Soil Biology & Biochemistry 42 (2010) 40–47

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Field investigations of *Lumbricus terrestris* spatial distribution and dispersal through monitoring of manipulated, enclosed plots

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A R T I C L E I N F O

Article history:
Received 12 June 2009
Received in revised form
22 September 2009
Accepted 25 September 2009
Available online 12 October 2009

Keywords:
Dispersal
Earthworm
Lumbricus terrestris
Midden
Population density
Spatial distribution

A B S T R A C T

A field experiment in managed woodland was set up to examine the effects of manipulated population density and resource availability on spatial distribution and dispersal of the anecic earthworm *Lumbricus terrestris*. Experiments over 2 years, made use of 1 m^2 field enclosures with associated trapping units to assess emigration rates at control and enhanced *L. terrestris* densities and different levels of leaf litter availability. Densities were manipulated twice; at the outset and again after 1 year when visually tagged animals obtained from 2 origins were introduced. Population density had a significant effect on dispersal ($p < 0.01$, $p < 0.05$ in Year 1 and Year 2 respectively) with more captures (pro rata) at the higher density compared with controls over the experimental period. Food availability only had a significant effect during the initial week of the experiment. *L. terrestris* midden arrangement was found to be regular across 1 m^2 plots and regularity increased with an increase in midden number. Mean (±S.E.) midden number was 30.34 ± 0.77 m^{-2} and 28.06 ± 0.5 m^{-2}, during the first and second year of the experiment respectively and this was unaffected by additions. Inter-midden distance was recorded at 0.13 ± 0.0014 m. Results suggest that *L. terrestris* dispersal can be affected by population density and resource availability.

1. Introduction

Lumbricus terrestris L. (1758), a temperate deep burrowing earthworm, is considered to be an ecosystem engineer (Jones et al., 1994) able to affect the availability of resources to other organisms. Unlike most subterranean organisms, some of the behaviours of this species can be directly observed, due to its above ground food collection, mating and dispersal. *L. terrestris* constructs a burrow system with a low branching rate (Jégou et al., 2000), usually a single burrow, that can extend to a depth of 2.5 m (Edwards and Bohlen, 1996). The energy expenditure in creating and maintaining a burrow is high and field observations suggest that usually only one large individual occupies each burrow (e.g. Shipitalo nd Butt, 1999).

This species feeds on organic material at the soil surface by emerging from its burrow within the hours of darkness, with an activity peak 2–3 h into the night (Butt et al., 2003; Field and Michiels, 2006). At the soil surface, activities occur with the caudal segments remaining within the burrow but allowing exploration, foraging and mating within a circular area of 0.28–0.63 m^2 centred on its burrow (Nuutinen and Butt, 2005). Exceptionally, *L. terrestris* may detach from its burrow and travel short distances to feed and mate and then displays an ability to return to and re-enter the burrow (Nuutinen and Butt, 2005). The authors suggested that the evolution of a homing ability in *L. terrestris* is most likely related to the importance of the burrow and may provide individuals with an expanded area of influence and aid survival.

While feeding on the soil surface, *L. terrestris* accumulates leaves and other organic and inorganic materials into the entrance of its burrow forming a "midden" with associated faecal casts. The functions of this are uncertain, but it could protect from predators by partially concealing individuals feeding on the soil surface, protect the earthworm and cocoons from environmental fluctuations by moderating moisture and temperature levels in the burrow and could serve as a food store for adults and hatchlings (Butt and Nuutinen, 2005). Such possibilities suggest that *L. terrestris* individuals would not easily abandon their burrow–midden complex which is of great importance to their survival (Butt and Nuutinen, 2005; Valckx et al., 2008). Therefore low dispersal rates would be expected in adults, while juveniles may be more efficient in dispersing either by expanding the population size within an area, or colonising adjacent areas. Biotic factors such as population

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0038-0717/$ – see front matter
doi:10.1016/j.soilbio.2009.09.021

density and inter-/intra-specific interactions, and abiotic factors such as habitat quality and seasonal changes and their combined effects, may influence dispersal.

In the field, surface migration of *L. terrestris* has been reported by Christensen and Mather (2004) for adults and juveniles with the former having greater dispersal rates. Nevertheless, this species is considered a sedentary, K-selected organism with low dispersal rates, a long period for maturation, low reproductive rate, and intense intraspecific competition (Satchell, 1980; Daniel, 1992). Dispersal of *L. terrestris* into previously unoccupied soil has been estimated to occur at a rate of 4.5 m yr^{-1} (Hoogerkamp et al., 1983), although over-surface dispersal distance has been reported to reach 19 m in one night from field observations (Mather and Christensen, 1988). In laboratory-based work assessing the effects of waterlogging, Valckx et al. (2008) found *L. terrestris* to move up to 15 m per night at a maximum speed of 0.1 m s^{-1}. In a field study by Shuster et al. (2003) dispersal velocity of *L. terrestris* was found to be approximately 6 m yr^{-1} as similarly reported by Ligthart and Peek (1997). Lower dispersal rates of 1.1 m y^{-1} have been reported by Nuutinen et al. (2006) in unfavourable colder climates and heavy clay soils.

From numerous studies of *L. terrestris* in recent years, much has been learned e.g. of mating behaviour (Nuutinen and Butt, 1997; Koene et al., 2002 and references within) but there still remains little information on other aspects of its behavioural ecology. This includes questions that relate to dispersal and factors affecting this, such as population density, resource availability and developmental stage of individuals. Equally important aspects are how spatial distribution is determined in a given habitat and the part(s) played by intraspecific interactions.

To address such questions, field experiments were constructed that aimed to examine the effect of increased population density and resource availability on dispersal and horizontal distribution of *L. terrestris*. Specific objectives were to examine dispersal of *L. terrestris* (1) at different population densities, (2) at different levels of resource availability, (3) of animals obtained from different sources and in addition to examine (4) the spatial arrangement of *L. terrestris* middens within small (1 m^2) plots and (5) the temporal stability of observed midden patterns.

2. Materials and methods

2.1. Site description

Experiments were conducted at Bank Hall (53°40′33″N, 02°48′54″W; 14 m asl), 15 km south of Preston. The site contains deciduous trees planted in the 1970s. These include *Acer*, *Betula*, *Fagus*, *Quercus* and *Tilia* species. Prior to tree planting, the area had been grassland. The soil, part of the Hesketh complex, is a silty clay loam with pH 6.3. Previous work on site (Butt and Lowe, 2007a) had shown an earthworm community of ten species. These were; epigeics - *Eiseniella tetraedra* (Sav.), *Lumbricus castaneus* (Sav.), *Satchellius mammalis* (Sav.); endogeics – *Allolobophora chlorotica* (Sav.), *Aporrectodea caliginosa* (Sav.), *Aporrectodea rosea* (Sav.), *Octolasion cyaneum* (Sav.), *Octolasion tyrtaeum* (Sav.) and anecics – *Aporrectodea longa* (Ude) and *L. terrestris* L. Current experiments were set up within an area of approximately 10 × 10 m where field observations of middens had revealed a relatively high abundance of *L. terrestris*.

Temperature and precipitation levels throughout the experimental period (September 2005 to October 2007), were obtained from Jeremiah Horrocks Observatory weather station, Preston, UK; monthly averages (±S.D.) were 10.97 ± 4.47 °C (Min. 4.77 °C in January 2006, Max. 19.67 °C in July 2006) and 3.04 ± 1.42 mm $month^{-1}$ (Min. 0.29 mm in July 2006, Max. 5.8 mm in June 2007), respectively.

2.2. Experimental design

To investigate the effects of population density and resource availability on *L. terrestris* dispersal and distribution, over a lengthy period of time, an experiment was set up in October 2005. This required measurement and preparation of 1 m^2 soil blocks, by digging surrounding trenches. Heavy duty (500 μm thick) polythene sheeting was inserted into and buried in the trenches, extending 0.2 m above and 0.15 m below the soil surface to form earthworm fencing (Blair et al., 1997; Lachnicht et al., 1997; Shuster et al., 2001; Perreault et al., 2007), effectively isolating these from the surrounding soil environment. Thirty of these enclosures were created in five blocks.

Information on the ambient *L. terrestris* population in enclosures (large individuals) was collected by recording midden positions. (Initial results were used to assist determination of numbers for experimental manipulations). Midden centres were located in the field and marked (for photography) with white plastic squares (2 × 2 cm). White string (2 mm diameter) was used to delineate midden areas. A 1 m ruler was placed on the lower side of the enclosure from point (0, 0), (lower left corner of square) to (1, 0), (lower right corner of square). These 2 points were set as constants and used in subsequent midden mapping of plots. Enclosures were photographed from above (vertical shot) with a hand-held camera, positioned at a height of approximately 1.80 m above the soil surface. The digital images were inserted into AutoCAD® (AutoDesk Inc, 2006), scaled accordingly to allow determination of midden coordinates and areas.

Field monitoring of *L. terrestris* movements was achieved using "tunnel traps" attached to the earthworm fencing, to capture individuals dispersing from the 1 m^2 enclosed plots. These traps (4 $plot^{-1}$) were constructed using 1 L, lidded plastic pots connected through the fence via PVC tubing (10 mm ID, 50 mm long) aligned at the soil surface. The pots were buried in the ground leaving lids exposed and half-filled with sterilised soil and provided with air-dried leaves from beside the experimental site. Small holes (0.5 mm) were made in each lid to allow aeration and also at the base of each trap to permit drainage and prevent waterlogging of the soil within.

2.3. Year 1 experiment

Experimental manipulation within enclosures was undertaken in October 2005, where earthworm and leaf litter additions resulted in six treatments that comprised three *L. terrestris* densities, each with two dry mass (dm) leaf litter quantities:

1. No *L. terrestris* addition – ambient numbers (CTRL).
2. Addition of 30 *L. terrestris* m^{-2} (LLt).
3. Addition of 60 *L. terrestris* m^{-2} (HLt).

With

A. Supply of 100 g dm of leaf litter m^{-2} (LF).
B. Supply of 300 g dm of leaf litter m^{-2} (HF).

These treatments were replicated five times, giving a total of 30, 1 m^2 plots, allocated to the enclosures in a stratified random design.

Commercially obtained (Wiggly Wigglers, Blakemere, U.K.) adult and sub-adult *L. terrestris* (mean (±S.D.) mass 4.51 ± 1.47 g), were placed in a group at the centre of each plot as per treatment. A mixture of leaf species collected from close to the experimental site,