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Earthworm-mediated maternal effects on seed germination and seedling growth in three annual plants

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ABSTRACT

Many ecological studies have pointed out maternal effects in plants and shown that plant maternal environment influences germination of their seed and subsequent seedling growth. However, few have tested for maternal effects induced by soil macroorganisms. We tested whether two earthworm species (*Aporrectodea caliginosa* and *Lumbricus terrestris*) trigger such maternal effects on seed germination and seedling growth of three plant species (*Veronica persica*, *Poa annua* and *Cerastium glomeratum*). Our results show that, through maternal effects, *A. caliginosa* enhanced seed germination (*V. persica* and *P. annua*) and seedling growth (*C. glomeratum* and *P. annua*) while *L. terrestris* reduced seed germination only in *V. persica*. In some cases, the increase in germination rates of seeds produced in the presence of earthworms was associated with a reduction of nitrogen content in seeds. These results show that earthworms induce maternal effects in plants and that the size and direction of these effects depend on the combination of plant and earthworm species.

1. Introduction

The phenotype of plant individuals is determined not only by their genotype and environment but also by maternal effects, i.e. the direct contribution of the maternal phenotype to the phenotype of its offspring. Indeed, the tissues immediately surrounding the developing embryo and endosperm are all maternal. These tissues, the integuments of the ovule and the wall of the ovary form the seed coat, the fruit and accessory seed structures such as the hairs, awns and barbs. They are important determinants of seed dormancy, dispersal, and germination traits (Roach and Wulff, 1987). Variation in these traits, such as germination rates, seed survival or seedling growth rate, can carry over to influence the earliest life stages through a transgenerational plasticity (Weiner et al., 1997; El-Keblawy and Lovett-Doust, 1998). Such effects may also influence later stages. Indeed, a small initial advantage – for instance earlier germination – for some seedlings may be maintained or amplified by competition (Weiner, 1990; Miao et al., 1991).

Several studies have shown that properties of the maternal abiotic environment such as light intensity (Galloway and Etterson, 2007; Contreras et al., 2008), temperature (Alexander and Wulff, 1985) and availability of soil nutrients (Wulff and Bazzaz, 1992; Wulff et al., 1994) lead to maternal effects. These characteristics have in turn been shown to influence seed germination and subsequent seedlings growth (Roach and Wulff, 1987). Soil macroorganisms often influence plant growth either directly or indirectly, through modifications of soil properties (Lavelle and Spain, 2001). They are thus likely to cause maternal effects in plants as any biotic or abiotic environmental feature impacting plant growth and resource allocation (Roach and Wulff, 1987). Yet, so far, it seems that no study has focused on the existence of such a maternal effect mediated by soil macroorganisms. Such an effect would constitute a new and original example of aboveground–belowground interaction. We have tested for the existence of such an interaction in the particular case of earthworms.

Although some studies have reported negative effects of earthworms on plants in North America (Hale et al., 2006, 2008), earthworms are generally known to affect positively plant growth, through five main mechanisms (Brown et al., 2004): (1) increased

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mineralization of soil organic matter, which increases nutrient availability (Bohlen et al., 2002, 2004), (2) change in soil structure (Brown et al., 2004), (3) production of plant growth regulating substances (Nardi et al., 1988; Muscolo et al., 1999), (4) stimulation of symbionts (Doube et al., 1994) and (5) biocontrol of pests and diseases (Blouin et al., 2005). These mechanisms affect not only plant biomass but their resource allocation, as well (Scheu, 2003; Laossi et al., 2009). Earthworms, thus, modify the shoot/root ratio (Scheu, 2003; Eisenhauer and Scheu, 2008), and the allocation to seed production. They modify the number of seeds produced (Poveda et al., 2005a; Laossi et al., 2009) and seed size (Poveda et al., 2005b). They have been shown to modify the C/N of vegetative organs (Eisenhauer and Scheu, 2008) and have thus also been shown to impact the seed nutrient content (Atlavinyte and Vanagas, 1982). Since earthworms are likely to affect various seed traits, they should lead to maternal effects. They should, in other words influence the germination of seeds produced by plants grown in their presence or the growth of seedlings germinating from these seeds. However, no study has ever tested the existence of such an earthworm-mediated maternal effect in plants. We thus tested the effect of an anecic (*Lumbricus terrestris* L.) and an endogeic (*Aporrectodea caliginosa* (Savigny)) earthworm species and the effect of the two species in combination on the germination of seeds and subsequent seedling growth. This has been tested in three annual plants (grassland species) belonging to two functional groups (*Poa annua* L. a grass; *Cerastium glomeratum* Thuill. and *Veronica persica* Poiret, two forbs).

It is known that anecic and endogeic earthworms have distinct influences on soils (Jégou et al., 1998; Brown et al., 2000). They are therefore likely to have different effects on plant growth. Endogeic earthworms keep moving inside the soil to feed on soil organic matter while anecic feed on plant litter at the soil surface and tend to stay in the same burrow. Anecic earthworms fragment plant litter and incorporate it into the soil where it can subsequently be ingested by endogeic earthworms. Such an interaction can lead to higher mineralization and plant growth (Jégou et al., 1998; Brown et al., 2000). Earthworm effects on plant growth vary with the identity of plant species and with the functional groups to which they belong (Brown et al., 2004; Eisenhauer et al., 2009). The germination of the seeds of plant species belonging to different functional groups is thus likely to be affected differently by earthworms through maternal effects. The general purpose of this study was to determine whether earthworms induce maternal effects and to make a first assessment of the frequency of these effects using more than one plant and earthworm species. We tested the existence of maternal effects based on results of a previous experiment (Laossi et al., 2009) in which we found that *L. terrestris* but not *A. caliginosa* enhanced the growth of *P. annua* and *V. persica* and increased seed mass of *V. persica*. No significant earthworm effect was found for *C. glomeratum* (Laossi et al., 2009). We thus expected that earthworm positive effects on biomasses would lead to maternal effects and conversely that the absence of effect on biomasses leads to an absence of maternal effect. We thus made three hypotheses: (1) *L. terrestris* but not *A. caliginosa* induces maternal effects. *L. terrestris* enhances through these maternal effects (2) seed germination and (3) seedling growth of *P. annua* and *V. persica* but not *C. glomeratum*.

2. Materials and methods

2.1. Experiment setup

Seeds used in the present experiment come from a previous experiment (Laossi et al., 2009) which used monocultures (4 plants per microcosm) of *P. annua, V. persica* and *C. glomeratum*. Monocultures of parent plants were grown in a greenhouse according to four earthworm treatments: no earthworm (control), in the presence of *A. caliginosa* (AC), in the presence of *L. terrestris* (LT) or in the presence of both earthworm species (LT + AC). There were five replicates for each earthworm treatment; there were thus 20 microcosms for each plant species. Microcosms consisted of PVC pots (diameter 18 cm, height 17 cm) filled with 3 kg of soil that were daily watered during 7 weeks with 12.5 ml and with 25 ml from week 8 to week 15- the end of the experiment. The soil used for both studies was a sandy cambisol supporting a wet meadow at the ecology station of the ENS – Ecole Normale Supérieure – at Foljuif in France (Laossi et al., 2009);organic matter content 2.55%, C/N 12.4, carbon content 1.47%, total nitrogen content 0.12%, pH 5.22. The soil was air-dried, sieved (2 mm), homogenized and maintained four months without earthworms before initiating the experiments.

Sixty Petri dishes were each filled with 10 g of soil and placed in a greenhouse. Seeds produced in the different earthworm treatments can therefore be considered to be grown in a common environment that has not been influenced by earthworm activities. Each Petri dish received 10 seeds of one of the three plant species. These seeds were randomly sampled among the seeds collected on the four conspecific plants of each microcosm of the first experiment. Two weeks after sowing, the number of seedlings was counted to determine the germination rate (no difference in time of germination between treatments was found within plant species) and the height of seedlings was measured. Petri dishes were watered every day (3 ml) during the experiment to maintain the moisture of the soil. Petri dish position within the greenhouse was randomized every 2 days. Nitrogen concentration in mother seed was measured using a ThermoFinnigan Flash EA 1112 elemental analyzer (ThermoFinnigan, Milan, Italy).

2.2. Statistical analyses

Data were analysed with ANOVAs using SAS GLM procedure (Sum of squares type III, SS3) (SAS, 1990). A full model was first used to test all possible factors (“AC”, “LT” and “plant species”) and all interactions between these factors (Table 1). To determine the direction of significant effects, we used multiple comparison tests based on least square means (LSmeans, LSmeans SAS statement). The residuals of each model were analysed to test normality and homogeneity of variances. All tests were conducted with a significance level $\alpha = 0.05$.

3. Results

The statistical analysis (Table 1 and LSmeans comparisons) showed that both earthworm species induced maternal effects in

Table 1
General ANOVA table for the effects of earthworms (*A. caliginosa* – AC and *L. terrestris* – LT) and plant species on the seed germination, on the height of seedlings and N content of seeds. Significant *P*-values are presented in bold. Total df = 59.

	df	Seedling height		Seed germination		Seed *N* content	
		F	*P*	*F*	*P*	*F*	*P*
AC	1	15.63	**<0.001**	62.16	**<0.001**	17.07	**<0.001**
LT	1	0.00	0.97	2.16	0.15	12.8	**<0.001**
AC*LT	1	1.67	**<0.0001**	11.16	**<0.001**	19.43	**<0.001**
Plant species	2	76.68	0.20	28.41	**<0.001**	87.78	**<0.001**
LT*plant species	2	2.92	**0.03**	2.80	0.07	14.91	**<0.001**
AC*plant species	2	3.89	0.06	26.38	**0.002**	6.43	**<0.01**
AC*LT*plant species	2	0.22	0.80	5.48	**0.007**	4.17	**0.02**
r^2		0.79		0.81		0.85	

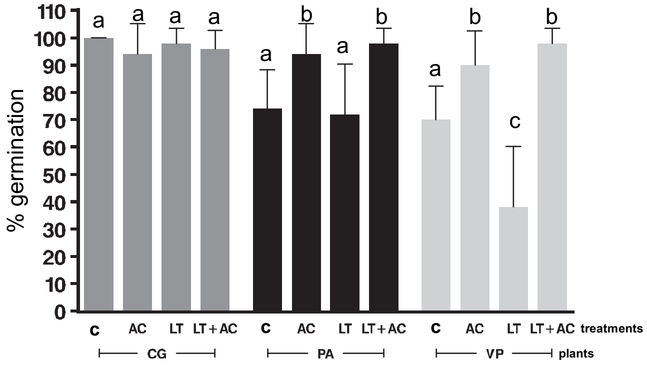

Fig. 1. Germination percentage of seeds coming from four maternal growth conditions. (AC, *A. caliginosa*; LT, *Lumbricus terrestris*; AC + LT, *A. caliginosa* + *Lumbricus terrestris*; C, Control). CG, *C. glomeratum*; PA; *P. annua*; VP; *V. persica* (mean + SD). For each plant species, bars with different letters are significantly different at $P < 0.05$.

the three plant species used with effects on their seed germination and/or seedling growth. N concentration in seeds was affected by earthworm treatments and this effect varied with plant species (significant AC × plants species, LT × plant species and AC × LT × plant species interactions).

In *P. annua* and *V. persica* seed germination was affected by maternal growth conditions. AC increased the germination rate of *V. persica* (+74%) and *P. annua* (+32%) seeds. On the contrary, *L. terrestris* decreased the germination rate of *V. persica* by 17% while when both earthworm species were present (AC + LT), the germination rate of *V. persica* was increased (+29%) (Fig. 1). Seedling height was affected by the maternal environment for *C. glomeratum* and *P. annua*, but not for *V. persica* (LSmeans comparisons). AC increased the height of seedlings of *C. glomeratum* (+23%) and *P. annua* (+27%) (Fig. 2).

Seed N concentrations of *V. persica* and *P. annua* were affected by AC, LT and the interaction AC × LT (Fig. 3). For *V. persica*, AC, LT and the combination of AC and LT reduced by 25% seed N concentration as compared to the control while, for *P. annua*, AC reduced N concentration by 22% and LT and the combination of LT and AC reduced it by 26% (Fig. 3).

4. Discussion

4.1. Synthesis of results

Contrary to our first hypothesis (see Introduction), *A. caliginosa* as well as *L. terrestris* induced maternal effects. Moreover, the main (and positive) induced maternal effects found are due to *A. caliginosa* while *L. terrestris* induced a maternal effect only on seed germination of *V. persica* (negative effect). Similarly, contrary to our second and third hypotheses, although earthworms did not affect the growth and seed size of *C. glomeratum* (Laossi et al., 2009), the germination of its seeds and the growth of its seedlings were affected by *A. caliginosa* through maternal effects. Taken together, this shows that effects of earthworms on plant and seed biomasses are not good indicators of earthworm-induced maternal effects.

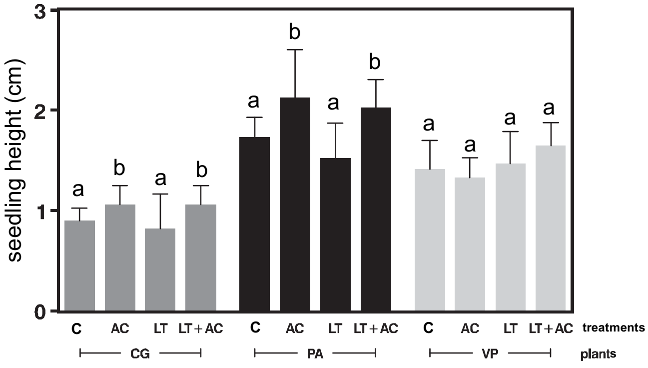

Fig. 2. Height of seedlings depending on the maternal growth conditions. (AC, *A. caliginosa*; LT, *Lumbricus terrestris*; AC + LT, *A. caliginosa* + *Lumbricus terrestris*; C, Control). CG, *C. glomeratum*; PA; *P. annua*; VP; *V. persica* (mean + SD). For each plant species, bars with different letters are significantly different at $P < 0.05$.

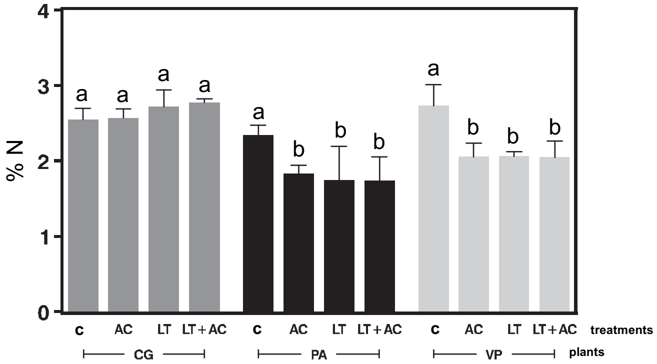

Fig. 3. Effect of earthworms on the nitrogen concentration in maternal seeds (AC, *A. caliginosa*; LT, *Lumbricus terrestris*; AC + LT, *A. caliginosa* + *Lumbricus terrestris*; C, Control). CG, *C. glomeratum*; PA; *P. annua*; VP; *V. persica* (mean + SD). For each plant species, bars with different letters are significantly different at $P < 0.05$.

4.2. Mechanisms of the observed maternal effects

Some of our results on seed germination and seedling growth can be explained by earthworm effects on seed characteristics. In our experiment, in the presence of AC, seeds of *P. annua* and *V. persica* contained less nitrogen and this probably explains partially their high germination rates (Laossi et al., 2009). This can be explained by observations showing that high nitrogen concentration in seeds can induce dormancy in some plant species (Luzuriaga et al., 2005; Roach and Wulff, 1987). Contrary to our second hypothesis, LT reduced the nitrogen concentration in *V. persica* seeds as well as their germination rate. This could be explained by the fact that in the previous experiment from which seeds were collected, LT also increased the seed weight of *V. persica* (Laossi et al., 2009). Although large seeds have often been shown to have higher germination rates, negative correlations between germination rates and seed size have also been reported for annuals (Baskin and Baskin, 2001). In addition to increasing the seed weight of *V. persica*, LT could also have induced modifications in seed structure and chemical composition that have not been measured and that could also be involved in the reduction in the rate of seed germination.

Other observed effect on seedlings cannot be explained by any of the seed characteristics we measured. Enhanced growth of *P. annua* and *C. glomeratum* seedlings from seeds produced in the presence of AC seems difficult to explain. First AC decreased the nitrogen content in *P. annua* seeds which has been shown to decrease seedling growth rate (Baskin and Baskin, 2001). Second, AC did not change the nitrogen content or the size of *C. glomeratum* seeds. This suggests that this earthworm species has changed other traits of *C. glomeratum* seeds that were not measured. Moreover, in the previous experiment, AC affected neither the growth of the three plant species nor their fecundity or the weight of their seeds (Laossi et al., 2009). This suggests that AC may affect in a subtle and not detected way the resource allocation of plants and may subsequently induce a maternal effect through modifications of their seeds.

Although LT increased the growth and N content of mother plants of *P. annua* in the experiment from which seeds were collected (Laossi et al., 2009), contrary to our expectation, it did not affect its seed germination and seedling growth through maternal effect. Moreover, LT increased the growth of mother plants of *V. persica* (Laossi et al., 2009) but decreased the germination of seeds through maternal effects. This shows that this earthworm species does not induce a maternal effect in all plant species. In addition, plant species which benefited during the first generation from its presence are not necessarily favoured by a maternal effect during the second generation. This could be due to the different resource allocation strategies evolved by plants. For example, earthworms (or any other soil treatment) may directly allow a plant to increase the nitrogen concentration in its leaves, but this plant does not necessarily allocate more nitrogen to its seeds. In addition, earthworms can directly trigger changes in plant resource allocation that are not correlated with earthworm effects on nutrient availability (Blouin et al., 2006; Noguera, 2009), i.e. through the release in the soil of phytohormones (probably produced by bacteria stimulated by earthworm activities) (Muscolo et al., 1999).

Earthworm effects on plant physiology (Wurst et al., 2003; Eisenhauer and Scheu, 2008) and resource allocation (Poveda et al., 2005a; Laossi et al., 2009) is likely to affect the chemical composition of seeds (Baskin and Baskin, 2001). Since the abiotic environment has already been shown to influence many other seed traits (e.g. seed structure, teguments thickness etc.) (Baskin and Baskin, 2001), effects of earthworms on soil properties as well as their effects on plant physiology should also affect such traits. Hence, undocumented earthworm-mediated modifications in the seed structure and in their content in various chemical compounds could both explain the positive effect of AC on the growth of *C. glomeratum* seedlings. It is however so far impossible to predict which plant species could benefit from the earthworm-mediated maternal effects we have pointed out, and how these effects should covary with earthworm species or functional group. Nevertheless, this type of maternal effect is an example of aboveground–belowground interaction that has hardly been recorded before.

Maternal effects might allow offspring to be adequately cued for their environment, if offspring and maternal environment properties are correlated (Roach and Wulff, 1987). Earthworm-mediated maternal effects and their direct effects on seed germination and offspring growth might interact. Of course, the germination rate of seeds and seedling growth vary with seed characteristics (influenced by their maternal environment) and soil properties and possible interactions between the two. Do the seeds produced in the presence of earthworms germinate better in a soil where earthworms are present? If it was the case, the maternal effect might correspond to an adaptive plasticity allowing offspring to be better fitted to their environment (Marshall and Uller, 2007).

5. Conclusion

Our study confirmed the existence of maternal effects induced by earthworms on seed germination and seedling growth. However, other experiments are needed to study underlying mechanisms in details. Four issues remain totally open: Can earthworm-mediated maternal effects influence plant growth after the seedling stage (Miao and Bazzaz, 1990)? How does interspecific competition between seedlings modulate such maternal effects? Can these effects persist in the third generation (Alexander and Wulff, 1985; Miao et al., 1991)? Are earthworm-induced adaptive?

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