Reviews and Syntheses: Ironing Out Wrinkles in the Soil Phosphorus Cycling Paradigm

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Abstract. Soil phosphorus (P) management remains a critical challenge for agriculture worldwide, and yet we are still unable to predict soil P dynamics as confidently as that of carbon (C) or nitrogen (N). This is due to both the complexity of inorganic P (P_i) and organic P (P_o) cycling and the methodological constraints that have limited our ability to trace P dynamics in the soil-plant system. In this review we describe the challenges to building parsimonious, accurate, and useful biogeochemical models that represent P dynamics and explore the potential of new techniques to usher P biogeochemistry research and modeling forward. We conclude that research efforts should focus on the following: 1) update the McGill and Cole (1981) model of P_o mineralization by clarifying the role and prevalence of "biochemical" and "biological" P_o mineralization which we suggest are not mutually exclusive and may co-occur along a continuum of P_o substrate stoichiometry; 2) further understand the dynamics of phytate, a 6-C compound that can regulate the poorly understood stoichiometry of soil P; 3) explore the effects of C and P_o saturation on P sorption and P_o mineralization; and 4) resolve discrepancies between hypotheses about P cycling and the methods used to test these hypotheses.

Introduction

Managing agricultural soil phosphorus (P) to maximize crop productivity and minimize P pollution is one of the critical challenges of contemporary agriculture. Our current understanding of soil P cycling lags carbon (C) and nitrogen (N) (Reed et al., 2015) and that lag is pronounced in simulation models (e.g. Vadas et al., 2006). Most P cycling components of biogeochemical models are structured after C and N despite key differences between the biogeochemical cycling of the three elements. Soil P has a significant inorganic component in addition to an organic one, both of which can cycle independently of C and N (McGill and Cole, 1981; Condron et al., 2005). Unlike C and N, investigating P cycling is limited by the existence of one P stable isotope (C and N have two each), making tracing studies dependent on P radioisotopes that are short-lived and hazardous. Phosphate-bound stable oxygen isotopes can also be used to trace P but are subject to biotically-mediated fractionation that complicate the interpretation of abiotic P transformations (Blake et al., 2005; Angert et al., 2011).

Gaps in our understanding of the P cycle are reflected in model conceptualizations and in model results that are rather uncertain regarding P cycling (Radcliffe et al., 2009). The mismatch or poor correlation between analytical-chemical P pools and conceptual P pools (Gijsman et al., 1996) only compounds this uncertainty. A manifestation of these limitations in model prediction was the failure to predict increased soluble P losses as agricultural management shifts from till to no-till systems (Duncan et al., 2019) even though it was long known that while no-till reduces erosion it stratifies immobile nutrients. Vertical stratification of P coupled with hydrological connectivity between fields and waterways via runoff or tile drains led to enhanced transport of soluble P from fields to water (Radcliffe et al., 2015; Dodd and Sharpley, 2016). The collective inability to predict

35   the behavior of P with current nutrient models (Radcliffe et al., 2015; García et al., 2016) highlights the limited holistic understanding of P cycling.

The goal of this review is to identify gaps in soil P cycling research that contribute to the observation-model disconnect and to clarify the path forward for a more seamless integration of experimental and theoretical progress. The objectives are to review the (1) discrepancies in P_o mineralization paradigms, (2) difficulties in incorporating phytate and C:P stoichiometry into these

40   paradigms, (3) dynamics of C and P_o saturation, and (4) methodological challenges in measuring P content, distribution, and sorption. These specific subjects were selected based on the extent of diverging evidence and the degree of importance to the conceptualization, or reconceptualization, of soil P cycling.

Overview of P cycle

In the soil-plant system, P exists in both inorganic (P_i) and organic (P_o) forms whose relative abundance depends on edaphic,

45   management, and climate conditions. Generally, P_o makes up 35-65%, and sometimes up to 90%, of total P in soil (Williams and Steinbergs, 1958; Harrison, 1987). Of the total P in most plant-soil systems, less than 10% is in living organisms (Ozanne, 1980; Arai and Sparks, 2007). Usually, less than 1% is in solution as either a dissolved organic species or as a free inorganic phosphate (PO_4) ion immediately useable by plants and microorganisms (Pierzynski, 1991; Frossard et al., 2000). For PO_4 to become available in the soil solution for organism uptake, soil P_i and soil P_o must undergo abiotic and biotic transformations (Figure 1).

50   Soil P_i is either in a primary mineral form, precipitated as various inorganic phosphates (mainly as $AlPO_4$, $FePO_4$, $CaPO_4$), occluded by precipitates and other minerals, sorbed to mineral surfaces, or dissolved in the soil solution. In inorganic "physiochemical" pathways PO_4 is released into solution by the dissolution of minerals, precipitates, and sorbed P_i (Hedley et al., 1982; Cross and Schlesinger, 1995; Arai and Sparks, 2007). However, PO_4 equilibrium favors sorption to the solid phase rather than desorption (Okajima et al., 1983; Menezes-Blackburn et al., 2016). PO_4 undergoes sorption to mineral and colloid surfaces

55   by electrostatic interaction or fast chemisorption (ligand exchange on external mineral sites).

Once PO_4 is sorbed it is either desorbed back to the soil solution or stabilized through further ligand exchange and slow incorporation into aggregates or clays (Holtan et al., 1988; Arai and Sparks, 2007). The methods of Hedley et al. (1982), later refined by Tiessen and Moir (1993), attempted to quantify P into pools along this continuum of P stabilization using sequential chemical extraction methods. The so-called "Hedley fractionation" is the most widely used method to quantify both P_i and P_o in

60   fractions of varying lability and indirectly, plant availability (Guppy et al., 2000).

The dissolution of solid phase P_i, and thus plant availability, depends on the ecosystem type (Cleveland et al., 2013; Bünemann, 2015), degree of soil development (Smeck, 1985), parent material (Bünemann et al., 2016), P_i lability relative to P_o (Pistocchi et al., 2018), and human inputs (Oehl et al., 2004). Soils in early stages of development have low soil P_o levels so plant P acquisition relies on physiochemical processes for P_i dissolution. These physiochemical processes also tend to control P

65   availability for plants in agroecosystems supplied with P_i-rich fertilizers (Guo et al., 2000; Oehl et al., 2004; Bünemann, 2015). While P_o can play a less significant role in agricultural systems (Bünemann, 2015), it can be an important P source via mineralization in forested or highly weathered soils (Yang and Post, 2011; Cleveland et al., 2013; Bünemann, 2015), particularly when labile P_i availability is low (Pistocchi et al., 2018).

The most common soil P_o forms are orthophosphate monoesters, orthophosphate diesters, organic polyphosphates, and phosphonates (Turner et al. 2007). The orthophosphate monoester inositol phosphate comprises a significant fraction of total P_o in most measured soils, principally due its recalcitrance to mineralization (Turner et al. 2002). Sugar phosphate monoesters and phosphate diesters like DNA and RNA are more labile sources of mineralizable P_o (Condron et al., 2005; Turner, 2008).

The agents responsible for P_o mineralization are plant and microbial phosphatases that are periplasmic, membrane-bound, or exuded into the soil solution. One function of extracellular enzymes is to depolymerize P_o compounds, thus increasing their solubility and accessibility by microbes and plants (Quiquampoix and Mousain, 2005). After depolymerization, P_o monomers may be assimilated by a microorganism depending on compound-specific membrane transport proteins and other organismal and environmental controls such as the concentration of P_i or the P_o compound (Wanner, 1996; Heath, 2005; Quiquampoix and Mousain, 2005). However, only a few P_o compounds are known to have direct transmembrane mobility (Wanner, 1996) and to our knowledge studies of direct P_o uptake were not conducted in soils. The indirect uptake of PO_4 from non-transportable P_o compounds is regulated by phosphatase enzymes.

The mechanisms by which non-transportable P_o is mineralized by microbes and plants are not clearly described in the literature; there is no unifying principle of P_o mineralization considering recent advances in P biogeochemistry research. Initially, microbial P_o mineralization was described similarly to N mineralization, whereby P_o is mineralized in conjunction with C for energy and thus coupled to C dynamics (Thompson et al., 1954; Dalal, 1979). This "biological" P_o mineralization model was challenged by McGill and Cole 1981 who posited a "biochemical" mineralization pathway. Under their definition, P_o mineralization is driven by P demand met by phosphatase enzymes to acquire P independent of C. This model demonstrates a decoupling of P from C dynamics. Although this conceptualization has been generally accepted to occur under low labile P_i conditions and provides a potential explanation for the observed variability in soil and microbial nutrient stoichiometry, it is not complete (see section 1).

The biological and biochemical pathways were regarded as mutually exclusive in the McGill and Cole 1981 model and in some cases continue to be (McGill and Cole, 1981; Heuck et al., 2015); however, it is simpler to assume that they coexist as, for example, in Goll et al. 2012 and Thum et al 2019. P_o mineralization can result in acquisition of P, C, or both, depending on the relative demand for either element or the relative lability of the P_o substrate. The biological and biochemical terms are misleading as P_o mineralization is always biochemical, i.e. phosphatase enzymes are used regardless of whether mineralization is driven by C or P demand. We propose to substitute "C-driven P_o mineralization" for biological and "P-driven P_o mineralization" for biochemical to distinguish the drivers leading to P_o mineralization but without confounding the paths. We understand that C-driven P_o mineralization as a concept might be narrow in scope, as organic matter can be decomposed to mine organic N or sulfur as well, but the proposed language is unequivocal with respect to P.

1 Deconstructing P_o mineralization and updating the McGill and Cole conceptual model

McGill and Cole (1981) proposed that P_o mineralization is independent of C and N mineralization (Smeck, 1985). However, this model is not uniformly true, as elucidated by Condron et al. 2005 and further evidenced by recent research. Phosphatase enzymes play a key role in P_o mineralization, yet phosphatase-mediated dephosphorylation may also be a requisite step in the acquisition of C (Spohn et al., 2015; Wang et al., 2016) as the polar PO_4 groups may hinder direct P_o uptake (Steenbergh et al., 2011). The extent to and conditions under which either C-driven or P-driven P_o mineralization occur is debated and requires clarification (Smeck, 1985; Gressel et al., 1996; Oehl et al., 2004; Guppy and McLaughlin, 2009; Spohn and Kuzyakov, 2013; Heuck and

Spohn, 2016). We will therefore highlight the evidence supporting both P_o mineralization pathways and describe methodological limitations to measure enzyme activity and P_o mineralization.

1.1 Evidence supporting P-driven P_o mineralization

Phosphatase enzymes can mineralize P_o independent of the C moiety. There is substantial evidence relating P_o depletion to increased phosphatase activity (Tarafdar and Jungk, 1987; Häussling and Marschner, 1989; Rojo et al., 1990; Speir and Cowling, 1991; Asmar et al., 1995; Chen et al., 2002) suggesting a mineralization pathway driven by P demand and decoupled from C dynamics. Increased phosphatase activity is also observed when decomposition is limited by P availability (Sinsabaugh et al., 1993), the soil has a high organic carbon (C_o) content (Halstead, 1964), or organic material is added to a soil (Li et al., 2015). Furthermore, there is a general negative relationship between available P_i and phosphatase activity, suggesting that P-driven mineralization is suppressed when labile P_i is no longer limiting (Juma and Tabatabai, 1977, 1978; Nannipieri et al., 1978; Spiers and McGill, 1979; Dick et al., 1988; Clarholm, 1993; Colvan et al., 2001; Moscatelli et al., 2005; Marklein and Houlton, 2012; Turner and Joseph Wright, 2014).

A tighter coupling of C mineralization with soil organic matter (SOM) C:N ratios rather than C:P ratios (Heuck and Spohn, 2016) and a relatively poor correlation of P_o with C or N (Yang and Post, 2011) indicate a greater independence of P mineralization from C than does N, a relationship captured by some simulation models (Yu et al., 2020). Furthermore, phosphatase activity responds quicker to changes in mineral P availability than analogous N enzymes to N availability (Marklein et al., 2016) indicating the reliance on phosphatase enzymes for P acquisition under P-limited scenarios.

1.2 Conflicting evidence in discerning P-driven and C-driven mineralization

The relative contribution of plants and microbes to exuded phosphatase enzymes is unknown (Richardson et al., 2009b). Because plants acquire C through photosynthesis, P-driven P_o mineralization seems uncontroversial for autotrophic plants. In contrast, heterotrophic microbes may mineralize P_o compounds for C or P rather than solely P. Discriminating microbial and plant phosphatase activity in the rhizosphere and linking C- or P-driven P_o mineralization pathways to either organism is challenging.

Phosphatase activity is higher in the rhizosphere than in the bulk soil (Nannipieri et al., 1978; Häussling and Marschner, 1989) likely due to the greater abundance of P_o substrates from decomposing root and microbial matter and combined plant and microbial activity in the rhizosphere (Jones et al., 2009; Spohn et al., 2015). The rhizosphere also tends to exhibit lower phosphatase activity with higher P_i availability compared to the bulk soil (Hedley et al., 1983). This response cannot be conclusively linked to plants or microbes (Richardson et al., 2009b) because, with a few exceptions, plant and microbial phosphatases are indistinguishable (Nannipieri et al., 2011). Among the exceptions are the microbe-specific alkaline phosphatases, which in some studies have exhibited a negative response to P_i fertilization when measured in the rhizosphere (Spohn et al., 2015) indicating an active microbe-mediated P-driven P_o mineralization. It must be noted however that alkaline phosphatases are only a subset of the microbially-produced phosphatase enzymes and are produced in neutral to basic conditions (Juma and Tabatabai, 1978), which cautions against broad generalizations.

Outside of the rhizosphere in the bulk soil, it has been shown that the alkaline phosphatase activity response to P_i availability is subdued (Spohn et al., 2015) or even positive (Colvan et al., 2001). This pattern is consistent with C-driven P_o mineralization by non-rhizosphere microbes, stripping the P group as a prerequisite for further C processing (Spohn and Kuzyakov, 2013; Spohn et

al., 2015). Supporting this interpretation, bulk or incubated soil isolated from roots (with phosphatases more likely of microbial origin) have not shown a decline in either acid or alkaline phosphatase activity when P_i availability increases (Adams and Pate, 1992; Lima et al., 1996).

Additionally some studies have either found no relationship between P_o mineralization and phosphatase activity (Dissing Nielsen and Eiland, 1980; Trasar-Cepeda et al., 1991; Chen et al., 2000; Allison and Vitousek, 2005) or did not observe a negative relationship of phosphatase activity with P_i availability or P_i fertilization (Halstead, 1964; Harrison, 1983; Li et al., 2015). The lack of an immediate negative response to P_i availability may be caused by recalcitrant phosphatase enzymes stabilized by soil minerals and colloids that remain active in the soil (Clarholm, 1993; Turner and Joseph Wright, 2014). Turner and Wright (2014) proposed that longer term studies must be conducted to ensure that a change in overall phosphatase production can be observed. But an equally plausible explanation for a lack of a phosphatase response to P_i availability may be that microbes are releasing phosphatase as a means of C acquisition (Spohn and Kuzyakov, 2013; Heuck et al., 2015), so phosphatase production can be on occasion unrelated to increased P_i availability (Figure 2).

1.3 Evidence supporting C-driven P_o mineralization

While P_o compounds are a C source for microbes, there is limited to no evidence of direct P_o assimilation by soil microbes (George et al., 2017). A lack of evidence does not exclude the possibility of phosphorylated compound uptake, but dephosphorylation either facilitates or is a requisite step in the acquisition of C from P_o. Evidence for C-driven P_o mineralization comes from studies showing the coupling of P_o mineralization and SOM decomposition (Dalal, 1979; Gressel et al., 1996; Moller et al., 2000). In dual-labeling experiments with ^{33}P and ^{14}C, the preferential microbial uptake of C from labeled glucose phosphate was greater than that of P, even under C saturation (Spohn and Kuzyakov, 2013; Heuck et al., 2015). Fransson and Jones (2007) found that organic compounds like adenosine were preferentially mineralized over their phosphorylated counterparts (AMP, ADP, ATP), and that low phosphatase activity may limit the use of phosphorylated compounds at elevated P_o concentrations. Accordingly, the activity of the C mineralizing enzyme β-glucosidase explained 41 to 69% of the variation in phosphatase activity (Wang et al., 2016) indicating the two groups of mineralization enzymes can be closely related (Sinsabaugh et al., 2009).

1.4 The co-existence of C-driven and P-driven P_o mineralization

It may only be on the extremes of a continuum of C or P limitation where C- or P-driven P_o mineralization dominates (Figure 3) with co-existence of these mechanisms under co-limiting conditions. In a temperate P-limited system, Heuck et al. 2015 found that C-driven P_o mineralization dominated, likely due to concurrent C-limitation that drove mineralization. Similarly, different microsites in the soil can be P- or C-limited, further complicating data interpretation when analyses are done in soil volumes that cannot distinguish processes at microscales.

Strict P-driven mineralization may not apply to soils and microbial communities that are C-limited, but soils and microbes are not always C-limited (Zechmeister-Boltenstern et al., 2015), particularly in tropical systems that can have significant P limitations (Camenzind et al., 2018). In highly-weathered soils the strong P_i fixation potential and overall low P_i makes P_o the dominant P source in the soil (McDowell et al., 2007; Vincent et al., 2010); thus, P-scavenging P acquisition strategies may be more prevalent. Soil type does not completely explain the dominance of P-driven P_o mineralization, as it may also depend on P_o speciation. Vincent et al. 2010 observed that litter manipulations did not impact soil C:N:P stoichiometry in a lowland tropical

forest indicating a non-discriminating mineralization behavior. As noted by these authors, the observed absence of inositol phosphates, which are very recalcitrant P_o compounds, may have reduced the prevalence of P-driven mineralization. A depletion in inositol phosphate, as seen in other studies (McDowell et al., 2007), may have been caused by earlier P-driven P_o mineralization (McDowell et al., 2007; Turner et al., 2007). Organic substrates of varying composition and their varying propensity to specific mineralization pathways may influence P stoichiometry and P_o mineralization.

1.5 Synthesis

Measuring and differentiating P_o mineralization pathways is an important step for modeling P biogeochemistry. Some land surface and catchment models simulate P-driven P_o mineralization (Wang et al., 2010; Goll et al., 2012, 2017; Davies et al., 2016; Yu et al., 2018, 2020; Thum et al., 2019; Zhu et al., 2019), but they are parameterized on limited observations (Reed et al., 2015; Thum et al., 2019) that are measured using unrepresentative or inaccurate methods. The first of these methodological limitations is the inaccuracy of P-driven mineralization measurements. It is difficult to quantify P-driven relative to C-driven mineralization with current assays (Oehl et al., 2004; Achat et al., 2016), particularly as phosphatase may play a role in both P and C-driven mineralization, complicating the use of phosphatase assays. Secondly, phosphatase enzyme assays are used as a proxy for P-driven mineralization (Goll et al., 2017), but the assays often overestimate real phosphatase activity and cannot be conducted in the field (Goll et al., 2012). Lastly, the mechanisms of phosphatase production and the relationship between phosphatase activity and mineralization are difficult to measure and are therefore poorly understood and not explicitly simulated in models (Oehl et al., 2004; Achat et al., 2016). Schimel and Weintraub (2003) took an enzyme-mediated approach to SOM decomposition/mineralization, but applying this approach to P_o decomposition/mineralization would require more accurate phosphatase activity assays and an ability to differentiate between extracellular and intracellular soil phosphatase. Better representing the P cycle in models is less a question of calibration and more a need to improve our fundamental understanding of P and C-driven P_o mineralization. However, further investigation of Po mineralization is hindered by the nature of P isotope chemistry, accessibility of appropriate methods, and currently held assumptions of the two pathways.

The co-regulation of P_o mineralization by substrate properties and by plant and microbial P-demand needs to be clarified. Developing methods to measure real instead of potential phosphatase activity will allow a more accurate estimation of P_o mineralization from actively produced phosphatase enzymes (Nannipieri et al., 2011; Bünemann, 2015). This will reduce the overestimation problem of current *in-vitro* phosphatase enzyme assays (Nannipieri et al., 2011; Spohn et al., 2013) enabling more accurate parameterization of models based on the explicit simulation of phosphatase activity.

Microbial or plant demand for P can also regulate phosphatase production, and the properties of P_o would determine the effectiveness of these phosphatases. A typical approach in modeling is to determine the maximum turnover rate of a given pool, which in this case can be equated to the rate of P_o mineralization in systems that are flooded with phosphatase. This rate can be reduced by the actual phosphatase activity that in turn would depend on a calculated demand from microbes and plants. Although not simulating the relative plant and microbe phosphatase activity in this manner, Yu et al. 2020 simulated P_o mineralization by combining the soil enzyme allocation model (SEAM) (Wutzler et al. 2017) and the equilibrium chemistry approximation (ECA) (Tang and Riley 2013) to estimate the allocation of enzymes between P_o sources and the subsequent microbial-plant uptake.

P turnover and the linkage with organic C mineralization can be studied with ^{32}P and ^{33}P isotope dilution (Frossard et al., 2011) and ^{18}O-P tracing to obtain mineralization rates alongside enzyme activity assays. ^{18}O isotope P tracing techniques has been used as a safe alternative to radioisotopes in tracing inorganic phosphate (Tamburini et al., 2010, 2014), and recent methods have

demonstrated the efficacy of ^{18}O tracing of organic phosphate (Liang and Blake, 2006; Tamburini et al., 2018). However, P_o tracing methods using oxygen isotopes are in their infancy and have not been applied outside of a proof-of-concept. Experiments employing ^{18}O tracing techniques for both P_i and P_o must be conducted on a wider range of soils (Nannipieri et al., 2011). Further employment of these methods could help discern biological processes and the turnover of phosphate in natural abundance (Roberts et al., 2015) and tracer studies (Joshi et al., 2016). They can also be used for P source characterization (Zohar et al., 2010; Frossard et al., 2011).

Discriminating the activity of microorganisms from those of stabilized enzymes is also tractable (Turner and Joseph Wright, 2014). One way would be to measure the expression of phosphatase genes in plants and microorganisms as a response to changes in P availability. A characterization of microbial or plant responsiveness to shifts in P availability would further help integrating P-driven P_o mineralization into models, as it is determined by specific environmental and biological conditions. This requires further work identifying conditions that lead to changes in gene expression (Grafe et al., 2018).

2 Phytate dynamics and the unpredictability of P stoichiometry

2.1 Phytate

P_o species differ in abundance due to their variable affinity for mineral or SOM sorption and recalcitrance to mineralization. Commonly, the most prevalent P_o forms in soil are inositol phosphates consisting of six-carbon rings with one to six phosphate groups. Myo-inositol hexakisphosphate, also known as phytate in its salt form, is the most abundant inositol phosphate and has six P groups (Harrison, 1987; Turner et al., 2002). Phytate is stabilized in the soil through ligand exchange, formation of metal-phosphate bridges to SOM, and precipitation as insoluble salts (Celi et al., 1999; Jørgensen et al., 2015). The phosphate groups bind to mineral surfaces by ligand exchange with hydroxyls and to mineral and SOM cationic surfaces via electrostatic binding (Celi et al., 1999; Arai and Sparks, 2007; Jørgensen et al., 2015). Phytate's tendency to bind to the soil phase contributes to its abundance and recalcitrance to mineralization (Anderson et al., 1974; Turner et al., 2002; Berg and Joern, 2006). A majority, from 29 to 65% and even up to 90%, of soil P_o can be phytate (Harrison, 1987; Turner et al., 2002) but this can vary substantially depending on factors that are not fully understood (Figure 4).

A thorough review on inositol phosphates is found in Turner (2007), but relevant information and new findings will be covered here. Phytate is prevalently stored in grain (and pollen, which is a small pool) but is also found in roots, crowns, and leaves, potentially as a transient storage compound (Campbell et al., 1991; Hubel and Beck, 1996). Turner (2007) noted that despite prevalent research on phytate and other soil inositol phosphates, their abundance varies widely and often unpredictably. As described by McGill and Cole (1981) and later supported by Shang et al. (1990), phytate sorption dynamics is similar to that of orthophosphate and is partially controlled by similar factors (sorption capacity, Fe and Al oxide content) (Yan et al., 2014). The abundance of phytate measured in agricultural systems is attributed to their recalcitrance and stability through sorption and precipitation (Yan et al., 2014) and prevalence in manures (particularly non-ruminants) and animal feeds (Sun and Jaisi, 2018).

2.1.1 Controls on phytate mineralization

The solubility and lability of phytate compounds, the principal controls on phytate mineralization, and the extent and efficacy of its mineralization by plants remain unclear (Richardson et al., 2000; Gerke, 2015a). We do know that phytate mineralization is a two-step process whereby phytate is first solubilized and made accessible to phytate-hydrolyzing enzymes called "phytases"

(Mullaney and Ullah, 2007; Gerke, 2015b, 2015a). In this review, the term phytase is used rather than the more general term "phytate-degrading enzymes", which refers to any enzyme *in vivo* or *in vitro* that can hydrolyze phosphate from phytate (Greiner, 2007). Because this review focuses on the *in vivo* processes, the term phytase is preferred.

The two principal controls on phytate mineralization are the production of phytase and the solubility of phytate, but their relative influence on mineralization is not fully understood. Phytate is expected to undergo hydrolysis in the soil solution (Ognalaga et al., 1994), but for that to happen it must first be solubilized from the soil phase through abiotic or biotic processes (Gerke, 2015b, 2015a). Akin to other organic phosphates, biotically-mediated dissolution of phytate can be facilitated by organic anions that chelate Fe, Al, or Ca (Tang et al., 2006). While solubilization is thought to be the limiting step in the hydrolysis of phytate (Greaves and Webley, 1969; Lung and Lim, 2006; Patel et al., 2010; Gerke, 2015a), other studies have shown that hydrolysis and phytase production are also limiting steps (Findenegg and Nelemans, 1993; Hayes et al., 2000; Richardson et al., 2001; George et al., 2004).

Microorganisms are key regulators of phytate mineralization. They produce both phytate-solubilizing organic acids (Richardson and Simpson, 2011) and multiple classes of phytate mineralizing enzymes (Hill and Richardson, 2007; Mullaney and Ullah, 2007). Soil microbial communities appear to be crucial agents in increasing phytate availability for plant acquisition (Richardson and Simpson, 2011). The extent to which plants themselves control phytate mineralization outside of in-vitro studies or genetic modification is less clear.

2.1.2 Plant-mediated phytate mineralization

A limited number of reports indicate that some plant species can secrete phytase (Li et al., 1997; Belinque et al., 2015). This is likely a response to limited P_i availability (Tarafdar and Claassen, 2003) and would be a prime example of P-driven P_o mineralization with phytate as the substrate. Steffens et al. (2010) demonstrated plant-mediated phytate mineralization in a growth chamber experiment with negligible microbial activity. While studies of this nature are scarce, Belinque et al. (2015) found that oilseed rape, sunflower, and soybean grown under sterile conditions could use phytate as a P source and that microbial inoculation had a minimal effect on overall plant acquisition of phytate P.

Contrary to these findings, other authors have reported that phytate mineralization and subsequent uptake of phytate-derived P by plants is minimal or absent (Findenegg and Nelemans, 1993; Richardson et al., 2000, 2001; Lung and Lim, 2006) or that detected phytase was plant-derived but involved in intracellular root phytate regulation rather than extracellular phytate scavenging (Hubel and Beck, 1996; Asmar, 1997; Richardson et al., 2000). If extracellular phytase release from plants is truly minimal or absent, effective plant use of soil phytate would depend heavily on phytase-producing microorganisms (Richardson et al., 2000; Idriss et al., 2002) or expression of microbial phytase genes in transgenic plants (Richardson et al., 2001; Lung et al., 2005; Giles et al., 2017). Furthermore, phytate use may still be limited by either microbial exoenzyme production (Findenegg and Nelemans, 1993) or phytate accessibility (Gerke, 2015a, 2015b).

2.1.3 Variable abundance and mineralization rates of soil phytate

There are exceptions that do not fit, or question, a neat pattern of phytate stabilization and retention in soil. Contrary to the widespread abundance of phytate often attributed to its recalcitrance to mineralization, rapid phytate mineralization has been observed in non-calcareous (Dou et al., 2009) and calcareous soils (Leytem et al., 2006; Doolette et al., 2010). Possible

explanations to rapid mineralization are that certain soil conditions increase phytate solubility or that some phytates are inherently more soluble or susceptible to hydrolysis depending on interactions with specific minerals or SOM.

As explained by Turner and Blackwell (2013), unless the soil solution of a calcareous soil has excess dissolved Ca^{2+}, Ca-phytate is slightly more soluble than Fe/Al phytates (Jackman and Black, 1951). Furthermore, Ca-phytate mineralizes more rapidly than insoluble Fe or Al-associated phytates (Greenwood and Lewis, 1977; Quiquampoix and Mousain, 2005; Tang et al., 2006) even at a pH 6-8 (Greaves and Webley, 1969)

Working in a non-calcareous soil, Dou et al. 2009 found a lack of phytate accumulation and presumed rapid mineralization. In this case, although Al and Fe contents and fixation capacity may have been high, the soil was likely saturated with C_o from previous manure applications. This would have increased the solubilization of phytate and contributed to its observed rapid mineralization, a subject discussed further below in section 3, Organic P and C saturation.

2.1.4 Synthesis

Although both plants and microbes can release phytase and phytate-solubilizing organic acids (Richardson et al., 2009b), microbes indirectly facilitate phytate acquisition (Richardson et al., 2001, 2009a) likely due to greater production of phytate solubilization or mineralization enzymes. It is therefore necessary to further investigate the interplay between microbes and plants, particularly *in vivo*, where experimentation is limited (Giles and Cade-Menun, 2014).

Although phytate makes up a large percentage of soil P_o in many soils, its dynamics are not explicitly simulated in models. Instead of constructing general pools with presumed P_o turnover rates, specific forms of C and P should be identified and their roles in the turnover of P_o investigated (Arenberg and Arai, 2019) with the ultimate goal of incorporating phytate-specific pools in models, such as that depicted in Figure 5. However, this will require elucidating the actual phytate abundance, as it is likely overestimated due to limitations in phytate analysis (Smernik and Dougherty, 2007; Doolette et al., 2011).

Integrating phytate pools into models would be facilitated by further research on the sorption of phytate and its mobility (Gerke, 2015b), the complementary effects of organic acid and phytase exudation from both plants and microbes on phytate depletion (Giles et al., 2017), and the observations of rapid phytate mineralization (Doolette et al., 2010) and reduced stabilization (Dou et al., 2009) resulting in variable phytate abundance. Coupling isotope tracing and ^{31}P NMR spectroscopy techniques will also provide important insights into the fate of P_o compounds like phytate (Giles and Cade-Menun, 2014; Tamburini et al., 2018). However, further study on plant and microbial strategies for improving phytate acquisition must also be conducted at the field scale (Giles and Cade-Menun, 2014). There is also a need to eliminate or reduce the ambiguities in ^{31}P NMR techniques when characterizing or quantifying Po, a topic covered in Kruse et al. (2015). The lack of clarity surrounding the different mineralization pathways, the varying recalcitrance of P_o species, or a combination of the two may contribute to the observed wide global variation in C:P or N:P stoichiometry (Vincent et al., 2010; Tipping et al., 2016).

2.2 Stoichiometry

The flux of nutrients between soil and organisms can be modeled by tying C fluxes to C:N:P stoichiometry, if it is known and predictable. Knowledge of C:N ratios has enabled accurate modeling of N limitation and mineralization-immobilization dynamics (White et al., 2014). This modeling success can be attributed to the tight coupling of C and N in soils across ecosystems, which is largely because organic N makes up 95% of soil N (Duxbury et al., 1989; Kirkby et al., 2011; Yang and

Post, 2011). Soil C:P and N:P ratios are currently used in simulation models, but P_i and P_o are often poorly correlated with soil C or N content (Yang and Post, 2011; Hartman and Richardson, 2013; Tipping et al., 2016; Zhou et al., 2018). Variation in soil C:P ratios, flexible microbial stoichiometry or not strictly homeostatic behavior (Hartman and Richardson, 2013), and unpredictable microbial critical ratios (CRs) contribute to model uncertainty. Variability in soil and microbial stoichiometry derive from methodological or analytical discrepancies (Kirkby et al., 2011), edaphic and ecosystem properties, and microorganism-specific characteristics (Mooshammer et al., 2014; Čapek et al., 2016), all of which must be considered when modeling plant litter and SOM decomposition.

2.2.1 Soil Stoichiometry

The use of P_o, P_i, or P_t (total P) in stoichiometry measurements requires clarification as methodological differences (Kirkby et al., 2011) can confuse matters. Including P_i in $C:P_t$ ratios introduces more variability in relating C and P because P_i can cycle independent of C and N. The $C:P_o$ ratio, where C only includes organic C, may better represent P_o stoichiometry in the soil, but it too can vary widely depending on the plant and microbial communities, ecosystem, and management (Figure 6) (Hartman and Richardson, 2013; Mooshammer et al., 2014; Čapek et al., 2016, 2018; Tipping et al., 2016). The decoupling of $C:P_t$ and $N:P_t$ is also seen as soil weathers (Yang and Post, 2011) where P_o becomes the predominant contributor to P fertility (Yang and Post, 2011; Cleveland et al., 2013; Bünemann, 2015) and nutrient acquisition strategies shift from physiochemical P_i acquisition to closed P_o cycling (Lang et al., 2017). Another possibility for this stoichiometric decoupling is the varying abundance of specific P_o forms between systems (Kirkby et al., 2011). Because the C:P ratio of phytate is 1, shifting or variable phytate abundance would reflect in the soil C:P stoichiometry. A depletion of mineral Pi, an absence of a strong C limitation, changes in abundance of certain P_o forms, or a potential shift to P-driven P_o mineralization processes may explain this decoupling.

2.2.2 Plant and Microbial Stoichiometry

The variability seen in soil C:P stoichiometry is also seen in C:P ratios of plants and microbes across and within ecosystems (Cleveland and Liptzin, 2007; Hartman and Richardson, 2013; Xu et al., 2013; Čapek et al., 2016). Plant stoichiometry is an important control on the flux of soil nutrients as it influences the decomposition activity of microbes (Manzoni et al., 2008, 2010). Microbes are the principal decomposers of litter and SOM and thus a major driver of P transformation in the soil (Zechmeister-Boltenstern et al., 2015), which is thought to be controlled by their own stoichiometry (Hall et al., 2011).

Microbial stoichiometry is more constrained than that of plants (Xu et al., 2013; Arenberg and Arai, 2019) and is often purported to be strictly homeostatic (Cleveland and Liptzin, 2007). Although microbial stoichiometry is roughly constrained on the global level, microbes at the population, ecosystem, or community scale may not be strictly homeostatic, as found in aquatic systems (Cotner et al., 2010). Soil microbes may also display the same level of stoichiometric flexibility (Hartman and Richardson, 2013), varying due to population size-dependent scaling, habitat and ecosystem differences, or shifts in microbial community composition (Hartman and Richardson, 2013; Mooshammer et a

l., 2014; Čapek et al., 2016).

Accounting for this variability in models is further complicated by the difficulties in calculating microbial nutrient demand, governed by the ratio of C:P at which microbes shift between mineralization and immobilization (Manzoni et al., 2010; Hartman and Richardson, 2013). This critical ratio (CR) is often predicted using direct measurements of microbial biomass C:P, which

itself is poorly correlated to actual microbial nutrient requirements (Čapek et al., 2018). This is in part because microbes can store P in the form of polyphosphates (up to 30% of their dry weight) (Deinema et al., 1985; Kulaev et al., 1999), which reflects an indirect translation between C:P ratios and demand (Čapek et al., 2016, 2018).

The microbial $C:P_{CR}$ is an important factor to model because mineralized or immobilized substrates provide or restrict P to plants, respectively. Capek et al. 2016 attempted to predict the $C:P_{CR}$ using microbial biomass stoichiometry and soil P measurements but were unsuccessful, likely because $C:P_{CR}$ is not solely dependent on biomass C:P, but on various edaphic and community-specific factors as well. This may explain why previous studies have failed to see a strong relationship between P_o mineralization and C:P ratios of SOM (Enwezor, 1967, 1976; McLaughlin et al., 2011). Using a fixed microbial $C:P_{CR}$ may not capture the observed variability (Hartman and Richardson, 2013; Čapek et al., 2016), but implementing a flexible $C:P_{CR}$ in a model is not yet possible due to the ratio's unpredictability (Čapek et al., 2016). However, one can tentatively assume that microbial communities adjust their P requirements by increasing $C:P_{CR}$ as P becomes more limiting. The degree of P limitation depends in part on N availability, because to sustain P-driven P_o mineralization microbes need N sources to sustain phosphatase enzyme production (Olander and Vitousek, 2000; Houlton et al., 2008). Supporting this view, Margalef et al. (2017) found that total N content was strongly correlated to phosphatase activity across global soil measurements.

2.2.3 Synthesis

One of the difficulties in modeling soil P dynamics is predicting the C:N:P stoichiometry of plants, microbes, and SOM. This is due to the many, often interacting, sources of variation in P stoichiometry such as habitat, edaphic properties, soil C quality, microbial population dynamics, climate, season, and disturbance or management (Cleveland et al., 2004; Aponte et al., 2010; Hartman and Richardson, 2013; Čapek et al., 2016). Establishing better relationships between these sources of variability and observed nutrient stoichiometry as well as implementing a consistent measurement protocol for C:P ratios will help future data collection and consolidation efforts.

The variability of $C:P_{CR}$ or the microbial and C:P ratios presented in Figure 6 makes it difficult but not intractable to set constraints on P cycling models. Many models assume fixed stoichiometry for the soil or soil pools (Kemanian et al., 2011), which may only be applicable to certain soil systems. Using fixed P stoichiometry to model P biogeochemistry may not capture P dynamics across ecosystems, but implementing variable C:P ratios, like those in the CENTURY model, requires improved parameterization and understanding of the factors that control C:P ratios. Clarifying the role of phytates may simplify this task, because phytate's C:P = 1 is a ratio well below the $C:P_{CR}$ of any organism. It is also necessary to elucidate the mechanisms of P-driven P_o mineralization because first, CRs do not reflect P dynamics in systems dominated by such P_o mineralization pathways (McLaughlin et al., 2011) and second, P-driven P_o mineralization can drive the decoupling of P mineralization from SOM decomposition (Goll et al., 2012).

Including an explicit microbial pool that accounts for physiological and community dynamics (Allison, 2012; Wieder et al., 2014) when modeling the P cycle will better represent microbial adaptation to changing resource stoichiometry. However, further research into community specific drivers of microbial stoichiometry is needed, such as accounting for differences in the P acquisition strategies of bacteria and fungi (Waring et al., 2013). Representing this in models could be as simple as accounting for bacterial and fungal C:P or biomass ratios, akin to the approach of Waring et al. (2013) for C and N cycling, or a more complex trait-based approach (Allison, 2012; Wieder et al., 2014).

3 Organic P and C saturation

P saturation refers to the level of soil P, typically inorganic, in relation to the measured sorption capacity. P saturation is often expressed as the degree of P saturation (DPS), which is used as an environmental risk indicator of potential dissolved P losses (Breeuwsma et al., 1995). Soils with DPS levels that surpass a "change point" (hereafter referred to as threshold DPS) exhibit significant increases in dissolved P transport due to the saturation of high energy sorption sites and reduction in P_i retention strength (Hooda et al., 2000; Maguire and Sims, 2002; Butler and Coale, 2005; Abdala et al., 2012). This threshold DPS generally occurs between 25 and 56% saturation depending on the soil (Maguire and Sims, 2002).

Difficulties in narrowing the range of threshold DPS or creating a simple predictive framework can be partially attributed to the ambiguous treatment of C_o saturation and P_o abundance in DPS measurements. One such DPS measurement uses oxalate or Mehlich-3 extractions to obtain the molar ratio of extractable P to the sorption maximum determined by extractable Al and Fe (van der Zee and van Riemsdijk, 1988; Kleinman and Sharpley, 2002). This method ignores the soil C_o content, which if high enough, can reduce the physically obtainable P saturation potential of a soil (Table 1, Figure 7A) and influence the rate of P_o mineralization (Figure 7B). Furthermore, certain extractants and analytical methods do not target P_o (e.g. Mehlich-3 extraction, P_i sorption isotherms, spectrophotometric methods), leading to underestimation of the "actual" total P DPS (Table 1, Figure 7C). The extent to which DPS is affected by P_o and C_o depends on the relative concentrations of P_i and Po, the form of P_o and its sorption potential, and the interacting sorption relationships between P_o, P_i, and dissolved organic compounds from the breakdown of SOM.

Because P_o turnover and mineralization is partially controlled by its solubility (Greaves and Webley, 1969; Grafe et al., 2018), and saturation influences the solubility of both P_i and P_o (Heckrath et al., 1995), ignoring P_o sorption and C_o saturation dynamics may limit the predictive capability of DPS measurements and sorption indices. P_o and C_o saturation are generally not determined and are not explicitly simulated in models despite the potential interactions between P_i and P_o in the soil and the role of P_o in plant fertility.

3.1 Modelling the effects of C_o saturation on P_o mineralization

Similar to P, C_o can be stabilized in the soil by sorption to silts and clays (Hassink and Whitmore, 1997) and during aggregate formation (Six et al., 2002). Sorption proceeds with the formation of organo-mineral complexes. The C_o saturation (C_x) can be calculated based on the clay and silt content of the soil (Table 2, Eq. 1) (Hassink and Whitmore, 1997). The saturation of C_o has implications for the storage of C, decomposition, and the mineralization of nutrients (Kemanian and Stöckle, 2010; Kemanian et al., 2011; Castellano et al., 2012; White et al., 2014).

The dynamics of explicit C_o saturation are only included in a few models (Kemanian and Stöckle, 2010; White et al., 2014; Ahrens et al., 2015), and its effect on P_o mineralization is unexplored in models. The limited number of studies on C_o saturation and N cycling demonstrate that C_o saturation is positively correlated with N mineralization (Castellano et al., 2012), likely because C_o saturation reduces the C transfer efficiency or rate to stable pools thus increasing mineralization of labile N (White et al. 2014). This relationship is expected to be seen between P_o mineralization and C_o saturation (Figure 7B). The effects of C_o saturation are most readily seen in soils with high C_o accumulation (top layer of stratified, undisturbed no-till systems) (Mazzilli et al., 2014; Pravia et al., 2019), or soils with low clay content (Castellano et al., 2012). More studies are needed, especially in

areas with an C_o saturation gradient, to solidify the C_o saturation concept for N dynamics (White et al., 2014) and advance it for P, preferably in investigations pairing N and P.

3.2 Competitive C_o anion sorption

Experiments on C_o saturation suggest that as the C_o content of the soil increases, so does the lability, solubility, and ultimate transport of P_i from the soil (Reddy et al., 1980; Walbridge et al., 1991; Erich et al., 2002; Guppy et al., 2005; Abdala et al., 2012; Gao et al., 2014). On a molecular basis, this can be attributed to the competitive saturation of sorption sties by C_o anions as reported in other studies (Ohno and Crannell, 1996; Staunton and Leprince, 1996; Antelo et al., 2007; Hunt et al., 2007) (Figure 7A). Guppy et al. (2005) claim that the observed decrease in P_i sorption is not attributable to competition for sorption sites, but instead to the increased mineralization of P-bearing C_o compounds, akin to the White et al. 2014 model (Figure 7B). These mechanisms are not necessarily mutually exclusive. For example, as soils move closer to C saturation, N mineralization increases because the soils lack new sites for C_o to be stabilized on minerals (Castellano et al., 2012; White et al., 2014). Regardless of the proposed mechanisms, in order to improve P modeling, accounting for competitive sorption reactions (Regelink et al., 2015) or the increase in P_i content from mineralization or P_i release (Guppy et al., 2005) is a necessity.

3.3 The contribution of P_o to DPS and the interactions between P_i and P_o

A common method of characterizing sorption dynamics is to develop a soil sorption isotherm, or sorption curve, which requires equilibrating various concentrations of P_i with a soil sample. Although to a lesser extent, P_o sorption dynamics have also been studied using sorption isotherms. Instead of using P_i in the equilibrating solution, different forms of P_o can be added together or separately with Pi and their sorption dynamics compared (Anderson et al., 1974; McKercher and Anderson, 1989; Berg and Joern, 2006). The PO_4 ion on P_o partially controls its sorption so P_o compounds share similar sorption dynamics with P_i. P_o's affinity to the soil phase increases with the number of phosphate groups (Shang et al., 1990). Due to the steric hindrance of the C moiety (Celi et al., 1999) it is suspected that P_o does not readily penetrate mineral pores (Shang et al., 1992). However, the similar surface binding mechanisms of P_o and P_i likely means they compete for surface sorption sites, which has implications for the solubility of both P_o and P_i and thus its availability for plant uptake or hydrologic losses.

When multiple P_o species and P_i are added to the equilibration solution of a sorption isotherm experiment the affinity of each species can be measured in competition with one another. P_o generally exhibits less efficient sorption than Pi, except for phytate. Phytate sorption dynamics are debated, with some reports stating that phytate sorbs to a greater extent than P_i (McKercher and Anderson, 1989; Berg and Joern, 2006; Wang et al., 2007) and others showing the opposite result (Shang et al., 1990; Ognalaga et al., 1994; Lilienfein et al., 2004).

An explanation parsimonious with both results is that P_o with multiple phosphate groups may sorb more strongly while P_i may sorb more rapidly. The P_o sorption strength increases with the number of phosphate groups (Shang et al., 1990; Berg and Joern, 2006). When compounds like phytate are present in a soil, stabilized by mineral interactions and not readily mineralized, P_i saturation should decrease due to the lower net desorption of P_o (Table 1, Figure 7C). In contrast, cases showing preferential sorption of P_i over P_o might be explained by the lower activation energy needed for a PO_4 ion to bind to soil compared to a more complex mono or diester organic compound. Both processes are likely co-occurring; P_o may sorb stronger, particularly if it has more PO_4 groups, but P_i may sorb faster due to its low activation energy and lower steric hindrance (Shang et al., 1990). Yet, we lack an understanding of the conditions that cause one of these processes to dominate in a soil environment.

The accumulation of P_o has implications for how DPS measurements of P_i are in interpreted; P_o can competitively sorb with P_i and reduce the measured, but not actual, DPS. P_o saturation may influence P_o mineralization dynamics and should be the subject of future empirical and modeling work. This can be critical to understand P pollution from soils with high organic C and high P_o, a condition that is becoming more prevalent with the advance of no-till in manured soils or in any soil receiving ample supply of manure.

3.4 Synthesis

Advances in understanding P_o dynamics and its relation to P_i and C_o saturation are required in three areas. First, the contributing role of P_o to P saturation and thus to greater P sorption and cycling dynamics must be further investigated. This includes determining the effect of P_o on DPS measurements, for P_o is implicitly considered in the denominator but not always in the numerator of the DPS calculation. Second, the controls on P sorption of litter application, rhizosphere exudation/deposition, or native C_o needs to be clarified. Organic additions can increase P_i in the solution due to P_o mineralization (as proposed by Guppy et al., 2005) or by increasing the solubility of P_i (as proposed by Hunt et al., 2007; Oburger et al., 2011; Regelink et al., 2015). Both processes may be co-occurring but it is critical to define the conditions under which one or the other dominates. And lastly, modeling and experimental efforts are needed to determine the effect of C saturation on P_o mineralization, as has been done for N (White et al. 2014). These efforts may need to consider phytate and non-phytate compounds as two separate pools. In soils that are amended with manure, C saturation and P saturation can be critical controls of both C and P turnover.

4 Methodological discrepancies between P analyses and implied P dynamics

4.1 Soil P_i and P_o pools

Soil P_i and P_o forms vary in turnover rates along a continuum of stabilization (Tiessen and Moir, 1993). To model their dynamics, P_i and P_o are subdivided into pools, with the exception of ECOSYS that simulates P_i dynamics using dozens of element and mineral-specific equilibrium reactions (Grant and Heaney, 1997). In most models these pools are conceptual and are not representable as analytical fractions (Gijsman et al., 1996; Six et al., 2002), such as those determined by the Hedley Fractionation Method. This is in part because analytical fractions do not always respond in a quantifiable manner directly to inputs and outputs (Delve et al., 2009). Despite this limitation, conceptual pools are still estimated by establishing relationships between P stability and changes in pool sizes or transformations using isotope tracing (Hedley et al., 1982; Stewart and Tiessen, 1987; Taranto et al., 2000; Helfenstein et al., 2020).

Among the consequences of the lack of correspondence between modeled and measured pools are that these models may need calibration and that as P_i and P_o decrease or increase there is no assurance that the calibrated parameters values will remain valid outside the calibration domain. P is distributed into pools based on its stability and cycling rate and the more stable pools are thought to be available over decadal timescales (Richter et al., 2006) through the slow replenishment of labile fractions (Guo et al., 2000). However, both inorganic and organic P forms are likely accessible on shorter, seasonal timescales. For example, phytate which is often considered highly stable, has been observed to mineralize rapidly (Doolette et al., 2010). For Pi, extracted pools that are considered "stable", such as the HCl fraction, have a greater short-term turnover than previously thought (Joshi et al., 2016; Siebers et al., 2018), so models with invariable cycling rates will not be able to represent this dynamic.

4.2 Sorption Curves

495 Inherently linked to the stabilization of phosphate in various soil phases are the processes and rates of phosphate sorption. Sorption curves, often referred to as sorption isotherms, are used to determine the extent of rapid P sorption between the solution P and the soil (McGechan and Lewis, 2002). Three problems arise from the use of sorption curves: they are soil-dependent rather than generalizable, the methods involved in generating the curve can influence the sorption isotherm parameterization and the modeled P dynamics, and the P sorption-desorption pathways is hysteretic (Barrow, 1983, 2008; Okajima et al., 1983; Grant and
500 Heaney, 1997).

Because sorption isotherms are time-consuming and are not a part of routine soil analyses, P is often modeled using sorption curve parameters that do not always represent the simulated soil. The general applicability of sorption curves is further reduced because they are not mechanistic and do not account for site-specific differences in pH, ionic strength, or surface complexation (Grant et al. 1997; Arai and sparks 2007).

505 Typically, the generation of sorption curves involves shaking P solutions with a range of known concentrations with a soil sample. After 16-24 hours, the equilibrium P concentration is measured, and the curve is fitted. If the shaking is too vigorous, new sorption sites can be exposed, and the isotherm is no longer representative of P sorption (Barrow 2008). Furthermore, parameterizing the hysteretic nature of P involves time consuming methodologies (Limousin et al., 2007), but its exclusion results in model uncertainty.

510 Fitting curves generated by isotherm experiments can also be problematic. The equations by Langmuir (Table 2, Eq. 2) and Freundlich (Table 2, Eq. 3) are commonly used to fit sorption curves. The Langmuir isotherm assumes a reaction with a uniform sorption surface, which does not occur in soils. Freundlich isotherms assume an infinite number of sorption sites (Kruse et al., 2015), i.e. no sorption maximum is considered like in the Langmuir. Neither the general Langmuir nor Freundlich equations account for multiple possible sorption pathways, which may result in their underestimation of sorption (Hussain et al., 2012) and
515 reduced fit (McGechan and Lewis 2002). Two phase Langmuir equations (Table 2, Eq. 4) can be used, as they have provided better fit for sorption isotherms in some cases (Holford et al., 1974; Hussain et al., 2012). However, using the same soils as Holford et al. (1974), Barrow (1978) demonstrated the Freundlich had comparable fits with reduced parameters, which may explain the absence of two phase Langmuirs in simulation models.

Sharpley et al. (1984) employed a longer and more intensive approach to estimating a "P sorption parameter" (PSP), which is the
520 percentage of added P remaining in the soil solution after equilibrium is reached with a labile "active" pool (Vadas et al. 2013). In lieu of a 24-hour incubation, known P concentrations were added to subsamples that were dried and rewetted three times with deionized (DI) water over a period of six months. Three general equations were developed for calcareous, slightly weathered, and highly weathered soils. These equations were integrated into the Soil and Water Assessment Tool (SWAT) model (Arnold et al., 1998), which is built on the CREAMS, GLEAMS, and EPIC model structures (Knisel, 1980; Jones et al., 1984; Leonard et
525 al., 1987). Although this model accounts for temperature and moisture factors, pH is grouped into large categories which may limit its applicability to the highly variable nature of soils. Furthermore, equation 7 shows that C_o has a negative relationship with PSP, which is the opposite of the expected response as outlined in section 3.2, Competitive C_o anion sorption. In SWAT, this PSP variable and the solution P are used to calculate the size of pools in the model. However, solution P is assumed to be half of Mehlich-3 or other soil test phosphorus (STP) method. This may work for initialization before model spin up, or at least
530 provide a consistent method, but is not a representative method in determining P pool sizes.

An alternative to both isotherm methods is the use of known equilibrium constants of various soil minerals and precipitates to calculate an equilibrium of sorbed or mineral P with the soil. Such an approach was taken by Grant et al. 1997 in the ECOSYS model. Although based on first principles, it relies on obtaining concentrations of many soil minerals, which may be impractical or difficult. For reliable parameterization, it would also require knowing the effective mineral-solution contact; larger minerals or colloids would have a lower surface area for P exchange compared to smaller colloids.

4.3 Synthesis

Translating analytical P pools into models is complicated by the fact that extracted pools are not compound-specific and only provide an estimation of P_i and P_o turnover rates. This issue is exacerbated by the diversity among and within chemical extraction protocols. The most used extraction method, the Hedley Fractionation method, is also the most heavily modified, having dozens of variations. This is a weak foundation for the comparison and meta-analysis of data from studies employing variations of the Hedley protocol. If we are to incorporate measurable pools into models, these pools need to be measured with a consistent protocol and efforts towards measuring P turnover and transformations using P radioisotope (Helfenstein et al., 2020) and oxygen isotope tracing (Joshi et al., 2016) must be continued. Although efforts in this space have been made (Joshi et al. 2018), it is necessary to continue coupling ^{31}P spectroscopy and chemical extractions to determine pool compositions, as well as tracing to assess compound-specific lability.

Conducting sorption isotherms is tedious and is not a part of standard soil tests. Applying isotherm parameters, such as the binding energy constant (K_L), when predicting or generating data can result in poor validation, as the conditions from which the parameter was derived likely do not match the simulated conditions. If an isotherm approach is to be used, then it will be necessary to employ methods to rapidly estimate the sorption parameters from accessible and cost-effective techniques, such as in Dari et al. (2015). In future method development, factors that influence sorption, such as the C_o content of the soil, should be considered. This is of particular importance as P isotherms are sometimes used in determining the saturation capacity, a necessary component of DPS measurements. As previously discussed in the section 3, Organic P and C Saturation, the presence of P_o and C_o may influence the interpretation of DPS data.

Improved accessibility of mineral analysis methods will facilitate the application of a bottom-up, first principles approach such as the dynamic equilibrium approach of ECOSYS (Grant and Heaney 1997). If the approach of Sharpley et al. 1984 is to be revised and expanded, soil-specific properties (C_o, pH, clay content, etc.) must be accounted for in a continuum that can be generalized. Furthermore, pool-pool transfer functions could benefit from the application of isotope tracing techniques; this is an area which clearly requires more fundamental research.

Conclusions

Limitations in simulating P_i sorption, P_o mineralization, stoichiometry as it relates to P, and nutrient interactions, calls for an improved experimental and modeling framework to interpret P cycling. Our current knowledge of soil P dynamics suffices for the management of crop nutrition, but still lags C and N in terms of process-based modeling (Beegle, 2005). We recommend focusing specifically on 1) updating the McGill and Cole model; 2) understanding the dynamics of phytate and soil stoichiometry; 3) exploring the role of C_o and P_o saturation on P sorption and P_o mineralization, and 4) resolving discrepancies between hypotheses about P cycling and methods to measure P pools and fluxes.

It is necessary to better understand P processes to build the most representative simulation models. Understanding the controls on plant, microbial biomass, and microbial stoichiometry will help determine bottom up controls on ecosystem, biome, and even global P cycling. The challenges summarized in this review will hopefully steer research efforts towards a better empirical understanding of the P cycle that will ultimately reduce the reliance on intensive calibration (Beven et al., 2006). A better understanding of P cycling will lay the stratum upon which better predictive models will be developed, enabling foresight of both plant P nutrition and P pollution challenges rather than reacting to them when symptoms like surface water eutrophication manifest visibly and in full force.

Author Contribution

ARK, CM, and JPK conceived the manuscript; CM conducted the literature search, organized and summarized information; CM, ARK and JPK defined the organizational structure after the literature search, CM drafted the manuscript and prepared the figures; ARK and JPK contributed to the discussion and edited the manuscript. ARK and JPK secured funding to support this research.

Competing Interests

The authors declare that they have no conflict of interest.

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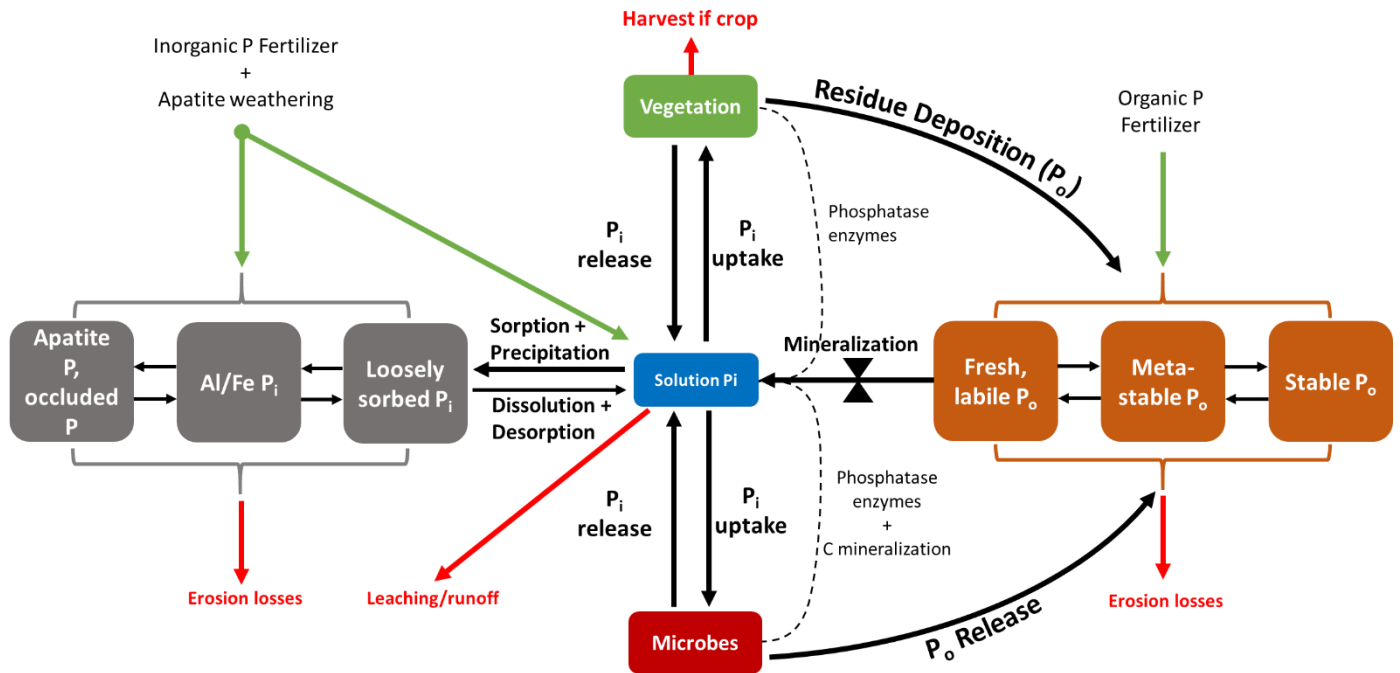
Figure 1. Conceptual diagram of the soil P cycle. P_i and P_o represent inorganic (gray) and organic (orange) phosphates, respectively. The P_i and P_o pools that are situated farthest from the depicted solution pool in this diagram are considered more stable. There are small amounts of organic P in solution that are not explicitly depicted here. The bowtie represents the control mineralization exerts on the transformation of P from P_o pools to the solution pool. The dotted lines represent enzymes in the mineralization of P_o. There are other abiotic controls of mineralization excluded from this diagram.

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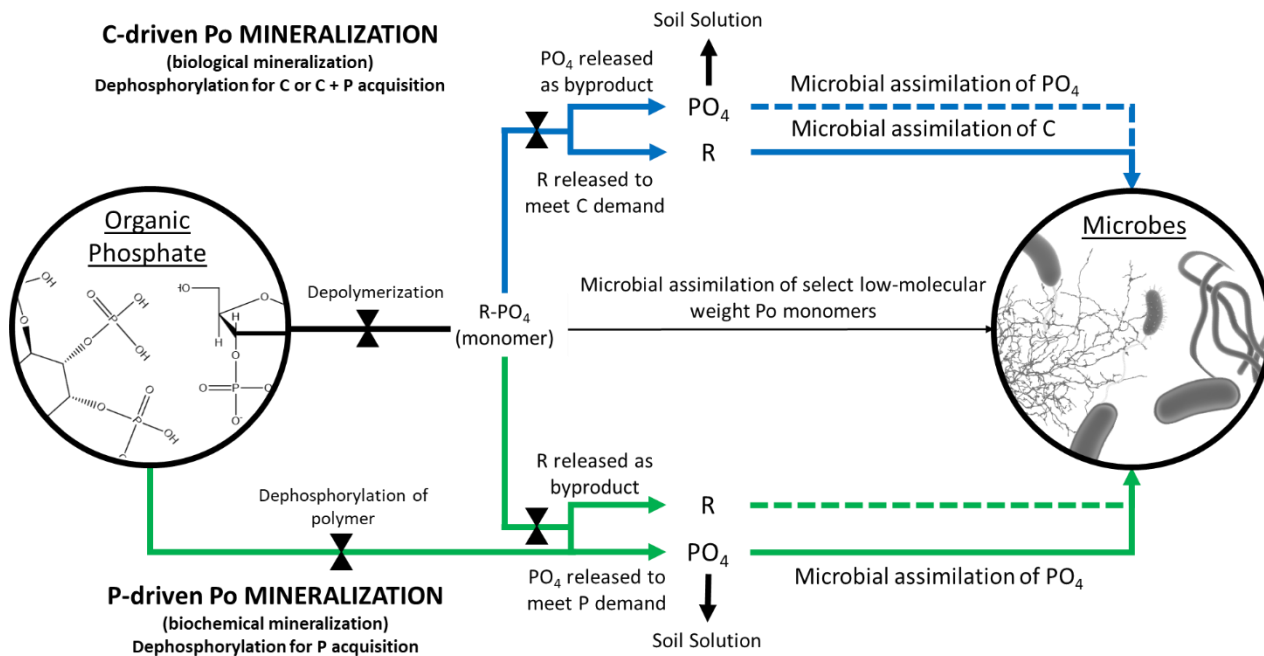
Figure 2. Conceptual diagram of C and P-driven Po mineralization. Because microorganisms can only directly uptake specific types of orthophosphate ester (Po) monomers directly (thin middle black arrow), the accessibility of Po is controlled by the action of phosphatase enzymes (indicated by bowties). The blue arrows represent C-driven Po mineralization, whereby the organic compound is mineralized for C acquisition, and depending on P demand, for P acquisition (immobilization, indicated by dotted blue line). P that is unused by microbes is left in the soil solution. The green arrows represent P-driven Po mineralization, whereby PO_4 is hydrolyzed from the Po compound and assimilated without further C processing (unless the C is available for uptake and is needed, and is circumstantially assimilated, indicated by green dotted line).

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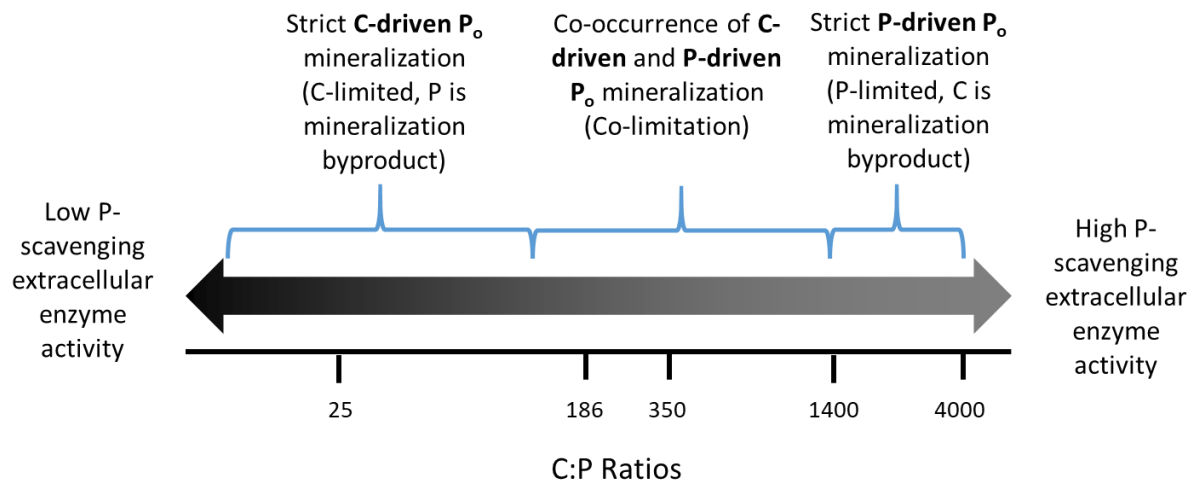
Figure 3. Hypothesis of stoichiometric controls on C-driven and P-driven Po mineralization. The log-scaled numbers are C:P ratios taken from the literature that include stoichiometry of microbes, litter, soil, and critical ratios. The brackets represent where biological or biochemical mineralization may begin to dominate. Values in figures are as follows: 25-Microbial biomass C:P ratio, low of study range (Capek et al. 2016); 186-Soil C:P ratio, global average (Cleveland et al. 2007); 350-Microbial biomass C:P ratio, high of study range (Capek et al. 2016); 1400-Threshold Elemental Ratio (Heuck et al. 2016); 4000-Decomposition stop point (Zechmeister-Boltenstern et al. 2015)

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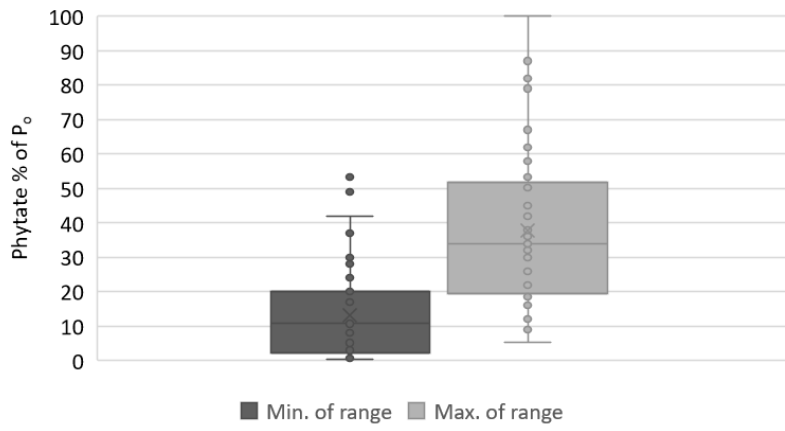
Figure 4. Minimum and maximum % of P_o comprised of phytate observed in a variety of natural and agricultural systems (n=41). Sources: Giles 2014; Turner 2002; Turner 2007.

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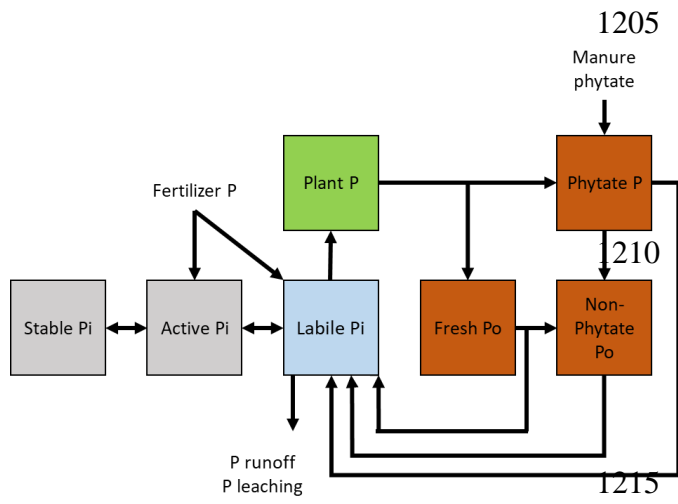
Figure 5: Simple conceptual diagram for modeling inorganic and organic phosphorus cycling, which includes an explicit phytate pool.

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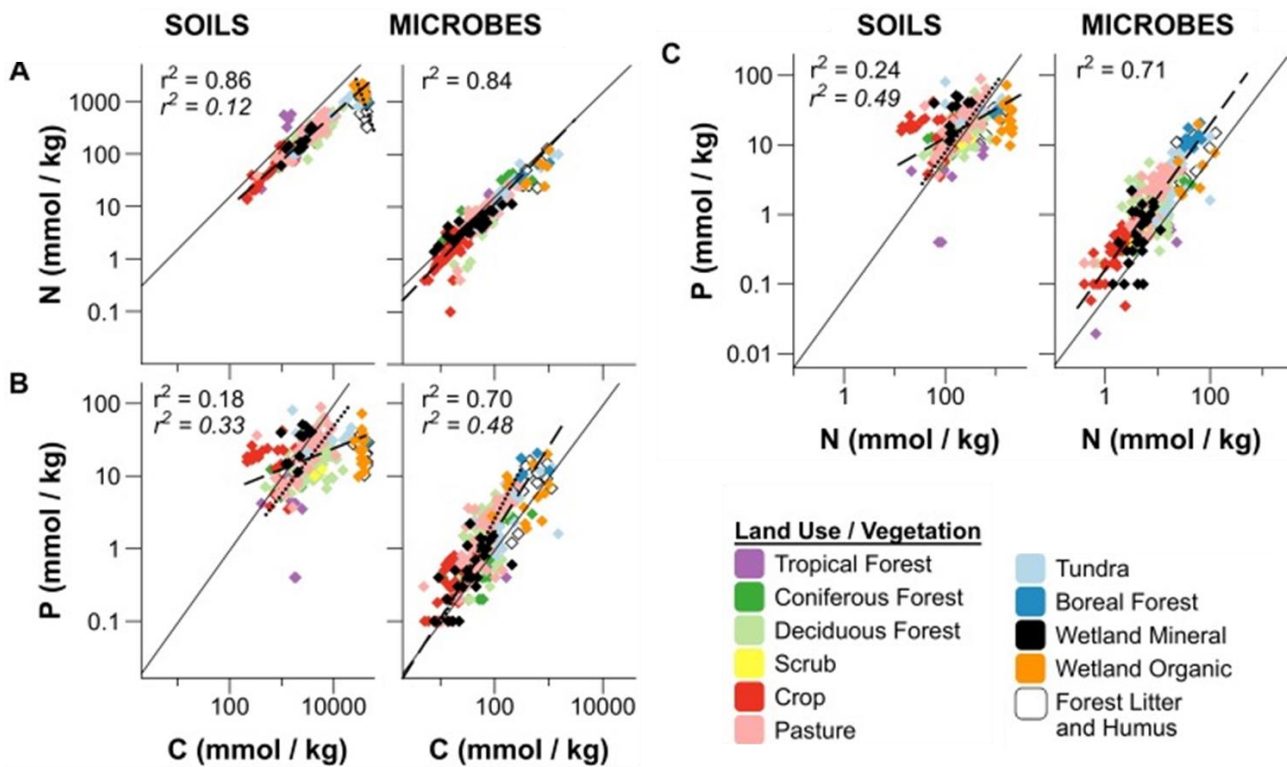
Figure 6. Regressions of C:N (A), C:P (B), and N:P (C) ratios in soils and microbial biomass using a log$_{10}$ transformation. The dashed lines (standard font r^2) are regressions of soil or microbial biomass stoichiometry for all land use/vegetation types that do not differ significantly. The dotted lines are slopes of stoichiometries that differ significantly from the other land use/vegetation types. For C:N (A), these land use/vegetation types were wetland organic, boreal forest, and humic horizons. For C:P (B) and N:P (C) the forest and pasture soils differed significantly from the other land/use vegetation types. The solid lines represent the Redfield (1958) ratio. Modified from Hartman and Richardson 2013.

Table 1. Hypothetical scenarios comparing the measured Pi saturation (DPS) and actual total P saturation.

Figure	Scenario	Presence of C_o	Total P_i (mg P/kg)	Total P_o (mg P/kg)	P_i and P_o saturaton cap. (mg P/kg)	Measured P_i saturation [DPS] (%)	P_o saturation (%)	Actual total P saturation (%)
N/A	**Fe/Al Oxide Mineral** (No P_i, P_o)	No	0	0	500	0	0	0
N/A	**Complete P_i saturation** (No P_o)	No	500	0	500	100	0	100
7A	**Incomplete P_i saturation** (No P_o. C_o competing with P_i for sorption)	Yes	400	0	500	80	0	100
7C	**Incomplete Pi saturation** (P_o competing with P_i for sorption)	No	300	200	500	60	40	100

Actual P saturation is defined as the total saturation of both P_o and P_i species. The competition with non-P-bearing C_o anions (7A) would lower the measured DPS despite the saturation of all available sorption sites. When P_o successfully competes with Pi for sorption (7C), the resulting measured DPS will be lower than the actual P saturation. It is important to note that, as opposed to colorimetric methods, if inductively coupled plasma optical emission spectrometry (ICP-OES) is used in DPS analysis, any circumstantially extracted Po would be included in the measurement, resulting in a higher % DPS than presented here.

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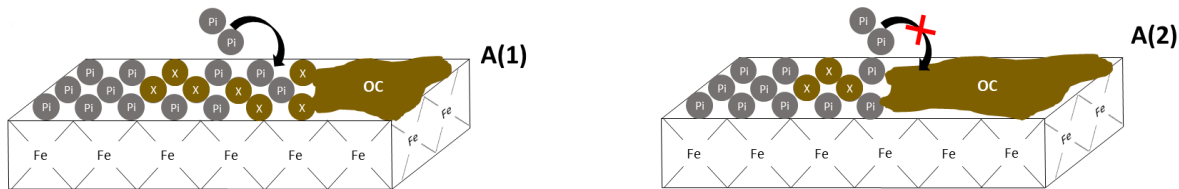
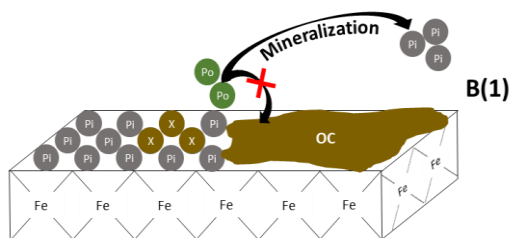
C_o anion-P_i competitive sorption (A)

C_o saturation increases P_o mineralization (B)

Disparities in DPS (C)

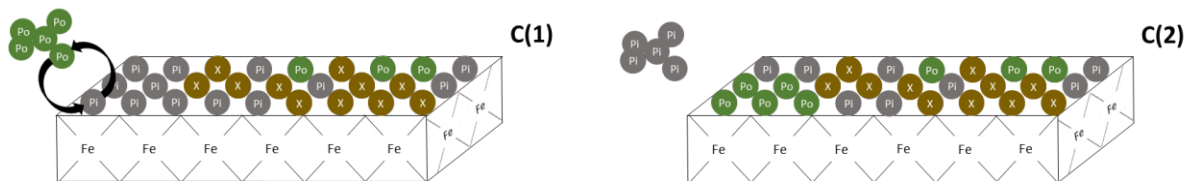



Figure 7. Conceptual depiction of P_i and P_o saturation dynamics. The green P_o bubbles are organic phosphate, the gray P_i bubbles are inorganic phosphate, and the brown "X" bubbles are non-P bearing organic and inorganic compounds. (A) represents the competitive sorption of non-P-bearing organic carbon (C_o) compounds on the sorption of P_i. As C_o saturation increases (A2), so does the solution concentration of P_i. (B) shows the increase in C_o from A2 causing an increase in P_o mineralization rather than a decrease in P_i sorption. (C) depicts the replacement of P_i with P_o on an iron oxide mineral surface, resulting in a change in composition of the saturated surface. Because DPS measurements do not target P_o, the measured DPS would be lower for mineral C2, despite having the same overall P content. The replacement of P_i with P_o on sorption surfaces would increase the C:P ratio of the soil.

Table 2: Equations for modeling sorption dynamics

#	Name	Equation	Parameters
1	C sorption capacity	$C_x = 21.1 + 37.5 \times f_{clay}$	C_x: maximum sorption C capacity (g C kg^{-1}) soil f_{clay}: clay concentration (g kg^{-1})
2	Langmuir	$\dfrac{C}{S} = \dfrac{C}{S_{max}} + \dfrac{1}{K_L \times S_{max}}$	S: sorbed P (mg kg^{-1}) C: equilibrium P concentration (mg L^{-1}) S_{max}: sorption maximum (mg kg^{-1}) K_L: binding energy constant
3	Freundlich	$S = a \times c^b$	S: sorbed P (mg kg^{-1}) a: proportionality constant (mg kg^{-1}/ mg L^{-1}) b: empirical binding energy coefficient (dimensionless) c: P concentration in solution (mg L^{-1})
4	Two-surface Langmuir	$\dfrac{x}{m} = \dfrac{b_I K_I EPC}{1 + K_I EPC} + \dfrac{b_{II} K_{II} EPC}{1 + K_{II} EPC}$	x/m: sorbed P (mg kg^{-1}) K_I/K_{II}: bonding energy, regions I and II (L mg^{-1}) b_I/b_{II}: adsorption maximum, regions I and II (mg kg^{-1} soil) EPC: equilibrium P concentration (mg L^{-1})
5	PSP: Calcareous soils	$PSP = 0.58 - 0.0061 * CaCO_3$	PSP: P sorption parameter[*] $CaCO_3$: calcium carbonate (%)
6	PSP: Slightly weathered soils	$PSP = -.70 - 0.0043 * BS$ $+0.0034 * Pi_l + 0.11 * pH$	BS: base saturation (%) P_{il}: labile P (µg g^{-1} soil) pH
7	PSP: Highly weathered soils	$PSP = 0.038 - 0.047 * \ln\left(\dfrac{f_{clay}}{10}\right)$ $+0.045 * P_{il} - 0.053 * OC$	f_{clay}: clay concentration (g kg^{-1}) OC: organic carbon (%)

Equations mentioned that take different approaches to describing P and C sorption dynamics
Equation 1: Hassink and Whitmore 1997
Equation 2, 3: Barrow 2008, Dari et al. 2015
Equation 4: Zhang et al. 2005
Equation 5-7: Sharpley et al. 1984; Vadas et al. 2010
[*] Also known as "phosphorus availability index" (PAI)