	5.6 ± 0.4	$\textbf{26.5} \pm \textbf{2.1}$	9.2 ± 3.3
Clay	СТ	Low	6.1 ± 0.3	$\textbf{26.3} \pm \textbf{1.5}$	5.4 ± 3.6
		High	6.1 ± 0.2	$\textbf{27.6} \pm \textbf{2.3}$	10.7 ± 2.4
	RT	Low	$\textbf{6.3} \pm \textbf{0.3}$	$\textbf{33.8} \pm \textbf{1.7}$	9.7 ± 2.3
		High	$\textbf{6.3} \pm \textbf{0.1}$	35.5 ± 2.7	18.0 ± 2.6
	NT	Low	$\textbf{6.4} \pm \textbf{0.2}$	37.4 ± 1.7	11.6 ± 1.7
		High	$\textbf{6.2}\pm\textbf{0.4}$	38.4 ± 2.9	11.3 ± 1.1
Effect		Analysis of variance			
		df	P > F	P > F	P > F
Soil		1	0.0018	<0.0001	NS
Tillage		2	NS	0.0037	0.0090
Residue input		1	NS	NS	0.0048
Tillage × residue		5	0.0164	NS	0.0444

adult does not exceed 0.5 g). In contrast, *L. terrestris* were relatively more abundant in the NT and RT plots of the clay soil, and earthworm biomass in these plots (Fig. 1B) reflects the fact that a formalin-preserved adult *L. terrestris* can weigh more than 4 g.

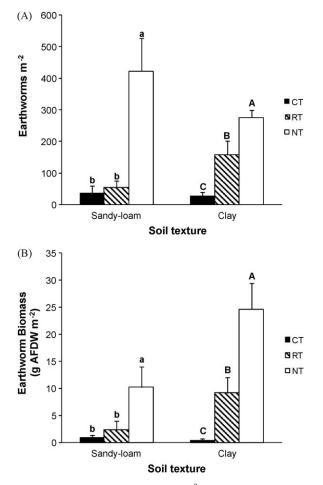


Fig. 1. (A) Earthworm population (individuals m^{-2}) and (B) earthworm biomass in g ash-free dry weight (AFDW) m^{-2} from long-term experiments on sandy-loam and clay soils with conventional (CT), reduced (RT) and no-tillage (NT) treatments. Within a soil, treatments with the same letter are not significantly different (P < 0.05, Tukey–Kramer test). Columns are the mean values with standard error bars.

Earthworm populations and biomass were greatest in the NT plots and similar in the RT and CT plots of the sandy-loam soil (Fig. 1A and B). We did not find earthworms in any of the RT-low residue plots (all three replicates), which were also observed in an earlier earthworm survey at the field site (Burgess, personal communication). This observation appears related to site-specific variables, as earthworms were absent from six plots (two per block) in a clearly defined section of the field site, and it is by coincidence that all RT-low residue treatments were randomly assigned to this section when the experiment was established. Further work is needed to determine why earthworms from adjacent plots have not migrated and established populations in this area. In the clay soil, earthworm populations and biomass were more homogenously distributed and exhibited the following pattern: NT > RT > CT (Fig. 1A and B). This is consistent with many studies that have reported larger earthworm populations and greater earthworm biomass in NT than other tillage systems (Edwards and Lofty, 1982; House and Parmelee, 1985; Wardle, 1995; Clapperton et al., 1997; Kladivko et al., 1997). In general, CT systems have 2-9 times fewer earthworms than in NT systems (Chan. 2001).

The retention of crop residues in agroecosystems, especially those with conservation tillage, is expected to increase earthworm numbers and biomass (House and Parmelee, 1985; Chan, 2001; Chan and Heenan, 2006). However, we did not observe an effect of residue input on earthworm populations and biomass. In the clay soil, it could be because the corn crop grown in 2006 obscured preexisting differences in residue inputs from barley monoculture and barley–legume rotations. It was surprising that there was no difference in earthworm populations and biomass in the sandy-loam soil because the high residue treatment received an additional 7–9 Mg dry matter ha⁻¹ year⁻¹ of corn residues than the low residue treatment (Dam et al., 2005).

Corn residues can protect against soil erosion and conserve moisture, especially in conservation tillage systems (Hubbard et al., 1999). In Wisconsin, Karlen et al. (1994) reported a significant reduction in earthworms, from 78 individuals m^{-2} to 53 individuals m^{-2} , in NT plots when corn stover was removed. When soil moisture is not limiting, as in the cold humid climate where our long-term experimental sites are located, crop residue quality is perhaps more important. Corn residues have a high C:N ratio – corn stover has a C:N ratio of 60 (Havlin et al., 2005) – and are not particularly palatable to earthworms. In laboratory studies,

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earthworms gain more weight when provided with alfalfa, red clover or soybean residues than corn residues (Mackay and Kladivko, 1985; Shipitalo et al., 1988). Earthworm populations are generally lower in corn monoculture systems than arable cropping systems that include legumes or perennial cropping systems such as hayfields and pastures (De St. Remy and Daynard, 1982; Mackay and Kladivko, 1985; Hubbard et al., 1999). While our results suggest that high corn residue inputs provided no direct benefit as a food resource for earthworms, other factors such as site-specific variability in soil texture and hydrology, agrochemicals, predation, climate and weather have also been proposed to explain why earthworm populations are sometimes unresponsive to crop residue inputs (Haukka, 1988; Nuutinen, 1992; Kladivko et al., 1997; Virto et al., 2007).

3.2. Earthworm growth in intact soil cores

Earthworms gained weight in all but two cores during the study, indicating favorable soil conditions and sufficient organic substrates for growth. There was no difference in earthworm growth due to soil texture, but tillage, residue input and the tillage \times residue interaction were significant (Table 1). The effect of tillage on earthworm growth varied according to residue management level (*P* = 0.044). Earthworm growth rates were nearly twice as great in the high residue than low residue treatment in CT and RT but were similar across residue treatments in NT plots (Table 1). Earthworm growth rates were highest in cores from the RT plus high residue plots, and lowest in cores from the CT plus low residue plots (Table 1).

At the outset, we predicted that differences in soil physical properties and food resources resulting from long-term tillage and residue management would affect earthworm growth. The soil moisture content was controlled by periodically adding water to replace evaporative loss. Soil bulk density was similar at the experimental sites (1.18 ± 0.02 g cm⁻³ in the sandy-loam soil and 1.17 ± 0.02 g cm⁻³ in the clay soil) and not affected by tillage or residue treatments. This indicates little difference in soil bulk density and porosity in treatments when the cores were collected. The soil pH was slightly acidic at both sites and exhibited some variability in the sandy-loam soil due to site heterogeneity (Table 1), but pH values should not have constrained earthworm growth. Since these soil physical and chemical properties were quite similar, we assumed that earthworm growth in soil cores was controlled primarily by food availability.

Soil organic C could be considered a general indicator of the availability of organic substrates for earthworm consumption. The soil organic C content was affected by tillage as follows: NT > RT > CT (Table 1), which is consistent with the findings from other long-term tillage experiments (Karlen et al., 1994; Wardle, 1995; Kladivko et al., 1997). There was a positive correlation between earthworm growth rates and the soil organic C pool (Fig. 2), suggesting that tillage and residue management practices that increase the soil organic C pool provide more organic substrates for earthworm growth. The correlation was mainly driven by the soil organic C content in the clay soil, since there was little change in the soil organic C in the sandy-loam soil due to long-term tillage and residue management practices. However, we cannot explain why the RT plus high residue treatment in both sandy-loam and clay soils was so favorable for earthworm growth. Harrowing and chisel plowing operations in RT systems fragment and incorporate crop residues in the soil profile, which may speed residue decomposition. Earthworms grow more rapidly when they are provided with shredded, ground or partially decomposed organic residues (Boström and Lofs-Holmin, 1986; Whalen and Parmelee, 1999; Lowe and Butt, 2003). At the field scale,

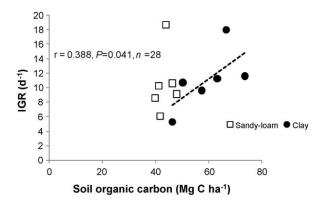


Fig. 2. Relationship between the instantaneous growth rates (IGRs, d^{-1}) of three juvenile *A. turgida* in intact soil cores and the soil organic C pool (Mg ha⁻¹, to a depth of 15 cm) in field sites with crop residue and tillage treatments. Symbols represent the mean IGR and soil organic C values from each treatment, with a trendline to illustrate the correlation. The Pearson correlation coefficient (*r*) was significant at the 95% probability level (*P*) for data pooled among sandy-loam and clay soils (*n* = 28).

tillage practices that mix crop residues into the soil profile are beneficial for endogeic earthworms like *A. turgida* (Boström, 1995; Kladivko, 2001; Wuest et al., 2005).

Under controlled environmental conditions, soils from RT systems with a history of high crop residue inputs were most effective at promoting *A. turgida* growth, but this did not correspond to the size and biomass of earthworm populations at the field sites. If food availability limits earthworm growth under field conditions, then crop residue management should have a significant effect on earthworm populations, which was not the case at either field site. In this study and many others, earthworm populations and biomass are consistently greater with NT than in tilled soils (Wardle, 1995; Kladivko et al., 1997; Chan, 2001). We conclude that NT supports the largest earthworm populations in cool, humid agroecosystems because it does not disturb the earthworm habitat or cause physical injury to these soft-bodied invertebrates.

4. Conclusions

As expected, earthworm populations were larger in long-term (15+ years) experimental sites with NT than CT practices, but crop residue management practices had no effect on earthworm populations. The annual input of 7–9 Mg ha⁻¹ of corn residues for 15 years did not change population levels, perhaps because the high C:N ratio of this residue (C:N > 60) limits its consumption by earthworms. Increasing the size of the earthworm population would require a balance between the amount of residue returned to soil and crop residue quality (low C:N ratio). The growth of *A. turgida* in intact soil cores was positively correlated with the size of the soil organic C pool, although RT plots with high residue inputs provided more organic substrates for *A. turgida* growth than other treatments. Our work suggests that physical disturbance, rather than food availability, may control the earthworm populations in cool, humid agroecosystems.

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