Applied Soil Ecology 75 (2014) 145–149

Contents lists available at ScienceDirect

Applied Soil Ecology

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

Non-native anecic earthworms (*Lumbricus terrestris* L.) reduce seed germination and seedling survival of temperate and boreal trees species

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ARTICLE INFO

Article history:
Received 14 July 2013
Received in revised form 3 November 2013
Accepted 8 November 2013

Keywords:
Lumbricus terrestris
Northern temperate and boreal tree species
Seed germination
Seedling survival

ABSTRACT

Recent studies have shown that the introduction of non-native earthworms in previously earthworm-free soils may have negative impacts on the recruitment of certain understory plant species in northern temperate forests. There is a need, therefore, to understand the mechanisms that may underlie this phenomenon. A microcosm study was conducted to test the effects of the anecic earthworm, *Lumbricus terrestris* L., on the number of days for germination, % seed germination, seedling survival and seedling biomass of 14 tree species native to southern Quebec (Canada). Seeds of these species were germinated and grown in the presence or absence of *L. terrestris*. The presence of earthworms significantly reduced % seed germination of seven tree species, as well as seedling survival of three tree species. The germination date of three tree species was significantly affected, either positively or negatively, by the presence of earthworms. Earthworms had no effect on seedling biomass. Results suggest that the introduction of *L. terrestris* into forested ecosystems of southern Québec may potentially alter overstory composition through several mechanisms that differentially affect the recruitment of various tree species in the understory.

1. Introduction

It is generally accepted that indigenous earthworm species of North America did not survive the Wisconsinian glaciation that receded approximately 11,000 years ago (Gates, 1970). Thus, in the province of Quebec (Canada), 17 of the 19 known earthworm species are believed to have been introduced by European settlers (Reynolds and Reynolds, 1992; Addison, 2009). These earthworm species migrate no faster than 5–10 m per year (Addison, 2009), and they are often confined to specific locations because of natural obstacles obstructing their movement. Their seemingly non-random distribution in agricultural fields, near roads and around lakes strongly suggests that their introduction into new areas is mainly mediated by humans, such as transport within tire treads or dumping of bait by fishermen (Hendrix and Bohlen, 2002; Callaham et al., 2006; Hale, 2008). Deciding whether or not measures should be taken to thwart this biological invasion requires an understanding of the impacts of non-native earthworms in previously earthworm-free soils.

In agroecosystems of southern Quebec, earthworms have traditionally been considered beneficial soil organisms that facilitate litter decomposition, increase nutrient availability and improve soil structure (e.g., Ramsay and Hill, 1978). Earthworm activities could have, however, a negative impact on the integrity of natural forest ecosystems. For example, some earthworm species dig vertical burrows to depths of 2–3 m, which may increase hydraulic conductivity in soils and nutrient export from watersheds (Domínguez et al., 2004). This phenomenon could be further exacerbated by the earthworm mediated removal of organic forest floors, which retain more moisture than mineral soil horizons. Secondly, earthworms may accelerate the decomposition of humified soil organic matter, thereby reducing the C storage capacity of forest soils and increasing atmospheric CO_2. Thirdly, studies in Northern Minnesota and Wisconsin have shown that exotic earthworm invasions in northern temperate forests coincide with a loss of understory herbaceous species and a low recruitment of sugar maple (*Acer saccharum* Marsh.) (Hale et al., 2006; Corio et al., 2009). Regarding this latter point, Forey et al. (2011) summarized our current state of knowledge on earthworm–seed interactions, and suggested a need for manipulative experiments that would

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http://dx.doi.org/10.1016/j.apsoil.2013.11.006

help us to mechanistically understand these interactions in driving plant community assembly. For example, it remains unclear whether the reduced abundance of some plant species is due to lower seed germination rates or to lower seedling survival.

The reported negative impact of exotic earthworms on sugar maple recruitment is of particular concern in Quebec (Canada). Sugar maple is not only a commercially valued tree species that is widespread across southern Quebec, it is also a cultural icon due to the popular celebration of the maple syrup industry. Moreover, southern Quebec is the region with the highest plant species richness in the province, where natural mixedwood stands may often contain more than 10 co-occurring tree species (Leckie et al., 2000). Many of these species also have high economic value, and it is hypothesized that they may vary in their vulnerability to earthworms. For example, Milcu et al. (2006) found that the recruitment of herbaceous species (i.e., grasses, legumes and herbs) was related to seed-size, with small seeded species being repressed and large-seeded species being promoted. Thus, a species whose seed germination rate and seedling survival are not negatively affected by earthworms, may increase its competitive ability relative to those species that are more vulnerable. For example, Holdsworth et al. (2007) found a decrease in sugar maple recruitment, and a concomitant increase in the abundance of ash (*Fraxinus* sp.) seedlings, as earthworm abundances increased in a Minnesota forest. It is especially important, therefore, to test the vulnerability of seeds and seedlings of sugar maple to the presence of exotic earthworms, relative to other tree species from southern Quebec.

Here we report on a microcosm study where we tested the effect of the anecic earthworm species, *Lumbricus terrestris* L., on the number of days for germination, % seed germination, seedling survival and seedling biomass of 14 tree species native to southern Quebec. We chose to work with *L. terrestris* because it is widespread in this region, because it is the most commonly used as fishing bait (Keller et al., 2007) and thus most prone to be dispersed in forests by anglers, and because its anecic lifestyle will likely have an important impact on soil processes.

2. Materials and method

2.1. Soil and litter collection

The soil and the litter used for this experiment were collected in October 2011 from an earthworm-free mature sugar maple stand near the town of Windsor, Canada (ca. 45°36′N, 71°44′W). Approximately 0.75 m^3 of fresh mineral soil (0–30 cm depth) was transported to a greenhouse at Laval University (Ste-Foy, Quebec, Canada). The soil was sieved to pass a 5 mm mesh and homogenized by gently mixing. Approximately 5 kg (dry wt. equiv.) of newly fallen sugar maple and red maple (*Acer rubrum* L.) leaf litter was handpicked from the same site. The litter was then air-dried at 35 °C, coarsely shred by hand, and kept in plastic buckets with lids.

2.2. Microcosm design and bioassay

In order to test the effects of earthworms on the germination and survival of tree seedling species from Eastern Canada, we constructed 170 microcosms consisting of 30 cm long PVC tubes with an inner dia. of 10 cm. The bottom end of each tube was lined with a 1 mm mesh nylon net, and the tubes were then placed vertically on metal mesh tables in a greenhouse where the lighting was set to a day:night cycle of 14:10 h. Approximately 2.65 kg (dry wt. equiv.) of soil was transferred in each tube and gently tamped up to 5 cm from the upper edge.

The experimental design consisted of a factorial array of two earthworm levels (i.e., with or without earthworms) × seeds from 15 plant species. Four mature specimens of *L. terrestris*, which were obtained from a local fishing supplies store, were added to 85 microcosms. The top of each microcosm was then lined with 1 mm mesh nylon net to prevent earthworms from escaping. Seeds from 1 of 15 plant species were sown at ca. 1–2 cm depth in each microcosm. The plant species consisted of 14 northern temperate forest tree species + tomato (*Solanum lycopersicum*). Tomato was used as a “reference” species, as a preliminary study had shown tomato seeds and seedlings to be readily damaged by *L. terrestris* (data not shown). The tree species were American elm (*Ulmus Americana* L.), balsam fir (*Abies balsamea* (L.) Mill.), bitternut hickory (*Carya cordiformis* Sarg.), black spruce (*Picea mariana* (Mill.) B.S.P.), bur oak (*Quercus macrocarpa* Michx.), eastern white cedar (*Thuja occidentalis* L.), jack pine (*Pinus banksiana* Lamb.), paper birch (*Betula papyrifera* Marsh.), tamarack (*Larix laricina* (Du Roi) Koch), white pine (*Pinus strobus* L.), white spruce (*Picea glauca* (Moench) Voss.), yellow birch (*Betula alleghaniensis* Britt.), red maple and sugar maple. All seeds were obtained from the *Ministère des ressources naturelles du Québec*. Thirty seeds were planted in each microcosm except those of bitternut hickory and bur oak, whose larger size incited us to plant only 15 seeds per microcosm. All treatments were replicated 5 times, except those with bitternut hickory and bur oak, which were replicated 10 times. Litterfall was simulated by adding 5 g of litter to all microcosms at the beginning of the bioassay experiment, and 3 g of litter each week thereafter.

Plants were grown from January to June 2012. At 2–3 day intervals during this period, each microcosm was watered to field capacity and seedlings were counted and marked, which allowed us to note the germination date and the survival of all individual seedlings. The % germination in each microcosm was calculated as the number of germinated seeds within 30 days of the first seed germination. At the end of this 30 day period, soil was sieved and buried seeds that had germinated were also included in our calculation of % seed germination. The % survival in each microcosm was calculated as the number of thriving seedlings at the end of the 30 day period, relative to the total number of germinated seeds. The mean number of days for germination of each treatment was based on the median germination date within each microcosm, that is, the day corresponding to 50% of total germination. At the end of the bioassay, we measured the average dry mass of surviving seedlings in each microcosm. Earthworm survival rate at the end of the study was >95%.

2.3. Statistical analyses

We first used two-way ANOVA to test the effects of tree species, earthworms, and tree species × earthworm interactions, on all response variables. The proportional data were arcsine–square root transformed prior to these analyses. When significant tree species × earthworm interactions were found, the effects of earthworms within each tree species were tested using generalized linear models (GLM). First, the overall earthworm effects on % germination and % survival were tested by logistic regression for proportional data with binomial distributions. However, these models were over-dispersed, so we re-analyzed the data after specifying a quasibinomial distribution, and tested the significance of these models with *F*-tests. We then tested, in the same way, the effects of earthworms on % germination and % survival within each plant species. Given that comparisons of survival rates are less robust as % germination rates decrease, the effect of earthworms on survival rates was not tested for the five tree species that had less than 15% seed germination in one or both earthworm treatments. The remaining 10 comparisons were more robust as they all had 20–100% seed germination rates (i.e., 30–150 germinated seeds per treatment). The effects of earthworms on the number of days for germination and on seedling biomass were tested within

Table 1
Effect of earthworms on % seed germination of 14 tree species and tomato plants ($n = 5$) as determined by logistic regressions for proportional data with binomial distributions.

Species	−Earthworms (%)	+Earthworms (%)	*t*-Value	$P > \|t\|$
Tomato	97	61	4.34	**0.002**
Sugar maple	91	90	1.66	0.135
Red maple	80	70	0.51	0.627
Balsam fir	79	47	3.01	**0.017**
Black spruce	73	32	4.49	**<0.001**
Bur oak	63	29	5.11	**<0.001**
Jack pine	57	25	5.32	**<0.001**
White spruce	50	21	2.50	**0.037**
White pine	46	17	4.81	**0.001**
American elm	27	27	0.00	1.000
Bitternut hickory	15	9	4.47	**<0.001**
Yellow birch	11	6	1.97	0.084
Paper birch	9	7	0.80	0.447
Tamarack	9	3	1.95	0.087
Eastern white cedar	7	15	−1.59	0.150

Significant comparisons are highlighted in bold.

each tree species using Student *t*-tests. All statistical analyses were performed using *R* statistical software (Version 2.14.0).

3. Results

Germination rates ranged from 97% (tomato) to only 7% (Eastern white cedar) across all species (Table 1). Two-way ANOVA revealed significant effects of tree species ($F_{14,120} = 61.77$, $P < 0.001$), earthworms ($F_{1,120} = 56.44$, $P < 0.001$), and tree species × earthworm interaction ($F_{14,120} = 5.63$, $P < 0.001$) on % seed germination. The average % germination rate was significantly higher in microcosms without earthworms (48%) than with earthworms (26%). Results of logistic regressions confirmed that earthworms significantly reduced % seed germination for 8 of the 15 species (Table 1). Among the seven non-significant comparisons, five of these were among those species with the lowest % germination rates, which reduced the statistical power of the tests.

Seedling survival rates ranged from 100% (bur oak) to only 13% (black spruce) across all species (Table 2). Two-way ANOVA revealed significant effects of tree species ($F_{14,120} = 29.91$, $P < 0.001$), earthworms ($F_{1,120} = 20.96$, $P < 0.001$), and tree species × earthworm interaction ($F_{14,120} = 4.79$, $P < 0.001$) on % seedling survival. The average % survival rate was significantly higher in microcosms without earthworms (64%) than with earthworms (50%). Results of logistic regressions confirmed that earthworms significantly reduced % survival for 4 of the 10 species that were tested (Table 2). There was no trend among the five species that had been excluded from these analyses (i.e., species not meeting our criterion for sample size).

The median number of days for germination ranged from 3 days (red maple) to 111 days (bitternut hickory) across all species. Two-way ANOVA revealed no effect of earthworms ($F_{1,120} = 0.13$, $P = 0.717$), but significant effects of tree species ($F_{14,120} = 157.97$, $P < 0.001$) and tree species × earthworm interaction ($F_{14,120} = 2.19$, $P < 0.01$) on the median number of days for germination. Individual *t*-tests within each tree species found that earthworms significantly delayed germination for bitternut hickory (86 vs. 103 days), but significantly hastened germination for balsam fir (35 vs. 30 days) and eastern white pine (39 vs. 33 days).

Two-way ANOVA showed a significant effect of tree species ($F = 57.80$, $P < 0.001$) on mean seedling biomass, but no significant effects of earthworms ($F = 0.69$, $P = 0.409$) or species × earthworm interaction ($F = 0.34$, $P = 0.984$), on seedling biomass.

4. Discussion

Taken collectively, our data suggest that the introduction of *L. terrestris* into forested ecosystems of southern Québec may potentially alter overstory composition through several mechanisms that differentially affect the recruitment of various tree species in the understory. Firstly, our data show that earthworms may reduce seed germination of some tree species, while others are unaffected. It has been reported that smaller seeds of graminoid and herbaceous species are more prone to be buried and/or ingested by earthworms, which ostensibly reduces their germination rate (Milcu et al., 2006; Aira and Piearce, 2009). However, smaller seed size did not seem to play a part in our study, as earthworms significantly reduced the germination of two species with the largest seeds (i.e., bitternut hickory and bur oak). For these two species, we did not detect any seed burial but rather the opposite, that is, earthworm activity unearthed these larger seeds. Combined to the removal of the surface litter by earthworms, it is possible that a lower germination rate for these two species resulted from desiccation due to exposure. Regardless of the mechanism, we posit that selective seed caching and/or seed predation and/or seed desiccation occurring under field conditions could alter tree recruitment

Table 2
The effect of earthworms (− EW *vs.* + EW) on % survival of tree seedlings and tomato plants as determined by logistic regressions for proportional data with binomial distributions.

Species	No. of seeds germinated		No. of surviving seedlings		% Survival			
	−EW	+EW	−EW	+EW	−EW (%)	+EW (%)	*t*-value	$P > \|t\|$
Tomato	154	91	148	37	96	41	6.86	**<0.001**
Sugar maple	137	135	79	107	58	79	−1.74	0.120
Red maple	120	105	58	20	48	19	2.98	**0.018**
Balsam fir	118	71	109	48	92	68	4.14	**0.003**
Black spruce	110	48	28	6	25	13	1.53	0.164
Bur oak	94	44	94	44	100	100	n.a.	n.a.
Jack pine	86	37	36	15	42	41	0.38	0.712
White spruce	75	31	37	8	49	26	3.06	**0.016**
White pine	69	26	64	21	93	81	1.27	0.239
American elm	41	41	32	30	78	73	−0.36	0.727
Bitternut hickory	22	13	20	12	91	92	excluded	excluded
Yellow birch	17	9	9	2	53	22	excluded	excluded
Paper birch	14	10	7	4	50	40	excluded	excluded
Tamarack	14	4	9	1	64	25	excluded	excluded
East. white cedar	10	23	2	6	20	26	excluded	excluded

Species that had less than 15% seed germination in one (or both) earthworm treatment were excluded from the analyses; no *t*-value was computed for bur oak (n.a. = not applicable) because perfect data (i.e., all replicates have 100% survival) cannot be analyzed with a *t*-test; n.s. = not significant; statistically significant ($P < 0.05$) comparisons are highlighted in bold.

dynamics in southern Quebec. Equally of concern is the fact that the five conifer species whose seed germination was reduced by earthworms (i.e., balsam fir, black spruce, jack pine, white spruce and white pine) have a natural range that extends north into the boreal forest, where the presence of earthworms in previously earthworm-free soils was recently reported (Cameron and Bayne, 2009).

Although earthworms may favor the growth of some herbaceous plants and tree seedlings (e.g., Haimi et al., 1992; Milcu et al., 2006), we did not observe a positive effect on seedling biomass due to earthworms. In fact, seedling survival of three tree species was significantly reduced in the presence of earthworms. The main mechanism that we observed for the reduced survival was the downward transport and burial of seedlings in earthworm burrows. The question, then, is why did some tree species resist to this disturbance? A likely explanation is seedling size, which is related to seed size. This is corroborated by the fact that survival of the two species with the largest seed size (i.e., bur oak and sugar maple) was not affected by earthworms. Likewise, bitternut hickory seedlings (i.e., larger seeds than sugar maple) also had relatively high survival rates, although low germination rates prompted us to exclude this species from our analyses. Another possible way by which seedlings may escape earthworm disturbance is by producing chemical compounds that incite avoidance. While there is little direct empirical evidence for this, it is known that earthworms preferentially aggregate under certain plant species (e.g., Westernacher and Graff, 1987) and that their growth rates are linked to the chemical quality of the plant litter they consume (Bradley et al., 2011).

The fact that seed germination and seedling survival of sugar maple were unaffected by the presence of earthworms came as a surprise to us, as previous field studies had shown a decrease in the recruitment of this species along invasion fronts of *Lumbricus* sp. (Hale et al., 2006; Holdsworth et al., 2007; Corio et al., 2009). Perhaps this antagonist effect observed under field conditions is related to a decrease in sugar maple root colonization by arbuscular mycorrhizal fungi (AMF) due to earthworms, as reported by Lawrence et al. (2003). Fully beneficial AMF networks most likely take more time to establish than the time allotted in our study, which would preclude any possible effects of earthworms on AMF. Furthermore, AMF are expected to provide benefits to seedlings only in stressful environments, which may not have occurred in our microcosms. Another possible explanation for the discrepancy between our results and previous field studies is that extensive litter consumption by earthworms in the field may eventually expose the shallow sugar maple root system to loss of moisture (Corio et al., 2009). Our study did not allow for this to occur, as microcosms were regularly watered and replenished with litter.

Past studies have shown that earthworms exert variable effects on average seed germination dates. For example, Tomati et al. (1988) and Ayanlaja et al. (2001) reported earlier seed germination due to earthworm compounds breaking seed dormancy (e.g.,), whereas Grant (1983) reported delayed seed germination after the gut passage through *L. terrestris*. Likewise, our study revealed significant yet divergent effects of *L. terrestris* on the germination of 3 of the tested tree species. If such idiosyncratic changes in seed germination dates were to occur under natural field conditions, it could possibly lead to unpredictable changes in tree community assembly due to stochastic changes in establishment and growth conditions at the time of germination.

Diamond (1986) provided an insightful analysis of the strength and weaknesses of laboratory (or greenhouse) microcosm experiments, relative to field experiments and natural field surveys. Microcosm experiments allow us to control experimental conditions thereby maximizing the variability ascribed to experimental factors (i.e., high precision); they lack, however, in realism and generalizability (i.e., low accuracy). Thus, our study could be criticized for its artificial conditions. For example, Milcu et al. (2006) performed a similar microcosm study using herbaceous plant species and earthworm (also *L. terrestris*) densities approximately 4 times lower than ours. The earthworm density that we used (i.e., 509 individuals m^{-2} at furrow depth) was conceived to verge on the highest densities (i.e., 466 individuals m^{-2} at furrow depth) of mixed earthworm communities (that included *L. terrestris*) observed by Kernecker (2013) in mixedwood forests of southern Québec. Our experimental conditions were meant, therefore, to represent realistic, albeit above average, earthworm densities in southern Quebec. Thus, the value of our study is in showing the relative vulnerability of seeds and seedlings of different tree species to earthworm disturbances, rather than in providing data that immediately can be extrapolated to the real world. In a forthcoming paper, we will report on an extensive field survey that will draw some parallels between the microcosm experiment reported here, and the relationship between earthworm densities, soil properties and understory plant community structure.

Acknowledgments

This study was made possible thanks to a “Team Grant” awarded by the Fonds québécois de la recherche sur la nature et les technologies.

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