

Review paper

Assessment of gross and net mineralization rates of soil organic phosphorus – A review



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ARTICLE INFO

Article history:

Received 20 April 2015

Received in revised form

23 June 2015

Accepted 24 June 2015

Available online 7 July 2015

Keywords:

P radioisotopes

Organic P mineralization

Isotopic exchange

Microbial immobilization

Extracellular enzymes

ABSTRACT

The quantification of net soil organic P mineralization rates is hampered by the potentially rapid sorption of released phosphate. Here, isotopic dilution approaches to assess gross and net organic P mineralization rates under steady-state conditions are reviewed, including different analytical and numerical solutions to assess P transformation rates based on incubation experiments with ^{32}P - or ^{33}P -labeled soils. Non-isotopic approaches are also commented on. Published isotopic dilution studies show that isotopically exchangeable P during incubation can partly or even predominantly (20–90%) result from biological and biochemical rather than physicochemical processes. The relative contribution of biological and biochemical processes tends to be lower in arable soils than under grassland and forests and is negatively related to the availability of inorganic P and positively to concentrations of soil organic carbon. Typical basal gross organic P mineralization rates range between 0.1 and 2.5 $\text{mg P kg}^{-1} \text{d}^{-1}$, but rates up to 12.6 $\text{mg P kg}^{-1} \text{d}^{-1}$ have been observed in grassland and forest soils. The further partitioning of gross organic P mineralization remains uncertain, but a dominance of microbial immobilization and remineralization is likely under most conditions, at least during the initial weeks of incubation. Over longer time periods, the relative importance of mineralization of non-living soil organic P increases, with the contribution of extracellular hydrolysis remaining to be elucidated. This requires other approaches than enzyme activity assays, since measurements of phosphomonoesterase activity in soil render organic P mineralization rates that are one to two orders of magnitude greater than those determined by isotopic dilution. The numerical modeling approach will enable assessment of soil P transformation rates under non-steady-state conditions, where P fluxes are likely to be greater than under steady-state conditions. Ultimately, an improved understanding of the biological and biochemical processes in soil P dynamics may help to improve P management in agroecosystems.

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1. Introduction

Phosphorus (P) is an essential element for all organisms (Westheimer, 1987). Efficient P management in agroecosystems is mandatory because P often limits primary productivity, mineralable P deposits are finite and losses of P to natural environments cause eutrophication, with adverse effects on terrestrial (Ceulemans et al., 2011) and especially aquatic ecosystems (Carpenter, 2005). Only a thorough understanding of the pools and processes of P dynamics in soil–plant systems (Fig. 1) can form a solid basis for efficient P management.

In soils, P occurs in inorganic as well as organic forms. The most common primary P mineral is apatite, while secondary P minerals include various calcium phosphates and predominantly amorphous aluminum and iron phosphates (Frossard et al., 1995). Soil organic P is present as orthophosphate monoesters, including inositol phosphates, and as orthophosphate diesters, organic polyphosphates and phosphonates (Condon et al., 2005). The stocks and relative proportions of these different forms of P change during pedogenesis, with a decrease of calcium phosphates and a build-up of organic P, non-occluded P_i (P_i on surfaces) and occluded P_i (P_i within secondary minerals) over time (Walker and Syers, 1976). When revisiting one of the soil chronosequences studied by Walker and Syers, Turner et al. (2013) found that microbial biomass P represented up to 40% of total organic P. Soil microorganisms contain inorganic as well as organic P (Bünemann et al., 2011). By (operational) definition, however, they are often included in the

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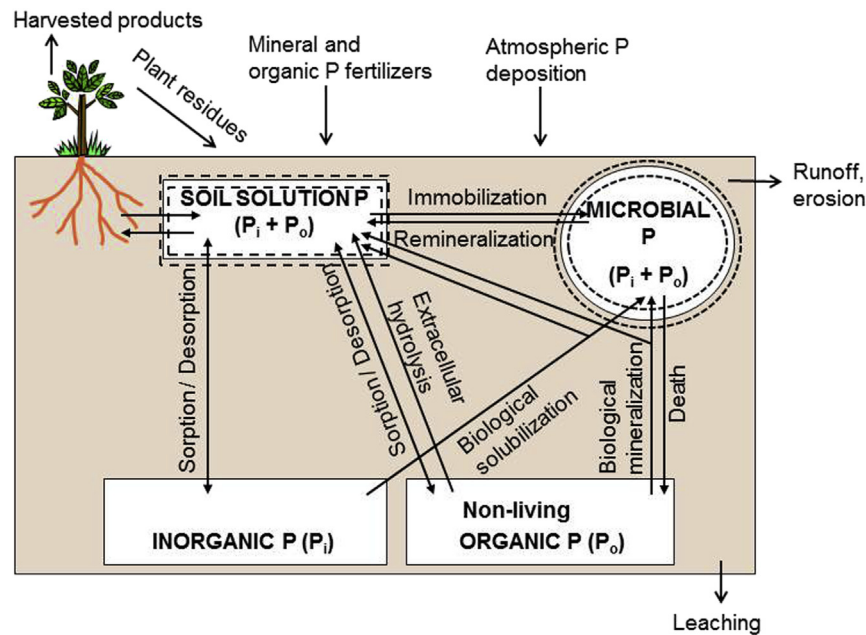


Fig. 1. Conceptual diagram of pools and pathways in P cycling in soil–plant systems. The large pools of inorganic P (inorganic P) and non-living organic P (organic P) are relatively constant in size, whereas the smaller pools of soil solution and microbial biomass containing both inorganic P and organic P can fluctuate in size as indicated by the dashed borders. The physicochemical sorption/desorption processes are meant to include both adsorption/desorption and precipitation/dissolution processes. The biological and biochemical processes include microbial immobilization and remineralization, biological mineralization of non-living organic P (microbial oxidation with or without assimilation of P), extracellular enzymatic hydrolysis of organic P (biochemical mineralization), and stabilization of microbial P in non-living organic P upon death. Inputs and outputs from the system are also shown but not further addressed in this review.

total organic P of the soil. The central role of the microbial biomass in the dynamics of soil organic P was stressed by Stewart and Tiessen (1987).

The interchange of nutrients between different forms, in particular between inorganic and organic forms, is often referred to as nutrient transformations. Plants and microorganism take up P (predominantly as phosphate) from the soil solution, but only a small fraction (<1%) of total P_i and also of total organic P is dissolved at any given time. Thus, this pool needs to be replenished repeatedly to satisfy plant demand (Frossard et al., 2000). The removal of P from the soil solution as well as its replenishment result from a combination of physicochemical (adsorption/desorption and precipitation/dissolution) and biological/biochemical processes (mineralization/immobilization). However, this distinction is complicated by the fact that the physicochemical processes of desorption and dissolution can also be mediated by plants and microorganisms, e.g. by exudation of organic anions (Richardson et al., 2011). This pathway is shown as biological solubilization in Fig. 1. Inputs and outputs of P are also indicated but not specifically addressed in this review.

The abiotic retention of P on soil particles is a continuum of precipitation and adsorption processes. The resulting P sorption capacity of soils is governed mainly by the concentration, types and surfaces of aluminum and iron oxides, even in calcareous soils (Frossard et al., 1995). Adsorption of inorganic P consists of a rapid ligand exchange reaction of phosphate groups with water or hydroxyl groups on the reactive surface, followed by slow reactions resulting from diffusion into the adsorbing material (Barrow, 1985; Goldberg and Sposito, 1985). Similar reactions account for adsorption of organic P compounds, although the slow reactions remain understudied (Celi and Barberis, 2005). For example, myo-inositol hexakisphosphate (phytate) can be removed from the soil solution via precipitation with Ca (Celi et al., 2000), or via

adsorption of up to four phosphate groups (Ognalaga et al., 1994; Celi et al., 1999). This makes adsorbed phytate less bioavailable than orthophosphate or glucose-6-phosphate which are adsorbed with only one phosphate group (Shang et al., 1996). Enzymatic hydrolysis of adsorbed phytate depends mainly on the strength of binding to a given soil mineral, but is generally rather limited (Giaveno et al., 2010). The availability of adsorbed organic P to microorganisms or enzymes can increase with increasing surface coverage (Shang et al., 1996; Olsson et al., 2012) as well as with exudation of organic anions (Giles et al., 2012).

The distinction between biological mineralization and extracellular hydrolysis of non-living organic P in Fig. 1 is based on McGill and Cole (1981). In their concept, biological mineralization is defined as microbial oxidation of organic matter driven by the need for energy, which may be associated with the release of inorganic nutrients before or after microbial uptake. In contrast, biochemical mineralization is defined as the release of inorganic nutrients through extracellular enzymatic processes driven by the need for the nutrient, thus followed by uptake from the soil solution. Extracellular enzymes can be located in the periplasmic space and on the surface of cells as well as in the soil solution or associated with soil organic matter and clay minerals (Burns et al., 2013). The most important enzymes in soil P cycling are phosphomonoesterases (including phytases), phosphodiesterases, and pyrophosphatase and polyphosphatase which hydrolyze P-containing anhydrides (Nannipieri et al., 2011). Acid and alkaline phosphomonoesterases dominate in acid and alkaline soils, respectively. The majority of phosphatase enzymes in soil probably originate from microorganisms, although plants also exude acid phosphomonoesterases and other enzymes, especially under P deficiency (George et al., 2011). The depletion of organic P in the rhizospheres of wheat and clover grown in alkaline soils was shown to be related to the sum of acid and alkaline phosphomonoesterase activity

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