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Effects of an endogeic and an anecic earthworm on the competition between four annual plants and their relative fecundity

Kam-Rigne Laossi [a,*], Diana Cristina Noguera [a], Abraham Bartolomé-Lasa [a],
Jérôme Mathieu [a], Manuel Blouin [b], Sébastien Barot [a,c]

[a] *Bioemco (UMR 7618) – IBIOS, Centre IRD d'Ile de France 32, avenue Henri Varagnat, 93140 Bondy Cedex, France*
[b] *Bioemco (UMR 7618) – IBIOS/Université Paris 12, 61 avenue du Général De gaulle, 94010 Créteil Cedex, France*
[c] *IRD, Bioemco (UMR 7618), Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris cedex 05, France*

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ABSTRACT

Competition between plants for essential resources determines the distribution of biomasses between species as well as the composition of plant communities through effects on species reproductive potentials. Soil organisms influence plant competitive ability and access to resources; thus they should modify plant community composition. The effects of an endogeic (*Aporrectodea caliginosa*) and an anecic (*Lumbricus terrestris*) earthworm species on the competition between grass (*Poa annua*), two forbs (*Veronica persica and Cerastium glomeratum*) and legume (*Trifolium dubium*) were investigated in a greenhouse experiment. We established two types of plant communities: monocultures and polycultures of the four species. *L. terrestris* increased the biomass of *P. annua* and *V. persica* (in monocultures as well as in polycultures). However, the presence of *L. terrestris* allowed the grass to produce the highest biomass in polycultures suggesting that this earthworm species promoted the growth of *P. annua* against the other plant species. In monocultures as well as in polycultures, the presence of *L. terrestris* to increased the number of seeds of *T. dubium* and the total seed mass of *V. persica*. These results suggest that *L. terrestris* enhanced the short term competitive ability of *P. annua* by promoting its growth. The increased number of seeds of *T. dubium* in the presence of *L. terrestris* suggests that this earthworm species could enhance the long-term competitive ability of this legume and may increase its number of individuals after several generations.

1. Introduction

Soil organisms are known to affect plant growth by enhancing mineralization of soil organic matter, modifying soil physical and chemical properties, consuming plant roots or maintaining symbiotic and parasitic relations with plants (Lavelle and Spain, 2001; Wardle et al., 2004; Bardgett, 2005). Many studies have been published on this topic. Most of them examine effects of soils organisms on plant growth, are short term microcosm experiments that focus on plant monocultures (Scheu, 2003). However, over a longer period, during an entire generation, soil organisms may also influence plant survival and fecundity (Poveda et al., 2005a,b). Moreover, few experiments have determined the effect of soil organisms on plant communities and compare the response of plant species when grown in monocultures and in polycultures (Bliss et al., 2002; Bonkowski and Roy, 2005; Eisenhauer et al., 2008a,b). Since these responses might be different, soil organisms may change the relative competitive ability of plant species and not only their growth and reproductive potential in monocultures (Bever, 2003; Reynolds et al., 2003; Wurst et al., 2004; Eisenhauer et al., 2008a,b). Both interspecific competition and soil organisms are likely to change interactively the plant hierarchy in growth, survival and reproductive ability. This may simply occur because a small initial advantage in their growth allows them to capture a higher proportion of resources (Weiner, 1990). It may also occur when soil organisms release mineral nutrients that benefit all plant species when grown in monocultures, but mostly benefit the species that are more efficient at absorbing these nutrients in polycultures. Taken together, the comparison of soil organism effects on the growth and reproduction of different plant species in monocultures and polycultures is necessary to predict the long-term effect of soil organisms on plant communities.

Among soil organisms, earthworms are known to generally affect positively plant (Scheu, 2003; Brown et al., 2004). They are also known to affect seed germination (Grant, 1983; Decaëns et al., 2003; Milcu et al., 2006). However, few studies have investigated their effects on plant competition and plant community structure –

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* Corresponding author. Tel.: +33 1 44 32 37 03; fax: +33 1 48 02 59 70.
E-mail address: laossi@bondy.ird.fr (K.-R. Laossi).

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as compared to the abundance of studies on single plant species (Scheu, 2003; Brown et al., 2004). To our knowledge, none has tested the effects of earthworms on plant competition taking into account the whole plant life-cycle (from germination to seed production). Furthermore, despite the evidence that different functional groups of earthworms can differentially affect plant growth (Lavelle et al., 1998), no study has tested for the effect of earthworm species belonging to different functional groups and their interaction on plant performance in the same laboratory experiment.

We performed a microcosm experiment and we evaluated the effects of an anecic and an endogeic earthworm species on seed germination, plant growth and seed production in four annual plant species growing in monocultures (intraspecific competition) or polycultures (interspecific competition). 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 (Lavelle et al., 1998). 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). We hypothesized that different plant species belonging to different functional groups should be affected differently by earthworms (Eisenhauer et al., 2008a,b). For example, legumes are supposed to be relatively insensitive to earthworm effects via an acceleration of mineralization since they have a direct access to atmospheric nitrogen (Brown et al., 2004). Specifically we tested four hypotheses: (1) earthworms change plant relative competitive ability in term of growth; (2) earthworms also influence plant relative reproductive potentials; (3) *Aporrectodea caliginosa* (endogeic earthworm) and *Lumbricus terrestris* (anecic earthworm) affect differently plant competition; (4) there is an interactive effect between *A. caliginosa* (an endogeic species) and *L. terrestris* (an anecic species) on plant growth and reproductive potential.

2. Materials and methods

2.1. Experiment set up

Experiment containers (microcosms) consisted of PVC pots (diameter 18 cm, height 17 cm). Drains at the bottom of pots were covered with 1 mm plastic mesh to prevent earthworms from escaping. Soil was collected at the ecology station of the Ecole Normale Supérieure at Foljuif (France). It is a sandy cambisol supporting a meadow (OM = 2.55%, C/N = 12.4, C content 1.47%, Ntotal = 0.12%, pH = 5.22). A total of 100 microcosms were filled with 3 kg of sieved (2 mm) dry soil. Before starting our experiment, the microcosms were watered regularly for two weeks and germinating weeds from the seedbank were removed. Prior to the addition of earthworms and seeds, 8 g of dried litter (72 h at 60 °C) of grass leaves were placed at the soil surface and 1 g was mixed with the first centimeter of soil. This constituted the essential food resource for the anecic earthworm species.

We used an anecic earthworm, *L. terrestris* (L.) (LT), and an endogeic earthworm, *A. caliginosa* (Savigny) (AC). These earthworm species are among the most abundant in temperate ecosystems (Edwards and Bohlen, 1996; Bohlen et al., 2004). LT was purchased in a store and AC was collected in the park of the IRD centre in Bondy (France). Our experiment had three earthworm treatments (AC, LT, AC + LT) and a control without earthworm. Five replicates were implemented for each treatment combination, resulting in 20 microcosms for the 4 earthworm treatments and for each plant treatment (see below). One individual of LT (4.2 ± 0.5 g) and four of AC (2.8 ± 0.4 g, i.e. total biomass of 4 AC individuals with gut contents) were introduced in each treatment including these species. The biomass of specimens added was equivalent to 165 g/m^2 and 110 g/m^2 for LT and AC respectively, which is comparable to the biomasses found in grassland ecosystems (Edwards and Bohlen, 1996).

Five days after introducing earthworms, 20 seeds of *Veronica persica*, *Trifolium dubium*, *Cerastium glomeratum* or/and *Poa annua* were sown, either in monocultures (4 × 20 microcosms) or in polycultures of the four species (20 microcosms). The seed size of the plant species were respectively 0.4 × 0.6 mm (±0.08) for *C. glomeratum*, 1.0 × 1.1 mm (±0.2) in *V. persica*, 1.1 × 1.3 mm (±0.1) in *T. dubium* and 1.9 × 1 mm (±0.1) in *P. annua* (obtained by measurement of 20 seeds of each plant species). Three weeks later, seedlings of each monoculture were counted to determine the germination rate. Four plants per microcosm (4 plants of the same species in monocultures, one plant of each species in polycultures) were kept (other seedlings were removed). Microcosms were weeded weekly during the experiment. Microcosms were watered during 7 weeks with 12.5 ml and from the eighth week to the end (week 15) with 25 ml each day. This allowed us to maintain the soil near its field capacity (this was checked through regular weighing of some pots).

2.2. Sampling

Seeds were harvested from plants as they matured. On week 15, shoots of the four species were cut at the soil surface and dried separately at 60 °C for 72 h. Roots were separated from soil by washing on a 600 µm mesh, but the roots of the individual plant species were not recognizable in polycultures. Individual dried shoot biomass and total root biomass were weighed. Twenty seeds from each plant were randomly selected and weighed as well as the biomass of all seeds. These data were used to calculate the number of seeds per plant and mean seed mass. 95% of the earthworms were recovered at the end of the experiment (77% of the total mortality was due to *A. caliginosa* [10 individuals] and 27% to *L. errestris* [3 individuals]). N concentration in plant leaves was measured using a ThermoFinnigan Flash EA 1112 elemental analyzer (ThermoFinnigan, Milan, Italy).

Table 1
General ANOVA table forthe effects of earthworms (AC and LT), plant species and composition (monocultures or mixtures) on shoot biomass, number of seeds, total seed mass and mean seed mass. *F*-values and the corresponding *p*-values are displayed. Data on seeds were log transformed.

	df	Shoot biomass	Number of seeds	Total seed mass	Mean seed mass
		F	*F*	*F*	*F*
AC	1	1.94	0.79	0.47	0.00
LT	1	10.66^{**}	1.30	1.78	0.09
Composition	1	63.07^{***}	3.81^{*}	35.39^{***}	103.46^{***}
Plant species	3	183.72^{***}	39.77^{**}	77.19^{***}	6.86^{***}
AC × LT	1	1.73	0.00	0.03	0.04
LT × plant species	3	12.46^{***}	2.23^{+}	4.40^{**}	4.41^{**}
AC × plant species	3	0.65	1.62	1.98	0.87
AC × composition	1	0.08	0.42	0.29	0.05
LT × composition	1	3.28	0.77	0.11	0.23
Composition × plant species	3	29.71^{***}	1.28	2.70	0.57
AC × LT × plant species	3	0.37	2.29^{+}	2.25	1.70
AC × LT × composition	1	0.00	0.02	0.20	0.90
AC × plant species × composition	3	0.50	0.57	1.65	0.68
LT × plant species × composition	3	6.07^{***}	0.23	0.14	0.33
AC × LT × plant species × composition	3	2.04	0.14	0.11	0.82
r^2		0.87	0.62	0.77	0.64

$^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$; $^{+}p < 0.1$.

Table 2
ANOVA table for the effects of earthworms (AC and LT) and plant species on the number of seedlings (seed germination), root biomass, total specific biomass and shoot-to-root ratio in monoculture. *F*-values and the corresponding *p*-values are displayed. Total df = 79.

	df	Number of seedlings	Root biomass	Total biomass	Shoot-to-root ratio
		F	*F*	*F*	*F*
AC	1	0.12	0.49	2.07	0.56
LT	1	60.38***	3.50*	4.32*	0.56
AC × LT	1	0.01	0.35	2.70	0.37
Plant species	3	107.81***	97.43***	139.40***	17.99***
LT × plant species	3	4.36**	3.20*	3.77**	1.20
AC × plant species	3	0.66	0.23	0.13	0.34
AC × LT × plant species	3	0.34	0.67	2.27	0.48
r^2		0.86	0.83	0.87	0.49

$^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

2.3. Statistical analyses

Data were analysed with ANOVAs using SAS GLM procedure (Sum of squares type III, SS3) (SAS, 1990). A full model was used to test all possible factors ("AC", "LT", "plant species" and "composition" i.e. monocultures or polycultures) and all interactions between these factors (Table 1). The factor "composition" indicates whether plant species are grown in polycultures or monocultures. Testing the interaction between this factor and earthworm effects allowed us to determine whether earthworm effects on plant depend on the nature of competition (intraspecific vs. interspecific). Similarly, testing the interaction between plant species and earthworm effects allowed us to determine whether plant species responded differently to earthworm species. Since roots of the four species were not distinguished in polycultures, analyses of specific root biomass and specific total biomass (shoot + root) were only achieved on monocultures (Table 2). Seed germination was also only analysed in monocultures (Table 2). In these analyses, biomasses from monocultures were divided by 4 to allow comparing monocultures and polycultures (since in monocultures we had 4 individuals of the same species while in polycultures we had one individual of each plant species). To determine the direction of significant effects, we used multiple comparison tests based on least square means (LSmeans, LSmeans SAS statement) but we only present the general outcome of these comparisons without displaying them in detail. The residuals of each model were analysed to test for normality and homogeneity of variances. Logarithm transformation was used for the number of seeds and seed mass. All tests were achieved with a significance level $\alpha = 0.05$.

3. Results

The statistical analysis (Table 1) showed that LT differently affected intra- and interspecific competition between the different plant species (significant LT × plant species × composition interaction). Reproductive parameters of the plant species, such as seed number and seed biomass were also differently affected by LT ($p < 0.1$). Earthworms did not affect the shoot/root ratio of any plant species and no simple effect of AC on plants was found.

At the end of the experiment we found a decline in earthworm biomass per microcosm when compared to the initial biomass, average final biomass of *L. terrestris* 2.62 g (−48%) and *A. caliginosa* 1.39 g (−51%). This is probably due to the low organic matter concentration of the soil in the case of *A. caliginosa*, and to the total disappearance of plant litter before the end of the experiment in the case of *L. terrestris*. We checked that earthworm biomass (initial

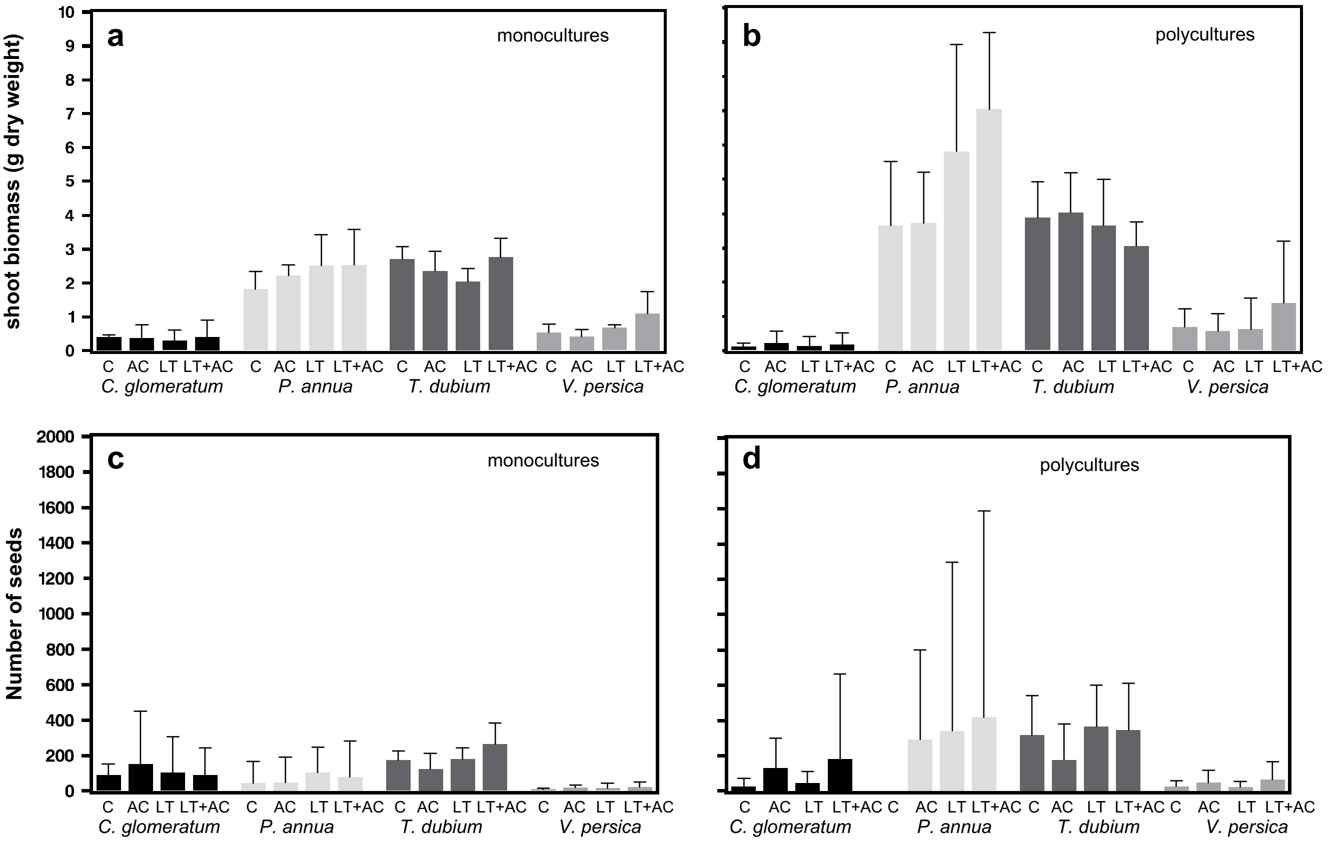

Fig. 1. Effects of earthworms on shoot biomass in monocultures (a) and polycultures (b), and on the number of seeds in monocultures (c) and in polycultures (d). C, control treatment; AC, *A. caliginosa* only; LT, *L. terrestris* only; LT + AC, combined treatment with *A. caliginosa* and *L. terrestris*. Means are displayed together with SD.

biomass as well as final biomass) did not affect plant performance ($p > 0.05$) so that earthworm biomasses were not taken into account in the other analyses.

The presence of LT increased the shoot biomass of *P. annua* (+36%) and *V. persica* (+80%). In *V. persica* the highest shoot biomass was obtained in the treatment with both earthworm species (Fig. 1a and b). Shoot biomasses of *T. dubium* and *C. glomeratum* were not affected by *L. terrestris* (Fig. 1a and b). Differences in shoot biomass between monoculture and polycultures were found for all plant species except *V. persica*. *P. annua* and *T. dubium* produced higher shoot biomass in polycultures than in monocultures, demonstrating that these species gained relative dominance in interspecific competition; while the opposite was found for *C. glomeratum*, which had a higher shoot biomass in monoculture (see Fig. 1a and b). The effects of the community composition on the shoot biomass of *P. annua*, however, depended on the presence of LT (Table 1, significant LT × plant species × composition interaction). The highest shoot biomass was found for *P. annua* in polycultures and in the presence of LT (detailed results not presented but see Fig. 1b). Its contribution to the community aboveground biomass increased in presence of the anecic earthworm (Fig. 3a).

The presence of LT increased the number of seeds per *T. dubium* individual by 60%. Also the highest number of seeds per plant was obtained in the treatment with both earthworm species. The presence of LT decreased (−42%) the mean seed mass of *T. dubium* (indicating that plants produced more but smaller seeds) and increased (+60%) the total seed mass of *V. persica* (LSmeans comparisons and significant LT × plant species interaction in Table 1). *T. dubium* and *V. persica* produced higher number of seeds in polycultures while the opposite was found for *C. glomeratum* (Fig. 1c and d). The total seed mass of *V. persica* (2.5 times) and *C. glomeratum* (5 times) were higher in monocultures than in polycultures and the mean seed mass of *C. glomeratum* was four times higher in monocultures.

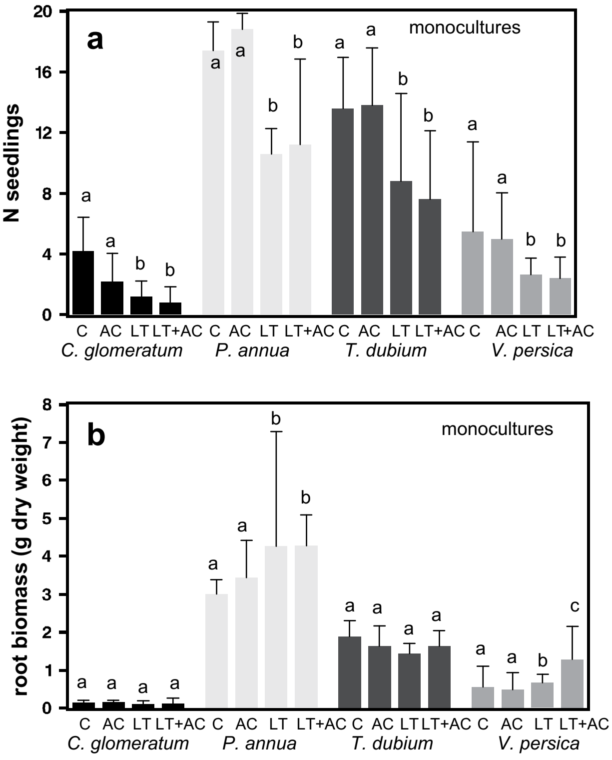

Fig. 2. Effects of earthworms on (a) the number of seedlings in monocultures, (b) root biomass in monocultures. C, control treatment; AC, *A. caliginosa* only; LT, *L. terrestris* only; LT + AC, combined treatment with *A. caliginosa* and *L. terrestris*. Bars with different letters are significantly different at $p < 0.05$ according to LSmeans comparisons. Means are displayed together with SD.

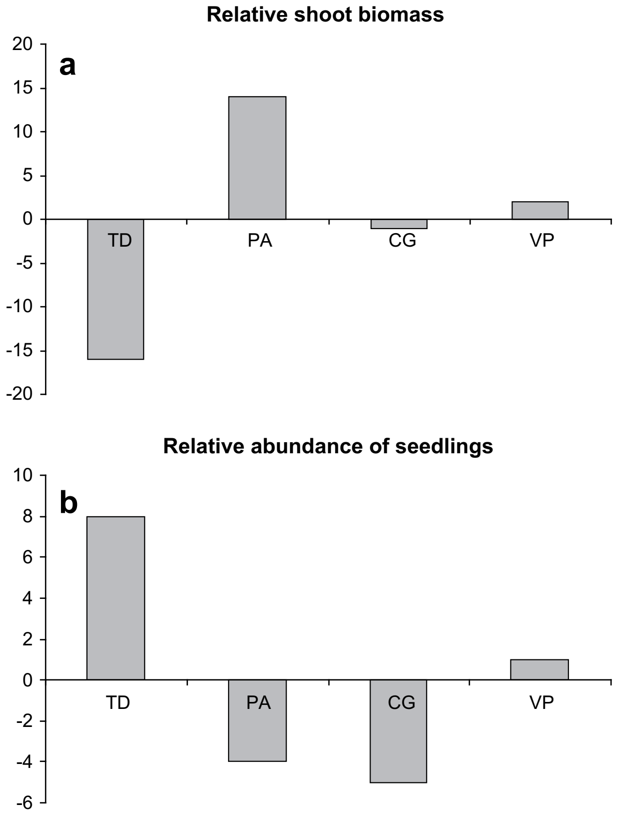

Fig. 3. Effect of the presence of LT on relative shoot biomass of each species (a) in the plant community calculated as [% in shoot biomass of the community; in presence of LT] − [% in shoot biomass of the community; in absence of LT] and (b) on the relative abundance of plant species in the hypothetical second generation community calculated as [% seedlings, i.e. germination × number of seeds; in presence of LT] − [% seedlings, i.e. germination × number of seeds; in absence of LT]. TD, *Trifolium dubium*; PA, *Poa annua*; CG, *Cerastium glomeratum*; VP, *Veronica persica*.

The presence of LT decreased the number of seedlings for all plant species in monocultures. However, plant species were affected differently (Fig. 2a and significant interaction LT × plant species in Table 2). The presence of LT decreased less the seed germination of *T. dubium* (−59%) and *P. annua* (−44.5%) than for *V. persica* (−88%) and *C. glomeratum* (−95%). LT increased the root biomass (+33%) and the total biomass (+27%) of *P. annua* while it did not affect the root and the total biomass of the other plant species (Table 2 and LSmeans comparisons).

Earthworm presence affected the nitrogen concentration in plant leaves (Table 3 and Fig. 4). LT activity increased the N content of *P. annua* (+14%) but decreased N content of *V. persica* (−25%). The presence of AC increased the N content in *C. glomeratum* (+44%) and *V. persica* (+33%).

Table 3
ANOVA table for the effects of earthworms (AC and LT) on the nitrogen content in plant leaves in mixture. *F*-values and the corresponding *p*-values are displayed. Total df = 19.

	df	*T. dubium*	*P. annua*	*C. glomeratum*	*V. persica*
		F	*F*	*F*	*F*
AC	1	0.78	3.29	19.02***	43.52
LT	1	3.72	4.91*	1.68	51.47***
AC × LT	1	1.48	0.34	14.21**	69.55***
r^2		0.26	0.34	0.68	0.92

$^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

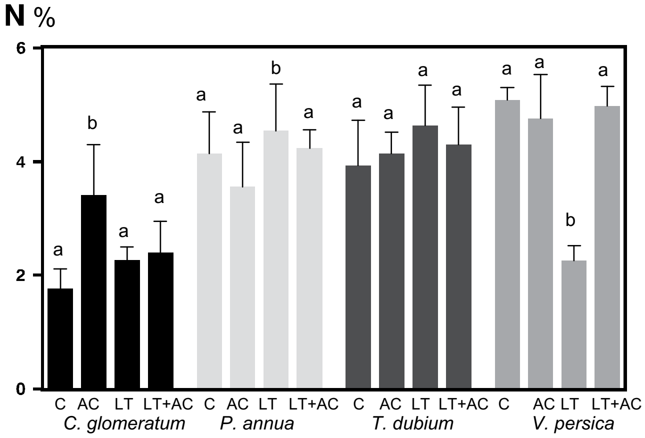

Fig. 4. Effects of earthworms on N concentration in leaves of *Trifolium dubium*; *Poa annua*; *Cerastium glomeratum* and *Veronica persica*. Bars with different letters are significantly different at $p < 0.05$ according to LSmeans comparisons. Means are displayed together with SD.

4. Discussion

Taking into account the whole life-cycle of four annual plants, we have found that (1) LT decreased less the germination of *T. dubium* and *P. annua* relative to the two other plant species. (2) LT increased the biomass production and the nitrogen concentration in *P. annua* relatively to the three other plants species. (3) LT increased the production of seeds by *T. dubium* relative to the three other plant species. (4) The presence of AC and its interaction with LT (AC × LT) increased the nitrogen concentration of the aerial system of *C. glomeratum* and *V. persica*. However, despite this effect, AC did not affect the growth and seed production of the four plant species.

4.1. Earthworm effects on plant competition

Our findings on seed germination are consistent with those of Milcu et al. (2006) showing that LT reduced strongly the germination rate of small seeds such as the seeds of *Poa pratensis*, *Trifolium repens*, *Bellis perennis* and *Festuca pratensis*. Such a decrease in the germination rate might either be due to seed burrowing by earthworms or to the fact that seeds are damaged during their ingestions by earthworms (Mc Rill and Sagar, 1979; Grant, 1983). Besides, the main positive effects of earthworms on plant growth found in our study are consistent with others showing that earthworms enhance the growth of grasses while legumes barely responded to earthworms (Wurst et al., 2003, 2008; Brown et al., 2004; Eisenhauer et al., 2008a,b). Since legumes fix atmospheric nitrogen through their association with *Rhizobium*, they are more independent than other plants from the availability of soil nitrogen. The small effect of the anecic earthworm on *P. annua* shoot biomass in monoculture was amplified when the grass was in mixture probably as a result of interspecific competition: in competition with other plant species *P. annua* is likely to have absorbed a greater share of the nutrient made available by LT than the other plant species. This argument is supported by the fact that LT increased N concentration in *P. annua* leaves. The increased seed production of *T. dubium* in the presence of LT could be an indirect result of a stimulation of symbiotic fixation by earthworms which has already been pointed out (Doube et al., 1994). It is less clear why *C. glomeratum* and *V. persica* did not react to the likely increase in mineral nutrient availability in presence of LT either in monoculture or mixture.

The positive effect of an earthworm species on the production of seeds has previously been reported by Poveda et al. (2005a,b) for wild mustard. However, the effect of earthworms on plant fecundity (and not only the seed biomass) has rarely been examined. In our case, LT did not increase the biomass of whole *T. dubium* individuals but enhanced the productions of seeds (+60%) that were smaller. This shows that LT changes the resource allocation of *T. dubium* in such a way that it increased its fecundity. This result might explain why the studies reporting a promotion of clover by earthworms were generally long-term (more than 9 months and at least two plants generations) experiments (Hopp and Slatter, 1948; Thompson et al., 1993) while short term experiments usually show very small effects of earthworms on the biomass of legumes (Brown et al., 2004; Kreuzer et al., 2004).

Contrary to many former results (Wurst et al., 2003, 2005; Kreuzer et al., 2004), no effect of AC and few effects of the interaction between AC and LT were found on plant growth and reproduction in this study. This general pattern could be due to the low content of the soil in organic matter. Indeed, in such a soil endogeic earthworms do not necessarily promote plant growth because there is little organic matter to be mineralized, thus few nutrients are released. However, AC increased the N content of the aerial system of *C. glomeratum* and *V. persica*. This suggests that AC can influence the physiology of these plants, for example the allocation of N to the root and aerial systems without affecting their biomass. Up to our knowledge, despite the fact that plant nutrient allocation has been widely studied (Lambers et al., 1998), predicting such effects of soil organisms on this allocation and determining the involved mechanisms remains very difficult.

Taking into account LT effect on seed germination and on seed production in our experiment we can theoretically estimate that, in similar conditions, this earthworm species should increase, at least at an early stage of the second generation, the abundances of *T. dubium* and *V. persica* seedlings in the community but decrease the abundances of *C. glomeratum* and *P. annua* (see Fig. 3a). These results contrast with LT effect on the contribution of each species to the shoot biomass of the whole community (+14.8% for *P. annua*, −15% for *T. dubium*, Fig. 3a; comparison between Fig. 3a and b). Hence, earthworm could promote one species at the individual scale, on a short time scale (a generation), but disadvantage this species at the community scale, on a longer time scale (across-generations) and vice versa. We have thus pointed out a potentially important mechanism but making predictions on the long-term effect of earthworms on plant community structure in the field would require taking into account many other processes, for example the effects of other organisms such as herbivores which can alter plant responses to earthworms (Poveda et al., 2005a,b).

4.2. Plant community type effects on plant growth

Plants responded differently when grown in monocultures and polycultures. Polycultures had a higher total biomass than monocultures (detailed statistical analysis not displayed in the results section). This suggests that the four species communities were dominated by the effect of complementary resource use, which decreased the negative impact of interspecific competition. More specifically, both *T. dubium* and *P. annua* produced higher shoot biomasses by individual in polycultures, which suggests that their relation is driven by complementary resource use. This could be explained by the fact that grasses are generally limited by N and legumes by P (Hooper, 1998). On the contrary, when *T. dubium* and *P. annua* were grown with *C. glomeratum*; the shoot biomass of the later decreased. This suggests, that *C. glomeratum* is a poorer competitor than the two other species, and that its relation with these species is driven by the competition for common resources. In the same vein, *T. dubium* and *C. glomeratum* individuals produced respectively more and less seeds and shoot biomass in interspecific than in intraspecific competition. This is probably merely a consequence of the respectively high and low abilities of these two species to capture resources, and thus of their short term competitive abilities. On the contrary, interspecific competition did not significantly change the biomass of *V. persica* but increased the number of seeds produced by individual and decreased the total seed biomass (i.e. interspecific competition led to a shift in the resource allocation). This should increase the number of *V. persica* individuals within the community in the next generation and thus could enhance its across-generation competitive ability. Up to our knowledge such a response to interspecific competition has never been pointed out, and very few studies have tackled the issue (Aarssen and Keogh, 2002).

4.3. Conclusions

Through its effect on germination and seed production LT is likely to modify the demography of the different plant species and to change the relative abundance of the plant species in the community after several generations. Earthworms can thus be considered to modulate long-term competition between plants. These results show that belowground–aboveground interactions have not only short term effects on plant growth (Wilson et al., 2001). They should also have demographic consequences that have so far been seldom studied. This emphasizes the importance of studying the effects of belowground–aboveground interactions on the whole life-cycles of plants, because first these effects might differ at different stages of the life-cycle and second to predict their consequences on plant demography and plant community structure (Wurst et al., 2008). In our case, it still remains to study the effect of earthworms on plant survival after the seedling stage. The effect of soil organisms on biomass production has often been documented, however, their effects on resource allocation are seldom documented, and there is so far no theory to predict how plant species shift their resource allocation strategies. For example the percentage of biomass and nitrogen allocated to seeds and the size of each seed, in the presence of different soil organisms must be investigated. Such a theory is nevertheless required to predict plant population or plant community responses to soil organisms.

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