Pedobiologia 43, 1–10 (1999)
Urban & Fischer Verlag

Pedo biologia

Growth of *Aporrectodea tuberculata* (Eisen) and *Lumbricus terrestris* L. under laboratory and field conditions

Joann K. Whalen and Robert W. Parmelee

Soil Ecology Laboratory, Ohio State University, Columbus OH 43210 USA

Accepted: 21. August 1998

Summary. The growth of juvenile *A. tuberculata* and *L. terrestris* under different conditions of soil temperature (10 °C and 18 °C) and moisture (20 %, 25 % and 30 % (w/w) soil moisture content) was determined in a laboratory experiment. The instantaneous growth rates (IGR) of *A. tuberculata* were between 10.8×10^{-3} d^{-1} and 18.7×10^{-3} d^{-1} and the IGR was lowest when *A. tuberculata* was placed in soil at 10 °C and 30 % (w/w) soil moisture content. The growth of *L. terrestris* tended to be lower than that of *A. tuberculata*, and the IGR of *L. terrestris* ranged from 7.1×10^{-3} d^{-1} to 13.9×10^{-3} d^{-1} under laboratory conditions. *L. terrestris* growth was greatest in soil maintained at 10 °C and 20 % (w/w) soil moisture content. The growth of juveniles of *A. tuberculata* and *L. terrestris* was also examined in the field in large cores containing soil from long-term manure-amended and inorganic fertilizer-treated plots during the spring and autumn of 1995 and 1996. The IGR of *A. tuberculata* in the field ranged from 7.5×10^{-3} d^{-1} to 14.6×10^{-3} d^{-1} when soil temperatures were between 10 °C and 18 °C, and was comparable to the IGR of *A. tuberculata* under similar environmental conditions in the laboratory. The growth of *L. terrestris* in the field was much lower than *L. terrestris* growth in the laboratory under similar environmental conditions, and the IGR of *L. terrestris* in the field ranged from -1.0×10^{-3} d^{-1} to 5.3×10^{-3} d^{-1} when soil temperatures were between 10 °C and 18 °C. The growth of *A. tuberculata* and *L. terrestris* was not significantly different for individuals placed in cores containing soil from either manure-amended or inorganic fertilizer-treated plots. While there appeared to be adequate soil organic substrates for *A. tuberculata* growth in the field, *L. terrestris* growth was probably limited by the absence of sufficient surface organic residues. The IGR equation can be used to predict the nonlinear growth of earthworms under laboratory and field conditions.

Key words: Earthworms, growth, instantaneous growth rate, manure, inorganic fertilizer, agroecosystem

Correspondence to: Joann Whalen, Agriculture and Agri-Food Canada, Research Centre, PO Box 3000, Lethbridge, AB, T1J 4B1, Canada. Phone 403-317-2280. Fax 403-382-3156. EMail whalenj@em.agr.ca

0031-4056/99/43/01/1/$ 12.00/0

Introduction

It is well known that earthworms are important soil-dwelling invertebrates whose activity can significantly influence soil physical, chemical and biological processes (Blair et al. 1995; Edwards & Bohlen 1996; Lee 1985). The dynamics of earthworm populations in terrestrial ecosystems are a function of the growth, survivorship and fecundity of individuals. By measuring the rate of production of new tissues through growth and reproduction (secondary production) in earthworm populations, it is possible to quantify the role of earthworms in ecosystem-level processes.

Earthworm growth is influenced by the age and stage of development of individuals because, as earthworms reach maturity, a greater proportion of the energy from food resources is probably used in the formation of sexual organs and reproduction rather than the formation of new tissues (Daniel et al. 1996). It has been well established that earthworm growth through time proceeds logistically (Daniel et al. 1996; Andersen 1987; Lakhani & Satchell 1970), and there are several ways to measure earthworm growth rates. Instantaneous growth rates have been used to estimate earthworm secondary production, which is the accumulation of biomass through growth and reproduction of a population through time, and the flux of nitrogen through earthworm populations in agroecosystems (Parmelee & Crossley 1988; J. K. Whalen unpublished Ph.D thesis).

Much of our present knowledge on how earthworm growth is affected by environmental factors comes from laboratory studies. Soil temperature and water potential strongly influence the growth of earthworm species, and optimal conditions for *Lumbricus terrestris* L. range from 10 °C to 15 °C and 20 % to 25 % (w/w) soil water content, depending on the soil type (Daniel 1991; Daugbjerg 1988). The availability and quality of food resources also influence earthworm growth (Böström & Lofs-Holmin 1986; Curry & Bolger 1984; Moody et al. 1995; Shipitalo et al. 1988). Böström (1987) found that organic substrates with higher N content and smaller particle size promoted greater weight gain in *Aporrectodea caliginosa* (Savigny). High earthworm abundance in cultures has a negative influence on earthworm growth and reproduction (Butt et al. 1994).

The use of laboratory growth rates to estimate earthworm secondary production in the field is questionable; however, there have been relatively few attempts to determine earthworm growth in the field. Hughes et al. (1994) found that earthworm growth and survival were greater in the laboratory than in the field for *Microscolex dubius* (Fletcher) grown in pots with varying proportions of soil and manure. Seasonal variation influenced the growth of *L. terrestris* in litter bags in a deciduous woodland, and earthworm growth was greater in laboratory cultures than under field conditions (Lakhani & Satchell 1970).

Spatial and temporal variation in the field, which include soil physicochemical properties (soil texture and organic matter content), availability and quality of food resources, and seasonal fluctuations in soil temperature and moisture content, probably have tremendous effects on earthworm growth in the field (Hendrix et al. 1992). Agricultural practices that alter the availability and quality of food resources for earthworms may influence their growth under field conditions. Earthworm populations are often higher in agroecosystems in which organic materials are retained in residues or added in organic fertilizers compared to agroecosystems in which organic matter retention or addition is low (Berry & Karlen 1993; Edwards & Lofty 1982; Edwards et al. 1995; Francis & Knight 1993; Tiwari 1993; Werner & Dindal 1989; Whalen et al. 1998). However, there have been no studies that have examined the effects of long-term additions of organic or inorganic fertilizers on earthworm growth under field conditions.

The objectives of this study were 1) to examine the growth of *Lumbricus terrestris* L. and *Aporrectodea tuberculata* (Eisen), the dominant species in corn agroecosystems, under controlled conditions of temperature and moisture in the laboratory; 2) to determine whether the growth of *L. terrestris* and *A. tuberculata* under field conditions in corn agroecosystems is comparable to their growth in the laboratory; and 3) to determine whether long-term amendments of manure and inorganic fertilizers to corn agroecosystems can significantly affect earthworm growth in the field.

Materials and Methods

Measurement of earthworm growth in the laboratory

The growth of *Aporrectodea tuberculata* (Eisen) and *Lumbricus terrestris* L. was determined using juvenile earthworms, ranging in age from newly hatched to pre-clitellate. Growth was measured using juveniles because they are actively growing and represent the greatest proportion of the earthworm population in corn agroecosystems (Whalen et al. 1998). Earthworms were collected from an area adjacent to the field sites (described below) by hand-sorting and extraction with a dilute (5 %) formaldehyde solution. The mass of juvenile *A. tuberculata* ranged from 0.02 g to 0.8 g fresh weight per individual, while juvenile *L. terrestris* were 0.5 g to 4 g fresh weight per individual. *Lumbricus rubellus* (Hoffmeister), another *Lumbricus species*, is present at the field site. Since it was not possible to distinguish individuals of *L. rubellus* and *L. terrestris* until the earthworms had reached approximately 0.5 g (fresh weight), it was not possible to include newly hatched *L. terrestris* in the laboratory and field studies. Individual earthworms were placed on wet filter paper for 24 h to void their guts and weighed (wet weight) before being placed in separate containers to follow the growth of individuals through time.

A. tuberculata growth was determined in 120 cm^3 plastic containers with 40 g (dry weight (dw)) of soil and 0.5 g (dw) of soybean leaves, while *L. terrestris* growth was determined in 300 cm^3 containers with 80 g (dw) of soil and 1 g (dw) of soybean leaves. Soybean leaves were either finely ground to pass through a 1 mm mesh and mixed with soil for *A. tuberculata* or crushed into 2 cm fragments and placed on the soil surface for *L. terrestris*. The containers were covered with perforated lids to prevent earthworm escape. The soil and soybean leaf mixtures were moistened to 20 %, 25 % or 30 % (w/w) water content prior to the addition of earthworms. Soil moisture of 20 %, 25 % and 30 % (w/w) water content corresponded to 62, 69, and 76 % of field capacity for this soil, respectively. Soil moisture contents at the field site generally range from 20 % to 30 % during the spring (April to June) and autumn (September to November) months. The containers were placed in controlled environmental chambers at 8 °C to 12° C (average daily temperature = 10 °C) and 16 °C to 20 °C (average daily temperature = 18 °C) to simulate daily diurnal flux. These temperatures were chosen to simulate mean seasonal temperature flux in soil during the spring and autumn under field conditions. The growth of juveniles of each species was examined with 8 replicate containers at each combination of temperature and moisture from January to November, 1995.

Earthworms were removed from the containers at approximately two week intervals, and after 24 h gut clearance, their mass (wet weight) was recorded. Individual earthworms were then returned to their container or replaced with a new individual, depending on earthworm health and stage of development. Earthworms were replaced once they had reached the pre-clitellate stage of development when tubercula pubertatis were present. Aestivating *A. tuberculata* and earthworms that were injured were also replaced. Worm-worked soil was removed, and fresh soil and soybean leaf mixtures were placed in each container at each sampling interval.

Measurement of earthworm growth in the field

The field study was conducted at the Ohio Agricultural Research and Development Center in Wooster, Ohio, USA. Mean monthly temperatures range from –4.8 °C in January to 21.2 °C in July and the mean annual precipitation is 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. Since 1992, the site has been used for continuous corn (*Zea mays*) production under a conventional disk tillage system. Twelve field plots (20 × 30 m) have been established in a randomized complete block design with four replicates of each receiving one of three agroecosystem nutrient treatments. The three nutrient treatments, NH_4NO_3 fertilizer (inorganic), straw-pack cow manure (manure), and legume/rye (Vicia villosa/Secale cereale) cover crop (legume) were applied at a rate of approximately 150 kg N ha^{-1} y^{-1} and disk incorporated in late spring. After harvest, corn residues were left on the plots and disk incorporated the following spring. Detailed information regarding the field site and agroecosystem treatments have been given by Bohlen et al. (1997).

The growth of the dominant earthworm species in these agroecosystems, *L. terrestris* and *A. tuberculata*, was determined during the spring and autumn of 1995 and 1996 when temperature and moisture conditions were suitable for earthworm growth. Earthworms were placed in 15 cm (diameter) × 45 cm (height) PVC cores that were sealed on both ends with fiberglass mesh (0.1 cm mesh) to prevent earthworm escape. Soil was collected by excavating a trench in two plots that had received long-term amendments of either inorganic fertilizer or manure, separated into A and B horizons, and sieved through a 25 mm mesh screen to remove any existing earthworms yet retain below ground organic materials that may have served as a food source for the earthworms. Approximately 8 kg (on a dry weight basis) of field-moist B horizon soil and 4 kg (dry weight basis) of field-moist A horizon soil were packed in each core to field bulk density, and 12 g (dry weight basis) of corn stalks and leaves collected from the plots were placed on the soil surface of each core. Four to twelve replicate cores per treatment were used to determine growth rates for each earthworm species. The cores were placed in the excavated trench and extra soil was packed around each core.

Juveniles of *A. tuberculata* and *L. terrestris* were obtained from a site about one meter north of the plots and taken to the lab where they were placed on wet filter paper for 24 h to void their guts, weighed (wet weight) and returned to the field. The growth of individuals through time was followed by adding earthworms of distinct, identifiable sizes to each core at field densities. Each core received either three identifiable size classes of *L. terrestris* or five size classes of *A. tuberculata*. These numbers are equivalent to 168 earthworms m^{-2} for *L. terrestris* and 280 earthworms m^{-2} for *A. tuberculata*, which are realistic field populations in corn agroecosystems for these species (Whalen et al. 1998).

At three to four week intervals, the cores were removed from the trench and taken to the lab where the soil was removed and carefully handsorted to collect earthworms. The earthworms were placed on wet filter paper to void their guts for 24 h, weighed (wet weight) and returned to the field. Earthworms were replaced once they had reached the pre-clitellate stage of development when tubercula pubertatis were present. Aestivating *A. tuberculata*, injured, missing and dead earthworms were also replaced.

Calculation of earthworm growth rates

The instantaneous growth rate (d^{-1}) of earthworms was calculated using:

$$IGR = \ln [Y_T/y_t] / (T - t) \qquad (1)$$

where IGR is instantaneous growth rate, Y_T is final earthworm mass (g) at time T, y_t is initial earthworm mass (g) at time t and the growth interval T – t is measured in days (Brafield & Llewellyn, 1982).

Meterological data

Meterological data were obtained from the Ohio Agricultural Research and Development Center weather station which reports daily mean soil temperatures, precipitation, and evapotranspiration. Monthly precipitation and mean monthly soil temperatures measured at a 10 cm depth at the study site from 1995-1996 have been reported by Whalen et al. (1998).

Statistical analyses

Earthworm growth rates in the laboratory and in the field were evaluated statistically using ANOVA procedures in a general linear model (GLM) with SAS software (SAS Institute, 1990). For earthworms growing in the laboratory, the effects of soil temperature, soil moisture and the interaction between soil temperature and moisture on the growth rates of *A. tuberculata* and *L. terrestris* were determined using a two-factor ANOVA. Variables that significantly affected earthworm growth rates were adjusted for multiple comparisons and analyzed using a t-test (LSD) at the 95 % confidence level. For earthworms growing under field conditions, the effects of fertilizer treatment on the growth rates of *A. tuberculata* and *L. terrestris* were determined using a two-factor ANOVA. Variables that significantly affected earthworm growth rates were analyzed using a t-test (LSD) for means comparison at the 95 % confidence level.

Results

The growth interval (T – t) in the laboratory ranged from 12 to 30 d, although most measurements were made at approximately 2 week intervals. The growth interval affected the relationship between the growth ratio (Y_T/y_t) and the instantaneous growth rate (IGR) (Figure 1). This relationship was observed for both species over the range of soil temperature and moisture conditions examined in the laboratory (data not shown). Since IGR was not independent of the growth interval, laboratory data with growth intervals greater than 17 d were not included in the analysis.

Earthworm growth rates in the laboratory

The IGR of juvenile *A. tuberculata* tended to be higher than that of juvenile *L. terrestris* under laboratory conditions, and the IGR for *A. tuberculata* ranged from 10.8×10^{-3} d^{-1} to 18.7×10^{-3} d^{-1} (Table 1). The mean growth ratio was between 1.18 and 1.30 for *A. tuberculata* in the laboratory, and weight gain tended to be higher at 18 °C than 10 °C (Table 1). The interaction between soil temperature and moisture was examined to determine what conditions were most conducive to *A. tuberculata* growth. The IGR of *A. tuberculata* was lowest at 10 °C and 30 % (w/w) soil moisture, significantly lower than the IGR at 10 °C and 20 % (w/w) soil moisture and the IGR of all soil moisture conditions at 18 °C (Table 1).

The IGR for juvenile *L. terrestris* ranged from 7.1×10^{-3} d^{-1} to 13.9×10^{-3} d^{-1} across the range of temperature and moisture conditions examined (Table 2). The mean growth ratio was between 1.14 and 1.33, and was highest when the soil moisture was 20 % (w/w) at 10 °C and 18 °C (Table 2). When the soil temperature was 10 °C, the IGR was significantly greater at 20 % (w/w) soil moisture than at 25 % (w/w) or 30 % (w/w) soil moisture (Table 2). At 18 °C, the IGR was significantly greater at 20 % (w/w) soil moisture than at 30 % (w/w) soil moisture (Table 2).

Table 1. Effect of soil temperature and moisture on *A. tuberculata* growth under laboratory conditions

Soil temperature (°C)	Soil moisture (% w/w)	Mean initial earthworm mass (g)	Mean growth interval T – t (d)	Mean growth ratio Y_T/y_t	IGR ($\times 10^{-3}$ d^{-1})
10	20	0.27 ± 0.03	13	1.25	16.7 ± 1.9 A
10	25	0.26 ± 0.02	13.9	1.22	14.0 ± 1.2 AB
10	30	0.26 ± 0.02	14.1	1.18	10.8 ± 1.4 B
18	20	0.28 ± 0.03	13	1.30	18.7 ± 3.8 A
18	25	0.29 ± 0.02	13.9	1.28	16.8 ± 1.6 A
18	30	0.24 ± 0.02	14.1	1.30	17.0 ± 1.6 A

Mean values (± standard errors) followed by the same letter within a column are not statistically significantly different ($p < 0.05$, LSD)

Table 2. Effect of soil temperature and moisture on *L. terrestris* growth under laboratory conditions

Soil temperature (°C)	Soil moisture (% w/w)	Mean initial earthworm mass (g)	Mean growth interval T – t (d)	Mean growth ratio Y_T/y_t	IGR ($\times 10^{-3}$ d^{-1})
10	20	2.07 ± 0.12	13	1.33	13.9 ± 3.3 A
10	25	2.11 ± 0.10	14.6	1.15	8.3 ± 1.2 B
10	30	2.11 ± 0.11	15	1.15	7.1 ± 1.0 B
18	20	2.07 ± 0.14	13	1.24	11.9 ± 2.1 A
18	25	2.23 ± 0.11	14.6	1.17	9.1 ± 1.0 AB
18	30	2.18 ± 0.12	15	1.14	7.9 ± 1.1 B

Mean values (± standard errors) followed by the same letter within a column are not statistically significantly different ($p < 0.05$, LSD)

Earthworm growth rates in the field

Earthworm growth rates in the field were measured over a wide range of temperature and moisture conditions. Mean soil temperatures at a 10 cm depth ranged from 3.4 °C to 20.2 °C, and the mean monthly precipitation ranged from 46.2 to 397.0 mm (Whalen et al. 1998). The recovery of earthworms from the cores in the field was between 75–100 %, and only a few intrusive earthworms (mostly newly hatched earthworms from cocoons that were not removed during sieving) were found during the study. The growth intervals for *A. tuberculata* and *L. terrestris* in the field ranged from 20 to 42 d (Tables 3 and 4). Since the growth interval appears to affect IGR (Fig. 1), we were not able to determine whether the IGR was influenced by soil temperature because the effect may have been confounded by the variation in growth intervals. However, we were able to examine the effect of fertilizer treatments on the IGR of earthworms within each growth interval.

Table 3. Effect of manure and inorganic NH_4NO_3 fertilizer amendments on *A. tuberculata* growth under field conditions

Fertilizer treatment	Mean soil temperature (°C)	Mean initial earthworm mass (g)	Mean growth interval T – t (d)	Mean growth ratio Y_T/y_t	IGR ($\times 10^{-3}$ d^{-1})
Manure	3.4	0.44 ± 0.05	42	1.09	2.0 ± 0.5
NH_4NO_3	3.4	0.47 ± 0.04	42	1.13	1.7 ± 1.3
Manure	9.7	0.20 ± 0.04	37	1.78	14.6 ± 1.7
NH_4NO_3	9.7	0.18 ± 0.03	37	1.71	13.6 ± 1.6
Manure	13	0.22 ± 0.03	37	1.51	10.4 ± 1.3
NH_4NO_3	13	0.20 ± 0.04	37	1.57	10.9 ± 1.6
Manure	18.4	0.31 ± 0.03	24	1.39	12.7 ± 1.2
NH_4NO_3	18.4	0.28 ± 0.03	24	1.22	7.5 ± 0.8
Manure	20.2	0.34 ± 0.04	20	1.15	5.9 ± 1.8
NH_4NO_3	20.2	0.36 ± 0.03	20	1.08	3.7 ± 1.2

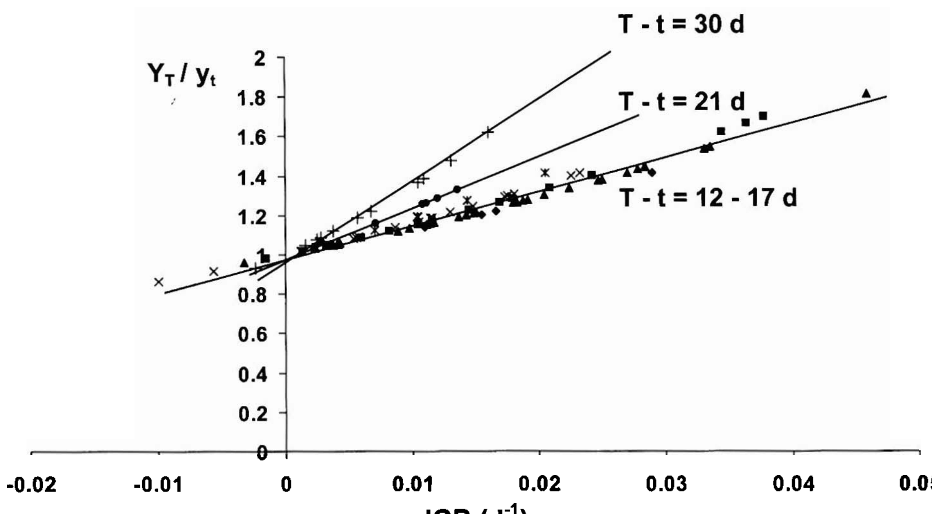

Fig. 1. Influence of the growth interval (T – t) on the relationship between the instantaneous growth rate (IGR) and growth ratio (Y_T/y_t). Growth data were from juvenile *A. tuberculata* in the laboratory at 10 °C and 25 % (w/w) soil moisture

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and 20.2 °C (Table 4).
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Table 4. Effect of manure
field conditions

Fertilizer treatment	Mean soi temperat (°C)
Manure	3.4
NH_4NO_3	3.4
Manure	9.7
NH_4NO_3	9.7
Manure	13
NH_4NO_3	13
Manure	18.4
NH_4NO_3	18.4
Manure	20.2
NH_4NO_3	20.2

Discussion

The instantaneous gr
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The growth of juvenile *A. tuberculata* in the field was comparable to *A. tuberculata* growth in the laboratory under similar conditions of soil temperature and moisture. The IGR of *A. tuberculata* in the field when soil temperatures were approximately 10 °C to 18 °C ranged from 10.4×10^{-3} d^{-1} to 14.6×10^{-3} d^{-1} in cores containing soil from manure-amended plots and 7.5×10^{-3} d^{-1} to 13.6×10^{-3} d^{-1} in cores containing soil from inorganic fertilizer-treated plots (Table 3). The mean growth ratio ranged from 1.08 to 1.78, and was lowest when the soil temperature was 3.4 °C and 20.2 °C (Table 3). There was no significant effect of fertilizer treatment on *A. tuberculata* growth at any temperature.

Juvenile *L. terrestris* growth in the field was much lower than *L. terrestris* growth in the laboratory under similar conditions of soil temperature and moisture. The IGR of *L. terrestris* in the field when soil temperatures were approximately 10 °C to 18 °C ranged from 0.9×10^{-3} d^{-1} to 2.9×10^{-3} d^{-1} in cores containing soil from manure-amended plots and -1.0×10^{-3} d^{-1} to 5.3×10^{-3} d^{-1} in cores containing soil from inorganic fertilizer-treated plots (Table 4). The mean growth ratio ranged from 0.98 to 1.15, and was highest when the soil temperature was 9.7 °C (Table 4). The IGR of *L. terrestris* was negative, indicating weight loss, in the cores containing soil from the inorganic fertilizer-treated plots at all temperatures except 9.7 °C, and in cores with soil from the manure-amended plots when soil temperatures were 3.4 °C and 20.2 °C (Table 4). There was no significant effect of fertilizer treatment on *L. terrestris* growth at any temperature.

Table 4. Effect of manure and inorganic NH_4NO_3 fertilizer amendments on *L. terrestris* growth under field conditions

Fertilizer treatment	Mean soil temperature (°C)	Mean initial earthworm mass (g)	Mean growth interval T – t (d)	Mean growth ratio Y_T/y_t	IGR ($\times 10^{-3}$ d^{-1})
Manure	3.4	2.70 ± 0.29	42	1.00	–0.1 ± 0.4
NH_4NO_3	3.4	2.83 ± 0.32	42	1.00	–0.2 ± 0.6
Manure	9.7	2.02 ± 0.19	25	1.07	2.9 ± 0.8
NH_4NO_3	9.7	1.96 ± 0.23	25	1.15	5.3 ± 0.9
Manure	13	2.18 ± 0.20	37	1.05	1.3 ± 0.5
NH_4NO_3	13	2.44 ± 0.15	37	0.98	–0.8 ± 0.8
Manure	18.4	2.44 ± 0.28	24	1.01	0.9 ± 0.9
NH_4NO_3	18.4	2.37 ± 0.24	24	0.98	–1.0 ± 0.7
Manure	20.2	2.03 ± 0.21	20	0.98	–1.3 ± 1.3
NH_4NO_3	20.2	1.93 ± 0.17	20	0.98	–1.3 ± 1.1

Discussion

The instantaneous growth rate equation we used to calculate earthworm growth provides information on the daily change in earthworm mass, and can be used to predict non-linear earthworm growth under laboratory and field conditions by transforming equation (1) to:

$$Y_T = y_t \cdot e^{(-IGR \cdot t)} \qquad (2)$$

We observed a negative relationship between the IGR and earthworm initial mass (data not shown) where the IGR tended to decline as the initial mass of earthworms increased. Similarly, Andersen (1987) reported an exponential decline with increasing body weight of the relative specific growth rates of *A. tuberculata, A. caliginosa, Aporrectodea longa* (Ude) and *Octolasion cyaneum* (Savigny). In the laboratory study, we assumed that the mean IGR values we reported were not confounded by differences in earthworm initial mass because the mean initial earthworm mass of *A. tuberculata* and *L. terrestris* were quite similar (Tables 1 and 2).

Under laboratory conditions, *A. tuberculata* growth tended to be higher at 18 °C, regardless of the soil moisture content, than at 10 °C. The IGR of *A. tuberculata* was lowest at 10 °C and 30 % (w/w), which was unexpected because we observed a greater tendency of *A. tuberculata* to aestivate when placed in containers with soil at 20 % moisture than when placed in soil moistened to 25 % or 30 % (w/w) soil water content. Using data from Andersen (1987), we calculated an IGR of 17.3×10^{-3} d^{-1} for an individual *A. tuberculata*, which was consistent with our results for *A. tuberculata* under laboratory conditions.

The growth of *A. tuberculata* in the laboratory and field was comparable under similar environmental conditions. In the field, *A. tuberculata* growth rates were greatest from about 10 °C to 18 °C, and declined when the soil temperature dropped below 10 °C or rose above 18 °C. In a laboratory study, Daugbjerg (1988) found that adults of related species, *A. caliginosa* and *A. longa*, had the greatest preference for soil temperatures between 10 °C and 15 °C and soil moisture content of 20 % to 25 %. However, even when the mean soil temperature was 3.4 °C or 20.2 °C, *A. tuberculata* exhibited positive growth rates, which indicates that this species can grow in the field even under seemingly quite unfavorable soil temperature conditions. *A. tuberculata* grew equally well in cores containing soil from either manure-amended or inorganic fertilizer-treated plots.

L. terrestris growth tended to be lower than *A. tuberculata* growth under both laboratory and field conditions. In the laboratory, the highest IGR for *L. terrestris* was at soil temperatures of 10 °C and 18 °C when the soil moisture was 20 % (w/w). Daugbjerg (1988) found that when earthworms were given a gradient of possible soil temperature and moisture conditions, the greatest proportion of *L. terrestris* adults migrated to soil at 10 °C with 20 % soil moisture content. The IGR of *L. terrestris* in the laboratory ranged from 7.1×10^{-3} d^{-1} to 14.5×10^{-3} d^{-1}, which were similar to the relative growth rates of 6 to 20×10^{-3} g weight gain g^{-1} initial earthworm mass d^{-1} that have been reported for this species (Butt et al. 1994; Curry & Bolger 1984; Hartenstein & Amico 1983). The growth of *L. terrestris* was much lower in the field than in the laboratory under similar environmental conditions. When the mean soil temperature in the field was 9.7 °C, the IGR of *L. terrestris* was as much as 80 % lower than the IGR of *L. terrestris* at 10 °C in the laboratory.

The number of individuals in a given area can influence earthworm growth due to competition for resources (Butt et al. 1994; Kaushal et al. 1995). In the field, the numbers of earthworms placed in each core were equivalent to 280 earthworms m^{-2} for *A. tuberculata* and 168 m^{-2} for *L. terrestris*. In the manure-amended plots, an average of 71 *A. tuberculata* m^{-2} were present from October 1994 to October 1996, while in the inorganic fertilizer-treated plots, the mean number of *A. tuberculata* was 42 m^{-2} during the same interval. The number of *L. terrestris* present during October 1994 to October 1996 was 68 m^{-2} and 43 m^{-2} in the manure-amended and inorganic fertilizer-treated plots, respectively (Whalen et al. 1998). However, the earthworm populations in these agroecosystems have declined by nearly 90 % since the fertilizer treatments were established in 1992 (Whalen et al. 1998), so we felt that the number of earthworms added to each core was a fairly good representation of earthworm numbers under natural conditions.

It was interesting that the growth rates of *A. tuberculata* and *L. terrestris* in cores with soil from either manure- or inorganic fertilizer-amended plots were not significantly different. There appeared to be adequate organic substrates to support the growth of *A. tuberculata*, which is thought to feed primarily on soil organic matter, in soil from both manure-amended and inorganic fertilizer-treated soils. *L. terrestris* growth under field conditions was probably limited by the availability of nutrient-rich organic substrates. In the laboratory, *L. terrestris* was provided with soybean leaves which had a C:N ratio of 12. However, in the field, the C:N ratio of the manure and corn residues in soil from the manure-amended plots was 30, while the C:N ratio of surface corn residues from the inorganic fertilizer-amended plots was 40 (Bohlen et al. 1997). Shipitalo et al. (1988) found that *L. terrestris* growth was much greater when individuals were provided with alfalfa and red clover leaves (C:N ratio = 14 and 12, repectively) than with corn leaves (C:N ratio = 21). Since *L. terrestris* feeds primarily on surface residues, it seems probable that the growth of this species was limited by the poorer quality resources in the field.

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Another difference between the laboratory and field study was the nature of the containers in which the earthworms were placed to grow. The small laboratory containers were suitable for *A. tuberculata*, which inhabits the top 10 cm of soil. However, the small laboratory containers did not provide *L. terrestris* with the opportunity to undertake its natural activities, such as the creation of permanent vertical burrows. During the field study, *L. terrestris* created deep vertical burrows in their cores and probably expended considerable energy building burrows rather than using energy for growth and tissue production.

While we are not aware of any studies that have examined the growth of *A. tuberculata* under field conditions, our results indicate that the growth of *A. tuberculata* was very similar under laboratory and field conditions. While it may be acceptable to extrapolate laboratory IGR for this species to *A. tuberculata* populations in the field, *L. terrestris* growth in the laboratory bore little resemblance to its growth in the field. It may be more appropriate to obtain large intact soil cores in the field for growth experiments to avoid negatively impacting *L. terrestris* growth. In addition, care must be taken in designing earthworm growth experiments to avoid confounding environmental effects (e.g. soil temperature) with other factors, such as the growth interval $(T - t)$ and the mean earthworm initial mass (y_t), that affect earthworm growth.

Acknowledgements

Thanks are extended to Jessie VanArsdale for help in collecting and weighing earthworms in the laboratory and field experiments, to Dave McCartney for assistance in designing the cores used in the field experiment, and to Cliff Pereira for advice on the statistical analysis. This work was supported by a grant from the US Department of Agriculture.

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