



Earthworms modify plant biomass and nitrogen capture under conditions of soil nutrient heterogeneity and elevated atmospheric CO₂ concentrations



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ABSTRACT

Earthworms modify the way roots respond to soil nutrient patchiness. However, few studies have evaluated the joint effects of earthworms and soil heterogeneity on plant community biomass and species dominance, and none of them have assessed the influence of different patch features and environmental conditions on such effects. We evaluated how soil nutrient heterogeneity, earthworms (*Eisenia fetida*), organic material quality (¹⁵N-labelled leaves and roots of contrasting C: N ratios) and elevated atmospheric CO₂ concentrations (phytotron chambers) affected the resource-use strategy, biomass and species dominance of mixtures formed by *Lolium perenne* L. and *Plantago lanceolata* L. Soil heterogeneity decreased N capture from the organic material, especially in the presence of earthworms. Mixtures experienced a 26 and 36% decrease in shoot and root biomass when earthworms were added to the heterogeneous microcosms, but only with high quality organic material. The dominance of *L. perenne* was lower under conditions of elevated CO₂, nutrient heterogeneity and earthworms. Our data suggest that earthworms can neutralize positive plant growth responses to soil heterogeneity by exacerbating decreases in the supply of N to the plant. Specifically, earthworms foraging for high quality patches may stimulate microbial N immobilization, translating into lower N capture by plants. Increases in casting activity under elevated CO₂, and hence in microbial N immobilization, may also explain why earthworms modulated the effects of soil heterogeneity and CO₂ concentrations on plant community structure. We show that earthworms, absent from most soil nutrient heterogeneity studies, mediate plant biomass responses to nutrient patchiness by affecting N capture. Future plant-foraging behaviour studies should consider the roles played by soil engineers such as earthworms, so that results can be better extrapolated to natural communities.

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1. Introduction

The distribution of nutrients in soils is naturally heterogeneous at multiple spatial scales (Jackson and Caldwell, 1993; Farley and Fitter, 1999). Soil nutrient heterogeneity promotes a variety of plant responses, including morphological (e.g., root proliferation into nutrient patches; Hutchings and de Kroon, 1994) and

physiological adjustments (e.g., changes in nutrient uptake kinetics; Jackson et al., 1990). These individual responses have performance implications, which are well addressed in the root foraging literature, both at the population (Day et al., 2003; Maestre and Reynolds, 2006a) and community (Wijesinghe et al., 2005; García-Palacios et al., 2011) levels. However, most previous research on soil heterogeneity has concentrated on the addition of inorganic patches of phosphate or nitrate (Hodge, 2004), whose patterns of nutrient release differ markedly to those of organic patches. Indeed, organic patches generally require degradation by soil biota before the nutrients become plant available (Fransen and

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de Kroon, 2001). Soil ecosystem engineers, such as earthworms, may then be important drivers of plant growth responses to organic nutrient patchiness because their actions directly redistribute patch material through the soil and indirectly affect patch decay because they change the environment and hence activities of decomposer microbes (Kreuzer et al., 2004; Lavelle et al., 2006; Bradford et al., 2007).

Earthworms are one of the most conspicuous groups of detritivores in terrestrial ecosystems. Their high consumption rates and burrowing activity profoundly modify the physical structure of soils and the rate at which soil microbes carry out important ecosystem processes such as N mineralization (Willems et al., 1996; Lavelle et al., 1997; Eisenhauer, 2010). Earthworms also influence root architecture and growth (Setälä and Huhta, 1991) – metrics that strongly influence N capture by plants from nutrient patches – potentially through root feeding and their effects on the distribution of patches. Together these effects of earthworms may play a key role modulating nutrient availability from organic patches, and therefore ultimately plant growth. Yet earthworms have been excluded from most soil heterogeneity studies, probably because the majority has used artificial growing media or potting soil (Hodge, 2004). To our knowledge, only a few studies have evaluated the joint effects of earthworms and nutrient heterogeneity on plant biomass (Bonkowski et al., 2000; Wurst et al., 2003; Kreuzer et al., 2004; Bradford et al., 2007), and none of them have assessed how different patch features and environmental conditions modify these effects.

The quality of the organic patch material (e.g., lignin: N and C: N ratios) may be particularly relevant in determining plant responses to soil heterogeneity, as it largely determines the rate of decomposition (Cornwell et al., 2008), and strongly regulates the effects of soil fauna on litter decay (García-Palacios et al., 2013). For example, the activity of earthworms may change in response to patches of contrasting qualities, as they selectively forage for high quality organic matter (Bradford et al., 2007). Thus, earthworms may particularly influence plant responses to patches of high quality because they redistribute them more rapidly, reducing the opportunity for roots to capture nutrients from the patch. The patch quality may also interact with abiotic environmental factors affecting the traits that determine the plant resource use strategy (García-Palacios et al., 2012). The rise in the atmospheric concentration of CO₂ is a major driver of ongoing global environmental change (IPCC, 2013). Elevated CO₂ concentrations have been found to alter plant nutrient uptake responses to soil nutrient heterogeneity, which in turn changes plant dominance (Maestre et al., 2005; Maestre and Reynolds, 2006b). Earthworms could also modify such effects because these soil engineers have been shown to influence plant biomass responses to nutrient heterogeneity and elevated CO₂ separately (Wurst et al., 2003; Arnone et al., 2013). Thus, our broader understanding of the ecological consequences of soil heterogeneity is hindered by the limited evaluation of the combined effects of earthworms, patch quality and projected global change scenarios.

Using a microcosm approach, natural soil and ¹⁵N-labelled organic material, we examined the simultaneous effects of soil nutrient heterogeneity, earthworm presence, organic material quality and elevated atmospheric CO₂ on plant resource-use strategy, biomass and species dominance in mixtures formed by *Lolium perenne* L. and *Plantago lanceolata* L. We tested the following two hypotheses: i) Earthworms reduce plant biomass under heterogeneous nutrient distribution through reduction in a set of morphological (root foraging precision) and physiological (N capture) plant responses caused by earthworm preemptive use of nutrient patches. The decrease in plant biomass will be highest with high (versus low) quality nutrient patches because earthworms

selectively forage for these (Bradford et al., 2007); and ii) elevated CO₂-induced increases in earthworm activity (Arnone et al., 2013) alter plant dominance in the mixtures when nutrient are heterogeneously distributed. The dominance of the more competitive species *L. perenne* – which is usually favoured by nutrient heterogeneity under elevated CO₂ (Maestre et al., 2005) – will therefore be reduced when earthworms are present under these conditions.

2. Materials and methods

The experiment was conducted at the Duke University Phytotron. The design consisted of a fully-crossed combination of two levels of spatial distribution of the organic material (NH: homogeneous and heterogeneous), earthworms (E: with and without), organic material quality (NQ: low and high) and atmospheric CO₂ concentration (ambient and elevated). *L. perenne* and *P. lanceolata* seeds were used to form two-species plant mixtures. Both species commonly co-occur in semi-natural temperate grasslands (Fowler and Antonovics, 1981), and have been previously employed in soil heterogeneity studies evaluating the interaction with earthworms (Wurst et al., 2003) and elevated CO₂ (Maestre et al., 2005).

2.1. ¹⁵N-labelled organic material

We obtained ¹⁵N-labelled organic material by growing *L. perenne* from seed in microcosms made out of a section of PVC pipe (length 40 cm, internal diameter 10 cm) and filled with 3: 1 sand: vermiculite mix. Seeds were germinated in a dark room on agar plates, and three days after germination were planted into the microcosms (7 seedlings per tube). These were then placed in a walk-in growth chamber that was maintained at day/night air temperature of 21/16 °C, PAR of 1000 μmol m⁻² s⁻¹ with a 16 h photoperiod, atmospheric CO₂ partial pressure of 35 Pa, and an average relative humidity of 80%. Each microcosm unit was irrigated to free drainage with distilled water twice a day, and received a modified ½ strength Hoagland's solution containing 800 mg L⁻¹ of ¹⁵NH₄¹⁵NO₃ (5 atom% ¹⁵N, Isotec, Miamisburg, USA) twice a week for eight weeks. After eight weeks, the plants were harvested and the roots and shoots were dried at 60 °C. For the experiment, we used finely cut (2 mm length) green shoots (5.30 atom% ¹⁵N, 2.88% N, 14.6C:N) and roots (4.30 atom% ¹⁵N, 0.88% N, 45.2C:N) to provide nutrient patches of high and low quality for decomposition, respectively.

2.2. Microcosm setup

Plants were grown in microcosms made out of sections of PVC pipe (length 38 cm, internal diameter 10 cm) closed at the bottom by caps with a 5 mm diameter hole to allow drainage (see Maestre and Reynolds, 2007 for details). At 15 cm from the top of the pots we placed two 31-cm³ open plastic cylinders (hair rollers with length and internal diameter of 75 and 23 mm, respectively, and a light mesh of 5 × 10 mm) separated from each other by 2 cm. The cylinders were introduced to measure root proliferation, and to enable the placement of the organic material in the heterogeneous treatments (see below). All the microcosms were filled as follows (from the bottom to the top): a 5-cm layer of gravel, a 28-cm layer (corresponding to 2.38 L) of a 50: 50 mixture of mineral soil: sand (hereafter background soil), and a 2-cm layer of a 50:50 mixture of organic soil: peat. Both the mineral (a nutrient-poor sandy loam soil) and organic soils were obtained from the Duke Forest two months prior to the beginning of the experiment. The mineral soil was a low-fertility, sandy loam classified as an ultisol-type soil. Total percentage of soil C, N and P were 1.20 ± 0.049, 0.05 ± 0.002 and 0.01 ± 0.002, respectively (mean ± 1 SE; n = 8; Bradford et al.,

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