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Original article

Selective vertical seed transport by earthworms: Implications for the diversity of grassland ecosystems

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Abstract

Earthworms are suggested to play an important role for the plant diversity of grassland ecosystems. Here we tested whether (i) *Lumbricus terrestris* L. selectively feeds on seeds of grassland species, (ii) feeding patterns match with seed species present in surface casts in a permanent grassland, and (iii) grassland plant seeds deposited in different soil depths are transported by earthworms. Food choice experiments with 10 plant species (3 grass spp., 4 non-leguminous herb spp., 3 leguminous spp.) showed that earthworms significantly selected between the offered seeds and generally preferred herbaceous species over grass species. Seed species in grassland surface casts did not correlate with seed species preferred by earthworms in the feeding experiment. Mesocosm experiments with *L. terrestris* in sterilized soil where 3500 seeds m^{-2} of *Dactylis glomerata* (grass), *Taraxacum officinale*, *Rumex obtusifolius* (non-leguminous herbs) and *Trifolium repens* (legume) were deposited in 2, 10, 20 and 30 cm depth showed a significantly different species-specific transport of the seeds both downward and upward the soil profile. Dependent on the initial deposition depth between 26% (seeds initially at 10 cm depth) and 56% (20 cm depth) of the seeds were transported by earthworms. After 90 days on average 585 germinable seeds m^{-2} of *D. glomerata*, 94 seeds m^{-2} of *T. officinale*, 38 seeds m^{-2} of *R. obtusifolius* but no seeds of *T. repens* were transported from deeper soil layers to the soil surface. Results suggest that seed herbivory and seed transport are important mechanisms by which earthworms can selectively alter the diversity of grassland ecosystems.

Keywords: Earthworm activity; Grassland diversity; Seed herbivory; Seed transport

1. Introduction

Evidence is increasing that earthworm activity and grassland plant diversity are closely linked. Declining plant species diversity has been shown to reduce the size (biomass and number) of earthworm communities [13,21] most likely due to declining fine root biomass in less diverse communities [1]. Plant species have also been shown to differ in their degree of association with nutrient-rich earthworm surface casts leading to a higher growth of species more frequently associated with casts (e.g., graminoid species) than those less frequently associated with casts (e.g., herbaceous species; 19). These species-specific relationships between plants and casts together with the effects of earthworms on soil seedbank dynamics via seed transport [4,5,15,16], seed burial [2,4,14–16] and seed herbivory [6,12] are suggested to influence the structure and diversity of grassland ecosystems. While earthworm activity in grassland

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is suggested to affect plant diversity it may not necessarily affect the aboveground biomass production, indicating that apparent earthworm-induced increases in plant nutrient availability might not be sufficient to promote the growth of perennial plant species in native grasslands [20].

The aim of this study is (i) to quantify the degree of selective ingestion of seeds from grassland species in the laboratory, (ii) to assess whether feeding patterns match with abundances of seed species in surface casts collected in a grassland, and (iii) to quantify the ability of earthworms to transport seeds placed in different soil depths using mesocosms.

2. Materials and methods

2.1. Experiment to test seed herbivory

Twenty-five seeds of the following species were offered to two adult similar-sized individuals of *L. terrestris* (average fresh mass 4.4 g, 24 hour starvation period prior to use) in plastic trays (16 × 12 × 5 cm): *Alopecurus pratensis* (average seed size: 5.5 × 2.3 mm), *Arrhenatherum elatius* (8.5 × 2.0 mm), *Dactylis glomerata* (5.5 × 1.3 mm)—grasses; *Plantago lanceolata* (2.8 × 1.3 mm), *Rumex obtusifolius* (2.3 × 1.2 mm), *Sanguisorba officinalis* (2.9 × 1.4 mm), *Taraxacum officinale* (3.8 × 1.0 mm)—non-leguminous herbs; *Trifolium pretense* (1.9 × 1.3 mm), *T. repens* (1.3 × 1.0 mm), *Vicia cracca* (2.3 × 3.2 mm)—leguminous herbs. These species are frequently abundant in permanent grasslands, vary in their size and shape and are—with the exception of *R. obtusifolius*—considered as species with a high feeding value for cattle. Seeds of two plant species were simultaneously placed in one feeding tray; additionally species were recombined to avoid a possible bias by testing similar species pairs ($n = 10$). Trays were lined with moist filter paper at the bottom and stored in growth chambers in darkness at 10 °C and at 60% relative humidity. Number of seeds removed relative to number of seeds offered was assessed after 24 h.

2.2. Seeds in earthworm surface casts from the field

In a permanent grassland of the organic research farm of the University of Bonn, Germany (65 m a.s.l.; 7°17′ E, 50°48′ N), surface casts were collected on 10 marked 50 × 50 cm areas over a period of 5 weeks starting in November 2003. Collected casts were spread in plastic trays and the germination capacity monitored over six months in a greenhouse. Some seedlings were additionally cultivated in pots until identification was possible.

2.3. Experiments to test vertical seed transport by earthworms

To test the effect of earthworms on the vertical movement of seeds in the soil, 24 opaque polyethylene tubes (40 cm high, 15 cm diameter) were filled with sterilized substrate (steamed for 24 h at 100 °C) consisting of field soil (Fluvisol), peat moss, sand and chopped rye straw in the ratio 4:2:1:1, respectively. Soil in the tubes was compacted to approximate field bulk densities (c 1.4 g cm^{-3}). All mesocosms were covered with a fine mesh at both ends to prevent earthworms from escaping. Soil moisture content in the mesocosms was stabilized by keeping the cylinders in plastic trays filled with water. During the filling of the soil into tubes, 62 seeds (equivalent to about 3500 seeds m^{-2}) of the grass *D. glomerata* non-leguminous herbs *R. obtusifolius* and *T. officinale* and the leguminous herb *T. repens* were deposited at four depths (2, 10, 20 and 30 cm). All four species were simultaneously present in a mesocosm, but placed at different depths to facilitate tracking of the seeds after earthworm activity ($n = 6$). All seed material was obtained from a professional supplier that guaranteed high germination rates (Rieger-Hofmann GmbH, Blaufelden-Raboldshausen, Germany).

After filling, 4 adult individuals of *L. terrestris* (average fresh mass 4.6 g) were introduced, resembling a density of about 200 earthworms m^{-2}, which is slightly higher than the ambient density in permanent grassland of this location. The mesocosms were randomly placed on benches of an unheated greenhouse under natural light conditions between December 2003 and March 2004. Surface casts were collected daily from the top of the soil in the mesocosms and investigated for germinable seeds.

After 90 days, the mesocosms were destructively harvested by carefully pressing the soil column out of the tube and cutting the soil in 4–8 cm thick slices. Slices had different thickness because we wanted accurately sample the layers where seeds were initially deposited. Seed numbers were standardized to account for different thickness. The soil slices were spread in thin layers on plastic trays placed in the greenhouse in order to facilitate germination of seeds present in these slices.

2.4. Statistical analyses

We used a GLM-ANOVA model in SAS (vers. 8.02 for Windows, SAS Inc., Cary, NC, USA) to analyse the data. Therefore, for each depth of seed placement a two-way ANOVA with the factors Species (spp.) and Location depth (LD) and their interactions was used.