Soil Biology & Biochemistry 41 (2009) 1668–1673

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

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

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A R T I C L E I N F O

Article history:
Received 26 December 2008
Received in revised form
6 May 2009
Accepted 18 May 2009
Available online 13 June 2009

Keywords:
Aboveground–belowground interactions
Earthworms
Plant competition
Plant fitness
Plant community

A B S T R A C T

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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doi:10.1016/j.soilbio.2009.05.009

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

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; +$p < 0.1$.