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Herbivore behavior in the anecic earthworm species *Lumbricus terrestris* L.?

Brad Griffith [a], Manfred Türke [b], Wolfgang W. Weisser [b], Nico Eisenhauer [a,b,c,*]

[a] University of Minnesota, Department of Forest Resources, 1530 Cleveland Ave. N., St. Paul, MN 55108, USA
[b] Technische Universität München, Department of Ecology and Ecosystem Management, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany
[c] Friedrich Schiller University Jena, Institute of Ecology, Dornburger Str. 159, 07743 Jena, Germany

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ABSTRACT

Earthworms dominate invertebrate biomass in many non-acidic terrestrial ecosystems and represent key detritivores. Anecic earthworms live in the soil but primarily feed on soil surface litter. Recent studies indicate that predation of seeds and seedlings may also contribute to earthworm nutrition. However, the biological significance of this behavior is unknown. Here, we present to our knowledge the first photographic and video evidence that the anecic earthworm species *Lumbricus terrestris* L. attacks living plants and damages leaves still attached to plants. This behavior could be observed repeatedly and in different locations, indicating that it may be a common process. Though based on uncontrolled observations and in situations of low litter availability, this herbivore behavior suggests that the role of earthworms within ecosystems should not be restricted to litter burial and decomposition, but should include aboveground herbivory. Our observations do not allow us to determine with certainty if the earthworms directly fed on fresh plant material or – more likely – transported it to its permanent burrows to facilitate microbial decay. We propose that this behavior and its implications for the composition and functioning of plant communities merits further scientific attention. For instance, given the detrimental effects of some common molluscicides on earthworm performance, assumed mollusk effects on plant growth and seedling survival reported in previous studies could be – at least in part – due to the action of anecic earthworms. Future studies should investigate the biological significance and the context-dependency of this behavior.

1. Introduction

Earthworms often dominate invertebrate biomass of non-acidic, temperate and tropical terrestrial ecosystems and function as ecosystem engineers by driving biological, chemical and physical soil properties [5,9,10,28]. Though considered to utilize plant litter material and carbon-rich soil layers of mineral soil as food source [5,9,10,34], earthworms are functionally diverse and are classified by a combination of the location and orientation of their burrows and their feeding behavior as epigeic, endogeic or anecic earthworms [4]. Consequently, the mechanisms how earthworms affect plants are also manifold and span from direct to indirect ones: changing soil structure, mineralization of nutrients, hormone-like effects, dispersal of plant growth stimulating microorganisms, dispersal of microorganisms antagonistic to root pathogens, root feeding, and transposal of plant seeds [34].

The ecological group of anecic earthworms is intermediate between litter-dwelling epigeics (usually living in holorganic soil layers) and soil-dwelling endogeics (living in organo-mineral soil layers) in that they feed, at least partly, on soil surface litter, but always live in the soil in burrows. These moderate to large earthworms (e.g., 120–300 mm in adult *Lumbricus terrestris*) form vertical permanent burrows in the soil and incorporate litter from the soil surface into deeper soil layers, but also transport mineral soil materials to the surface by casting [4,37]. *L. terrestris*, one of the most common anecic earthworm species in Europe, has been the subject of several studies and functions as a model earthworm species [11,22,36]. At the entrance of its burrows *L. terrestris* forms middens, which are distributed regularly [23] indicating quasi-territorial behavior [13,33]. Anecic earthworms are likely to exert direct effects on plants and seeds due to their pronounced soil surface activity [6,15].

* Corresponding author. Technische Universität München, Department of Ecology and Ecosystem Management, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany. Tel.: +49 3641 949410; fax: +49 3641 949402.
E-mail address: nico.eisenhauer@web.de (N. Eisenhauer).

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Recent work further stressed the significance of earthworm–seed interactions, amongst others encompassing seed predation [21]. Indeed, seed predation may be crucial for earthworm nutrition [14,19] with consequences for plant community composition [17,20]. In addition, results from a laboratory experiment of Eisenhauer et al. [19] indicate that anecic earthworms feed on seedlings, and that seedlings with high tissue nitrogen concentrations may indeed contribute significantly to earthworm nutrition. In this experiment, *L. terrestris* had the choice between feeding on plant seeds (sterile seeds) or plant seedlings (viable seeds) from either grass or legume species and soil surface litter material. The objective of the experiment was to investigate if earthworms feed on seeds and/or seedlings despite the availability of surface litter and if seeds and seedlings contribute to earthworm nutrition. However, experimental as well as observational evidence of such a herbivore behavior in earthworms in the field is extremely scarce. Here, we provide to our knowledge the first photograph and video evidence showing the anecic earthworm species *L. terrestris* tearing living plant parts and damaging leaves still attached to plants. This behavior could be observed repeatedly and in various locations, indicating that it may be a common process. The aim of the present paper is to discuss the causes and consequences of this behavior and to encourage readers to consider herbivorous behavior of anecic – but also other – earthworms in future studies as well as to explore its biological significance.

2. Assessment of anecic behavior

All observations were performed and pictures and video clips were taken in the urban area of Sequim, Washington, USA (48°4′41″N 123°6′5″W) mostly in gardens and gravel driveways with little plant litter at the soil surface and a high proportion of stones. The vegetation was dominated by grasses and forbs. Soil surface activity of *L. terrestris* has been reported to peak approximately 1 h after on-set of darkness [6]. Thus, most of the footage was taken between 10:00 and 11:00 pm in spring and fall 2010–2012 during light rainy nights at air temperatures of approximately 5–15 °C. The footage was taken using a standard camera (Aiptek HD-DV 1080P with 3× optical zoom) with the help of a small handhold flashlight. The videos were edited using the software Video Studio ProX4 (Corel). Most individuals of *L. terrestris* sensed the vibration caused by approaching steps and moved back into their vertical burrows. The observer waited at the location quietly. After some time, earthworms came back to the soil surface when they were photographed or filmed. However, we are unable to estimate the commonness of the behavior due to the uncontrolled conditions during field observations.

L. terrestris searched the soil surface for plant litter, little stones and living plants. It frequently tore apart living plant parts and damaged leaves still attached to plants (Fig. 1). It attacked withered (Fig. 1a; Online Supplementary Material: Video S1) as well as living plant parts (Fig. 1b and c; Video S2, S3, S4) and both grasses (Fig. 1a) and forbs (Fig. 1b; Video S1–S4). We did not follow if *L. terrestris* directly fed on living plant parts or transported the plant material to its burrows to facilitate microbial decay. However, most of the litter and plant material was pulled toward the earthworm midden.

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3. Earthworm nutrition and herbivore behavior: ideas and perspectives

Earthworms mainly consume organic materials in various stages of decay mixed with mineral soil components [8,30]. The bulk of the organic matter consumed is dead plant material, though also

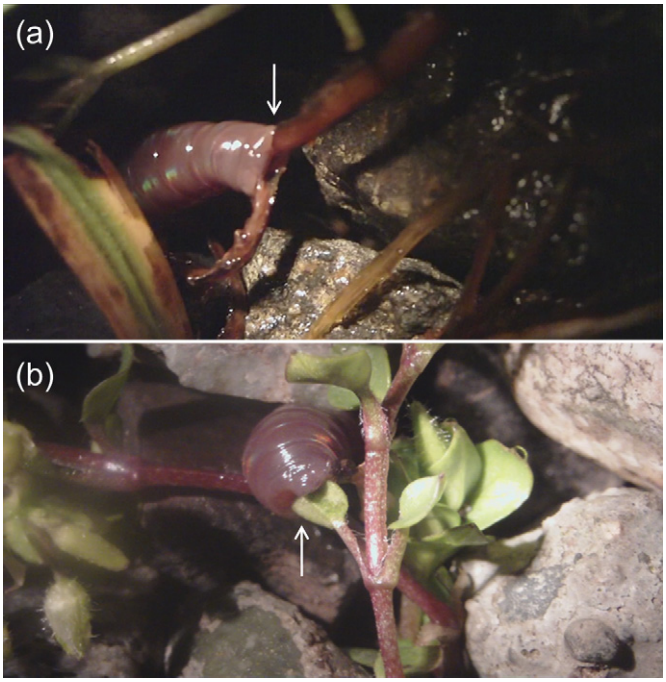

Fig. 1. *Lumbricus terrestris* attacking plant parts attached to live plants: (a) unknown grass species and (b) *Sempervivum tectorum*. Photos were taken in the urban area of Sequim, Washington, USA between 10:00 and 11:00 pm in spring and fall 2010–2012 during light rainy nights. Arrows point to the mouth opening of the *L. terrestris* individual. Photo credit: Brad Griffith.

soil microorganisms, micro- and mesofauna are ingested and likely digested together with the swallowed material. Although some studies found cellulase activity in earthworm guts [39] and earthworms produce several enzymes in their guts, cellulases are likely to be of microbial origin and are also ingested with organic materials [8]. It is thus likely that anecic earthworms fragment plant litter and increase its surface for microbial enzymes and facilitate microbial growth. It is possible that earthworm nutrition relies not only on dead plant material but also on soil microorganisms themselves. If this is the case, the relationship between earthworms and some microorganisms may be regarded as mutualistic partners in litter degradation. Indeed, earthworms have been reported to show a preference for specific types of fungi (mostly dark pigmented fungi [3,32]) and/or plant litter (protein- and carbohydrate-rich litter; reviewed in Curry and Schmidt [8]).

There is some evidence that earthworms may also show herbivore behavior: some studies reported earthworms to feed on plant roots [2,7,24,30] and seeds [19,21]. Results of a recent greenhouse experiment furthermore suggest that *L. terrestris* feeds on seedlings as indicated by changes in earthworm biomass as well as ^{15}N signatures in earthworm tissue when earthworms were offered living and sterile seeds [19]. The video clips shown in the present paper are, however, the first direct evidence for aboveground herbivore behavior suggesting that anecic earthworms actively damage living plants and that this is a common behavior. Notably, however, our observations were performed at locations with little plant litter material at the soil surface, which might have fostered the frequency of the behavior.

By removing and burrowing tissue from living plants earthworms may increase the inputs of organic material to the soil and pave the way for microbial decay in their burrows. It remains to be investigated if fresh plant material is ingested and/or digested by *L. terrestris*, but it is possible that they just bury the plant material