ABSTRACT

Belowground biotic interactions are known to influence soil fertility and plant growth by changing the physical environment and the soil nutrient cycles. Among the great diversity of soil biota, earthworms are key soil organisms in regulating nutrient cycling through: (i) their own metabolism that leads to high availability of carbon (C) and nitrogen (N) from metabolic wastes such as urine, mucus and tissue, (ii) the dispersal and the stimulation of soil microorganism activity associated with passage through the intestinal tract and (iii) the distribution of organic matter and soil mineral particles. While many studies have examined impacts of earthworm on C and N fluxes in soils, less attention has been paid to the impact of earthworms on soil phosphorus (P). This paper reviews the current state of knowledge of the global earthworm’s impact on soil P dynamics in order to evaluate further involvements: i) on plant production and ii) on P transfer by runoff waters at the plot scale. This mini-review aims at considering research issues at several ecological levels, from individual earthworms (P distribution during food assimilation and excretion; gut microbial activities) to earthworm populations and communities (ecological categories and their influence on P dynamics) and, to the full extent, to the ecosystem scale (storage and/or loss of P). Interacting effects with other organisms (plants, microorganisms) are taken into account as well as the role of earthworms on physiochemical parameters (casting and burrowing activities, soil stability). Such a synthesis highlights the necessity to conduct interdisciplinary studies on biological, chemical and physical processes to better understand the effects of earthworms on P cycling at the ecosystem and landscape levels.

Keywords: drilosphere, ecological level, erosion, microorganism, plant

INTRODUCTION

Belowground biotic interactions in terrestrial ecosystems are known to influence soil fertility and plant growth by changing soil nutrient cycling and the physical environment (Wardle 2002). Belowground communities include a large variety of organisms showing highly complex interactions across trophic or non-trophic groups (Coleman 2008). Among the great diversity of soil biota, earthworms are key components to regulate nutrient cycling processes in many ecosystems (Edwards and Bohlen 1996; Bohlen et al. 2004). Already in 1881, Darwin was one of the first scientists who noted that the topsoil consisted mostly of earthworm castings thus highlighting the importance of earthworms in pedogenesis processes. Darwin’s observations pointed out the importance of earthworm activities in the decomposition of organic matter and its intimate mixing with mineral particles leading to the formation of the so called “vegetable mould”. Indeed, earthworms function as ecosystem engineers, i.e. they modify directly or indirectly the chemical, physical and biochemical properties of the soil thus affecting the availability of resources to other organisms (Stork and Eggleton 1992; Jones et al. 1994, 1997; Lavelle et al. 1997). At the heart of the engineering concept is the great ability to move through the soil and to create organo-mineral structures as faeces (casts) and burrows, activities commonly referred to as “bioturbation”. As pointed out by Lavelle (1997), the soil biogenic structures created by earthworms, commonly termed drilosphere (Beare et al. 1995; Brown et al. 2000), may have several functions in the soil system: i) they serve as a food resource, or even habitat (Tiunov and Scheu 2000), for smaller organisms, mainly microorganisms, because of their high energetic status and especially the high contents of organic matter (Jégou et al. 1998; Buck et al. 1999; Jégou et al. 2000; Le Bayon and Binet 2006) and, ii) they are directly involved in the formation and/or stabilization of soil structure (porosity, aggregation) and thus contribute to the soil maintenance and fertility. The abundance and variety of biogenic structures are also known to modulate the turnover of soil organic matter which is entrapped in earthworm dejections (McInerney et al. 2001; Marhan and Scheu 2006; Don et al. 2008). While many studies have examined impacts of earthworm on carbon (C) and nitrogen (N) fluxes in soils (Bohlen et al. 1997; Bouché et al. 1997; Lavelle et al. 1997; Whalen and Janzen 2002), less attention has been paid to how and to the extent to which earthworms influence the dynamics of soil phosphorus (P).
Growing interest in the dynamics of P is mainly due to two aspects. On the one hand, after N, P is the second most limiting element for plant growth (Vance et al. 2000; Hinsinger 2001; Vance 2001). In addition, P is by far less soluble in water and consequently less mobile and available to plants in comparison with the other major nutrients in soils, especially N. Indeed, P ions (mainly $\text{H}_2\text{PO}_4^-$ and $\text{HPO}_4^{2-}$, which are the effective P forms absorbed by plant roots) tend to strongly react with numerous soil constituents on which they adsorb, thus inducing a lower proportion of P ions in the soil solution. The weak availability of P in soils is related to several factors as (i) the pH, (ii) the concentrations of anions that compete with P ions for ligand exchange reactions and, (iii) the concentrations of metals (Ca, Fe and Al) that can co-precipitate with P ions (Hinsinger 2001). As commonly observed in the vicinity of plant roots in the so-called rhizosphere soil (Li et al. 2008a, 2008b; Guppy and McLaughlin 2009), the physicochemical conditions of the drilosphere may considerably differ from those of the bulk soil, as a consequence of a range of processes that are induced either directly by the activity of earthworms themselves or by those of the specific microflora living in earthworm biogenic structures (faeces, burrow-linings) (Devliegher and Verstraete 1997; Brown et al. 2000). On the other hand, at a larger scale, the second reason that leads us to focus on P is that runoff and potential transfer of this element from soils is a primary factor in the eutrophication of continental waters (rivers, lakes, etc.). In particular, available forms of P, comprising P in dissolved and particulate forms, are mostly involved in surface water eutrophication (Sharpley 1993). Several studies have focused on particular soil detachment; however, less attention has been directed towards the contribution of earthworm surface casts to soil erosion despite their enrichment in P compared to the surrounding soil (Sharpley and Syers 1976, 1977; Sharpley et al. 1979; Le Bayon and Binet 1999; Le Bayon et al. 2002; Le Bayon and Binet 2006).

This paper aims to review the current state of knowledge of the global earthworm’s impact on soil P dynamics in order to evaluate further involvements: i) on plant production and, ii) on P transfer by runoff waters at the plot scale. Research issues at several levels of the ecological hierarchy are considered, from individual earthworms (P distribution during food assimilation and excretion; gut microbial activities) to earthworm populations and communities (ecological categories and their influence on P dynamics) and, to the full extent, to the ecosystem scale (storage and/or loss of P).

EARTHWORMS AND PHOSPHORUS CYCLING: A HIERARCHICAL APPROACH

By studying the effect of earthworms on nutrient cycling, and especially on P, many investigations have focused on small-scale processes and functions, i.e. in casts and burrows. The extrapolation of the results obtained to the ecosystem scale is therefore quite difficult. In addition to this spatial dimension, taking into account the temporal variation is also a challenge for future modelling approaches in order to better understand the whole role of earthworms. The schematic diagram proposed by Brown et al. (2000) outlines the combination of all of these aspects by illustrating the drilosphere effects on soil organic matter (C, N) and microbial activity (Fig. 1). These authors highlight the drilosphere as a “dynamic sphere” of earthworm influence on soil which is constantly changing in space and in time depending for instance on the periods of activity of earthworms, the duration of the different structures they have created, the horizontal and vertical distribution of earthworms according to biotic and abiotic factors, etc. This concept may be applied to P and the following section gathers together several ecological levels to better understand how earthworms influence the P cycle.

The earthworm individual level

Earthworms are known to preferentially ingest a mixture of organic matter and sand grains (Schulmann and Tsinn 1999; Lavelle and Spain 2001) with the latter facilitating the mechanical fragmentation of organic residues during gut transition, thus enhancing microbial accessibility to organic matter (Marhan and Scheu 2005; Curry and Schmidt 2007). The diet of earthworms mainly consists of organic material in various stages of decay and of the microorganisms that colonize it (Lee 1985; Curry and Schmidt 2007). Earthworm guts actually act as bioreactors where the microbial
activity is enhanced due to favourable conditions with readily available C of mucus and water (Lattaad et al. 1997; Tiunov and Scheu 2000). Microorganisms have been reported to proliferate in the gut and dejections of earthworms (Parle 1963a, 1963b; Edwards and Bohlen 1996; Brown et al. 2000). Microclimatic conditions in surface-casts and burrows are favourable for a high microbial activity and several studies have described the taxonomic composition of the gut community in earthworms (Tiunov and Scheu 2000; Tiunov et al. 2001; Orazova et al. 2003; Prakash et al. 2008). Evidence of a mutualistic digestion involving earthworms and their microflora was brought by Laplace and Spain (2001), Brown et al. (2000) and Trigo et al. (1999), where it was demonstrated that the favourable conditions of the earthworm’s gut enhance the digestion of organic matter by microorganisms. During the gut transit, the ingested soil is completely rearranged and restructured (Barois and Lavelle 1986; Barois et al. 1993) leading to the mobilization of clay particles (Marinissen et al. 1996) and the disruption of the existing cation bridges in the aggregates, but also conversely to the formation of new bonds (Shipitalo and Protz 1988, 1989). The global reorganization of mineral and organic particles generally occurs in the posterior intestine of earthworms (Barois et al. 1993) thus leading to the fine processes of P dynamics in the earthworm’s gut remain already partially unknown. According to several authors and reviewed by Kuczak et al. (2006), the increase of P in soil that passes through the intestinal tract of earthworms is probably due to several factors: (i) a significantly greater pH of the gut contents along the earthworm intestinal tract (6.8 and 6.0 for the anterior and posterior parts and 5.0-5.4 for the soil, respectively) (Barois and Lavelle 1986); (ii) large amounts of mucus secreted in the earthworm gut, which release carbohydrates from carbohydrate compounds that may block and compete for P sorbing places, and in turn, increase soluble P (López-Hernández et al. 1993); and (iii) an increase in the microbial activity during digestion processes (López-Hernández et al. 1993). In addition, the ingestion and thorough mixing of soil in the intestinal tract of Lumbriicus rubellus and Aporrectodea caliginosa favors the dissolution of phosphate rock and thus the availability of the derived-P in soils (extracted with resin strips, NaHCO3 0.5 M, NaOH 0.1 M, HCl 1 M) in casts through gut passage and/or selection of ingested materials in several ecosystems (agroforestry, secondary forest, pasture). Looking at earthworm burrows that are usually lined by a layer of flattened casts and mucus, they seem to follow the opposite trend in terms of P dynamics. The few researches that have been conducted thus showed a lower Olsen-P content in burrow linings than in surface casts and surrounding soil (Le Bayon and Binet 2006). Moreover, Jensen et al. (2002) observed that lining material desorbed quite large amounts of labile P at solution concentrations below approximately 1 mg PO4-P L−1 and at short contact times ranging from 5 minutes to 2 hours.

Concomitantly to the P behavior in earthworm biogenic structures, an increased P mobilization and release of easily soluble basic and acid phosphate has been found in Lumbricus terrestris burrow-linings and casts from a temperate agroecosystem in France (Le Bayon and Binet 2006). In the United Kingdom’s, Satchell and Martin (1984) also previously recorded a high phosphatase activity (both acid and alkaline forms) in wormcasts from cultures of paper waste sludge inoculated with Eisenia fetida, Dendrobaena veneta, L. rubellus and A. caliginosa. Similar results were obtained in Germany by Buck et al. (1999) with L. terrestris and Octolasion cyanenum varying mulch types, as well as by Flegel and Schrader (2000) working with D. octaedra. As a consequence, the enzymatic activities may be influenced by the food quality provided that could affect the specific nutrient state of the casts. Indeed, Flegel and Schrader (2000) showed an interesting correlation between acid and alkaline phosphatase activities and the organic C and total N contents in casts. Not only the food nutrient status but also the enhanced mineralization of nutrients, the high substrate concentrations and the high moisture favor enzymes activities in fresh casts (Parhasarathi and Ranganathan 1999) that tend to decline with cast ageing (Parhasarathi and Ranganathan 1999; Le Bayon and Binet 2006). However, finding a better phosphatase activity in earthworm faeces was not systematically verified as pointed out by Zhang et al. (2000) in China for the earthworms Metaphire guillelmi and E. fetida.

More interestingly, the recent finding of an alkaline phosphatase in burrow-linings; this enzyme activity was strictly allocated to the earthworm proper gut microflora (Satchell and Martin 1984; Le Bayon and Binet 2006). This latter result raised the question about the origin of the earthworm’s gut microflora: while it is now commonly accepted that the ingestion of P-rich particles thus modifying the relative proportions of different P forms. Recently, Kuczak et al. (2006) in China for the earthworms Metaphire guillelmi and E. fetida.

### The earthworm population and community levels

As described above, earthworms affect soil physical and chemical properties and contribute to the transfer of organic matter and soil into organo-mineral and mineral soil layers. It becomes obvious that at the plot scale, parameters as the earthworm population and community size, growth, reproduction rate, survival and mortality have clear consequences on casting and burrowing activities. Moreover, the ecological and functional group of earthworms is quite obviously crucial regarding bioturbation processes that depend...
mostly on the location and availability of food resources. As reviewed by Bouché (1977), Lee (1985) and Curry and Schmidt (2007), earthworms are divided into detritivores (epigeic and anecic species) which usually feed at or near the soil surface mainly on plant litter, and geophages (endo-geic species) feeding deeper in the soil profile and ingesting large quantities of soil. As a consequence, the spatial distribution of field earthworm populations and communities varies and is usually closely linked to soil pedotopes (Lavelle 1997; Brown 2000). Therefore, the aggregate distribution of earthworms leads to hot spots of activity and a recent review of Feller et al. (2003) pointed out that the amount of soil brought up to the surface by worms in various temperate ecosystems ranged from 2.2 to 91.6 t ha⁻¹ yr⁻¹ in North Vietnam (Jouquet et al. 2008a). Such large amounts of fine soil materials surfaced at the top soil layers may increase P stocks in the first 1 cm, especially with exotic earthworms and deep-burrowing species (Suarez et al. 2003). A positive association between earthworms and soil P content was also previously observed by Nuutinen et al. (1998) and thus reinforces the importance of earthworm activities on P cycling.

However, the great majority of the studies (or even the totality) has focused on earthworm surface-casts, which may constitute only a small proportion of the total cast production, i.e. aboveground and belowground dejections, as they may constitute only a small proportion of the total cast production. Such studies should be conducted both in laboratory experiments and at the field scale to give an overview of the global impact of earthworm on P cycling. Phosphorus balance, i.e. the importance of earthworm activities on P cycling. Phosphorus balance, i.e. the importance of earthworm activities on P cycling.

The ecosystem and landscape levels

How earthworms affect the balance between P storage and conservation versus P losses from the system is one of the main topical questions that would help to satisfy requirements of the necessity to fertilize cultivated lands and to preserve concomitantly waters quality. At the ecosystem level, Kuczak et al. (2006) estimated that earthworm casts could constitute 41.0, 38.2, and 26.0 kg ha⁻¹ of total available P stocks in an agroforestry system, pasture and secondary forest, respectively. The stability of P forms may also be modified in biogenic structures (Brossard et al. 1996) and once egested, fresh earthworm casts are initially subject to soil destabilization (Schrader and Zhang 1997) and then prone to stabilization processes through thixotropic or age gardening (Shipitalo and Protz 1988, 1989; Marinissen et al. 1996) that may be reversible. Regarding lifetimes of surface-casts, Deé (2000) observed in Colom approach of various P concentrations and plant growth by using an original compartmentalization (Lavelle 1997; Brown 2000) and potentially organic P, the most important P pool in soils that may represent 30 to 80% of the total P. The enclosure of organic matter in stable earthworm casts of L. terrestris and L. rubellus has already been demonstrated, especially for dried aged casts that were less dispersible than moist fresh ones, the effects of ageing and drying increasing as cast organic C content increased (Shipitalo and Protz 1988). On a long-term scale, McInerney et al. (2011) assumed that organic matter accreted in casts of anecic and endogeic earthworms could remain as it is and could maintain its stabilization status more than two years before changes may occur. One of the most important factors that govern stabilization/de-stabilization processes is clearly the soil texture. Indeed, an increased sand content generally increases carbon mineralization of enclosed organic matter in earthworm casts (Marinissen and Then 1990) and may promote inorganic P in the presence of earthworms (Scullion and Malik 2000) may contribute to the stabilization of organic matter and its protection against microbial degradation (Feller and Beare 1997; Six et al. 2004; Lehmann et al. 2007).

In contrast to these phenomena of stabilization, earthworm casts and burrows may also contribute to nutrient losses through soil erosion or lixiviation. Nevertheless, how earthworms affect soil erosion is not clear: on the one hand, the general idea from the literature is that the presence of earthworms decreases runoff up to 2-15 times by increasing soil water infiltration. Using dye and tracer techniques, several studies have shown that burrows from endogeic and anecic worms may conduct water (Joschko et al. 1992; Shipitalo et al. 2000). Edwards et al. (1990) estimated that monitored burrows of L. terrestris over 12 season storms collected until 10% of the rainfall and an ave-
range of 13 times more water than predicted based solely on the diameter of the burrows at the soil surface. Burrows from anecic species are usually the most efficient on water infiltration (Bouché and Al-Addan 1997), in particular *L. terrestris* in no-till systems (Willoughby et al. 1997). Using artificial burrows, Joschko *et al.* (1989) and Roth and Joschko (1991) showed that earthworms enhance macroporosity by the burrows network or continuous channels they created, and the persistence of open burrow holes at the soil surface led to decreased runoff from crusted soils. Moreover, by their surface casting activities i.e. egesting soil and burying organic matter, earthworm casts enhance the soil surface roughness and then reduce soil crusting, which in turn improves water flow into the soil (Kladivko *et al.* 1986).

On the other hand, earthworm casts that are deposited on soil surface are subject to splash erosion (Vanhooff 1983) and the fine soil materials as well as plant nutrients they contain are exposed to an easy detachment and transport during rainfall events. Sharpley and Syers (1976, 1977) and Sharpely *et al.* (1979) reported the potential role of earthworm casts for the P enrichment of runoff waters under permanent pasture in New Zealand. These results partly contradict those of Le Bayon and Binet (2001) who used a simulated rainfall and demonstrated that earthworm activities act as a physical brake for soil erosion by (i) creating a surface roughness with the deposition of surface casts and (ii) reducing water runoff by associated enhanced water percolation. Only once the breaking-down point of the physical resistance of casts was reached, all surface casts were then quickly disintegrated and finally completely washed away. Transfers of nutrients (C, N and P) occurred then subsequently over a short-distance through successive deposition/suspension of soil particles in the water runoff. Cast erosion was also significantly and positively correlated to initial mass when casts were young but not when they were old (Le Bayon and Binet 2001). The erodibility of casts at different stages of their ageing process was also studied in Colombia by Mariani *et al.* (2007) who showed that under simulated rainfall, dry casts were slowly eroded into large aggregates, showing thus a progressive detachment of soil particles. These authors suggested that nutrients as C, N and P might have deposited around the cast during the rainfall events in the rainy season. At the opposite of all these results, a recent study in North Vietnam using a water runoff simulation showed that, despite the study was conducted under a tropical climate leading to strong rainfall intensities, earthworm casting activity significantly decreased water runoff velocity (Jouquet *et al.* 2008b). The authors assumed that the high stability of casts from the anecic *Amynthas khami* and particularly the rapid drying of the faeces might explain the low contribution of earthworms to soil loss even under intense rainfalls. Therefore, with regards to these three main studies, it appears that further work is needed on earthworm casts erosion to better predict their effects on soil and nutrient losses, especially P.

**CONCLUSION**

As illustrated in Fig. 2, several questions remain unsolved about the global earthworm’s impact on soil P dynamics. At the finest scale, i.e. in the digestive tract of the earthworm itself, the biochemical processes during the gut transit are still not clearly understood, especially regarding the microflora specialized in the organic P mineralization and the re-

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**Fig. 2 Dynamics of phosphorus at the ecosystem level.** Four compartments are represented: the soil profile as a whole, plant shoots, the rhizosphere and the drilosphere. Questions still unsolved are raised and ecosystem outputs are underlined.
lease of available P ions. At the community level, the ecological category of earthworms appears to be predominant in the P transformation and storage. Thus, mainly due to their earthworms, with Observations on Their Habits, John Murray, London, UK, 326 pp.


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Earthworms and phosphorus dynamics. Le Bayon and Millereet