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Review Article

Can We Predict How Earthworm Effects on Plant Growth Vary with Soil Properties?

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Earthworms are usually assumed to enhance plant growth through different mechanisms which are now clearly identified. It is however difficult to determine their relative importance, and to predict a priori the strength and direction of the effects of a given earthworm species on a given plant. Soil properties are likely to be very influential in determining plant responses to earthworm activities. They are likely to change the relative strength of the various mechanisms involved in plant-earthworm interactions. In this paper, we review the different rationales used to explain changes in earthworm effect due to soil type. Then, we systematically discuss the effect of main soil characteristics (soil texture, OM, and nutrient contents) on the different mechanisms allowing earthworm to influence plant growth. Finally, we identify the main shortcomings in our knowledge and point out the new experimental and meta-analytical approaches that need to be developed. An example of such a meta-analysis is given and means to go further are suggested. The result highlights a strong positive effect size in sandy soil and a weakly negative effect in clayey soil.

1. Introduction

Earthworms are among the most important detritivores in terrestrial ecosystems in terms of biomass and activity [1]. They are known to affect plant growth through five main mechanisms [2, 3]: (1) the enhancement of soil organic matter mineralization, (2) the production of plant growth regulators via the stimulation of microbial activity, (3) the control of pests and parasites, (4) the stimulation of symbionts, and (5) the modifications of soil porosity and aggregation, which induce changes in water and oxygen availability to plant roots. Although these mechanisms are well identified, it is difficult to determine their relative influence [4] and to predict the impact of a given earthworm species on a given plant species.

In a recent review, Brown et al. [2] proposed that the response of plants to earthworms should depend on soil properties such as texture, mineral nutrient levels, and

organic matter content. However, most studies tackling earthworm effects on plant growth used soils containing more sand than clay (Brown et al. [2] and see Table 1). Comparatively, few studies [5–7] have tested in the same experiment earthworm effects on plant growth using different soils. Doube et al. [5] showed that the endogeic *Aporrectodea trapezoides* may increase wheat growth in sandy soils but may have no significant effect with a clayey substrate. They also found that the growth and grain yield of barley were both increased by *A. trapezoides* and *Aporrectodea rosea* in the sandy soil but reduced in the clayey one. On the contrary, Laossi et al. [7] showed that *Lumbricus terrestris* increased the shoot and total biomasses of *Trifolium dubium* in a clayey and nutrient-rich soil but not in a sandy and nutrient-poor one. The hypothesis that earthworm effects on plant growth should vary with soil type is based on two main reasons. (1) Soil properties may inhibit or stimulate some of the mechanisms through which earthworms tend to increase

plant growth. (2) If earthworms are able to alleviate limiting factor for plant growth, their impacts are expected to be weak in soils where the factor is not limiting. According to this rationale, the main mechanism through which earthworms affect plants should depend on soil type and in some soils earthworms might have no detectable or negative effect on plant growth.

2. How Soil Properties Should Modulate Earthworm Effects on Plant Growth?

Below, we go through the different mechanisms listed above and try to determine how soil properties should modulate their effect on plant growth.

(1) Earthworm activities usually have a positive impact on the mineralization of soil organic matter [8]. This effect is assumed to be a consequence of plant litter fragmentation and incorporation into the soil, as well as of the selective stimulation of microbial activity [9, 10]. Hence earthworms may enhance the release of nutrients that become available to plants and thus increase plant growth when they allow higher nutrient uptake than nutrient leaching [11, 12]. Anecic and endogeic earthworms have different feeding habits and affect differently soil organic matter composition and distribution [13]. Anecic earthworms feed on plant litter at the soil surface and tend to live in semipermanent vertical burrows while endogeic earthworms are active within the soil profile where they feed on soil organic matter [14]. This can lead to different effect on plant growth [15–17] which could also vary with soil properties such as organic matter and nutrient contents [18]. However, this rationale only holds if nutrients are limiting plant growth, that is, in soils where nutrients are poorly available. In contrast, in nutrient-rich soils, plants are less limited by the availability of mineral nutrients and earthworm-mediated mineralization should have less or no influence on plant growth [2]. Water is between the factors that limit plant growth and earthworms have been found to increase drought stress in plants [19]. This effect should be stronger in sandy soil which retains less water than in a clayey one.

(2) Earthworms affect plant growth through modifications of soil structure. They tend to increase soil porosity and the stability of organomineral aggregates by creating burrows and organomineral casts at different places within the soil profile [20, 21]. This effect is assumed to enhance plant growth in most situations [2] although opposite effects have also been reported [22]. It is difficult to predict how soil texture will modulate these effects. In clayey soils, earthworm might lead to very stable structures which could in turn strongly influence plant growth. This influence could be positive if the casts produced by earthworms do not lead to soil compaction [22], or negative with a physical protection of organic matter that impedes the release of mineral nutrients. In sandy soils, structures created by earthworms are more fragile [23] but more mineral nutrients can be released since the soil organic matter is less protected.

(3) Earthworm effects on plant growth via the release of plant growth regulators may be modulated by soil properties

through several mechanisms, but here again the outcome is difficult to be predicted. First, plant growth regulators are thought to be released by bacteria [24] and may be differently available depending on the levels of microbial activity in the soil. Sandy soils and soil with low organic matter contents usually have lower microbial biomasses and low potential for plant growth regulator production [25]. Thus, in such soils, earthworm effects via production of plant growth regulator could lead to weak effects on plant growth. Second, soil texture and soil organic matter could also affect the short-term availability of the produced phytohormones. For instance, clays and organic matter are known to adsorb organic molecules [26] and could reduce plant growth regulator availability to plants and weaken earthworm effect on plant growth.

(4) Earthworms are known to alleviate the negative effect of some parasites on plant growth by reducing strongly their density [27], ingesting and killing some pathogens in their intestine, or producing unfavourable conditions in cast material or tunnel lining [28]. This kind of mechanism may be influential for plant growth, especially in soil properties (such as moisture and temperature) that allow the development of abundant parasite populations. We can thus expect more parasites and greater negative effect of earthworms on them in a clayey soil.

(5) Similarly, earthworms can increase plant growth through the stimulation of symbionts or the increase in the contact between plants and symbionts [29]. Besides, if symbionts such as mycorrhizae provide nutrients to plants, symbiont-mediated earthworm effect (as their effect through mineralization) on plants should be more marked in poor soils than in rich soils where mineral resources are already available.

Taken together, these elements show that earthworm effects on plants vary with soil type but that it is difficult to predict the direction and the intensity of these variations. To make relevant predictions, we need to develop studies comparing in the same experiment earthworm effects on plants under different soil conditions. It is also necessary to set up meta-analyses using data of previous earthworms—plants studies. We provide below an example of what could be done through computing the effect size of earthworms on plant growth using meta-analysis with the data of the studies listed in Table 1.

3. How Can We Go Further?

To determine how earthworms effects on plant growth change with soil properties a first approach would be to compare earthworm-induced effects in different soils but in the same experimental conditions (same plant and earthworm species, same watering protocol, same greenhouse, etc.). Such experiments have been so far very scarce (but see [5–7]). To help predicting earthworm effects on plant growth in different soil types one could also use the “all-minus-one” tests proposed by Brown et al. [2]. In such experiments, only one factor such as mineral nutrition [4] or a root parasite [27] is limiting plant growth so

TABLE 1: References included in the survey of C and N contents in soil and the soil texture used in earthworm effects on plant growth.

References	Soil classification	Soil texture	N total	Clay	Sand	C Total
Aira and Plearce 2009	John Innes potting compost no. 2	Loamy compost	?	?	20%	?
Blouin et al. 2005	Ultisol	Sandy soil	0.05%	6%	78%	0.91%
Blouin et al. 2006	Ultisol	Sandy soil	0.05%	6%	78%	0.91%
Blouin et al. 2007	Ultisol	Sandy soil	0.05%	6%	78%	0.91%
Bonkowski et al. 2001	?	Loam soil + sand	0.1%	?	>50%	1.52%
Clapperton et al. 2001	Chernozem	Loamy soil	?	?	?	?
Derouard et al. 1997	?	Sandy soil	0.11%	5%	87%	0.91%
Devliegheer and Verstraete 1997	Ardoyne	Sandy soil	?	?	?	0.9%
Daube et al. 1997	Xerosol, Palexeralf, wiesenboden	Sandy soil, loamy soil and clayey soil	?	?	?	?
Eisenhauer et al. 2009	Eutric Fluvisol	Loam soil	0.3%	?	?	4.6%
Eisenhauer et al. 2008	Gleyic cambisol	Silty soil	?	22%	9%	1.1%
Eisenhauer and Scheu 2008a	Eutric Fluvisol	Loam soil	0.3%	?	?	4.6%
Eisenhauer and Scheu 2008b	Eutric Fluvisol	Loam soil	0.3%	?	?	4.6%
Eriksen-Hamel and Whalen 2007	Typic endoquent	Sandy loam soil	?	12%	58%	2.45%
Eriksen-Hamel and Whalen 2008	Typic endoquent	Loam soil	?	?	?	5.6%–13.3%
Fraser et al. 2003	Udic dystrochrept	Silt loam soil	0.2%	?	?	2.6%
Gilot 1997	Ferralsol	Sandy soil	0.44%–0.59%	6%–10%	>75%	>1%
Gilot-Villeneuve et al. 1996	Ferralsol	Sandy soil	0.4%–1.2%	2.4%–4.5%	>80%	0.28%–1.18%
Hale et al. 2008	Eutroboralf	Silty clay loam soil	?	?	?	?
Hale et al. 2006	Eutroboralf	?	?	?	?	?
Hopp and Slatter 1948	?	Clayey soil	?	70%	16%	?
Kreuzer et al. 2004	?	?	<0.1%	?	?	1.8%
Taossi et al. 2009a	Cambisol	Sandy soil	0.12%	6.9%	74%	1.47%
Taossi et al. 2009b	Cambisol and leptosol	Sandy soil and clayey soil	0.12%; 0.46%	6.9%; 34.4%	74%; 27%	1.47%; 5.67%
Milcu et al. 2006	Eutric Fluvisol	Loam soil	0.3%	?	?	4.6%
Milleret et al. 2009	Anthrosol	Sandy soil + compost	?	26.7%	45.3%	?
Newington et al. 2004	?	Sandy loam + aquatic compost + leaf mulch	<0.01%	?	?	?
Ortiz-Ceballos et al. 2007a	Fluvisol	Silty clay loam soil	0.25%	26.8%	41.5%	?
Ortiz-Ceballos et al. 2007b	Fluvisol	Silty clay loam soil	0.25%	26.8%	41.5%	?
Partsch et al. 2006	Eutric Fluvisol	Loam soil	0.3%	?	15%	4.6%
Pashanasi et al. 1996	Paleudult	Sandy loam soil	?	23%	55%	?
Patron et al. 1999	Inceptisol	Sandy soil	0.08%	11%	82%	0.85%
Poveda et al. 2005a	?	?	?	?	?	?
Poveda et al. 2005b	?	?	?	?	?	?
Schmidt and Curry 1999	Podzol	Loam to clay loam soil	0.18%	19%	47%	1.88%
Stephens and Davoren 1995	Calcic Natrixeralf	Calcic soil	?	?	?	1.5%

TABLE 1: Continued.

References	Soil classification	Soil texture	N total	Clay	Sand	C Total
Stephens and Davoren 1997	Calcic Natrixeralf	Calcic soil	?	?	?	?
Thompson et al. 1993	?	Loam soil	?	?	?	?
Welke and Parkinson 2003	Dystric brunisols, grey-brown luvisols	Sandy loam soil	0.1%–1.07%	?	?	21.63%–43.73%
Wurst et al. 2008	?	Loamy sandy mineral soil	0.13%	?	?	2.1%
Wurst et al. 2005	Cambisol	Loam soil	0.087%	?	?	1.58%
Wurst et al. 2003	?	Loam soil	0.087%	?	?	1.58%
Zaller and Arnone 1999	Rendzina	Calcareous soil	?	?	?	?

that the capacity of earthworms to alleviate this limiting factor can be tested. This allows testing main mechanisms through which (see introduction) earthworms affect plant growth in particular conditions. Such experiments could be repeated in soils differing by only one property to determine how this property modulates the strength of each of these mechanisms. For example, previous experimental studies conducted in greenhouse conditions [27, 30] and using sandy soil have showed that earthworms enhanced the tolerance of plants to nematodes. This kind of study should be carried out using sandy and clayey soil in the same experiment to test whether soils properties change the strength and direction of this earthworm effect.

While comparing earthworm effect in different soils differing by only one parameter is easy, this is not likely to allow disentangling all factors because soil properties are often correlated. Clay soils are generally rich in organic matter. A solution would be to directly manipulate soil properties. Hence, it would be possible to add, for example, clay, sand, organic matter, or mineral nutrients to a soil. We would then study the effect of a gradient in clay, sand, organic matter, or mineral nutrient on earthworm-induced effect. In the same vein, earthworm effect on the nutrient input-output balance of ecosystems should determine the long-term effect of earthworm on plant primary production [31]. Thus, comparing earthworm effects in different soils could also allow measuring their effects on nutrient leaching in these different soils and to identify the type of soil in which nutrients made available are leached and in which other it remains in the superficial soil layers. This is important to determine the long-term effect of earthworm-soil type interaction on plant growth. Another possibility would be to conduct meta-analyses to take advantage of the numerous studies already published on the issue. We give below a first example of such meta-analyses.

4. Example of Meta-Analysis

We used the results of 25 experiments (Table 1) to perform a meta-analysis and calculate the effect size of earthworms influence on plant growth in different soil types with

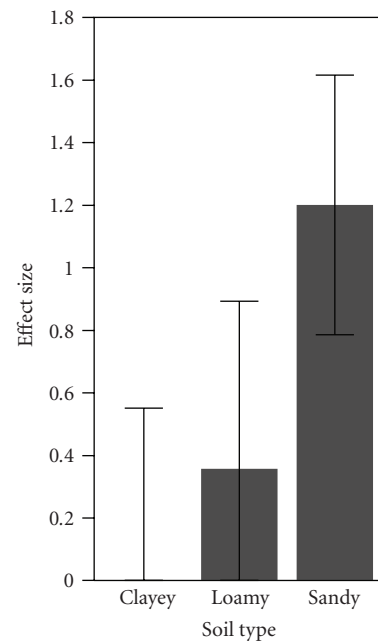


FIGURE 1: Effect size of earthworm effects on plant growth based on results of 25 experiments presented in Table 1. Mean effect size calculated as $[M1 - M2]/\sigma$ with $M1$: mean plant biomass in the presence of earthworms, $M2$: mean plant biomass without earthworm, and σ : standard deviation without earthworm. $P = .02$

contrasting texture properties (sandy, clayey, or loamy soil). The effect size was computed as $(M1 - M2)/\sigma$, with $M1$: mean plant biomass in the presence of earthworms, $M2$: mean plant biomass without earthworm, and σ : standard deviation without earthworm [32]. An ANOVA was then used to test for the effect of soil texture on the effect size, that is, on the magnitude of earthworm impact on plant biomass. This shows that soil texture influences significantly earthworm impact on plant growth ($r^2 = 0.11$ and $P = .02$). LS mean comparisons show that the effect size was in sandy and loamy soils, respectively, 60- and 17.5- fold higher than in clayey soil. The result highlights a strong positive effect size in sandy soil and a weakly negative effect in clayey soil (Figure 1).

This result supports the assertion of Brown et al. [2] that positive effects of earthworms on plant growth are more pronounced in sandy soils (generally nutrient-poor soils) than in clayey soils (generally nutrient-rich soil). However, as showed in Table 1 most studies used sandy soils while only few studies have used clayey ones. We thus need to release this bias by developing more studies for clayey soil. Nevertheless, our meta-analysis is the first formal test of the influence of soil properties on earthworm effect on plant growth.

5. Conclusion

Although the majority of authors provided detailed data on soil characteristics, this basic information was not available in all studies in earthworm impacts on plant production (Table 1). Further studies should pay attention to providing a standardized description of soil characteristics, which would thus be available for meta-analyses on earthworms—plants studies. For example, data on soil texture (sand and clay percentage), total C, total N content, NH_4^+ , and NO_3^- should be systematically published. Because such information, is not always given (see Table 1), we have only compared the effect of wide texture classes on earthworm effect. Finally, we have shown that these texture classes only explain 11% of the variations in effect sizes. This is probably due to a variety of other factors that we have not taken into account: soil properties mentioned above but also earthworm species (or its functional group) and plant species (or its functional group), and so forth [2, 3]. Gathering more studies on earthworm effects on plant growth and documenting for each of these studies all these factors would allow disentangling, through a unique meta-analysis statistical model, the respective effect of all these factors on earthworm-induced effect on plant growth, as well as interactions between these factors. This kind of general and systematic approach is required to derive general results on soil ecology and to develop the theoretical background needed to base soil ecology on solid bases [33].

Taken together, while a given earthworm species could have positive effects in a soil, it could have negative effects in another soil. To restore soil fertility or to enhance the sustainability of crop production [14], the right earthworm species has indeed to be chosen according to soil properties and crop type. Developing applications based on the use of earthworms would thus also require implementing the general meta-analysis (as suggested above) and the subsequent development of a general and comprehensive framework on earthworm-induced effect on plant growth that is so far missing.

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