Applied Soil Ecology 185 (2023) 104807

Contents lists available at ScienceDirect

Applied Soil Ecology

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

Short Communication

Soil grit influences the effects of earthworms (*Lumbricus terrestris*) on seed damage

Shu Han Gan[a], Michael J. McTavish[a,*], Robert S. Bourchier[a,b], Sandy M. Smith[a]

[a] *Institute of Forestry and Conservation, John H. Daniels Faculty of Architecture, Landscape and Design, University of Toronto, 33 Willcocks Street, Toronto M5S 3E8, ON, Canada*

[b] *Agriculture and Agri-Food Canada, 5403 – 1 Avenue South, Lethbridge, Alberta T1J 4B1, Canada*

ARTICLE INFO

Keywords:
Anecic earthworm
Granivory
Feeding experiment
Soil texture
Seed coat
Alliaria petiolata

ABSTRACT

Ingested soil grit is thought to enhance the grinding action of the earthworm gizzard but its role in earthworm-seed interactions is unknown. This study used feeding trials to investigate how different levels of supplemental soil grit (+0 %, +25 %, and +50 % sand additions by weight) influenced the impacts of the cosmopolitan anecic earthworm *Lumbricus terrestris* L. on seed ingestion, egestion, seed coat damage, and germination of garlic mustard (*Alliaria petiolata*). Added grit increased the amount of seed coat damage on garlic mustard seeds egested by *L. terrestris*. Earthworm egestion also increased the speed of garlic mustard germination (~20 days control, ~14 days with L. *terrestris* and +0 % grit, ~11 days with *L. terrestris* and +25–50 % grit). The results demonstrate how earthworm ingestion and soil grit can modify the impacts of earthworms on seeds and highlight the importance of considering soil texture in field and laboratory earthworm experiments.

1. Introduction

One of the poorly studied aspects of earthworm feeding ecology is the importance of inorganic soil grit. Generally, ingested sand grains are thought to enhance the grinding action of the earthworm gizzard and facilitate the breakdown and assimilation of nutrients from organic matter (Curry and Schmidt, 2007; Satchell, 1967). Earthworms prefer mixtures of grit and organic material over organic material alone (Doube et al., 1997) and will selectively ingest smaller particles of grit (*i.e.*, ≤1 mm) (Schulmann and Tiunov, 1999; Shumway and Koide, 1994). Moderate amounts of sand (*e.g.,* 25 % by weight) have been found to be beneficial to earthworm growth (Flack and Hartenstein, 1984; Marhan and Scheu, 2005). Soil grit is rarely controlled for in feeding experiments but has been associated with higher rates of earthworm leaf litter feeding and fragmentation (Schulmann and Tiunov, 1999) and increased carbon mineralization (Marhan and Scheu, 2005).

Soil grit is also suspected to help break down seeds in the earthworm gizzard (Shumway and Koide, 1994). Seeds ingested by earthworms may be digested and destroyed or egested into the soil largely intact (McRill and Sagar, 1973). Egested seeds have been anecdotally observed to be damaged (Decaëns et al., 2003; McTavish, unpublished data), but the role of grit in earthworm-seed interactions has yet to be experimentally tested. In addition, there is growing evidence that seeds experience both enhanced or impaired germination after earthworm egestion as a result of either physical grinding in the gut (Decaëns et al., 2003; Eisenhauer et al., 2009a) or increased seed scarification that breaks seed dormancy (Ayanlaja et al., 2001; Eisenhauer et al., 2009a). Investigating the role of grit is useful to understand the impacts of earthworms on native and non-native plant communities in various soil textures (Clause et al., 2015a; Forey et al., 2011) and to interpret the results of earthworm seed feeding experiments with (*e.g.,* Eisenhauer et al., 2009a) and without grit (*e.g.,* Quackenbush et al., 2012).

The purpose of the present study is to explore how soil grit influences the effects of earthworms on seeds. We conducted the work using the large-bodied anecic earthworm *Lumbricus terrestris* L., a major, non-native earthworm granivore in North America (Grant, 1983) and seeds of garlic mustard (*Alliaria petiolata* (Bieb.) Cavara & Grande), a non-native invasive herbaceous species in North America whose seeds are known to be palatable to L. *terrestris* (Cassin and Kotanen, 2016; Flinn, 2017; Quackenbush et al., 2012). The study included a feeding trial in which earthworms acclimated in soils containing three different levels of added soil grit (+0 %, +25 %, +50 %) were fed garlic mustard seeds to monitor impacts on seed ingestion, egestion, and seed coat damage. A second experiment was used to determine the effects of earthworm

---

* Corresponding author.
E-mail address: michael.mctavish@alum.utoronto.ca (M.J. McTavish).

https://doi.org/10.1016/j.apsoil.2023.104807
Received 5 August 2022; Received in revised form 5 January 2023; Accepted 9 January 2023

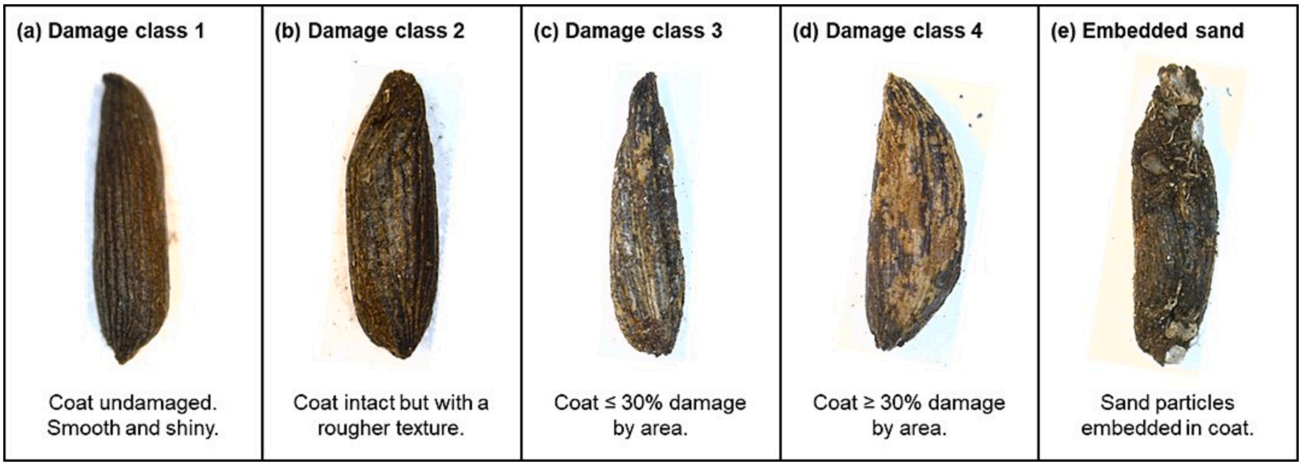

Fig. 1. Characteristic examples and descriptions of seed damage classes (1–4) and embedded sand for garlic mustard seeds.

egestion and grit levels on seed germination.

2. Materials and methods

The feeding experiment tested whether different amounts of added soil grit (+0 %, +25 %, or + 50 % sand by weight) affected earthworm granivory and the amount of damage on egested seeds. Garlic mustard seeds were collected in eastern Ontario, Canada during mid-August 2020 and stored dry at room temperature until the fall. Based on a random subsample of 20 seeds, garlic mustard seeds had a mean length (±SD) of 2.90 ± 0.37 mm and mean width of 1.02 ± 0.10 mm, placing them below the 3 mm width threshold thought to influence earthworm seed palatability (Clause et al., 2011). Adult L. *terrestris* were collected from the University of Toronto campus (Ontario, Canada) using hot mustard extraction (Lawrence and Bowers, 2002), rinsed off, and housed in separate containers (42 × 28 × 20 cm) filled with ~15 L of soil to acclimate to laboratory conditions and ingest sand particles. Commercial potting soil (ALL TREAT Farms All Purpose Premium Potting Soil, silt loam texture 40 % sand, 56 % silt, 4 % clay) was mixed with different quantities of commercially purchased playground sand sieved to retain particles between 0.5 and 1 mm (Schulmann and Tiunov, 1999; Shumway and Koide, 1994) to create three grit addition treatments (+0 %, +25 %, and + 50 %, by weight). Earthworms were fed crumbled leaf litter (Norway maple, *Acer platanoides* L.) and kept in the containers at 18 °C indoors in the dark for five days.

After acclimation in the different grit soil conditions, earthworms were used for granivory trials based on McRill and Sagar (1973). Earthworms were rinsed, weighed, and added singly to Petri dishes (15 cm diameter) lined with moistened filter paper and 25 garlic mustard seeds for a total of $n = 10$ dishes at each added grit level, including an earthworm free control (control, +0 %, +25 %, +50 %) (40 dishes in total). Allowing for an estimated gut transit time of ~8 h for L. *terrestris* (Hartenstein and Amico, 1983), earthworms were transferred immediately prior to feeding to minimize grit egestion and feeding dishes were kept grit-free to facilitate the accurate recollection of the small seeds (Schulmann and Tiunov, 1999). Dishes were covered with ventilated lids, placed in the dark at 18 °C, and left for 20 h for earthworms to ingest seeds. Earthworms were then transferred to fresh dishes to egest seeds for 24 h. Total seeds were counted from the non-ingested seeds and the egested seeds to determine ingestion (% of initial seeds) and egestion (% of ingested seeds).

Following the granivory trials, seeds were examined under a dissecting light microscope and assigned to categorical damage classes (1–4) based on the amount of seed coat area damaged and checked for embedded sand particles (Fig. 1). To avoid experimenter bias, seeds were assessed randomly without knowledge of the grit treatment they had been exposed to.

A follow-up germination trial was used to assess the effects of earthworm egestion and grit (control seeds or seeds egested by earthworms exposed to soils with +0 %, +25 %, or + 50 % grit) on the germination of garlic mustard seeds. Garlic mustard produces dormant seeds requiring scarification for germination, which is typically provided by cold stratification (Sosnoskie and Cardina, 2009). Prior to germination trials, seeds were cold stratified according to Baskin and Baskin (1992) and Raghu and Post (2008). Groups of 20 garlic mustard seeds from the control and each grit treatment were placed in individual Petri dishes (10 cm diameter) with 30 mL of potting soil and 6.25 mL tap water (~ 21 % *v*/v moisture content) ($n = 4$ dishes per treatment, 16 dishes total). Dishes were sealed with plastic film, wrapped in aluminum foil, and placed randomly under a 5-cm thick layer of mixed leaf litter and commercial coir mulch in Toronto, Ontario, Canada to overwinter for ~4 months.

After stratification, seed dishes were uncovered and counted for initial germination (≥1 mm radicle growth). Dishes with lids removed were placed randomly in planter trays of a growth chamber set to approximate March–April conditions at the seed collection site (10 °C/5 °C, 13 h/11 h, day/night). Seeds were lightly misted with tap water and checked for germination every 3–4 days over 50 days. For each dish, the initial and final germinations were calculated as percentages of the total seeds, and the time to first germination and peak germination (*i.e.*, the day after which no further germination was observed) were determined.

For the granivory trials, the effects of grit on seed ingestion and egestion were assessed using ANCOVAs with earthworm weight as a covariate. Chi-squared tests were used to examine the associations between grit level and the distribution of seeds across the four damage classes, and between grit level and the number of seeds with embedded sand. For the germination trials, the effect of earthworms and grit on initial germination (% of total seeds), final germination (% of total seeds), time to first germination (days), and time to peak germination (days) were assessed using One-Way ANOVAs or Welch's Test when assumptions of equal variance were violated, with omega-squared (ω^2) as an effect size and Tukey's HSD used as a post-hoc test. All statistical tests were conducted using R 3.6.2 (R Core Team, 2019).

3. Results

Earthworm egestion with different levels of added grit had no statistically significant effect on garlic mustard seed ingestion (ANCOVA, $F_{2,26} = 0.15$, $p = 0.86$) nor egestion ($F_{2,25} = 2.07$, $p = 0.15$). Across grit treatments, earthworms ingested 57 ± 26 % of available garlic mustard seeds (mean ± SD) and egested 66 ± 25 % of the ingested seeds.

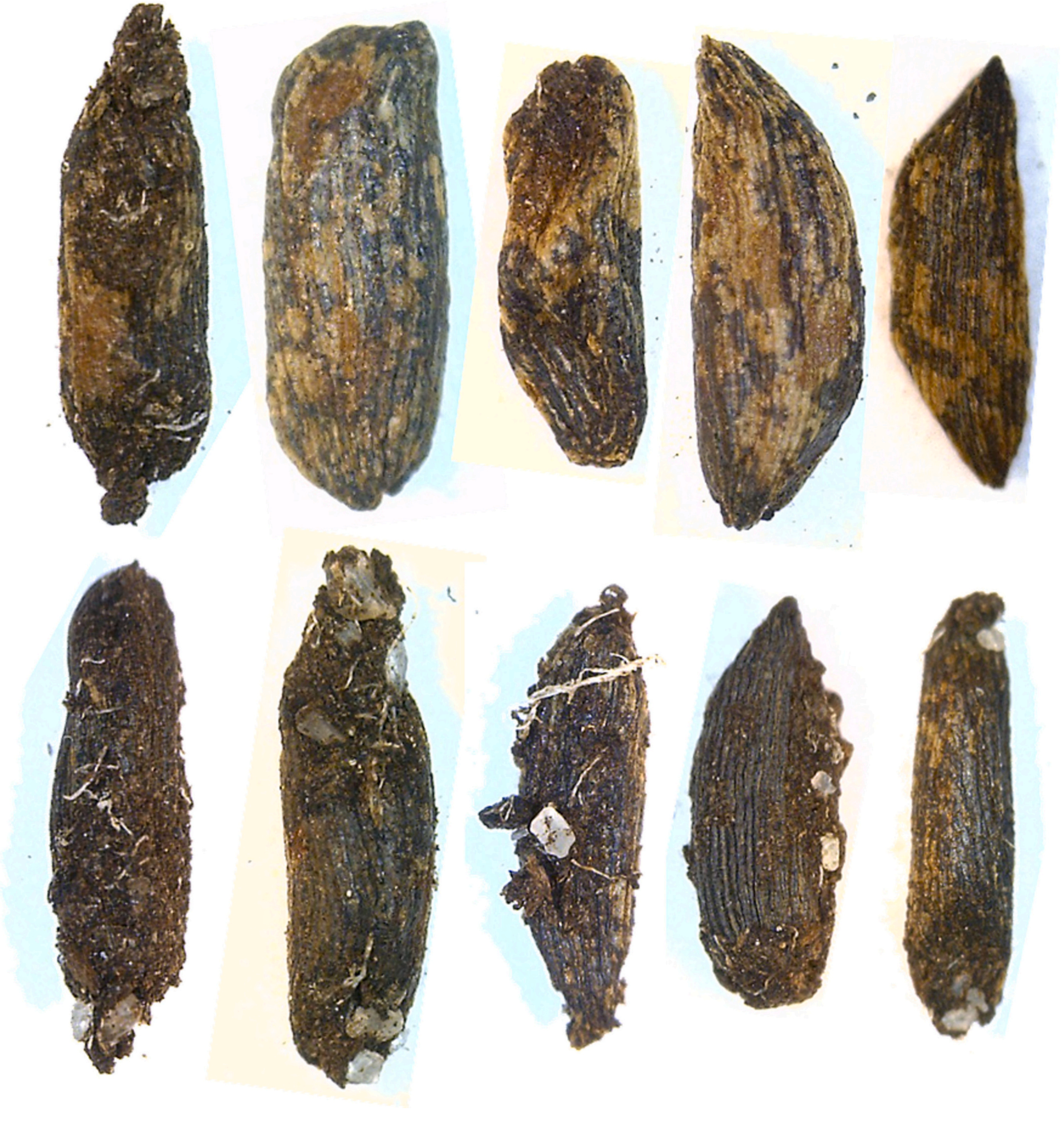

Fig. 2. Additional examples of earthworm egested garlic mustard seeds with the highest levels of damage (class 4) (top row) and embedded sand particles (bottom row).

Seeds egested by earthworms had visibly damaged seed coats and embedded sand particles (Fig. 2). Earthworm egestion and grit level affected both the distribution of seeds across different damage classes (Chi-Squared Test, X^2 (9, $n = 368$) = 41.2, $p < 0.001$) and the number of seeds with embedded sand particles (X^2 (3, n = 368) = 25.3, p < 0.001). At higher grit levels, there was more damage to seeds; the proportion of seeds assigned to lower damage classes decreased and the proportion assigned to higher damage classes increased (Fig. 3). Approximately twice as many seeds had the highest level of damage in the +50 % grit treatment (39 %) compared to those in the control or + 0 % grit treatments (11–18 %). Sand was never found embedded in seeds from the earthworm-free control (0 % of seeds), rare at the +0 % grit level (1.1 %), and more common in the +25 % grit (7.1 %) and + 50 % grit levels (15.9 %).

Earthworm egestion and grit affected the speed of garlic mustard seed germination (Table 1). The number of days required to reach peak germination was the highest for seeds from the earthworm-free control (~20 days), intermediate for seeds egested by earthworms from +0 % grit (~14 days), and shortest (~11 days) for seeds egested by earthworms from +25–50 % grit (Fig. 4). Earthworm egestion and grit did not affect initial seed germination, final germination, or the time to first germination (Table 1). Averaged across all treatment levels, initial seed

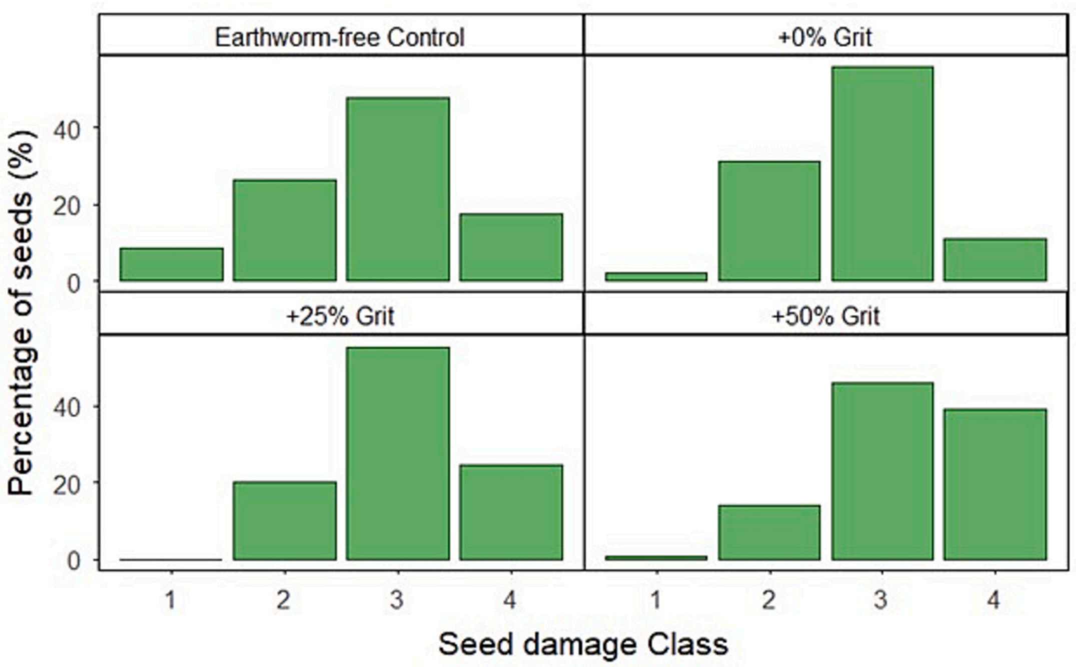

Fig. 3. Percentages of garlic mustard seeds assigned to damage classes with increasing seed coat damage (1, 2, 3, 4) from earthworm-free control conditions ($n = 80$ seeds) or egested by L. *terrestris* from soil with different added grit content (+0 %, $n = 90$ seeds; +25 %, $n = 85$ seeds; +50 %, $n = 113$ seeds).

Table 1
Summary of the effects of earthworm egestion and grit (earthworm-free control, +0 %, +25 %, +50 %) on garlic mustard initial germination, final germination, time to first germination, and time to peak germination ($n = 4$ dishes of 20 seeds for each treatment level).

Response	Test	F-statistic	p-value	Effect size (ω^2)
Initial germination (%)	Welch's Test	$F_{3,6.2} = 0.44$	0.73	–
Final germination (%)	One-Way ANOVA	$F_{3,12} = 2.15$	0.15	–
Time to first germination (days)	One-Way ANOVA	$F_{3,12} = 0.61$	0.62	–
Time to peak germination (days)	One-Way ANOVA	$F_{3,12} = 7.49$	**0.004**	0.55

germination was 6.6 ± 13.4 %, final germination was 97.5 ± 4.1 %, and the first germination was observed 5.2 ± 2.9 days after recovery from overwintering conditions (mean ± SD).

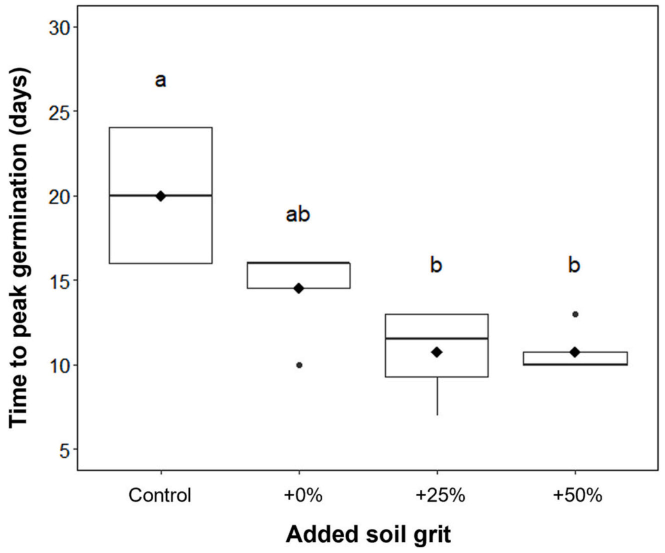

Fig. 4. Days to peak germination of garlic mustard seeds from earthworm-free control conditions or egested by L. *terrestris* from soil with different added grit content (+0 %, +25 %, +50 %) ($n = 4$ dishes of 20 initial seeds per grit level). Diamonds denote group means. Letters denote groupings from Tukey's HSD post-hoc test; means that do not share a letter are statistically significantly different.

4. Discussion

Our study provides the first direct investigation of how soil grit can influence earthworm-seed interactions. Adding soil grit increased the amount of seed coat damage sustained by garlic mustard seeds egested by L. *terrestris*, corroborating anecdotal observations of damage on earthworm egested seeds (Decaëns et al., 2003; McTavish, unpublished data). The increase in embedded sand particles in garlic mustard seeds egested by *L. terrestris* acclimated in higher grit soils supports the hypothesis that earthworms were ingesting more sand from the higher grit soils and that this directly contributed to increased seed coat damage.

Damage from earthworm egestion determined by soil grit could influence seed germination, vigour, and longevity (De Souza and Marcos-Filho, 2001; Harman, 1983). Seeds of specific plant species may benefit from seed coat damage (*e.g.,* increasing germination) (Eisenhauer et al., 2009a) while others may be negatively affected if damaged seeds experience higher digestion or infection by bacteria, fungi, or viruses (Harman, 1983). In our study, higher soil grit may have increased the germination speed of garlic mustard seeds, though it was impossible to statistically separate this effect from that of earthworm egestion (*i.e.,* earthworm egestion with +25–50 % grit accelerated germination compared to earthworm-free controls while earthworm egestion with +0 % grit had an intermediate effect). Given that garlic mustard seeds were cold stratified prior to the germination trial, it is unclear whether the seed damage caused by L. *terrestris* alone would be sufficient to break garlic mustard seed dormancy without cold stratification; this could be tested in future experiments comparing the germination of garlic mustard seeds egested by earthworms with and without cold stratification. Overall, accelerated germination through grit and egestion could be an additional mechanism by which non-native earthworms facilitate invasive plants such as garlic mustard, with which they often co-occur (Craven et al., 2017; Nuzzo et al., 2009).

In contrast to observations by Schulmann and Tiunov (1999) that showed soil grit facilitated greater earthworm feeding and fragmentation of leaf litter, we did not detect any effects of supplemental grit on earthworm seed ingestion or egestion. We suspect that if grit changes the assimilation efficiency of earthworm feeding (Curry and Schmidt, 2007; Marhan and Scheu, 2005), then effects of grit on ingestion rate may only become apparent over longer periods of time. In terms of egestion, *L. terrestris* was able to digest seeds at all grit levels, including without supplemental grit (+0 %), suggesting that the base sand content of the soil (40 %) may have been sufficient for digestion without supplemental grit. High grit levels may also be unnecessary to break down the relatively small, slim garlic mustard seeds that were chosen here for their known palatability to L. *terrestris* (Cassin and Kotanen, 2016; Flinn, 2017; Quackenbush et al., 2012). However, higher grit levels may have an increased impact for larger, tougher seeds.

Our work identifies soil grit as an additional factor that can influence the effects of earthworms on the post-dispersal fate of seeds. Variation in soil texture could contribute to variable impacts of earthworms on different vegetation communities (Clause et al., 2015b; Eisenhauer et al., 2009b; Fleri et al., 2021; Nuzzo et al., 2015). Soil texture should also be considered in laboratory-based earthworm feeding experiments (Fründ et al., 2010), especially when comparing granivory trials that provide grit (*e.g.,* Eisenhauer et al., 2009a) and those that do not (*e.g.,* Quackenbush et al., 2012). Given the known species-specificity of earthworm-seed interactions (Eisenhauer et al., 2009a), we recommend further experimentation with a range of earthworm species – including taxa from different functional groups – and plant species, including species with seeds that vary in size and seed coat toughness.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

We thank Carla Timm for laboratory technical assistance. This research was funded by the Institute of Forestry and Conservation at the University of Toronto, Agriculture and Agri-Food Canada, Mitacs Elevate, and Ducks Unlimited Canada.

References

Ayanlaja, S.A., Owa, S.O., Adigun, M.O., Senjobi, B.A., Olaleye, A.O., 2001. Leachate from earthworm castings breaks seed dormancy and preferentially promotes radicle growth in jute. HortScience 36, 143–144. https://doi.org/10.21273/HORTSCI.36.1.143.

Baskin, J.M., Baskin, C.C., 1992. Seed germination biology of the weedy biennial Alliaria petiolata. Nat. Areas J. 12, 191–197.

Cassin, C.M., Kotanen, P.M., 2016. Invasive earthworms as seed predators of temperate forest plants. Biol. Invasions 18, 1567–1580. https://doi.org/10.1007/s10530-016-1101-x.

Clause, J., Margerie, P., Langlois, E., Decaëns, T., Forey, E., 2011. Fat but slim: criteria of seed attractiveness for earthworms. Pedobiologia 54, S159–S165. https://doi.org/10.1016/j.pedobi.2011.08.007.

Clause, J., Barot, S., Forey, E., 2015a. Effects of cast properties and passage through the earthworm gut on seed germination and seedling growth. Appl. Soil Ecol. 96, 108–113. https://doi.org/10.1016/j.apsoil.2015.07.007.

Clause, J., Forey, E., Lortie, C.J., Lambert, A.M., Barot, S., 2015b. Non-native earthworms promote plant invasion by ingesting seeds and modifying soil properties. Acta Oecol. 64, 10–20. https://doi.org/10.1016/j.actao.2015.02.004.

Craven, D., Thakur, M.P., Cameron, E.K., Frelich, L.E., Beauséjour, R., Blair, R.B., Blossey, B., Burtis, J., Choi, A., Dávalos, A., Fahey, T.J., Fisichelli, N.A., Gibson, K., Handa, I.T., Hopfensperger, K., Loss, S.R., Nuzzo, V., Maerz, J.C., Sackett, T., Scharenbroch, B.C., Smith, S.M., Vellend, M., Umek, L.G., Eisenhauer, N., 2017. The unseen invaders: introduced earthworms as drivers of change in plant communities in North American forests (a meta-analysis). Glob. Chang. Biol. 23, 1065–1074. https://doi.org/10.1111/gcb.13446.

Curry, J.P., Schmidt, O., 2007. The feeding ecology of earthworms – a review. Pedobiologia 50, 463–477. https://doi.org/10.1016/j.pedobi.2006.09.001.

De Souza, F.H.D., Marcos-Filho, J., 2001. The seed coat as a modulator of seed-environment relationships in Fabaceae. Rev. Bras. Bot. 24, 365–375. https://doi.org/10.1590/S0100-84042001000400002.

Decaëns, T., Mariani, L., Betancourt, N., Jiménez, J.J., 2003. Seed dispersion by surface casting activities of earthworms in Colombian grasslands. Acta Oecol. 24, 175–185. https://doi.org/10.1016/S1146-609X(03)00083-3.

Doube, B.M., Schmidt, O., Killham, K., Correll, R., 1997. Influence of mineral soil on the palatability of organic matter for lumbricid earthworms: a simple food preference study. In: Soil Biol. Biochem. 5th International Symposium on Earthworm Ecology, 29, pp. 569–575. https://doi.org/10.1016/S0038-0717(96)00032-6.

Eisenhauer, N., Schuy, M., Butenschoen, O., Scheu, S., 2009a. Direct and indirect effects of endogeic earthworms on plant seeds. Pedobiologia 52, 151–162. https://doi.org/10.1016/j.pedobi.2008.07.002.

Eisenhauer, N., Straube, D., Johnson, E.A., Parkinson, D., Scheu, S., 2009b. Exotic ecosystem engineers change the emergence of plants from the seed bank of a deciduous forest. Ecosystems 12, 1008–1016. https://doi.org/10.1007/s10021-009-9275-z.

Flack, F.M., Hartenstein, R., 1984. Growth of the earthworm Eisenia foetida on microorganisms and cellulose. Soil Biol. Biochem. 16, 491–495. https://doi.org/10.1016/0038-0717(84)90057-9.

Fleri, J.R., Martin, T.G., Rodewald, A.D., Arcese, P., 2021. Non-native earthworms alter the assembly of a meadow plant community. Biol. Invasions 23, 2407–2415. https://doi.org/10.1007/s10530-021-02513-8.

Flinn, K.M., 2017. Invasive earthworms ingest and digest garlic mustard seeds at rates equal to native seeds. Northeast. Nat. 24, 413–420. https://doi.org/10.1656/045.024.0403.

Forey, E., Barot, S., Decaëns, T., Langlois, E., Laossi, K.-R., Margerie, P., Scheu, S., Eisenhauer, N., 2011. Importance of earthworm–seed interactions for the composition and structure of plant communities: a review. Acta Oecol. 37, 594–603. https://doi.org/10.1016/j.actao.2011.03.001.

Fründ, H.-C., Butt, K., Capowiez, Y., Eisenhauer, N., Emmerling, C., Ernst, G., Potthoff, M., Schädler, M., Schrader, S., 2010. Using earthworms as model organisms in the laboratory: recommendations for experimental implementations. Pedobiologia 53, 119–125. https://doi.org/10.1016/j.pedobi.2009.07.002.

Grant, J.D., 1983. The activities of earthworms and the fates of seeds. In: Satchell, J.E. (Ed.), Earthworm Ecology. Springer, Dordrecht, pp. 107–122. https://doi.org/10.1007/978-94-009-5965-1_9.

Harman, G.E., 1983. Mechanisms of seed infection and pathogenesis. Phytopathology 73.

Hartenstein, R., Amico, L., 1983. Production and carrying capacity for the earthworm Lumbricus terrestris in culture. Soil Biol. Biochem. 15, 51–54. https://doi.org/10.1016/0038-0717(83)90118-9.

Lawrence, A.P., Bowers, M.A., 2002. A test of the 'hot' mustard extraction method of sampling earthworms. Soil Biol. Biochem. 34, 549–552. https://doi.org/10.1016/S0038-0717(01)00211-5.

Marhan, S., Scheu, S., 2005. Effects of sand and litter availability on organic matter decomposition in soil and in casts of Lumbricus terrestris L. In: Geoderma. Mechanisms And Regulation of Organic Matter Stabilisation in Soils, 128, pp. 155–166. https://doi.org/10.1016/j.geoderma.2004.07.001.

McRill, M., Sagar, G.R., 1973. Earthworms and seeds. Nature 243, 482. https://doi.org/10.1038/243482a0.

Nuzzo, V., Dávalos, A., Blossey, B., 2015. Invasive earthworms shape forest seed bank composition. Divers. Distrib. 21, 560–570. https://doi.org/10.1111/ddi.12322.

Nuzzo, V.A., Maerz, J.C., Blossey, B., 2009. Earthworm invasion as the driving force behind plant invasion and community change in northeastern North American forests. Conserv. Biol. 23, 966–974.

Quackenbush, P.M., Butler, R.A., Emery, N.C., Jenkins, M.A., Kladivko, E.J., Gibson, K. D., 2012. Lumbricus terrestris prefers to consume garlic mustard (Alliaria petiolata) seeds. Invasive Plant Sci. Manag. 5, 148–154. https://doi.org/10.1614/IPSM-D-11-00057.1.

R Core Team, 2019. R: A Language And Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Raghu, S., Post, S.L., 2008. Cold stratification requirements for germination of Alliaria petiolata. Invasive Plant Sci. Manag. 1, 315–318. https://doi.org/10.1614/IPSM-07-027.1.

Satchell, J.E., 1967. Lumbricidae. In: Burges, A., Raw, F. (Eds.), Soil Biology. Academic Press, London, UK, pp. 259–322.

Schulmann, O.P., Tiunov, A.V., 1999. Leaf litter fragmentation by the earthworm Lumbricus terrestris L. Pedobiologia 43, 453–458.

Shumway, D.L., Koide, R.T., 1994. Seed preferences of Lumbricus terrestris L. Appl. Soil Ecol. 1, 11–15. https://doi.org/10.1016/0929-1393(94)90019-1.

Sosnoskie, L.M., Cardina, J., 2009. Laboratory methods for breaking dormancy in garlic mustard (Alliaria petiolata) seeds. Invasive Plant Sci. Manag. 2, 185–189. https://doi.org/10.1614/IPSM-08-126.1.