



Exploring the pathways of earthworm-induced phosphorus availability



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ABSTRACT

As many soils are unable to supply sufficient amounts of phosphorus (P) to plants, P availability is often a growth-limiting factor. Literature shows that levels of readily available P can be considerably higher in earthworm casts than in the surrounding bulk soil, possibly resulting in increased plant P uptake. However, the underlying mechanisms through which this increase of readily available P occurs are unclear. In a greenhouse pot experiment with annual ryegrass (*Lolium multiflorum*) on a soil with low P availability, we tested whether the presence of the anecic earthworm *Lumbricus terrestris* resulted in increased grass growth and P uptake and explored the possible mechanisms behind such an effect. During the pot experiment, earthworm casts were collected and analysed for water-extractable P as well as for most other relevant ions. The earthworm's presence significantly increased grass yield from 9.80 to 10.80 g dry matter per pot ($p = 0.044$) and P uptake from 6.32 to 8.04 mg per pot ($p = 0.002$). Due to increased microbial activity, the solution chemistry in the water extracts of the casts was dramatically changed compared to the bulk soil samples. The concentrations of dissolved inorganic P in cast were enhanced by a factor ~ 30 –1000 compared to the levels found in bulk soil. The pH in earthworm casts increased from 5.9 to values between 7.4 and 9.0 and the Ca concentrations decreased by about a factor ~ 2 –3 compared to bulk soil samples. In addition, there was an increase in dissolved organic carbon (35 mg L^{-1} in casts versus 3 mg L^{-1} in soil). Surface complexation modelling, using the Charge Distribution model, suggests that, besides an increase in pH, particularly an enhanced interaction of dissolved organic matter with reactive surface of metal (hydr)oxides is likely to be a major driving force for the augmented release of orthophosphate (PO_4) via competitive adsorption and desorption. This competition for adsorption sites is an alternative pathway, next to mineralisation of organic matter, through which earthworms can increase soil fertility.

1. Introduction

Phosphorus (P) is one of the macronutrients that are essential for plant growth; it is a structural element in biomolecules like nucleic acids, and is crucial in energy transfer processes (Hawkesford et al., 2012). Plants take up P from the soil solution in the form of orthophosphate (PO_4), which, depending on the soil pH, is most commonly present as HPO_4^{2-} or H_2PO_4^- . In most soils, the amount of PO_4 in the soil solution is limited and represents $< 1\%$ of the typical P uptake by crops (around 50 kg P ha^{-1}) over a growing season (Morel et al., 2000). The remaining P is provided by the release of PO_4 from the soil solid phase to the soil solution throughout the growing season. The rate at which PO_4 in soil solution is replenished is governed by an intricate interplay between various soil chemical and biological processes. Among these, desorption of PO_4 to the soil solution from reactive surfaces of metal (hydr)oxides and edges of clay minerals, or dissolution of calcium-phosphate and magnesium-phosphate minerals, as well as

subsequent diffusion of PO_4 towards the plant root surface where uptake occurs, is the dominant processes affecting P uptake by crops in many agricultural soils (Gérard, 2016; Hinsinger, 2001; Koopmans et al., 2004; Kovar and Claassen, 2005; Van Noordwijk et al., 1990). Moreover, mineralisation of soil organic matter (OM), microbial biomass, and plant residues can contribute substantially to P availability and subsequent plant P uptake, especially in soils with high OM content and microbial activity (Richardson et al., 2011, 2009). These processes, in turn, are affected by abiotic factors like pH, soil moisture, temperature, soil texture, as well as metal (hydr)oxide content.

As a result of a low P content and strong binding of PO_4 to mineral surfaces, most soils are unable to supply P to plants at sufficient rates for sustaining optimal growth. This is especially the case in highly weathered tropical soils, but also frequently occurs in non P-fertilised soils in temperate climates (Hinsinger, 2001). Application of P fertiliser is often used to avoid P deficiency in plants. In large parts of Europe and North America, however, application rates of P in the form of animal

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manure and mineral P fertiliser well above P crop removal have led to an accumulation of P in a so-called soil “legacy” P pool (Kleinman et al., 2011). This has increased the accompanying risk of P losses to ground- and surface waters that contribute to eutrophication (Csathó and Radimsky, 2009; Jarvie et al., 2015; Koopmans et al., 2007; MacDonald et al., 2011). In intensively managed soils with excessive P application rates, the legacy P pool can reach a substantial size. In the Netherlands, the average size of this pool has been estimated to be 2050 kg P ha⁻¹ in the upper 0.5 m of agricultural land (Schoumans and Chardon, 2015). Since global P reserves might be depleted within a century and prices of mineral P fertiliser will increase over the coming decades (Cordell et al., 2009), unsustainable P management has been identified as a key planetary boundary that has been crossed and needs to be addressed (Steffen et al., 2015). There is therefore an increasing need for alternative, sustainable ways that facilitate plants to acquire P from this legacy P pool.

Increasing plant P acquisition can possibly be achieved through adapting plants or their environment. Many plants have developed their own strategies to enhance P uptake, such as adaptation of their root morphology, excretion of organic acids and phosphatases, or forming mycorrhizal associations (Milleret et al., 2008; Shen et al., 2011). Using new plant genotypes (Lynch and Brown, 2001) or inoculating the soil with microbes (Richardson, 2001) may be effective strategies to increase plant P uptake. In a different line of research, recent studies have shown that earthworms might also increase P acquisition by plants. Earthworms are ecosystem engineers that can strongly alter physico-chemical soil properties. They create burrows and feed on litter and OM associated with soil particles (Doube et al., 1997). By doing so, earthworms affect soil structure, microbial activity, decomposition of OM, and nutrient cycling. Earthworms have been shown to increase yield of grasses and grain crops by 25% on average, and this effect has been linked to increased nitrogen (N) availability (Van Groenigen et al., 2014). Additionally, they stimulate microbial activity in their casts and can increase the amount of readily available P (Kuczak et al., 2006; Lopez-Hernandez et al., 1993; Sharpley and Syers, 1976; Vos et al., 2014). Although a variety of pathways through which earthworms might affect plant growth have been suggested (Brown et al., 2004), the relative importance of the mechanisms responsible for the increase in readily available P in earthworm casts still remains largely unclear (Le Bayon and Milleret, 2009).

In an earlier study (Vos et al., 2014), we established that earthworm species with different feeding strategies produced casts with different amounts of water-extractable P (a proxy for plant-available P), and that P uptake by grass was enhanced by earthworm presence when other nutrients were sufficiently supplied. Three possible mechanisms were hypothesised for this earthworm-induced increase in readily available P in casts: a) desorption of PO₄ from mineral surfaces due to the elevated pH in earthworm casts; b) increased mineralisation of organic P due to enhanced microbial activity; and c) desorption of PO₄ from mineral surfaces due to competitive adsorption of elevated dissolved organic matter (DOM) concentrations in casts (Vos et al., 2014). To facilitate plant uptake from the legacy P pool in the presence of earthworms, it is important to develop our understanding of how the cast environment enhances P availability. Additionally, the temporal dynamics of readily available P in earthworm casts are still unclear and may affect P uptake by plants. The objectives of this study are (i) to determine the effect of earthworm presence on grass growth and P uptake in relation to the increase of the amount of readily available P in their casts; (ii) to quantitatively distinguish between the main pathways for earthworm-induced elevated P availability; and (iii) to assess the persistence of the amount of readily available P in earthworm casts over time.

2. Materials and methods

In the present study, we addressed two of the proposed pathways for the increase of readily available P in earthworm casts, as well as the

temporal dynamics of this increase. We used a combination of pot and incubation experiments with a soil that is low in readily available P. In the pot experiment, we tested whether earthworms can increase the growth of grass through increased levels of readily available P in their casts. In a separate incubation experiment, we compared incubated cast and bulk soil material and quantify the temporal dynamics of elevated levels of readily available P in the casts. In a third experiment, we assessed the effect of pH on readily available P by adjusting the pH of bulk soil samples. Finally, for gaining insight in the complex chemical P dynamics of the earthworm casts, we used surface complexation modelling applying the Charge Distribution (CD) model (Hiemstra and Van Riemsdijk, 1996). This advanced mechanistic approach has been used to successfully predict the adsorption and desorption behaviour of PO₄ to metal (hydr)oxide surfaces in mono- and multiple component synthetic systems (Rietra et al., 2001; Weng et al., 2012, 2008) and soil samples (Hiemstra et al., 2013). The mechanistic nature of the model enables the prediction of the change in PO₄ adsorption as a result of variation in pH, concentrations of interacting cat- and anions, and the amount of OM adsorbed to metal (hydr)oxides. The CD model has not yet been used for analysing the role of these factors on the solubility of PO₄ in earthworm casts. This modelling approach will allow us to unravel the pathways through which earthworms influence the solubility of PO₄ in their casts.

2.1. Soil collection and physico-chemical characteristics

For the pot experiment, we used a non-calcareous sandy soil from the subsoil (30–60 cm) of an arable field of the Droeveendaal experimental farm in Wageningen, the Netherlands (51°59′32″N 5°39′45″E). This soil can be classified as a typic endoaquoll (USDA, Soil Survey Staff, 1999). The soil was air-dried and sieved (5 mm) prior to the experiment. For determination of relevant soil physico-chemical characteristics, a soil subsample was dried at 40 °C for 24 h and sieved (2 mm). Soil particle size distribution and OM content were determined using standard analytical methods (Houba et al., 1997). Soil particle size distribution was determined using the sieve and pipette method and OM content by loss-on-ignition. Soil pH-H₂O was measured in water extracts obtained at a solid to solution ratio (SSR) of 1:10 (w:v; based on dry weight). Total and inorganic soil P contents were measured according to Kuo (1996). In short, inorganic soil P was determined by digestion of soil with 0.5 M H₂SO₄, followed by measuring P colourimetrically using the molybdenum blue method (Murphy and Riley, 1962) and segmented flow analysis (SFA; Skalar, SAN⁺⁺); total soil P was determined by measuring P in a 0.5 M H₂SO₄ soil digest after OM combustion in a muffle furnace (550 °C). Organic P was calculated as the difference between total and inorganic soil P. The amounts of short-range ordered iron and aluminium oxides (Fe_{ox} and Al_{ox}) as well as P bound to these mineral oxides (P_{ox}) were determined by acid ammonium oxalate extraction (Schwertmann, 1964). Concentrations of P, Fe, and Al in the acid ammonium oxalate extracts were measured using inductively coupled plasma - atomic emission spectroscopy (ICP-AES; Varian Vista Pro). From these data, the P-saturation index (α) was calculated according to:

$$\alpha \equiv \frac{P_{ox}}{[Fe + Al]_{ox}} \quad (1)$$

with P_{ox} and [Fe + Al]_{ox} in mmol kg⁻¹. Additionally, P was measured in an ammonium lactate extract of the soil (P-AL; Egnér et al., 1960). This method is routinely used in the P fertiliser recommendation system of the Netherlands to assess the P status of grassland soils.

2.2. Experimental setup and chemical analyses

2.2.1. Pot experiment

For the 42-day greenhouse pot experiment, a full factorial, completely randomised block design was set up, with P fertilisation (present

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