

Dear Dr. Sönke Zaehle,

Please accept this revised version of the manuscript bg-2020-130 titled “Reviews and Syntheses: Ironing Out Wrinkles in the Soil Phosphorus Cycling Paradigm” in addition to our response to the referees. Their comments were insightful, and we appreciate the input. We thoroughly considered all referee comments and clarified our text or added citations accordingly. In the marked-up manuscript, new text is highlighted while removed text is indicated by a strikethrough. In this document, we include comments from both referees, our responses, and the corresponding change in line number for both the clean and marked-up versions of the manuscript. Any line number referenced will be from the clean version, and the number following in parentheses corresponds to the marked-up document. e.g. Line 118(123).

The principal updates to the document are as follows: 1) Changed the language from “improving models” to “incorporating new concepts into models”, which better represents the purpose of the paper. 2) Incorporated additional relevant work on modeling P biogeochemistry (most prominently P-driven P_o mineralization). 3) Added other relevant citations recommended by referees, 4) Restructured paragraphs in sections 1.3, 1.5, and 2.2.1. 5) Clarified the difficulties in incorporating P-driven P_o mineralization into models (section 1.5). Additionally, all instances of P_i , P_o , and OC were changed to P_i , P_o , and C_o respectively.

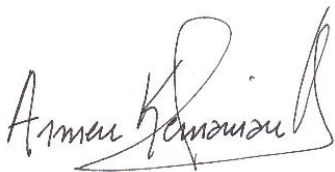
We look forward to your feedback. This letter, document, and revised manuscript represent the consensus of all co-authors.

Kind Regards,

Curt McConnell



Armen Kemanian



Jason Kaye



Referee 1

Dear reviewer, thank you for your incisive review of the MS. We hope to address all your comments here. The references that you provided are also pertinent and informative and will improve the manuscript.

[Referee 1]: "...it lacks in-depth insights of current "P models" to justify its statement that these processes should be improved in models. It is partly because some of the processes or features are simply ignored in current models, such as phytate, and partly because the proposed processes by authors are not particularly discussed by modeling community yet."

Authors: The original intent in the initial stages of the review, was to compare individual models by reconstructing their respective P cycling components. That intent veered to the current manuscript with emphasis on missing components. As Referee 1 noted, there are many terrestrial biosphere models (TBMs) and landscape/watershed models. It was tedious and not necessarily informative to reconstruct them all due to the many overlapping frameworks and processes.

With knowledge of individual models from this earlier research, we redirected our efforts to address concepts not generally or never included in these models (for example, phytate dynamics) or those that may not be representing a specific process completely (P-driven "biochemical" mineralization). We believe it is important to draw attention to those concepts ignored in models or not yet discussed by the modeling community, so that new hypotheses and experiments can be proposed, and models improved.

In response to the comment regarding "improving P models", we think that the matter is more semantic than conceptual. We changed the language to "including processes not addressed in current models", which of course would be done to improve models. Our aims are to highlight areas of knowledge that need to be included in models in relation to P cycling, to acknowledge the need to converge on common or complementary frameworks well supported by theory, and to acknowledge that uncertainty still exists due to conceptual ambiguity or the inability to measure P pools and fluxes with ease.

Revisions: Changed the language of "improving P models" to incorporating certain pools and processes or improving the modeling of P cycling generally.

Line 436(459): "Regardless of the proposed mechanisms, in order to improve P modeling, accounting for competitive sorption reactions..."

[Referee 1]: "...P cycling models', which in practice does not really count as a sub-category of models"

Authors: The semantics here can be subjective. Any model refers to a system with arbitrary boundaries. Whatever comes from outside the boundaries are "forcings" or inputs. Any model "component", which can be called a submodel if inside a well bounded model, is in itself a model with its own forcings. Maybe we can make a stop here and highlight that is difficult to be a purist: setting boundaries does not make the boundaries correct, as there are feedbacks that could affect the forcing variables themselves. For example, a change in land use will affect the air temperature and air moisture through changes in the surface energy balance. For models that couple the atmosphere with the earth surface, climate variables are mostly forced in, regardless of the land use, and the feedback is ignored. The errors introduced by ignoring the feedback are in most cases minor. And of course there is no assurance that including a feedback will make the outcome better, it may just make the model more cumbersome veering into arrogance without any predictive gain. In any case, the model and sub-model language is context dependent. We will try to avoid any confusion.

Revisions: Changed the language from "P models" to "P cycling" or "P components of biogeochemical models"

Line 21(21): "Most P cycling components of biogeochemical models are structured after C and N..."

Line 378(401): "Using fixed P stoichiometry to model P biogeochemistry may not capture P dynamics across ecosystems..."

[Referee 1]: "...perhaps the authors could try to narrow down the scope of models, for example, only to land surface models and TBMs"

Authors: Among the models referred to by Referee 1, it is important to realize that different names sometimes encapsulate the same or related P components. Referee 1 suggested including EPIC (Jones et al., 1984), GLEAMS (Leonard et al., 1987), and ANIMO (Schoumans and Groenendijk, 2000) in our review. GLEAMS was a standalone model. GLEAMS was absorbed into EPIC during the early stages of the EPIC model development. SWAT (as well as APEX) uses EPIC as the base crop and soil model for each simulation unit (SWAT is a semi-distributed watershed model and APEX is a pseudo-distributed model mostly applicable to smaller watersheds) (Gassman et al., 2007; Wang et al., 2012). By using SWAT, we were encompassing this conglomerate and trying to avoid long explanations and redundancy.

Revisions: Clarified the composition of SWAT and incorporated citations for CREAMS, GLEAMS, and EPIC

Line 523(547): "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 al., 1987)."

Section 1:

[Referee 1] in reference to Line 118 (original line #): "the modeling work has also supported that CP cycling is largely decoupled from CN cycling (Yu et al. 2020, GMD)"

Authors: We had missed the work of Yu et al. (2020) while finishing up the review. Indeed, Yu et al. 2020 is a good example of a model *representing* CP-CN decoupling. This reference will be included in our review. We agree with other comments in that work. The uncritical inclusion of a Century-like approach and the need to represent soil properties variation with depth as an emergent, and not an imposed property, has also been pointed out and partially addressed by using the carbon saturation concept (e.g. Kemanian and Stöckle, 2010), as so did Yu et al. (2020). We think that conceptually, Yu et al. (2020) and our review are convergent.

Revisions: Included Yu et al. 2020 as a work that represents the decoupling of CP-CN cycling.

Line 118(123): "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 Po 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)."

[Referee 1] in reference to Line 164 (original line #): "logically, I think it is better to place the last sentence at the beginning of this paragraph."

Revisions: Reordered paragraph as recommended

[Referee 1] in reference to Line 187 (original line #): "Schimel and Weintraub did not simulate phosphatase"

Authors: The intention was not to convey that Schimel and Weintraub (2003) used phosphatase activity in their theoretical model, rather to highlight that improving phosphatase activity assays would benefit model development employing approaches like that of Schimel and Weintraub, who account for enzymes in SOM decomposition. The text was changed as follows:

Revisions: Clarified the statement about the work of Schimel and Weintraub 2003.

Line 194(202): "Schimel and Weintraub (2003) took an enzyme-mediated approach to SOM decomposition/mineralization, but if applied to Po decomposition/mineralization, it would require more accurate phosphatase activity assays and an ability to differentiate between extracellular and intracellular soil phosphatase."

[Referee 1] in reference to Line 194 (original line #): “please check Yu et al. 2020, in which a dynamic enzyme allocation approach is used to mimic such a relationship”

Authors: The point that we were making referred to measuring or explicitly modeling the relative release of phosphatases by both plants and microbes. The Yu et al. (2020) use of SEAM (Wutzler et al., 2017) and the ECA approach (Tang and Riley, 2013) addresses a different if related area, pertaining to the dynamic allocation of microbial phosphatases to litter or microbial residue and nutrient acquisition by plants and microbes.

Revisions: Incorporated the work of Yu et al. 2020, Tang and Riley 2013, and Wutzler et al. 2017 to describe dynamic enzyme allocation, the ECA approach, and SEAM.

Line 209(218): “... Yu et al. 2020 simulated Po 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 Po sources and the subsequent microbial-plant uptake.”

[Referee 1] in reference to Line 209 (original line #): “I would argue many terrestrial ecosystem models (ESMs) did include the P-driven mineralization. From as early as the CENTURY model (Parton et al. 1988) to the more recent ESMs such as JSBACH (Goll et al., 2012), ORCHIDEE (Goll et al., 2017), For SAFE (Yu et al., 2018), E3SM (Zhu et al., 2019), QUINCY (Thum et al., 2019). And the overall role of P-driven mineralization (biochemical mineralization) is crucial for plant growth in some of these models.”

Authors: We agree that many models include P-driven mineralization implicitly (CENTURY) (Achat et al., 2016) but those that do so explicitly (Goll et al., 2012, 2017; Yang et al., 2014) are parameterized on limited data (Reed et al., 2015). Goll et al. 2012 stated in relation to P-driven (biochemical) mineralization “parameter values for the adjustment intensity is set arbitrarily” and that in-field P-driven mineralization assays are not currently possible, thus limiting data. This is similarly stated by Thum et al. 2019 in reference to P-driven mineralization: “Further observations are required to constrain this flux better (Reed et al., 2011).” In other words, one can easily come up with a P flux from P-driven mineralization given P demand through a sort of inverse modeling. Our argument was that P-driven mineralization is not always explicitly included, and it is difficult to obtain P-driven mineralization as an emergent property. When P-driven mineralization is explicitly modeled, it is not well constrained. We could include more models into that categorization to make things clear and the review more thorough.

Revisions: The works mentioned above were incorporated as examples of work that did simulate P-driven mineralization. We also added three methodological limitations and gaps in our understanding of P-driven mineralization:

- Difficult to differentiate P-driven vs. C-driven mineralization
- Phosphatase enzyme assays overestimate real phosphatase activity and cannot be conducted in the field
- Difficult to relate phosphatase activity to mineralization

Line 184-199(191-207): “Measuring and differentiating Po mineralization pathways is an important step for modeling P biogeochemistrythe P cycle. Some land surface and catchment models simulate P-driven Po 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), 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 is 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 if applied to Po decomposition/mineralization, it 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 Po mineralization, which itself is hindered by the nature of P isotope chemistry, accessibility of appropriate methods, and currently held assumptions of the two pathways.”

Section 2:

[Referee 1] in reference to Line 325 (original line #): “please check Lang et al. 2017, SBB.”

Authors: Lang et al. 2017 is a very fitting reference for the “potential shift to P-driven Po mineralization processes” statement (Line 358). The work by Lang et al. 2017 reflects the (Walker and Syers (1976), showing that as soils weather and overall P stocks degrade, Po becomes the more available P source as Pi is either lost from the system or occluded. Although not explicitly stated by Walker and Syers, McGill and Cole (1981) discussed the change in nutrient strategies with the depletion of P stocks: “Although Po has not started to decline, it has leveled off and the decline in total P is substantial. Under such conditions demand for internal cycling of Po to meet the needs for P increases.” (McGill and Cole 1981)

The objective of the paragraph in question referenced by Referee 1 was to describe how C:P ratios were variable and that they become more decoupled (wider range of possible C:P ratios) as soils weather. This may be due to the depletion in P stocks and changes in P nutrition strategies. It could also be due to variable C demand and the assumed prevalence of extracellular “P-driven ‘biochemical’ mineralization” to scavenge P. In a highly weathered soil where P availability is limiting, P could be scavenged without C mineralization, thus further decoupling C and P. Therefore, this decoupling would be dependent to some degree on the relative P to C demand and the extracellular mineralization of Po.

Revisions: Included Lang et al. 2017 as their work on nutrient strategies fit well in this discussion.

Line 333(355): “The decoupling of C:Pt and N:Pt is also seen as soil weathers (Yang and Post, 2011) where Po becomes the predominant contributor to P fertility (Yang and Post, 2011; Cleveland et al., 2013; Bünemann, 2015) and nutrient acquisition strategies shift from physiochemical Pi acquisition to closed Po cycling (Lang et al., 2017).”

[Referee 1] in reference to Line 366 (original line #): “The real challenge (for modeling) is to account for the huge stoichiometry differences between plant litter, microbe, and SOM, especially C:P ratio (Xu et al., 2013; Mooshammer et al., 2014). This requires an explicit microbial pool and a number of microbial adaptation processes to be included in models. Additionally, how to extrapolate these mechanisms from site-level to regional and global level is another complicated problem”

Authors: We agree. Our intention was to convey this in the review while acknowledging that phytate dynamics are possibly related to the wide ratios in C and Po stoichiometry. The issues identified by the reviewer are on point but were also well understood. On the one hand, we highlight that the dynamics of phytate is barely in the modeler’s radar. On the other hand, we acknowledge that phytate is just a component of the larger picture. We will rebalance the narrative.

Revisions: Added paragraph stressing the importance of an explicit microbial pool and microbial adaptation processes.

Line 385(408): “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).”

Section 3:

[Referee 1] in reference to Line 398 (original line #): “there are some models implementing the OC saturation dynamics (or similarly clay-related C sorption capacity), such as MIMICS (Wieder et al. 2014), MEND (Wang et al. 2015), RESOM (Tang and Riley 2015), and COMMISSION (Arhens et al. 2015). The recent JSM (Yu et al. 2020) has also include N and P in the OC sorption, which also complies with the saturation principle, although Po is not specifically separated as a competing sorbate of OC”

Authors: We are not certain we follow the reviewer, or if our point was clearly laid out and understood.

Wieder et al 2014 (MIMICS) include the effect of clay on SOM protection, not the concept of carbon saturation which is different (see Table 1 in that paper, row for C_{scalar}).

Wang et al 2013 and 2015 (MEND) does not address carbon saturation explicitly. There are parameters to represent C affinity to the mineral matrix, but no explicit mention of soil C saturation. Perhaps it is an emergent property of the model. However, the steady state mineral associated organic matter in equation 25 in Wang et al 2013 (variable M) does not seem to be saturating (when inputs go to infinity SOC should approach an asymptote to be “saturating”). That paper presents steady state equations, but not the limit when inputs go to infinity.

Tang and Riley (2015), figure 12b in the supplemental shows a linear increase in SOM with increasing mineral surface area (many models surrogate MSA with clay content despite the limitation of such simplification). There is however no indication of saturating behavior, although it might be an emergent property if the model is tested with increasing C inputs. It should also consider aggregation (see work by Six et al team, Kong et al., 2005), and Tang and Riley model does not address aggregation.

Arhens et al. (2015) is explicitly saturating (Table 1, Eq 6 in their paper) and as acknowledged in that paper, it follows work by Hassink and Whitmore (1997). Ignoring fluxes between layers, the soil carbon steady state in Arhens et al is:

$$C_q = K_{\text{ads}} * q_{\text{max}} / (K_{\text{ads}} + k_{\text{des}}/C_{\text{doc}})$$

C_q is soil organic carbon, q_{max} is the maximum allowed soc, C_{doc} is carbon in DOC, and K_{ads} and k_{des} are DOC sorption and desorption rates. As C_{doc} goes to infinity $C_q = q_x$.

This is conceptually and mathematically similar to Hassink and Whitmore (1997) model, Kemanian et al (2006), Kemanian and Stockle (2010), and in a more formal formulation in Kemanian et al. (2011). A paper by White et al. (2014) in Biogeosciences followed up on the impacts on N dynamics. Arhens et al. (2015) is a good reference to include in this review, acknowledging that there are earlier precedents. And there is always the possibility that we are missing other relevant work.

We think that the general point that organic C saturation (not the response to clay) is not explicitly included in many models stands, as well as the need to consider the implications for P cycling, much as White et al. (2014) addressed the implications for N.

Revisions: No major changes were made, but Arhens et al. 2015 was added, with justification mentioned above.

Line 419(442): “The dynamics of explicit C_o saturation are only included in a few models (Kemanian and Stöckle, 2010; White et al., 2014; Arhens et al., 2015), and its effect on Po mineralization is unexplored in models.”

[Referee 1] in reference to Line 445 (original line #): “in principle, what is discussed in this paragraph makes sense, however, given the existing uncertainties in Pi sorption (as discussed in section 4), it is really a challenge ahead of our current focus to consider the role of Po and interactions with OC saturation. The role of OC in Pi sorption has been partially considered in QUINCY (Thum et al. 2019), which proves to have an important role in regulating the P availability and thus affect plant growth, but this is not specifically discussed in the model description paper.”

Authors: Thank for the comment. It seems that Referee 1 agrees with the point. Stating the knowledge gap does neither ignore ongoing efforts to address it (even if they have not been published yet) nor the difficulties inherent to the problem.

Section 4:

Referee 1 in reference to Line 501, 506 (original line #): “DI and STP not defined”

Authors: Thank you. DI water = dionized water, STP = Soil test phosphorus

Revisions: DI and STP were defined in the text.

Line 521(545): “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.”

Line 529(552): “However, solution P is assumed to be half of Mehlich-3 or other soil test phosphorus (STP) method.”

[Referee 1] in reference to Line 517 (original line #): “The work by Helfenstein et al. 2020, BG, has shown that there is a certain level of correlation between the Hedley Pi pool and Isotopic Exchange Kinetics Pi pool. And our recent work actually shows, with the implementation of double-surface Langmuir on current Pi pool structure, there is a possibility of utilizing the Hedley data for model validation”

Authors: An excellent point and a noteworthy inclusion in our review. However, the point we were making was that the numerous modifications of the Hedley method complicate the analysis of Hedley data. We did not intend to say that correlations can’t be drawn, just that the lack of methodological consistency makes this difficult or contributes to a lingering uncertainty about the compatibility of chemically extracted and modeled P pools.

Revisions: We included Helfenstein et al. 2020 as a citation in two locations where P turnover and transformations were being discussed. Below is the more relevant example.

Line 541(565): “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.”

[Referee 1] in reference to Line 525 (original line #): “Dari et al. 2015 not found in reference. And the effect of OC content on Pi sorption is already partially implemented in QUINCY (Thum et al. 2019, GMD)”

Authors: Dari et al., 2015 reference is listed below. Its exclusion was unintentional.

Dari, B., Nair, V. D., Colee, J., Harris, W. G. and Mylavarapu, R.: Estimation of phosphorus isotherm parameters: a simple and cost-effective procedure, *Front. Environ. Sci.*, 3(October), 1–9, doi:10.3389/fenvs.2015.00070, 2015.

[Referee 1] in reference to Figure 1: “Isn’t the weathering of P coming from apatite P? are the three Pi and Po pools forming a continuum of stability? Do they transfer with each other? If they do, please add internal fluxes between pools. If they don’t, do they all directly transfer phosphate to solution Pi?”

Authors: Yes, apatite P is the most prevalent source, the use of “P minerals” was purposefully generic, and referring to it as apatite seems to be most common in the literature. There is likely exchange between the various pools through stabilization and destabilization as mineral-PO₄ bonds are formed and broken. However, there should be direct exchange between all soil pools and the soil solution. This is particularly pertinent to organic phosphates. There may be more “stable” Po forms, such as phytate, but P can be hydrolyzed using specific phosphatases such as phytase. P from any Po pool can be directly hydrolyzed into the soil solution, albeit at different rates depending on the stability of the Po form under consideration.

Actual “pools” are less well-defined than those operationally defined by chemical extractions. But for clarity, we will add arrows indicating internal fluxes between Pi and Po pools. All pools can directly transfer to the solution pool; P does not have to cascade down the gradient of pool stability until it reaches the “solution” pool. It is likely that all pools exchange P with the solution and with one another. Representing this will increase the number of arrows and complexity of diagram, but will make it more representative.

Revisions:

1. “Apatite” weathering replaced “Weathering of P minerals”
2. Arrows were added to indicate exchange between P pools

[Referee 1] in reference to Figure 3: “Are there any references for the C:P ratios values in the figure?”

Authors: Value (description) Reference. Microbial biomass (MB). Threshold Elemental Ratio (TER)

25 (MB C:P ratio, low of range) Capek et al. 2016;
186 (Soil C:P ratio, global average) Cleveland et al. 2007;
350 (MB C:P ratio, high of range) Capek et al. 2016;
1400 (Threshold Element Ratio), Heuck et al. 2016;
4000 (Decomposition stop point, Zechmeister-Boltenstern et al. 2015)

Revisions:

The references were added to Figure 3.

[Referee 1] in reference to Figure 6: “the resolution of the figure is too low to read. What are the differences between the two dash lines in each sub-panel?”

Authors: We improved the resolution. The dashed lines are regressions for all the Land Use/Vegetation categories in the study. The dotted lines are regressions for Land Use/Vegetation whose slope was significantly different than other systems (e.g. the “Wetland Organic” slope is negative in the top-left regression). We could describe which system regressions differ from the rest in the figure legend if that improves clarity. The important point is that the r^2 values are lower for C:P in soils and microbes than the C:N.

Revisions:

The resolution problem of Figure 6 was fixed. The legend is as follows:

“Figure 6. Regressions of C:N (A), C:P (B), and N:P (C) ratios in soils and the microbial biomass using a log10 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.”

Referee 1 in reference to Table 2: “it needs an appropriate caption. There are quite some different equations for C sorption capacity and PSP, why do you choose those specific ones. I am not particularly sure about the purpose of these equations here, particularly the ones calculating PSP.”

Authors: PSP equations are listed because they were described earlier in the text. Showing the equations makes the model structure unequivocal.

Referee 2

Dear Dr. Kirkby, Thank you for your incisive review of the MS. We hope to address all your comments here. We will include your suggestions in the revised manuscript.

[Referee 2] in reference to C:P variability: “While the authors mention methodological and analytical discrepancies it is done in just a couple of lines. Do the authors think it is really important or not so important, and why. While it is pretty obvious why P_i is generally poorly correlated with soil C do the authors think soil C is poorly correlated with P_o because of the unnamed methodological or analytical discrepancies or some other, perhaps unknown, reason.”

Authors: We believe investigating the methodological and analytical discrepancies in stoichiometry measurements to be an important pursuit. As stated in Kirkby et al. 2011, C: P_o ratios can vary widely across studies (Table 7) employing different P measurement methods (extraction, digestion, or ignition). However, C: P_o ratios also varied within studies applying the same methodology thus Kirkby et al. 2011 briefly explored some potential explanations for this weak correlation. We address these mechanisms below.

Revisions: We moved the first paragraph of 2.2.1 to 2.2 in order to better introduce the methodological vs. mechanical explanation for variation in soil and microbial stoichiometry. We also added the following to the of the paragraph in 2.2 to outline the drivers of variable soil and microbial C:P stoichiometry:

Line 324(341): “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.”

(1) Kirkby et al. 2011 hints to varying P_o forms and abundances as a possible driver of the variation in C to P_o ratios: “... P is found in many organic compounds and the proportions vary in different soils (e.g. Turner et al., 2003a, 2003b). The major organic P compounds are the inositol phosphates (up to 50% of total OP), which contain neither N nor S but are generally considered to be associated with the soil heavy fraction component (Borie et al., 1989; Dalal, 1977).”

Revisions: We mention P_o forms and their varying recalcitrance as a potential explanation to C:P decoupling (Line 330), briefly expounding on this at Line 358. The evidence of variable phytate abundance and mineralization is already outlined in section 2.1.3.

Line 336(358): “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.”

Mentioned later in our review are the differing mechanisms of stabilization of P_i and P_o . Phosphate groups can control the sorption of P_o , and some P_o substances do not have to pass through the microbial biomass and can therefore be directly stabilized in the soil. An example of this would be phytate. Its recalcitrance and resulting abundance in some systems would yield a higher soil C:P ratio when compared to a similar system with a lower phytate abundance.

(2) Another explanation mentioning diverging C:P ratios also appears in Kirkby et al. 2011: “differences in how microbes enzymatically attack OP vs N or S could also play a substantial role but we consider a detailed discussion on these issues beyond the scope of this paper”.

Revisions: We mentioned this in the review at line 360: “A depletion of mineral P_i , 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.” This was again mentioned again in a revised statement at line 405.

Line 383(405): “and second, P-driven Po mineralization can drive the decoupling of P mineralization from SOM decomposition (Goll et al., 2012)”

Overall, it is difficult to ascribe a relative importance to each mechanism potentially controlling the decoupling of Po and C. However, we describe the mechanisms that potentially explain this decoupling. When assessing if P cycling pathways or methodological difference explain this decoupling, we are inclined to say that both likely are at play (methods are described briefly in Kirkby et al. 2011 sec. 2.2), but that the review of P cycling mechanisms strongly suggests that no stability in this ratio should be expected. Rather, we should understand its controls.

[Referee 2]: “While obtaining such a measurement is probably expecting too much it might be worthwhile seeing if forest soils and top soils in no till agriculture (which generally have high fungi:bacteria ratios) can be modelled differently to soils that are often cultivated (which often have lower fungi:bacteria ratios).”

Authors: It would be interesting to follow this line of thinking, and it would be natural to explore the scenarios proposed by the reviewer in a focused study. While we think that this falls outside the scope of the review, it does fall in the scope of topics that should be explored further and we will incorporate this suggestion in the review.

Revisions: Research on fungi:bacterial C:P or biomass ratios was added to the paper to address the reviewer comment. See following comment.

[Referee 2]: “The difference in fungal and bacterial C:P ratios may help to explain differences in P driven Po mineralization compared to C-driven Po mineralization in different soils”

Authors: Yes, this could be a very useful area of study and the relative abundance of fungi and bacteria (as Referee 2 stated previously) is a worthwhile topic of investigation. Exploring fungi:bacteria ratios and the differences in their respective C:P ratios may reflect differences in P vs. C-driven mineralization and potentially, soil C:Po ratio discrepancies.

Revisions: Added paragraph briefly describing C:P decoupling and microbial adaptation and how accounting for fungal vs. bacterial stoichiometry may help modeling efforts.

Line 387(410): “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).”

Citations added and justification

General Papers:

- (Helfenstein et al., 2020): Included because the work uses P radioisotopes to study turnover of Hedley Fractions, a concept mentioned in the text.
- (Lang et al., 2017): Added in response to author comment as the work explores the nutrient strategies of plants/microbes as P stocks change.
- (Mooshammer et al., 2014): Added because it adds to the discussion of the non-strictly homeostatic nature of microbes. Review covering microbial/soil stoichiometry.

Models added:

- (Ahrens et al., 2015): Added as an example of a model that represents C saturation.
- (Allison, 2012): Added as an example of a trait-based model of litter decomposition.
- (Goll et al., 2017): Added as an example of a model that represents P-driven mineralization, but one that uses phosphatase activity as a proxy for P-driven mineralization.
- (Davies et al. 2016): Added as an example of a model that represents biochemical mineralization

- (Knisel, 1980; Jones et al., 1984; Leonard et al., 1987): All components of SWAT (GLEAMS, EPIC, and CREAMS).
- (Tang and Riley, 2013): Cited when describing the dynamic enzyme allocation approach of Yu et al. 2020.
- (Thum et al., 2019): Added as the paper supports the claim that biogeochemical models representing biochemical mineralization of P are parameterized on limited observations
- (Waring et al., 2013): Accounts for fungal:bacterial ratios in model (a recommended approach by Referee 2)
- (Wieder et al., 2014): Included because the work calls for explicitly modeling microbial processes.
- (Wutzler et al., 2017): Cited as a component of the dynamic enzyme allocation approach of Yu et al. 2020.
- (Yu et al., 2018): Included as model that represents P-driven Po mineralization.
- (Yu et al., 2020): Included as a model that represents CP decoupling from CN.
- (Zhu et al., 2019): Included as model that represents P-driven Po mineralization.

References

Achat, D. L., Augusto, L., Gallet-Budynek, A. and Loustau, D.: Future challenges in coupled C–N–P cycle models for terrestrial ecosystems under global change: a review, *Biogeochemistry*, 131(1–2), 173–202, doi:10.1007/s10533-016-0274-9, 2016.

Ahrens, B., Braakhekke, M. C., Guggenberger, G., Schrumppf, M. and Reichstein, M.: Contribution of sorption, DOC transport and microbial interactions to the 14C age of a soil organic carbon profile: Insights from a calibrated process model, *Soil Biol. Biochem.*, 88, 390–402, doi:10.1016/j.soilbio.2015.06.008, 2015.

Allison, S. D.: A trait-based approach for modelling microbial litter decomposition, *Ecol. Lett.*, 15(9), 1058–1070, doi:10.1111/j.1461-0248.2012.01807.x, 2012.

Arnold, J. G., Srinivasan, R., Muttiah, R. S. and Williams, J. R.: Large Area Hydrologic Modeling and Assessment Part I: Model Development, *J. Am. Water Resour. Assoc.*, 34(1), 73–89, doi:10.1111/j.1752-1688.1998.tb05961.x, 1998.

Borie, F., H. Zunino, and L. Martínez.: Macromolecule-P associations and inositol phosphates in some Chilean volcanic soils of temperate regions, *Communications in Soil Science and Plant Analysis* 20(17-18), 1881-1894, 1989.

Dalal, R. C.: Soil Organic Phosphorus, *Adv. Agron.*, 29(C), 83–117, doi:10.1016/S0065-2113(08)60216-3, 1977.

Dari, B., Nair, V. D., Colee, J., Harris, W. G. and Mylavaram, R.: Estimation of phosphorus isotherm parameters: a simple and cost-effective procedure, *Front. Environ. Sci.*, 3(October), 1–9, doi:10.3389/fenvs.2015.00070, 2015.

Gassman, P. W., Reyes, M. R., Green, C. H. and Arnold, J. G.: The Soil and Water Assessment Tool: Historical Development, Applications, and Future Research Directions, *Trans. ASABE*, 50(4), 1211–1250, doi:10.13031/2013.23637, 2007.

Goll, D. S., Brovkin, V., Parida, B. R., Reick, C. H., Kattge, J., Reich, P. B., Van Bodegom, P. M. and Niinemets, Ü.: Nutrient limitation reduces land carbon uptake in simulations with a model of combined carbon, nitrogen and phosphorus cycling, *Biogeosciences*, 9(9), 3547–3569, doi:10.5194/bg-9-3547-2012, 2012.

Goll, D. S., Vuichard, N., Maignan, F., Jornet-Puig, A., Sardans, J., Violette, A., Peng, S., Sun, Y., Kvakic, M., Guimberteau, M., Guenet, B., Zaehle, S., Penuelas, J., Janssens, I. and Ciais, P.: A representation of the

- phosphorus cycle for ORCHIDEE (revision 4520), *Geosci. Model Dev.*, 10(10), 3745–3770, doi:10.5194/gmd-10-3745-2017, 2017.
- Hassink, J. and Whitmore, A. P.: A Model of the Physical Protection of Organic Matter in Soils, *Soil Sci. Soc. Am. J.*, 61(1), 131–139, doi:10.2136/sssaj1997.03615995006100010020x, 1997.
- Helfenstein, J., Pistocchi, C., Oberson, A., Tamburini, F., Goll, D. S. and Frossard, E.: Estimates of mean residence times of phosphorus in commonly considered inorganic soil phosphorus pools, *Biogeosciences*, 17(2), 441–454, doi:10.5194/bg-17-441-2020, 2020.
- Heuck, C. and Spohn, M.: Carbon, nitrogen and phosphorus net mineralization in organic horizons of temperate forests: stoichiometry and relations to organic matter quality, *Biogeochemistry*, 131(1–2), 229–242, doi:10.1007/s10533-016-0276-7, 2016.
- Jones, C. A., Cole, C. V., Sharpley, A. N. and Williams, J. R.: A Simplified Soil and Plant Phosphorus Model: I. Documentation, *Soil Sci. Soc. Am. J.*, 48, 800–805, 1984.
- Kemanian, A. R. and Stöckle, C. O.: C-Farm: A simple model to evaluate the carbon balance of soil profiles, *Eur. J. Agron.*, 32(1), 22–29, doi:10.1016/j.eja.2009.08.003, 2010.
- Kemanian, A. R., Julich, S., Manoranjan, V. S. and Arnold, J. R.: Integrating soil carbon cycling with that of nitrogen and phosphorus in the watershed model SWAT: Theory and model testing, *Ecol. Modell.*, 222(12), 1913–1921, doi:10.1016/j.ecolmodel.2011.03.017, 2011.
- Knisel, W. G.: CREAMS: A field-scale model for chemicals, runoff, and erosion from agricultural management systems, USDA National Resources Conservation Service, Washington, D.C., 1980.
- Kong, A. Y. Y., Six, J., Bryant, D. C., Denison, R. F. and van Kessel, C.: The Relationship between Carbon Input, Aggregation, and Soil Organic Carbon Stabilization in Sustainable Cropping Systems, *Soil Sci. Soc. Am. J.*, 69(4), 1078–1085, doi:10.2136/sssaj2004.0215, 2005.
- Lang, F., Krüger, J., Amelung, W., Willbold, S., Frossard, E., Bünemann, E. K., Bauhus, J., Nitschke, R., Kandeler, E., Marhan, S., Schulz, S., Bergkemper, F., Schloter, M., Luster, J., Guggisberg, F., Kaiser, K., Mikutta, R., Guggenberger, G., Polle, A., Pena, R., Prietzel, J., Rodionov, A., Talkner, U., Meesenburg, H., von Wilpert, K., Hölscher, A., Dietrich, H. P. and Chmara, I.: Soil phosphorus supply controls P nutrition strategies of beech forest ecosystems in Central Europe, *Biogeochemistry*, 136(1), 5–29, doi:10.1007/s10533-017-0375-0, 2017.
- Leonard, R. A., Knisel, W. G. and Still, D. A.: GLEAMS: Groundwater Loading Effects of Agricultural Management Systems, *Trans. ASAE*, 30(5), 1403–1418, doi:10.13031/2013.30578, 1987.
- McGill, W. B. and Cole, C. V.: Comparative aspects of cycling of organic C, N, S and P through soil organic matter, *Geoderma*, 26(4), 267–286, doi:10.1016/0016-7061(81)90024-0, 1981.
- Mooshammer, M., Wanek, W., Zechmeister-Boltenstern, S. and Richter, A.: Stoichiometric imbalances between terrestrial decomposer communities and their resources: Mechanisms and implications of microbial adaptations to their resources, *Front. Microbiol.*, 5(FEB), 1–10, doi:10.3389/fmicb.2014.00022, 2014.
- Reed, S. C., Townsend, A. R., Taylor, P. G. and Cleveland, C. C.: Phosphorus Cycling in Tropical Forests Growing on Highly Weathered Soils, edited by E. Bünemann, A. Oberson, and E. Frossard, Springer Berlin Heidelberg, Berlin, Heidelberg., 2011.

- Reed, S. C., Yang, X. and Thornton, P. E.: Incorporating phosphorus cycling into global modeling efforts: A worthwhile, tractable endeavor, *New Phytol.*, 208(2), 324–329, doi:10.1111/nph.13521, 2015.
- Schimel, J. P. and Weintraub, M. N.: The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: A theoretical model, *Soil Biol. Biochem.*, 35(4), 549–563, doi:10.1016/S0038-0717(03)00015-4, 2003.
- Schoumans, O. F. and Groenendijk, P.: Modeling soil phosphorus levels and phosphorus leaching from agricultural land in the Netherlands, *J. Environ. Qual.*, 29(1), 111–116, doi:10.2134/jeq2000.00472425002900010014x, 2000.
- Tang, J. Y. and Riley, W. J.: A total quasi-steady-state formulation of substrate uptake kinetics in complex networks and an example application to microbial litter decomposition, *Biogeosciences Discuss.*, 10(6), 10615–10683, doi:10.5194/bg-10-10615-2013, 2013.
- Thum, T., Caldararu, S., Engel, J., Kern, M., Pallandt, M., Schnur, R., Yu, L. and Zaehle, S.: A new terrestrial biosphere model with coupled carbon, nitrogen, and phosphorus cycles (QUINCY v1.0; revision 1772), *Geosci. Model Dev. Discuss.*, (12), 4781–4802, doi:10.5194/gmd-2019-49, 2019.
- Turner, B. L., Cade-Menun, B. J. and Westermann, D. T.: Organic Phosphorus Composition and Potential Bioavailability in Semi-Arid Arable Soils of the Western United States, *Soil Sci. Soc. Am. J.*, 67(4), 1168–1179, doi:10.2136/sssaj2003.1168, 2003a.
- Turner, B. L., Chudek, J. A., Whitton, B. A. and Baxter, R.: Phosphorus composition of upland soils polluted by long-term atmospheric nitrogen deposition, *Biogeochemistry*, 65(2), 259–274, doi:10.1023/A:1026065719423, 2003b.
- Walker, T. W. and Syers, J. K.: The fate of phosphorus during pedogenesis, *Geoderma*, 15(1), 1–19, doi:10.1016/0016-7061(76)90066-5, 1976.
- Wang, X., Williams, J. R., Gassman, P. W., Baffaut, C., Izaurralde, R. C., Jeong, J. and Kiniry, J. R.: EPIC and APEX: Model Use, Calibration, and Validation, *Trans. ASABE*, 55(4), 1447–1462, doi:10.13031/2013.42253, 2012.
- Waring, B. G., Averill, C. and Hawkes, C. V.: Differences in fungal and bacterial physiology alter soil carbon and nitrogen cycling: Insights from meta-analysis and theoretical models, *Ecol. Lett.*, 16(7), 887–894, doi:10.1111/ele.12125, 2013.
- White, C. M., Kemanian, A. R. and Kaye, J. P.: Implications of carbon saturation model structures for simulated nitrogen mineralization dynamics, *Biogeosciences*, 11(23), 6725–6738, doi:10.5194/bg-11-6725-2014, 2014.
- Wieder, W. R., Grandy, A. S., Kallenbach, C. M. and Bonan, G. B.: Integrating microbial physiology and physio-chemical principles in soils with the MICROBIAL-MINERAL CARBON STABILIZATION (MIMICS) model, *Biogeosciences*, 11(14), 3899–3917, doi:10.5194/bg-11-3899-2014, 2014.
- Wutzler, T., Zaehle, S., Schrumpf, M., Ahrens, B. and Reichstein, M.: Adaptation of microbial resource allocation affects modelled long term soil organic matter and nutrient cycling, *Soil Biol. Biochem.*, 115, 322–336, doi:10.1016/j.soilbio.2017.08.031, 2017.
- Xu, X., Thornton, P. E. and Post, W. M.: A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems, *Glob. Ecol. Biogeogr.*, 22(6), 737–749, doi:10.1111/geb.12029, 2013.

Yang, X., Thornton, P. E., Ricciuto, D. M. and Post, W. M.: The role of phosphorus dynamics in tropical forests – a modeling study using CLM-CNP, *Biogeosciences*, 11(6), 1667–1681, doi:10.5194/bg-11-1667-2014, 2014.

Yu, L., Zanchi, G., Akselsson, C., Wallander, H. and Belyazid, S.: Modeling the forest phosphorus nutrition in a southwestern Swedish forest site, *Ecol. Modell.*, 369, 88–100, doi:10.1016/j.ecolmodel.2017.12.018, 2018.

Yu, L., Ahrens, B., Wutzler, T., Schrumpf, M. and Zaehle, S.: Jena Soil Model (JSM v1.0; Revision 1934): A microbial soil organic carbon model integrated with nitrogen and phosphorus processes, *Geosci. Model Dev.*, 13(2), 783–803, doi:10.5194/gmd-13-783-2020, 2020.

Zhu, Q., Riley, W. J., Tang, J., Collier, N., Hoffman, F. M., Yang, X. and Bisht, G.: Representing Nitrogen, Phosphorus, and Carbon Interactions in the E3SM Land Model: Development and Global Benchmarking, *J. Adv. Model. Earth Syst.*, 11(7), 2238–2258, doi:10.1029/2018MS001571, 2019.

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 P-models and to explore the potential of some new techniques to usher P biogeochemistry research and modeling forward. To advance our understanding and modeling of P biogeochemistry, 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 hypothesize 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 models components of biogeochemical models are structured after C and N models 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; Condon 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, or on phosphate-bound stable oxygen isotopes that are subject to biotically-mediated fractionation, complicating 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 (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 has led to enhanced transport of soluble P from fields to water (Radcliffe et al., 2015; Dodd and Sharpley, 2016). The collective inability to predict the behavior

35 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 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

45 In the soil-plant system, P exists in both inorganic (P_i) and organic (P_o) forms whose relative abundance depends on edaphic, 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). ~~Due to PO_4 's strong affinity to mineral and colloid surfaces, PO_4 equilibrium favors sorption to the solid phase rather than desorption to the soil solution (Okajima et al., 1983; Menezes-Blackburn et al., 2016).~~ 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 by electrostatic interaction or fast chemisorption (ligand exchange on external mineral sites).

60 Once PO_4 is sorbed, ~~sorbed to minerals by electrostatic interaction or fast chemisorption (ligand exchange on external mineral sites),~~ PO_4 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 fractions of varying lability and indirectly, plant availability (Guppy et al., 2000).

65 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 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

70 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 (Condrón et al., 2005; Turner, 2008).

75 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 ~~the presence of~~ 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.

85 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 therefore 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 and enabled by phosphatase enzymes to acquire P independent of C and is therefore decoupled 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 next section).

95 The biological and biochemical pathways ~~are generally~~ ~~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~~ ~~not the paths,~~ ~~leading to P_o mineralization.~~ 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 Condrón et al. 2005 and further evidenced by recent research. Phosphatase enzymes

105 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 some
110 limitations of methods in measuring methodological limitations to measure enzyme activity and P_o mineralization. (Smeck,
1985; Gressel et al., 1996; Oehl et al., 2004; Guppy and McLaughlin, 2009; Spohn and Kuzyakov, 2013; Heuck and Spohn,
2016).

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
115 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
120 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
125 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
130 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
135 microbial activity near roots (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).

140 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). ~~This indicates~~ **indicating an** active microbe-mediated P_o -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.

145 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).

150 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

160 **While P_o compounds are a C source for microbes, but 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).

170 ~~Although poorly understood and undertested in soils, dephosphorylation of P_o compounds may be such an important step in C acquisition from P_o because soil microbes may be limited in their ability to directly assimilate P_o compounds in the soil. So far there is limited to no evidence of direct P_o assimilation in soils (George et al. 2017).~~

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

175 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.

180 Strict P-driven mineralization may not apply to soils **and microbial communities** that are C-limited, but ~~many~~ 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), and 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), 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 is 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 if applied to P_o decomposition/mineralization, it 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, which itself 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); and may enable enabling more accurate parameterization of models based on the explicit simulation of phosphatase activity, such as that of Schimel and Weintraub (2003). However, this is clearly not enough.

215 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, which 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. Co-located organic C mineralization would also influence the P_o turnover rate. To our knowledge, no systematic effort has been conducted to elucidate such relationships.

220 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).

230 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).

235 Most models do not explicitly simulate P driven P_o mineralization independent of C demands, (Reed et al., 2015) largely because the general structure of P models mirrors that of N, which only includes C driven P_o mineralization. The global CNP models CLM CNP and CASA CNP incorporate P driven P_o mineralization of SOM pools but there are insufficient observations of this process for reliable parameterization (Wang et al., 2010; Yang et al., 2014; Reed et al., 2015; Achat et al., 2016). Although explicit inclusion of P driven P_o mineralization resulted in better agreement between simulated and measured P pool sizes (Wang et al., 2010), P driven P_o mineralization may only apply in specific circumstances (Olander and Vitousek, 2000). With major uncertainties in theory, there are limitations to venture far from data.

2 Phytate dynamics and the unpredictability of P stoichiometry

245 2.1 Phytate

Po 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-
250 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
255 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
260 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

265 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
270 (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
275 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).

280 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

285 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.

290 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

300 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.

305 As explained by Turner and Blackwell (2013), unless the soil solution of a calcareous soil has excess dissolved Ca²⁺, 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)

310 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 the “Organic P and C saturation” section.

2.1.4 Synthesis

315 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).

320 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).

325 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 techniques 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
330 when characterizing or quantifying P_o , 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

335 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 unlike N, 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).

340 However, variation in soil C:P ratios, flexible microbial stoichiometry or “not strictly homeostatic behavior”, 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 characteristics specific to microorganisms (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

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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 (total P) 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; Bünenmann, 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 P_i , 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 therefore 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 al., 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. Čapek 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 in P models 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, a ratio that is 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

420 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).

425 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
430 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 P_o , 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.

435 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

440 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).

445 **The dynamics of explicit** C_o saturation ~~dynamics~~ 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
450 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 sites 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 models 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 P_i , 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 P_i , 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, C1). 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.

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 (Gijssman 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 labile and P transformations P stability and changes in pool sizes or transformations using isotope tracing (Hedley et al., 1982; Tiessen et al., 1984; Stewart and Tiessen, 1987; Gijssman et al., 1996; Delve et al., 2009; 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 P_i , 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. a fact that must be incorporated into models that have invariable cycling rates of stable fractions.

4.2 Sorption Curves

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 Heaney, 1997).

525 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).

530 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.

535 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 reduced fit (McGechan and Lewis 2002). Two phase Langmuir equations (Table 2, Eq. 4) can be used, as they have provided 540 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.

545 Sharpley et al. (1984) employed a longer and more intensive approach to estimating a “P sorption parameter” (PSP), which is the 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 550 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 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 the C and P saturation section. 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 555 soil test phosphorus (STP) method-STP. This may work for initialization before model spin up, or at least provide a consistent method, but is not a representative method in determining P pool sizes.

555 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.

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 Organic P and C Saturation section, 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 P simulation models. Understanding the controls on plant, microbial biomass, and microbial stoichiometry will help determine bottom up controls on the 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

595 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

600 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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References

- Abdala, D. B., Ghosh, A. K., da Silva, I. R., de Novais, R. F. and Alvarez Venegas, V. H.: Phosphorus saturation of a tropical soil and related P leaching caused by poultry litter addition, *Agric. Ecosyst. Environ.*, 162, 15–23, doi:10.1016/j.agee.2012.08.004, 2012.
- 625 Achat, D. L., Augusto, L., Gallet-Budynek, A. and Loustau, D.: Future challenges in coupled C–N–P cycle models for terrestrial ecosystems under global change: a review, *Biogeochemistry*, 131(1–2), 173–202, doi:10.1007/s10533-016-0274-9, 2016.
- Adams, M. A. and Pate, J. S.: Availability of organic and inorganic forms of phosphorus to lupins (*Lupinus* spp.), *Plant Soil*, 145(1), 107–113, doi:10.1007/BF00009546, 1992.
- Ahrens, B., Braakhekke, M. C., Guggenberger, G., Schrumpf, M. and Reichstein, M.: Contribution of sorption, DOC transport and microbial interactions to the ¹⁴C age of a soil organic carbon profile: Insights from a calibrated process model, *Soil Biol. Biochem.*, 88, 390–402, doi:10.1016/j.soilbio.2015.06.008, 2015.
- 630 Allison, S. D.: A trait-based approach for modelling microbial litter decomposition, *Ecol. Lett.*, 15(9), 1058–1070, doi:10.1111/j.1461-0248.2012.01807.x, 2012.
- Allison, S. D. and Vitousek, P. M.: Responses of extracellular enzymes to simple and complex nutrient inputs, *Soil Biol. Biochem.*, 37(5), 937–944, doi:10.1016/j.soilbio.2004.09.014, 2005.
- 635 Anderson, G., Williams, E. G. and Moir, J. O.: A Comparison of the Sorption of Inorganic Orthophosphate and Inositol Hexaphosphate by Six Acid Soils, *J. Soil Sci.*, 25(1), 51–62, doi:10.1111/j.1365-2389.1974.tb01102.x, 1974.
- Angert, A., Weiner, T., Mazeh, S., Tamburini, F., Frossard, E., Bernasconi, S. M. and Sternberg, M.: Seasonal variability of soil phosphate stable oxygen isotopes in rainfall manipulation experiments, *Geochim. Cosmochim. Acta*, 75(15), 4216–4227, doi:10.1016/j.gca.2011.05.002, 2011.
- 640 Antelo, J., Arce, F., Avena, M., Fiol, S., López, R. and Macías, F.: Adsorption of a soil humic acid at the surface of goethite and its competitive interaction with phosphate, *Geoderma*, 138(1–2), 12–19, doi:10.1016/j.geoderma.2006.10.011, 2007.
- Aponte, C., Marañón, T. and García, L. V.: Microbial C, N and P in soils of Mediterranean oak forests: Influence of season, canopy cover and soil depth, *Biogeochemistry*, 101(1), 77–92, doi:10.1007/s10533-010-9418-5, 2010.
- 645 Arai, Y. and Sparks, D. L.: Phosphate Reaction Dynamics in Soils and Soil Components: A Multiscale Approach, *Adv. Agron.*, 94(06), 135–179, doi:10.1016/S0065-2113(06)94003-6, 2007.
- Arenberg, M. R. and Arai, Y.: Uncertainties in soil physicochemical factors controlling phosphorus mineralization and immobilization processes, in *Advances in Agronomy*, vol. 154, pp. 153–200, Elsevier., 2019.
- Arnold, J. G., Srinivasan, R., Muttiah, R. S. and Williams, J. R.: Large Area Hydrologic Modeling and Assessment Part I: Model Development, *J. Am. Water Resour. Assoc.*, 34(1), 73–89, doi:10.1111/j.1752-1688.1998.tb05961.x, 1998.
- 650 Asmar, F.: Variation in activity of root extracellular phytase between genotypes of barley, *Plant Soil*, 195(1), 61–64, doi:10.1023/A:1004291512285, 1997.
- Asmar, F., Singh, T., Gahoonia and Nielsen, N. E.: Barley genotypes differ in activity of soluble extracellular phosphatase and depletion of organic phosphorus in the rhizosphere soil, *Plant Soil*, 172(1), 117–122, doi:10.1007/BF00020865, 1995.
- 655 Barrow, N. J.: The Description of Phosphate Adsorption Curves, *J. Soil Sci.*, 29(4), 447–462, doi:10.1111/j.1365-2389.1978.tb00794.x, 1978.
- Barrow, N. J.: On the reversibility of phosphate sorption by soils, *J. Soil Sci.*, 34(4), 751–758, doi:10.1111/j.1365-2389.1983.tb01069.x, 1983.
- Barrow, N. J.: The description of sorption curves, *Eur. J. Soil Sci.*, 59(5), 900–910, doi:10.1111/j.1365-2389.2008.01041.x, 660 2008.

- Beegle, D.: Assessing soil phosphorus for crop production by soil testing, in *Phosphorus: Agriculture and the environment*, edited by J. T. Sims and A. N. Sharpley, pp. 123–143, ASA, CSSA, and SSSA, Madison, WI., 2005.
- Belinque, H., Pucheu, N., Kerber, N. and Rubio, G.: Utilization of organic phosphorus sources by oilseed rape, sunflower, and soybean, *J. Plant Nutr. Soil Sci.*, 178(2), 339–344, doi:10.1002/jpln.201400301, 2015.
- 665 Berg, A. S. and Joern, B. C.: Sorption Dynamics of Organic and Inorganic Phosphorus Compounds in Soil, *J. Environ. Qual.*, 35(5), 1855–1862, doi:10.2134/jeq2005.0420, 2006.
- Beven, K., Page, T. and McGechan, M.: Uncertainty Estimation in Phosphorus Models, in *Modeling Phosphorus in the Environment*, edited by D. E. Radcliffe and M. L. Cabrera, pp. 131–160, CRC Press, Boca Raton, FL., 2006.
- Blake, R. E., O’Neil, J. R. and Surkov, A. V.: Biogeochemical cycling of phosphorus: Insights from oxygen isotope effects of phosphoenzymes, *Am. J. Sci.*, 305(6-8 SPEC. ISS.), 596–620, doi:10.2475/ajs.305.6-8.596, 2005.
- 670 Breeuwsma, A., Reijerink, J. G. A. and Schoumans, O. F.: Impact of manure on accumulation and leaching of phosphate in areas of intensive livestock farming, in *Animal waste and the land-water interface*, edited by K. F. Steele, pp. 239–249, Lewis Publishers, Boca Raton. [online] Available from: <http://www.narcis.nl/publication/RecordID/oai%3Alibrary.wur.nl%3Awurpubs%2F302050>, 1995.
- 675 Bünemann, E. K.: Assessment of gross and net mineralization rates of soil organic phosphorus - A review, *Soil Biol. Biochem.*, 89, 82–98, doi:10.1016/j.soilbio.2015.06.026, 2015.
- Bünemann, E. K., Augstburger, S. and Frossard, E.: Dominance of either physicochemical or biological phosphorus cycling processes in temperate forest soils of contrasting phosphate availability, *Soil Biol. Biochem.*, 101, 85–95, doi:10.1016/j.soilbio.2016.07.005, 2016.
- 680 Butler, J. S. and Coale, F. J.: Phosphorus Leaching in Manure-Amended Atlantic Coastal Plain Soils, *J. Environ. Qual.*, 34(1), 370–381, doi:10.2134/jeq2005.0370, 2005.
- Camenzind, T., Hättenschwiler, S., Treseder, K. K., Lehmann, A. and Rillig, M. C.: Nutrient limitation of soil microbial processes in tropical forests, *Ecol. Monogr.*, 88(1), 4–21, doi:10.1002/ecm.1279, 2018.
- Campbell, M., Dunn, R., Ditterline, R., Pickett, S. and Raboy, V.: Phytic acid represents 10 to 15% of total phosphorus in alfalfa root and crown, *J. Plant Nutr.*, 14(9), 925–937, doi:10.1080/01904169109364253, 1991.
- 685 Čapek, P., Kotas, P., Manzoni, S. and Šantrůčková, H.: Drivers of phosphorus limitation across soil microbial communities, *Funct. Ecol.*, 30(10), 1705–1713, doi:10.1111/1365-2435.12650, 2016.
- Čapek, P., Manzoni, S., Kaštovská, E., Wild, B., Diáková, K., Bárta, J., Schneckner, J., Biasi, C., Martikainen, P. J., Alves, R. J. E., Guggenberger, G., Gentsch, N., Hugelius, G., Palmtag, J., Mikutta, R., Shibistova, O., Urich, T., Schleper, C., Richter, A. and Šantrůčková, H.: A plant–microbe interaction framework explaining nutrient effects on primary production, *Nat. Ecol. Evol.*, 2(October), 1588–1596, doi:10.1038/s41559-018-0662-8, 2018.
- 690 Castellano, M. J., Kaye, J. P., Lin, H. and Schmidt, J. P.: Linking Carbon Saturation Concepts to Nitrogen Saturation and Retention, *Ecosystems*, 15(2), 175–187, doi:10.1007/s10021-011-9501-3, 2012.
- Celi, L., Lamacchia, S., Marsan, F. A. and Barberis, E.: Interaction of inositol hexaphosphate on clays: Adsorption and charging phenomena, *Soil Sci.*, 164(8), 574–585, doi:10.1097/00010694-199908000-00005, 1999.
- 695 Chen, C. R., Condon, L. M., Davis, M. R. and Sherlock, R. R.: Effects of afforestation on phosphorus dynamics and biological properties in a New Zealand grassland soil, *Plant Soil*, 220(1–2), 151–163, doi:10.1023/A:1004712401721, 2000.
- Chen, C. R., Condon, L. M., Davis, M. R. and Sherlock, R. R.: Phosphorus dynamics in the rhizosphere of perennial ryegrass (*Lolium perenne* L.) and radiata pine (*Pinus radiata* D. Don.), *Soil Biol. Biochem.*, 34(4), 487–499, doi:10.1016/S0038-0717(01)00207-3, 2002.
- 700

- Clarholm, M.: Microbial biomass P, labile P, and acid phosphatase activity in the humus layer of a spruce forest, after repeated additions of fertilizers, *Biol. Fertil. Soils*, 16(4), 287–292, doi:10.1007/BF00369306, 1993.
- Cleveland, C. C. and Liptzin, D.: C:N:P stoichiometry in soil: Is there a “Redfield ratio” for the microbial biomass?, *Biogeochemistry*, 85(3), 235–252, doi:10.1007/s10533-007-9132-0, 2007.
- 705 Cleveland, C. C., Townsend, A. R., Constance, B. C., Ley, R. E. and Schmidt, S. K.: Soil Microbial Dynamics in Costa Rica: Seasonal and Biogeochemical Constraints, *Biotropica*, 36(2), 184–195, doi:10.1646/03115-q1562, 2004.
- Cleveland, C. C., Houlton, B. Z., Smith, W. K., Marklein, A. R., Reed, S. C., Parton, W., Del Grosso, S. J. and Running, S. W.: Patterns of new versus recycled primary production in the terrestrial biosphere, *Proc. Natl. Acad. Sci.*, 110(31), 12733–12737, doi:10.1073/pnas.1302768110, 2013.
- 710 Colvan, S. R., Syers, J. K. and O’Donnell, A. G. .: Effect of long-term fertiliser use on acid and alkaline phosphomonoesterase and phosphodiesterase activities in managed grassland, *Biol. Fertil. Soils*, 34, 258–263, doi:10.1007/s003740100411, 2001.
- Condrón, L. M., Turner, B. L. and Cade-Menun, B. J.: Chemistry and dynamics of soil organic phosphorus, in *Phosphorus: Agriculture and the environment*, edited by J. T. Sims and A. N. Sharpley, pp. 87–121, ASA, CSSA, and SSSA, Madison, WI., 2005.
- 715 Cotner, J. B., Hall, E. K., Scott, J. T. and Heldal, M.: Freshwater bacteria are stoichiometrically flexible with a nutrient composition similar to seston, *Front. Microbiol.*, (DEC), 1–11, doi:10.3389/fmicb.2010.00132, 2010.
- Cross, A. F. and Schlesinger, W. H.: A literature review and evaluation of the Hedley fractionation: Applications to the biogeochemical cycle of soil phosphorus in natural ecosystems, *Geoderma*, 64(3–4), 197–214, doi:10.1016/0016-7061(94)00023-4, 1995.
- 720 Dalal, R. C.: Mineralization of Carbon and Phosphorus from Carbon-14 and Phosphorus-32 Labelled Plant Material Added to Soil1, *Soil Sci. Soc. Am. J.*, 43(5), 913–916, doi:10.2136/sssaj1979.03615995004300050019x, 1979.
- Dari, B., Nair, V. D., Colee, J., Harris, W. G. and Mylavarapu, R.: Estimation of phosphorus isotherm parameters: a simple and cost-effective procedure, *Front. Environ. Sci.*, 3(October), 1–9, doi:10.3389/fenvs.2015.00070, 2015.
- Davies, J. A. C., Tipping, E., Rowe, E. C., Boyle, J. F., Graf Pannatier, E. and Martinsen, V.: Long-term P weathering and recent N deposition control contemporary plant-soil C, N, and P, *Global Biogeochem. Cycles*, 30(2), 231–249, doi:10.1002/2015GB005167, 2016.
- 725 Deinema, M. H., van Loosdrecht, M. and Scholten, A.: Some Physiological Characteristics of *Acinetobacter* spp. Accumulating Large Amounts of Phosphate, *Water Sci. Technol.*, 17(11–12), 119–125, doi:10.2166/wst.1985.0226, 1985.
- Delve, R. J., Probert, M. E., Cobo, J. G., Ricaurte, J., Rivera, M., Barrios, E. and Rao, I. M.: Simulating phosphorus responses in annual crops using APSIM: Model evaluation on contrasting soil types, *Nutr. Cycl. Agroecosystems*, 84(3), 293–306, doi:10.1007/s10705-008-9243-6, 2009.
- 730 Dick, R. P., Rasmussen, P. E. and Kerle, E. A.: Influence of long-term residue management on soil enzyme activities in relation to soil chemical properties of a wheat-fallow system, *Biol. Fertil. Soils*, 6(2), 159–164, doi:10.1007/BF00257667, 1988.
- Dissing Nielsen, J. and Eiland, F.: Investigations on the relationship between P-fertility, phosphatase activity and ATP content in soil, *Plant Soil*, 57(1), 95–103, doi:10.1007/BF02139645, 1980.
- 735 Dodd, R. J. and Sharpley, A. N.: Conservation practice effectiveness and adoption: unintended consequences and implications for sustainable phosphorus management, *Nutr. Cycl. Agroecosystems*, 104(3), 373–392, doi:10.1007/s10705-015-9748-8, 2016.
- Doolette, A. L., Smernik, R. J. and Dougherty, W. J.: Rapid decomposition of phytate applied to a calcareous soil demonstrated by a solution ³¹P NMR study, *Eur. J. Soil Sci.*, 61(4), 563–575, doi:10.1111/j.1365-2389.2010.01259.x, 2010.
- 740

- Doolette, A. L., Smernik, R. J. and Dougherty, W. J.: Overestimation of the importance of phytate in NaOH-EDTA soil extracts as assessed by ³¹P NMR analyses, *Org. Geochem.*, 42(8), 955–964, doi:10.1016/j.orggeochem.2011.04.004, 2011.
- Dou, Z., Ramberg, C. F., Toth, J. D., Wang, Y., Sharpley, A. N., Boyd, S. E., Chen, C. R., Williams, D. and Xu, Z. H.: Phosphorus Speciation and Sorption-Desorption Characteristics in Heavily Manured Soils, *Soil Sci. Soc. Am. J.*, 73(1), 93–101, doi:10.2136/sssaj2007.0416, 2009.
- 745 Duncan, E. W., Osmond, D. L., Shober, A. L., Starr, L., Tomlinson, P., Kovar, J. L., Moorman, T. B., Peterson, H. M., Fiorellino, N. M. and Reid, K.: Phosphorus and Soil Health Management Practices, *Agric. Environ. Lett.*, 4(1), 0, doi:10.2134/ael2019.04.0014, 2019.
- Duxbury, J., Smith, M. S. and Doran, J. W.: Soil organic matter as a source and a sink of plant nutrients, in *Dynamics of Soil Organic Matter in Tropical Ecosystems*, edited by D. Coleman, J. M. Oades, and G. Uehara, pp. 33–67, University of Hawaii Press, Honolulu, Hawaii., 1989.
- 750 Enwezor, W. O.: Significance of the C: Organic P ratio in the mineralization of soil organic phosphorus, *Soil Sci.*, 103(1), 62–66, doi:10.1097/00010694-196701000-00010, 1967.
- Enwezor, W. O.: The mineralization of nitrogen and phosphorus in organic materials of varying C:N and C:P ratios, *Plant Soil*, 44(1), 237–240, doi:10.1007/BF00016972, 1976.
- 755 Erich, M. S., Fitzgerald, C. B. and Porter, G. A.: The effect of organic amendments on phosphorus chemistry in a potato cropping system, *Agric. Ecosyst. Environ.*, 88(1), 79–88, doi:10.1016/S0167-8809(01)00147-5, 2002.
- Findenegg, G. R. and Nelemans, J. A.: The effect of phytase on the availability of P from myo-inositol hexaphosphate (phytate) for maize roots, *Plant Soil*, 154(2), 189–196, doi:10.1007/BF00012524, 1993.
- 760 Fransson, A. M. and Jones, D. L.: Phosphatase activity does not limit the microbial use of low molecular weight organic-P substrates in soil, *Soil Biol. Biochem.*, 39(5), 1213–1217, doi:10.1016/j.soilbio.2006.11.014, 2007.
- Frossard, E., Condrón, L. M., Oberson, A., Sinaj, S. and Fardeau, J. C.: Processes governing phosphorus availability in temperate soils, *J. Environ. Qual.*, 29(1), 15–23, doi:10.2134/jeq2000.00472425002900010003x, 2000.
- Frossard, E., Achat, D. L., Bernasconi, S. M., Bünemann, E. K., Fardeau, J., Jansa, J., Morel, C., Rabeharisoa, L., Randriamanantsoa, L., Sinaj, S., Tamburini, F. and Oberson, A.: The Use of Tracers to Investigate Phosphate Cycling in Soil-Plant Systems, in *Phosphorus in action: Biological processes in soil phosphorus cycling*, pp. 59–91, Springer, Heidelberg., 2011.
- 765 Gao, Y., Zhu, B., He, N., Yu, G., Wang, T., Chen, W. and Tian, J.: Phosphorus and carbon competitive sorption-desorption and associated non-point loss respond to natural rainfall events, *J. Hydrol.*, 517, 447–457, doi:10.1016/j.jhydrol.2014.05.057, 2014.
- 770 García, A. M., Alexander, R. B., Arnold, J. G., Norfleet, L., White, M. J., Robertson, D. M. and Schwarz, G.: Regional Effects of Agricultural Conservation Practices on Nutrient Transport in the Upper Mississippi River Basin, *Environ. Sci. Technol.*, 50(13), 6991–7000, doi:10.1021/acs.est.5b03543, 2016.
- George, T. S., Richardson, A. E., Hadobas, P. A. and Simpson, R. J.: Characterization of transgenic *Trifolium subterraneum* L. which expresses *phyA* and releases extracellular phytase: Growth and P nutrition in laboratory media and soil, *Plant, Cell Environ.*, 27(11), 1351–1361, doi:10.1111/j.1365-3040.2004.01225.x, 2004.
- 775 George, T. S., Giles, C. D., Menezes-Blackburn, D., Condrón, L. M., Gama-Rodrigues, A. C., Jaisi, D., Lang, F., Neal, A. L., Stutter, M. I., Almeida, D. S., Bol, R., Cabugao, K. G., Celi, L., Cotner, J. B., Feng, G., Goll, D. S., Hallama, M., Krueger, J., Plassard, C., Rosling, A., Darch, T., Fraser, T., Giesler, R., Richardson, A. E., Tamburini, F., Shand, C. A., Lumsdon, D. G., Zhang, H., Blackwell, M. S. A., Wearing, C., Mezeli, M. M., Almås, R., Audette, Y., Bertrand, I., Beyhaut, E.,
- 780

- Boitt, G., Bradshaw, N., Brearley, C. A., Bruulsema, T. W., Ciais, P., Cozzolino, V., Duran, P. C., Mora, M. L., de Menezes, A. B., Dodd, R. J., Dunfield, K., Engl, C., Frazão, J. J., Garland, G., González Jiménez, J. L., Graca, J., Granger, S. J., Harrison, A. F., Heuck, C., Hou, E. Q., Johnes, P. J., Kaiser, K., Kjær, H. A., Klumpp, E., Lamb, A. L., Macintosh, K. A., Mackay, E. B., McGrath, J., McIntyre, C., McLaren, T., Mészáros, E., Missong, A., Mooshammer, M., Negrón, C. P., Nelson, L. A., Pfahler, V., Poblete-Grant, P., Randall, M., Seguel, A., Seth, K., Smith, A. C., Smits, M. M., Sobarzo, J. A., Spohn, M., Tawaraya, K., Tibbett, M., Voroney, P., Wallander, H., Wang, L., Wasaki, J. and Haygarth, P. M.: Organic phosphorus in the terrestrial environment: a perspective on the state of the art and future priorities, *Plant Soil*, 1–18, doi:10.1007/s11104-017-3391-x, 2017.
- Gerke, J.: Phytate (Inositol Hexakisphosphate) in Soil and Phosphate Acquisition from Inositol Phosphates by Higher Plants. A Review, *Plants*, 4(2), 253–266, doi:10.3390/plants4020253, 2015a.
- Gerke, J.: The acquisition of phosphate by higher plants: Effect of carboxylate release by the roots. A critical review., *J. Plant Nutr. Soil Sci.*, 178(3), 351–364, doi:10.1002/jpln.201400590, 2015b.
- Gijsman, A. J., Oberson, A., Tiessen, H. and Friesen, D. K.: Limited Applicability of the CENTURY Model to Highly Weathered Tropical Soils, *Agron. J.*, 88(6), 894–903, doi:10.2134/agronj1996.00021962003600060008x, 1996.
- Giles, C. D. and Cade-Menun, B. J.: Phytate in Animal Manure and Soils: Abundance, Cycling and Bioavailability, in *Applied Manure and Nutrient Chemistry for Sustainable Agriculture and Environment*, pp. 163–190, Springer, Dordrecht., 2014.
- Giles, C. D., George, T. S., Brown, L. K., Mezeli, M. M., Richardson, A. E., Shand, C. A., Wendler, R., Darch, T., Menezes-Blackburn, D., Cooper, P., Stutter, M. I., Lumsdon, D. G., Blackwell, M. S. A., Wearing, C., Zhang, H. and Haygarth, P. M.: Does the combination of citrate and phytase exudation in *Nicotiana tabacum* promote the acquisition of endogenous soil organic phosphorus?, *Plant Soil*, 412(1–2), 43–59, doi:10.1007/s11104-016-2884-3, 2017.
- Goll, D. S., Brovkin, V., Parida, B. R., Reick, C. H., Kattge, J., Reich, P. B., Van Bodegom, P. M. and Niinemets, Ü.: Nutrient limitation reduces land carbon uptake in simulations with a model of combined carbon, nitrogen and phosphorus cycling, *Biogeosciences*, 9(9), 3547–3569, doi:10.5194/bg-9-3547-2012, 2012.
- Goll, D. S., Vuichard, N., Maignan, F., Jornet-Puig, A., Sardans, J., Violette, A., Peng, S., Sun, Y., Kvakic, M., Guimberteau, M., Guenet, B., Zaehle, S., Penuelas, J., Janssens, I. and Ciais, P.: A representation of the phosphorus cycle for ORCHIDEE (revision 4520), *Geosci. Model Dev.*, 10(10), 3745–3770, doi:10.5194/gmd-10-3745-2017, 2017.
- Grafe, M., Goers, M., von Tucher, S., Baum, C., Zimmer, D., Leinweber, P., Vestergaard, G., Kublik, S., Schloter, M. and Schulz, S.: Bacterial potentials for uptake, solubilization and mineralization of extracellular phosphorus in agricultural soils are highly stable under different fertilization regimes, *Environ. Microbiol. Rep.*, 10(3), 320–327, doi:10.1111/1758-2229.12651, 2018.
- Grant, R. F. and Heaney, D. J.: Inorganic phosphorus transformation and transport in soils: Mathematical modeling in ecosys, *Soil Sci. Soc. Am. J.*, 61(3), 752–764, doi:http://dx.doi.org/10.2136/sssaj1997.03615995006100030008x, 1997.
- Greaves, M. P. and Webley, D. M.: The hydrolysis of myoinositol hexaphosphate by soil microorganisms, *Soil Biol. Biochem.*, 1(1), 37–43, doi:10.1016/0038-0717(69)90032-7, 1969.
- Greenwood, A. . and Lewis, D. H.: Phosphatases and the utilisation of inositol hexaphosphate by soil yeasts of the genus *Cryptococcus*, *Soil Biol. Biochem.*, 9(3), 161–166, doi:10.1016/0038-0717(77)90069-4, 1977.
- Greiner, R.: Phytate-degrading enzymes: Regulation of synthesis in microorganisms and plants, in *Inositol Phosphates: Linking Agriculture and the Environment*, edited by B. L. Turner, A. E. Richardson, and E. J. Mullaney, pp. 78–96, CAB International, Wallingford., 2007.
- Gressel, N., McColl, J. G., Preston, C. M., Newman, R. H. and Powers, R. F.: Linkages between phosphorus transformations and

carbon decomposition in a forest soil, *Biogeochemistry*, 33(2), 97–123, doi:10.1007/BF02181034, 1996.

Guo, F., Yost, R. S., Hue, N. V., Evensen, C. I. and Silva, J. a.: Changes in Phosphorus Fractions in Soils under Intensive Plant Growth, *Soil Sci. Soc. Am. J.*, 64(5), 1681–1689, doi:10.2136/sssaj2000.6451681x, 2000.

825

Guppy, C. N. and McLaughlin, M. J.: Options for increasing the biological cycling of phosphorus in low-input and organic agricultural systems, *Crop Pasture Sci.*, 60(2), 116–123, doi:10.1071/CP07157, 2009.

Guppy, C. N., Menzies, N. W., Moody, P. W., Compton, B. L. and Blamey, F. P. C.: A simplified, sequential, phosphorus fractionation method, *Commun. Soil Sci. Plant Anal.*, 31(11–14), 1981–1991, doi:10.1080/00103620009370556, 2000.

Guppy, C. N., Menzies, N. W., Moody, P. W. and Blamey, F. P. C.: Competitive sorption reactions between phosphorus and organic matter in soil: A review, *Aust. J. Soil Res.*, 43(2), 189–202, doi:10.1071/SR04049, 2005.

830

Hall, E. K., Maixner, F., Franklin, O., Daims, H., Richter, A. and Battin, T.: Linking Microbial and Ecosystem Ecology Using Ecological Stoichiometry: A Synthesis of Conceptual and Empirical Approaches, *Ecosystems*, 14(2), 261–273, doi:10.1007/s10021-010-9408-4, 2011.

Halstead, R. L.: Phosphatase Activity of Soils as Influenced by Lime and Other Treatments, *Can. J. Soil Sci.*, 44(1), 137–144, doi:10.4141/cjss64-017, 1964.

835

Harrison, A. F.: Relationship between intensity of phosphatase activity and physico-chemical properties in woodland soils, *Soil Biol. Biochem.*, 15(1), 93–99, doi:10.1016/0038-0717(83)90124-4, 1983.

Harrison, A. F.: *Soil organic phosphorus: a review of world literature*, Cab International, Wallingord, UK., 1987.

Hartman, W. H. and Richardson, C. J.: Differential Nutrient Limitation of Soil Microbial Biomass and Metabolic Quotients (qCO₂): Is There a Biological Stoichiometry of Soil Microbes?, *PLoS One*, 8(3), 1–14, doi:10.1371/journal.pone.0057127, 2013.

840

Hassink, J. and Whitmore, A. P.: A Model of the Physical Protection of Organic Matter in Soils, *Soil Sci. Soc. Am. J.*, 61(1), 131–139, doi:10.2136/sssaj1997.03615995006100010020x, 1997.

Häussling, M. and Marschner, H.: Organic and inorganic soil phosphates and acid phosphatase activity in the rhizosphere of 80-year-old Norway spruce [*Picea abies* (L.) Karst.] trees, *Biol. Fertil. Soils*, 8(2), 128–133, doi:10.1007/BF00257756, 1989.

845

Hayes, J. E., Richardson, A. E. and Simpson, R. J.: Components of organic phosphorus in soil extracts that are hydrolysed by phytase and acid phosphatase, *Biol. Fertil. Soils*, 32(4), 279–286, doi:10.1007/s003740000249, 2000.

Heath, R. T.: Microbial turnover of organic phosphorus in aquatic systems, in *Organic Phosphorus in the Environment*, edited by B. L. Turner, E. Frossard, and D. S. Baldwin, pp. 185–203, CAB International, Wallingford., 2005.

Heckrath, G., Brookes, P. C., Poulton, P. R. and Goulding, K. W. T.: Phosphorus Leaching from Soils Containing Different Phosphorus Concentrations in the Broadbalk Experiment, *J. Environ. Qual.*, 24(5), 904–910, doi:10.2134/jeq1995.00472425002400050018x, 1995.

850

Hedley, M. J., Stewart, J. W. B. and Chauhan, B. S.: Changes in Inorganic and Organic Soil Phosphorus Fractions Induced by Cultivation Practices and by Laboratory Incubations, *Soil Sci. Soc. Am. J.*, 46(5), 970–976, doi:10.2136/sssaj1982.03615995004600050017x, 1982.

855

Hedley, M. J., Nye, P. H. and White, R. E.: Plant-Induced Changes in the Rhizosphere of Rape (*Brassica Napus* Var. Emerald) Seedlings, *New Phytol.*, 95(1), 69–82, doi:10.1111/j.1469-8137.1983.tb03470.x, 1983.

Helfenstein, J., Pistocchi, C., Oberson, A., Tamburini, F., Goll, D. S. and Frossard, E.: Estimates of mean residence times of phosphorus in commonly considered inorganic soil phosphorus pools, *Biogeosciences*, 17(2), 441–454, doi:10.5194/bg-17-441-2020, 2020.

860

Heuck, C. and Spohn, M.: Carbon, nitrogen and phosphorus net mineralization in organic horizons of temperate forests:

stoichiometry and relations to organic matter quality, *Biogeochemistry*, 131(1–2), 229–242, doi:10.1007/s10533-016-0276-7, 2016.

- Heuck, C., Weig, A. and Spohn, M.: Soil microbial biomass C: N: P stoichiometry and microbial use of organic phosphorus, *Soil Biol. Biochem.*, 85, 119–129, doi:10.1016/j.soilbio.2015.02.029, 2015.
- 865 Hill, J. E. and Richardson, A. E.: Microorganisms That Utilize Phytate, in *Inositol Phosphates: Linking Agriculture and the Environment*, edited by B. L. Turner, A. E. Richardson, and E. J. Mullaney, pp. 61–77, CAB International, Wallingford., 2007.
- Holford, I. C. R., Wedderburn, R. W. M. and Mattingly, G. E. G.: A Langmuir Two-Surface Equation as a Model for Phosphate Adsorption by Soils, *J. Soil Sci.*, 25(2), 242–255, doi:10.1111/j.1365-2389.1974.tb01121.x, 1974.
- 870 Holtan, H., Kamp-Nielsen, L. and Stuanes, A. O.: Phosphorus in soil, water and sediment: an overview, *Hydrobiologia*, 170(1), 19–34, doi:10.1007/BF00024896, 1988.
- Hooda, P. S., Rendell, A. R., Edwards, A. C., Withers, P. J. A., Aitken, M. N. and Truesdale, V. W.: Relating Soil Phosphorus Indices to Potential Phosphorus Release to Water, *J. Environ. Qual.*, 29(4), 1166–1171, doi:10.2134/jeq2000.00472425002900040018x, 2000.
- 875 Houlton, B. Z., Wang, Y. P., Vitousek, P. M. and Field, C. B.: A unifying framework for dinitrogen fixation in the terrestrial biosphere, *Nature*, 454(7202), 327–330, doi:10.1038/nature07028, 2008.
- Hubel, F. and Beck, E.: Maize Root Phytase (Purification, Characterization, and Localization of Enzyme Activity and Its Putative Substrate), *Plant Physiol.*, 112(4), 1429–1436, doi:10.1104/pp.112.4.1429, 1996.
- Hunt, J. F., Ohno, T., He, Z., Honeycutt, C. W. and Dail, D. B.: Inhibition of phosphorus sorption to goethite, gibbsite, and kaolin by fresh and decomposed organic matter, *Biol. Fertil. Soils*, 44(2), 277–288, doi:10.1007/s00374-007-0202-1, 2007.
- 880 Hussain, A., Murtaza, G., Ghafoor, A. and Mehdi, S. M.: Use of Two-Surface Langmuir-Type Equations for Assessment of Phosphorus Requirements of Lentil on Differently Textured Alluvial Soils, *Commun. Soil Sci. Plant Anal.*, 43(20), 2575–2589, doi:10.1080/00103624.2012.716121, 2012.
- Idriss, E. E., Makarewicz, O., Farouk, A., Rosner, K., Greiner, R., Bochow, H., Richter, T. and Borriss, R.: Extracellular phytase activity of *Bacillus amyloliquefaciens* FZB45 contributes to its plant-growth-promoting effect a, *Microbiology*, 148(7), 2097–2109, doi:10.1099/00221287-148-7-2097, 2002.
- 885 Jackman, R. H. and Black, C. A.: Solubility of Iron, Aluminum, Calcium, and Magnesium Inositol Phosphates at Different pH Values, *Soil Sci.*, 72(3), 179–186, doi:10.1097/00010694-195109000-00002, 1951.
- Jones, C. A., Cole, C. V., Sharpley, A. N. and Williams, J. R.: A Simplified Soil and Plant Phosphorus Model: I. Documentation, *Soil Sci. Soc. Am. J.*, 48, 800–805, 1984.
- 890 Jones, D. L., Nguyen, C. and Finlay, R. D.: Carbon flow in the rhizosphere: Carbon trading at the soil-root interface, *Plant Soil*, 321(1–2), 5–33, doi:10.1007/s11104-009-9925-0, 2009.
- Jørgensen, C., Turner, B. L. and Reitzel, K.: Identification of inositol hexakisphosphate binding sites in soils by selective extraction and solution ³¹P NMR spectroscopy, *Geoderma*, 257, 22–28, doi:10.1016/j.geoderma.2015.03.021, 2015.
- 895 Joshi, S. R., Li, X. and Jaisi, D. P.: Transformation of Phosphorus Pools in an Agricultural Soil: An Application of Oxygen-18 Labeling in Phosphate, *Soil Sci. Soc. Am. J.*, 80(1), 69–78, doi:10.2136/sssaj2015.06.0219, 2016.
- Juma, N. G. and Tabatabai, M. A.: Effects of Trace Elements on Phosphatase Activity in Soils, *Soil Sci. Soc. Am. J.*, 41(2), 343–346, doi:10.2136/sssaj1977.03615995004100020034x, 1977.
- Juma, N. G. and Tabatabai, M. A.: Distribution of phosphomonoesterases in soils, *Soil Sci.*, 126(2), 101–108, doi:10.1097/00010694-197808000-00006, 1978.
- 900

- Kemarian, A. R. and Stöckle, C. O.: C-Farm: A simple model to evaluate the carbon balance of soil profiles, *Eur. J. Agron.*, 32(1), 22–29, doi:10.1016/j.eja.2009.08.003, 2010.
- Kemarian, A. R., Julich, S., Manoranjan, V. S. and Arnold, J. R.: Integrating soil carbon cycling with that of nitrogen and phosphorus in the watershed model SWAT: Theory and model testing, *Ecol. Modell.*, 222(12), 1913–1921, doi:10.1016/j.ecolmodel.2011.03.017, 2011.
- 905 Kirkby, C. A., Kirkegaard, J. A., Richardson, A. E., Wade, L. J., Blanchard, C. and Batten, G.: Stable soil organic matter: A comparison of C:N:P:S ratios in Australian and other world soils, *Geoderma*, 163(3–4), 197–208, doi:10.1016/j.geoderma.2011.04.010, 2011.
- Kleinman, P. J. A. and Sharpley, A. N.: Estimating soil phosphorus sorption saturation from Mehlich-3 data, *Commun. Soil Sci. Plant Anal.*, 33(11/12), 1825–1839, doi:10.1081/CSS-120004825, 2002.
- 910 Knisel, W. G.: CREAMS: A field-scale model for chemicals, runoff, and erosion from agricultural management systems, USDA National Resources Conservation Service, Washington, D.C., 1980.
- Kruse, J., Abraham, M., Amelung, W., Baum, C., Bol, R., Kühn, O., Lewandowski, H., Niederberger, J., Oelmann, Y., Rieger, C., Santner, J., Siebers, M., Siebers, N., Spohn, M., Vestergren, J., Vogts, A. and Leinweber, P.: Innovative methods in soil phosphorus research: A review, *J. Plant Nutr. Soil Sci.*, 178(1), 43–88, doi:10.1002/jpln.201400327, 2015.
- 915 Kulaev, I., Vagabov, V. and Kulakovskaya, T.: New aspects of inorganic polyphosphate metabolism and function, *J. Biosci. Bioeng.*, 88(2), 111–129, doi:10.1016/S1389-1723(99)80189-3, 1999.
- Lang, F., Krüger, J., Amelung, W., Willbold, S., Frossard, E., Bünemann, E. K., Bauhus, J., Nitschke, R., Kandeler, E., Marhan, S., Schulz, S., Bergkemper, F., Schloter, M., Luster, J., Guggisberg, F., Kaiser, K., Mikutta, R., Guggenberger, G., Polle, A., Pena, R., Priezel, J., Rodionov, A., Talkner, U., Meesenburg, H., von Wilpert, K., Hölscher, A., Dietrich, H. P. and Chmara, I.: Soil phosphorus supply controls P nutrition strategies of beech forest ecosystems in Central Europe, *Biogeochemistry*, 136(1), 5–29, doi:10.1007/s10533-017-0375-0, 2017.
- 920 Leonard, R. A., Knisel, W. G. and Still, D. A.: GLEAMS: Groundwater Loading Effects of Agricultural Management Systems, *Trans. ASAE*, 30(5), 1403–1418, doi:10.13031/2013.30578, 1987.
- 925 Leytem, A. B., Smith, D. R., Applegate, T. J. and Thacker, P. A.: The Influence of Manure Phytic Acid on Phosphorus Solubility in Calcareous Soils, *Soil Sci. Soc. Am. J.*, 70(5), 1629–1638, doi:10.2136/sssaj2006.0003, 2006.
- Li, L., Liang, X., Ye, Y., Zhao, Y., Zhang, Y., Jin, Y., Yuan, J. and Chen, Y.: Effects of repeated swine manure applications on legacy phosphorus and phosphomonoesterase activities in a paddy soil, *Biol. Fertil. Soils*, 51(2), 167–181, doi:10.1007/s00374-014-0956-1, 2015.
- 930 Li, M., Osaki, M., Rao, I. M. and Tadano, T.: Secretion of phytase from the roots of several plant species under phosphorus-deficient conditions, *Plant Soil*, 195(1), 161–169, doi:10.1023/A:1004264002524, 1997.
- Liang, Y. and Blake, R. E.: Oxygen isotope composition of phosphate in organic compounds: Isotope effects of extraction methods, *Org. Geochem.*, 37(10), 1263–1277, doi:10.1016/j.orggeochem.2006.03.009, 2006.
- Lilienfein, J., Qualls, R. G., Uselman, S. M. and Bridgman, S. D.: Adsorption of Dissolved Organic and Inorganic Phosphorus in Soils of a Weathering Chronosequence, *Soil Sci. Soc. Am. J.*, 68(2), 620–628, doi:10.2136/sssaj2004.6200, 2004.
- 935 Lima, J. A., Nahas, E. and Gomes, A. C.: Microbial populations and activities in sewage sludge and phosphate fertilizer-amended soil, *Appl. Soil Ecol.*, 4(1), 75–82, doi:10.1016/0929-1393(96)00094-7, 1996.
- Limousin, G., Gaudet, J. P., Charlet, L., Szenknect, S., Barthès, V. and Krimissa, M.: Sorption isotherms: A review on physical bases, modeling and measurement, *Appl. Geochemistry*, 22(2), 249–275, doi:10.1016/j.apgeochem.2006.09.010, 2007.
- 940 Lung, S. C. and Lim, B. L.: Assimilation of phytate-phosphorus by the extracellular phytase activity of tobacco (*Nicotiana*

tabacum) is affected by the availability of soluble phytate, *Plant Soil*, 279(1–2), 187–199, doi:10.1007/s11104-005-1009-1, 2006.

- Lung, S. C., Chan, W. L., Yip, W., Wang, L., Yeung, E. C. and Lim, B. L.: Secretion of beta-propeller phytase from tobacco and *Arabidopsis* roots enhances phosphorus utilization, *Plant Sci.*, 169(2), 341–349, doi:10.1016/j.plantsci.2005.03.006, 2005.
- 945 Maguire, R. O. and Sims, J. T.: Measuring Agronomic and Environmental Soil Phosphorus Saturation and Predicting Phosphorus Leaching with Mehlich 3, *Soil Sci. Soc. Am. J.*, 66(6), 2033–2039, doi:10.2136/sssaj2002.2033, 2002.
- Manzoni, S., Jackson, R. B., Trofymow, J. A. and Porporato, A.: The Global Stoichiometry of Litter Nitrogen Mineralization, *Science* (80-), 321(5889), 684–686, doi:10.1126/science.1159792, 2008.
- Manzoni, S., Trofymow, J. A., Jackson, R. B. and Porporato, A.: Stoichiometric controls on carbon, nitrogen, and phosphorus
950 dynamics in decomposing litter, *Ecol. Monogr.*, 80(1), 89–106, doi:10.1890/09-0179.1, 2010.
- Margalef, O., Sardans, J., Fernández-Martínez, M., Molowny-Horas, R., Janssens, I. A., Ciais, P., Goll, D., Richter, A., Obersteiner, M., Asensio, D. and Peñuelas, J.: Global patterns of phosphatase activity in natural soils, *Sci. Rep.*, 7(1), 1–13, doi:10.1038/s41598-017-01418-8, 2017.
- Marklein, A. R. and Houlton, B. Z.: Nitrogen inputs accelerate phosphorus cycling rates across a wide variety of terrestrial
955 ecosystems, *New Phytol.*, 193(3), 696–704, doi:10.1111/j.1469-8137.2011.03967.x, 2012.
- Marklein, A. R., Winbourne, J. B., Enders, S. K., Gonzalez, D. J. X., van Huysen, T. L., Izquierdo, J. E., Light, D. R., Liptzin, D., Miller, K. E., Morford, S. L., Norton, R. A. and Houlton, B. Z.: Mineralization ratios of nitrogen and phosphorus from decomposing litter in temperate versus tropical forests, *Glob. Ecol. Biogeogr.*, 25(3), 335–346, doi:10.1111/geb.12414, 2016.
- 960 Mazzilli, S. R., Kemanian, A. R., Ernst, O. R., Jackson, R. B. and Piñeiro, G.: Priming of soil organic carbon decomposition induced by corn compared to soybean crops, *Soil Biol. Biochem.*, 75, 273–281, doi:10.1016/j.soilbio.2014.04.005, 2014.
- McDowell, R. W., Cade-Menun, B. and Stewart, I.: Organic phosphorus speciation and pedogenesis: Analysis by solution ³¹P nuclear magnetic resonance spectroscopy, *Eur. J. Soil Sci.*, 58(6), 1348–1357, doi:10.1111/j.1365-2389.2007.00933.x, 2007.
- 965 McGechan, M. B. and Lewis, D. R.: Sorption of phosphorus by soil, part 1: Principles, equations and models, *Biosyst. Eng.*, 82(1), 1–24, doi:10.1006/bioe.2002.0054, 2002.
- McGill, W. B. and Cole, C. V.: Comparative aspects of cycling of organic C, N, S and P through soil organic matter, *Geoderma*, 26(4), 267–286, doi:10.1016/0016-7061(81)90024-0, 1981.
- McKercher, R. B. and Anderson, G.: Organic phosphate sorption by neutral and basic soils, *Commun. Soil Sci. Plant Anal.*,
970 20(7–8), 723–732, doi:10.1080/00103628909368112, 1989.
- McLaughlin, M. J., McBeath, T. M., Smernik, R., Stacey, S. P., Ajiboye, B. and Guppy, C.: The chemical nature of P accumulation in agricultural soils-implications for fertiliser management and design: An Australian perspective, *Plant Soil*, 349(1–2), 69–87, doi:10.1007/s11104-011-0907-7, 2011.
- Menezes-Blackburn, D., Zhang, H., Stutter, M., Giles, C. D., Darch, T., George, T. S., Shand, C., Lumsdon, D., Blackwell, M.,
975 Wearing, C., Cooper, P., Wendler, R., Brown, L. and Haygarth, P. M.: A Holistic Approach to Understanding the Desorption of Phosphorus in Soils, *Environ. Sci. Technol.*, 50(7), 3371–3381, doi:10.1021/acs.est.5b05395, 2016.
- Moller, A., Kaiser, K., Amelung, W., Niamskul, C., Udomsri, S., Puthawong, M., Haumaier, L. and Zech, W.: Forms of organic C and P extracted from tropical soils as assessed by liquid-state ¹³C- and ³¹P-NMR spectroscopy, *Aust. J. Soil Res.*, 38(5), 1017–1035, doi:10.1071/SR99111, 2000.
- 980 Mooshammer, M., Wanek, W., Zechmeister-Boltenstern, S. and Richter, A.: Stoichiometric imbalances between terrestrial

decomposer communities and their resources: Mechanisms and implications of microbial adaptations to their resources, *Front. Microbiol.*, 5(FEB), 1–10, doi:10.3389/fmicb.2014.00022, 2014.

Moscatelli, M. C., Lagomarsino, A., De Angelis, P. and Grego, S.: Seasonality of soil biological properties in a poplar plantation growing under elevated atmospheric CO₂, *Appl. Soil Ecol.*, 30(3), 162–173, doi:10.1016/j.apsoil.2005.02.008, 2005.

985 Mullaney, E. J. and Ullah, A. H. J.: Phytases: Attributes, catalytic mechanisms and applications, in *Inositol Phosphates: Linking Agriculture and the Environment*, edited by B. L. Turner, A. E. Richardson, and E. J. Mullaney, pp. 97–110, CAB International, Wallingford., 2007.

Nannipieri, P., Johnson, R. L. and Paul, E. A.: Criteria for measurement of microbial growth and activity in soil, *Soil Biol. Biochem.*, 10(3), 223–229, doi:10.1016/0038-0717(78)90100-1, 1978.

990 Nannipieri, P., Giagnoni, L., Landi, L. and Renella, G.: Role of Phosphatase Enzymes in Soil, in *Phosphorus in action: Biological processes in soil phosphorus cycling*, pp. 215–243, Springer, Heidelberg., 2011.

Oburger, E., Jones, D. L. and Wenzel, W. W.: Phosphorus saturation and pH differentially regulate the efficiency of organic acid anion-mediated P solubilization mechanisms in soil, *Plant Soil*, 341(1–2), 363–382, doi:10.1007/s11104-010-0650-5, 2011.

995 Oehl, F., Frossard, E., Fliessbach, A., Dubois, D. and Oberson, A.: Basal organic phosphorus mineralization in soils under different farming systems, *Soil Biol. Biochem.*, 36(4), 667–675, doi:10.1016/j.soilbio.2003.12.010, 2004.

Ognalaga, M., Frossard, E. and Thomas, F.: Glucose-1-phosphate and Myo-inositol Hexaphosphate Adsorption Mechanisms on Goethite, *Soil Sci. Soc. Am. J.*, 58(2), 332–337, doi:10.2136/sssaj1994.03615995005800020011x, 1994.

1000 Ohno, T. and Crannell, B. S.: Green and Animal Manure-Derived Dissolved Organic Matter Effects on Phosphorus Sorption, *J. Environ. Qual.*, 25(5), 1137–1143, doi:10.2134/jeq1996.00472425002500050029x, 1996.

Okajima, H., Kubota, H. and Sakuma, T.: Hysteresis in the phosphorus sorption and desorption processes of soils, *Soil Sci. Plant Nutr.*, 29(3), 271–283, doi:10.1080/00380768.1983.10434628, 1983.

Olander, L. P. and Vitousek, P. M.: Regulation of soil phosphatase and chitinase activity by N and P availability, *Biogeochemistry*, 49(2), 175–190, doi:10.1023/A:1006316117817, 2000.

1005 Ozanne, P. G.: Phosphate Nutrition of Plants—a General Treatise, in *The Role of Phosphorus in Agriculture*, pp. 559–589, ASA, CSSA, and SSSA, Madison, WI., 1980.

Patel, K. J., Singh, A. K., Nareshkumar, G. and Archana, G.: Organic-acid-producing, phytate-mineralizing rhizobacteria and their effect on growth of pigeon pea (*Cajanus cajan*), *Appl. Soil Ecol.*, 44(3), 252–261, doi:10.1016/j.apsoil.2010.01.002, 2010.

1010 Pierzynski, G. M.: The chemistry and mineralogy of phosphorus in excessively fertilized soils, *Crit. Rev. Environ. Control*, 21(3–4), 265–295, doi:10.1080/10643389109388418, 1991.

Pistocchi, C., Mészáros, É., Tamburini, F., Frossard, E. and Bünemann, E. K.: Biological processes dominate phosphorus dynamics under low phosphorus availability in organic horizons of temperate forest soils, *Soil Biol. Biochem.*, 126(April), 64–75, doi:10.1016/j.soilbio.2018.08.013, 2018.

1015 Pravia, M. V., Kemanian, A. R., Terra, J. A., Shi, Y., Macedo, I. and Goslee, S.: Soil carbon saturation, productivity, and carbon and nitrogen cycling in crop-pasture rotations, *Agric. Syst.*, 171(January), 13–22, doi:10.1016/j.agry.2018.11.001, 2019.

Quiquampoix, H. and Mousain, D.: Enzymatic Hydrolysis of Organic Phosphorus, in *Organic Phosphorus in the environment*, edited by B. L. Turner, E. Frossard, and D. S. Baldwin, pp. 89–112, CAB International, Wallingford. [online] Available from: <http://www.cabi.org/cabebooks/ebook/20043210888>, 2005.

1020 Radcliffe, D. E., Freer, J. and Schoumans, O.: Diffuse phosphorus models in the United States and Europe: their usages, scales,

and uncertainties., *J. Environ. Qual.*, 38(5), 1956–1967, doi:10.2134/jeq2008.0060, 2009.

Radcliffe, D. E., Reid, D. K., Blombäck, K., Bolster, C. H., Collick, A. S., Easton, Z. M., Francesconi, W., Fuka, D. R., Johnsson, H., King, K., Larsbo, M., Youssef, M. A., Mulkey, A. S., Nelson, N. O., Persson, K., Ramirez-Avila, J. J., Schmieder, F. and Smith, D. R.: Applicability of Models to Predict Phosphorus Losses in Drained Fields: A Review, *J. Environ. Qual.*, 44(2), 614–628, doi:10.2134/jeq2014.05.0220, 2015.

Reddy, K. R., Overcash, M. R., Khaleel, R. and Westerman, P. W.: Phosphorus adsorption-desorption characteristics of two soils utilized for disposal of animal wastes, *J. Environ. Qual.*, 9(1), 86–92, doi:10.2134/jeq1980.00472425000900010020x, 1980.

Reed, S. C., Yang, X. and Thornton, P. E.: Incorporating phosphorus cycling into global modeling efforts: A worthwhile, tractable endeavor, *New Phytol.*, 208(2), 324–329, doi:10.1111/nph.13521, 2015.

Regelink, I. C., Weng, L., Lair, G. J. and Comans, R. N. J.: Adsorption of phosphate and organic matter on metal (hydr)oxides in arable and forest soil: A mechanistic modelling study, *Eur. J. Soil Sci.*, 66(5), 867–875, doi:10.1111/ejss.12285, 2015.

Richardson, A. E. and Simpson, R. J.: Soil Microorganisms Mediating Phosphorus Availability, *Plant Physiol.*, 156(3), 989–996, doi:10.1104/pp.111.175448, 2011.

Richardson, A. E., Hadobas, P. A. and Hayes, J. E.: Acid phosphomonoesterase and phytase activities of wheat (*Triticum aestivum* L.) roots and utilization of organic phosphorus substrates by seedlings grown in sterile culture, *Plant, Cell Environ.*, 23(4), 397–405, doi:10.1046/j.1365-3040.2000.00557.x, 2000.

Richardson, A. E., Hadobas, P. A. and Hayes, J. E.: Extracellular secretion of *Aspergillus* phytase from *Arabidopsis* roots enables plants to obtain phosphorus from phytate, *Plant J.*, 25(6), 641–649, doi:10.1046/j.1365-313X.2001.00998.x, 2001.

Richardson, A. E., Barea, J. M., McNeill, A. M. and Prigent-Combaret, C.: Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms, *Plant Soil*, 321(1–2), 305–339, doi:10.1007/s11104-009-9895-2, 2009a.

Richardson, A. E., Hocking, P. J., Simpson, R. J. and George, T. S.: Plant Mechanisms to Optimise Access to Soil Phosphorus, *Crop Pasture Sci.*, 60(2), 124–143, doi:10.1071/CP07125, 2009b.

Richter, D. D., Allen, H. L., Li, J., Markewitz, D. and Raikes, J.: Bioavailability of slowly cycling soil phosphorus: Major restructuring of soil P fractions over four decades in an aggrading forest, *Oecologia*, 150(2), 259–271, doi:10.1007/s00442-006-0510-4, 2006.

Roberts, K., Defforey, D., Turner, B. L., Condron, L. M., Peek, S., Silva, S., Kendall, C. and Paytan, A.: Oxygen isotopes of phosphate and soil phosphorus cycling across a 6500year chronosequence under lowland temperate rainforest, *Geoderma*, 257–258, 14–21, doi:10.1016/j.geoderma.2015.04.010, 2015.

Rojo, M. J., Carcedo, S. G. and Mateos, M. P.: Distribution and characterization of phosphatase and organic phosphorus in soil fractions, *Soil Biol. Biochem.*, 22(2), 169–174, doi:10.1016/0038-0717(90)90082-B, 1990.

Schimel, J. P. and Weintraub, M. N.: The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: A theoretical model, *Soil Biol. Biochem.*, 35(4), 549–563, doi:10.1016/S0038-0717(03)00015-4, 2003.

Shang, C., Huang, P. M. and Stewart, J. W. B.: Kinetics of Adsorption of Organic and Inorganic Phosphates by Short-Range Ordered Precipitate of Aluminum, *Can. J. Soil Sci.*, 70(3), 461–470, doi:10.4141/cjss90-045, 1990.

Shang, C., Stewart, J. W. B. and Huang, P. M.: pH effect on kinetics of adsorption of organic and inorganic phosphates by short-range ordered aluminum and iron precipitates, *Geoderma*, 53(1–2), 1–14, doi:10.1016/0016-7061(92)90017-2, 1992.

Siebers, N., Bauke, S. L., Tamburini, F. and Amelung, W.: Short-term impacts of forest clear-cut on P accessibility in soil microaggregates: An oxygen isotope study, *Geoderma*, 315, 59–64, doi:10.1016/j.geoderma.2017.11.024, 2018.

- Sinsabaugh, R. L., Antibus, R. K., Linkins, A. E., McClaugherty, C. A., Rayburn, L., Repert, D. and Weiland, T.: Wood Decomposition: Nitrogen and Phosphorus Dynamics in Relation to Extracellular Enzyme Activity, *Ecology*, 74(5), 1586–1593, doi:10.2307/1940086, 1993.
- 1065 Sinsabaugh, R. L., Hill, B. H. and Follstad Shah, J. J.: Ecoenzymatic stoichiometry of microbial organic nutrient acquisition in soil and sediment, *Nature*, 462(7274), 795–798, doi:10.1038/nature08632, 2009.
- Six, J., Conant, R. ., Paul, E. . and Paustian, K.: Stabilization mechanisms of soil organic matter: Implications for C-saturatin of soils, *Plant Soil*, 241, 155–176, doi:10.1023/A:1016125726789, 2002.
- Smeck, N. E.: Phosphorus dynamics in soils and landscapes, *Geoderma*, 36(3–4), 185–199, doi:10.1016/0016-7061(85)90001-1, 1985.
- 1070 Smernik, R. J. and Dougherty, W. J.: Identification of Phytate in Phosphorus-31 Nuclear Magnetic Resonance Spectra: The Need for Spiking, *Soil Sci. Soc. Am. J.*, 71(3), 1045–1050, doi:10.2136/sssaj2006.0295, 2007.
- Speir, T. W. and Cowling, J. C.: Phosphatase activities of pasture plants and soils: Relationship with plant productivity and soil P fertility indices, *Biol. Fertil. Soils*, 12(3), 189–194, doi:10.1007/BF00337200, 1991.
- 1075 Spiers, G. A. and McGill, W. B.: Effects of phosphorus addition and energy supply on acid phosphatase production and activity in soils, *Soil Biol. Biochem.*, 11(1), 3–8, doi:10.1016/0038-0717(79)90110-X, 1979.
- Spohn, M. and Kuzyakov, Y.: Phosphorus mineralization can be driven by microbial need for carbon, *Soil Biol. Biochem.*, 61, 69–75, doi:10.1016/j.soilbio.2013.02.013, 2013.
- Spohn, M., Ermak, A. and Kuzyakov, Y.: Microbial gross organic phosphorus mineralization can be stimulated by root exudates - A 33P isotopic dilution study, *Soil Biol. Biochem.*, 65, 254–263, doi:10.1016/j.soilbio.2013.05.028, 2013.
- 1080 Spohn, M., Treichel, N. S., Cormann, M., Schloter, M. and Fischer, D.: Distribution of phosphatase activity and various bacterial phyla in the rhizosphere of *Hordeum vulgare* L. depending on P availability, *Soil Biol. Biochem.*, 89, 44–51, doi:10.1016/j.soilbio.2015.06.018, 2015.
- Staunton, S. and Leprince, F.: Effect of pH and some organic anions on the solubility of soil phosphate: Implications for P bioavailability, *Eur. J. Soil Sci.*, 47(2), 231–239, doi:10.1111/j.1365-2389.1996.tb01394.x, 1996.
- 1085 Steenbergh, A. K., Bodelier, P. L. E., Hoogveld, H. L., Slomp, C. P. and Laanbroek, H. J.: Phosphatases relieve carbon limitation of microbial activity in Baltic Sea sediments along a redox-gradient, *Limnol. Oceanogr.*, 56(6), 2018–2026, doi:10.4319/lo.2011.56.6.2018, 2011.
- Stewart, J. W. B. and Tiessen, H.: Dynamics of soil organic phosphorus, *Biogeochemistry*, 4(1), 41–60, doi:10.1007/BF02187361, 1987.
- 1090 Sun, M. and Jaisi, D. P.: Distribution of inositol phosphates in animal feed grains and excreta: distinctions among isomers and phosphate oxygen isotope compositions, *Plant Soil*, 430(1–2), 291–305, doi:10.1007/s11104-018-3723-5, 2018.
- Tamburini, F., Bernasconi, S. M., Angert, A., Weiner, T. and Frossard, E.: A method for the analysis of the $\delta^{18}\text{O}$ of inorganic phosphate extracted from soils with HCl, *Eur. J. Soil Sci.*, 61(6), 1025–1032, doi:10.1111/j.1365-2389.2010.01290.x, 2010.
- 1095 Tamburini, F., Pfahler, V., von Sperber, C., Frossard, E. and Bernasconi, S. M.: Oxygen Isotopes for Unraveling Phosphorus Transformations in the Soil–Plant System: A Review, *Soil Sci. Soc. Am. J.*, 78(1), 38–46, doi:10.2136/sssaj2013.05.0186dgs, 2014.
- Tamburini, F., Pistocchi, C., Helfenstein, J. and Frossard, E.: A method to analyse the isotopic composition of oxygen associated with organic phosphorus in soil and plant material, *Eur. J. Soil Sci.*, 69(5), 816–826, doi:10.1111/ejss.12693, 2018.
- 1100 Tang, J., Leung, A., Leung, C. and Lim, B. L.: Hydrolysis of precipitated phytate by three distinct families of phytases, *Soil Biol.*

Biochem., 38(6), 1316–1324, doi:10.1016/j.soilbio.2005.08.021, 2006.

Tarafdar, J. C. and Claassen, N.: Organic phosphorus utilization by wheat plants under sterile conditions, *Biol. Fertil. Soils*, 39(1), 25–29, doi:10.1007/s00374-003-0671-9, 2003.

1105 Tarafdar, J. C. and Jungk, A.: Phosphatase activity in the rhizosphere and its relation to the depletion of soil organic phosphorus, *Biol. Fertil. Soils*, 3(4), 199–204, doi:10.1007/BF00640630, 1987.

Thompson, L. M., Black, C. A. and Zoellner, J. A.: Occurrence and mineralization of organic phosphorus in soils, with particular reference to associations with nitrogen, carbon, and pH, *Soil Sci.*, 77(3), 185–196, doi:10.1097/00010694-195403000-00002, 1954.

1110 Thum, T., Caldararu, S., Engel, J., Kern, M., Pallandt, M., Schnur, R., Yu, L. and Zaehle, S.: A new terrestrial biosphere model with coupled carbon, nitrogen, and phosphorus cycles (QUINCY v1.0; revision 1772), *Geosci. Model Dev. Discuss.*, (12), 4781–4802, doi:10.5194/gmd-2019-49, 2019.

Tiessen, H. and Moir, J. O.: Characterization of available P by sequential extraction, in *Soil Sampling and Methods of Analysis*, edited by M. R. Carter and E. G. Gregorich, pp. 75–86, Taylor & Francis, Boca Raton, FL., 1993.

1115 Tiessen, H., Stewart, J. W. B. and Cole, C. V.: Pathways of phosphorus transformations in soils of differing pedogenesis, *Soil Sci. Soc. Am. J.*, 48(4), 853–858, doi:10.2136/sssaj1984.03615995004800040031x, 1984.

Tipping, E., Somerville, C. J. and Luster, J.: The C:N:P:S stoichiometry of soil organic matter, *Biogeochemistry*, 130(1–2), 117–131, doi:10.1007/s10533-016-0247-z, 2016.

Trasar-Cepeda, M. C., Carballas, T., Gil-Sotres, F. and de Blas, E.: Liming and the phosphatase activity and mineralization of phosphorus in an andic soil, *Soil Biol. Biochem.*, 23(3), 209–215, doi:10.1016/0038-0717(91)90054-N, 1991.

1120 Turner, B. L.: Resource partitioning for soil phosphorus: A hypothesis, *J. Ecol.*, 96(4), 698–702, doi:10.1111/j.1365-2745.2008.01384.x, 2008.

Turner, B. L. and Joseph Wright, S.: The response of microbial biomass and hydrolytic enzymes to a decade of nitrogen, phosphorus, and potassium addition in a lowland tropical rain forest, *Biogeochemistry*, 117(1), 115–130, doi:10.1007/s10533-013-9848-y, 2014.

1125 Turner, B. L., Papházy, M. J., Haygarth, P. M. and Mckelvie, I. D.: Inositol phosphates in the environment, *Philos. Trans. R. Soc. London. Ser. B Biol. Sci.*, 357(1420), 449–469, doi:10.1098/rstb.2001.0837, 2002.

Turner, B. L., Condrón, L. M., Richardson, S. J., Peltzer, D. A. and Allison, V. J.: Soil Organic Phosphorus Transformations During Pedogenesis, *Ecosystems*, 10(7), 1166–1181, doi:10.1007/s10021-007-9086-z, 2007.

1130 Vadas, P. A., Krogstad, T. and Sharpley, A. N.: Modeling Phosphorus Transfer between Labile and Nonlabile Soil Pools, *Soil Sci. Soc. Am. J.*, 70(3), 736–743, doi:10.2136/sssaj2005.0067, 2006.

Vincent, A. G., Turner, B. L. and Tanner, E. V. J.: Soil organic phosphorus dynamics following perturbation of litter cycling in a tropical moist forest, *Eur. J. Soil Sci.*, 61(1), 48–57, doi:10.1111/j.1365-2389.2009.01200.x, 2010.

Walbridge, M. R., Richardson, C. J. and Swank, W. T.: Vertical Distribution of Biological and Geochemical Phosphorus Subcycles in two Southern Appalachian Forest Soils, *Biogeochemistry*, 13(1), 61–85 [online] Available from:

1135 <http://www.jstor.org/stable/1468576> 5Cnhttp://www.jstor.org/stable/1468576?seq=1&cid=pdf-reference#references_tab_contents 5Cn<http://about.jstor.org/terms> 5Cn%3CGo to ISI%3E://A1991FZ49500003, 1991.

Wang, J., Wu, Y., Zhou, J., Bing, H. and Sun, H.: Carbon demand drives microbial mineralization of organic phosphorus during the early stage of soil development, *Biol. Fertil. Soils*, 52(6), 825–839, doi:10.1007/s00374-016-1123-7, 2016.

1140 Wang, S., Jin, X., Zhao, H., Zhou, X. and Wu, F.: Effect of organic matter on the sorption of dissolved organic and inorganic phosphorus in lake sediments, *Colloids Surfaces A Physicochem. Eng. Asp.*, 297(1–3), 154–162,

doi:10.1016/j.colsurfa.2006.10.040, 2007.

Wang, Y. P., Law, R. M. and Pak, B.: A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere, *Biogeosciences*, 7(7), 2261–2282, doi:10.5194/bg-7-2261-2010, 2010.

1145 Wanner, B. L.: Phosphorus Assimilation and Control of the Phosphate Regulon, in *Escherichia coli and Salmonella typhimurium: Cellular and Molecular Biology*, vol. 1, pp. 1357–1381, American Society for Microbiology, Washington, DC., 1996.

Waring, B. G., Averill, C. and Hawkes, C. V.: Differences in fungal and bacterial physiology alter soil carbon and nitrogen cycling: Insights from meta-analysis and theoretical models, *Ecol. Lett.*, 16(7), 887–894, doi:10.1111/ele.12125, 2013.

1150 White, C. M., Kemanian, A. R. and Kaye, J. P.: Implications of carbon saturation model structures for simulated nitrogen mineralization dynamics, *Biogeosciences*, 11(23), 6725–6738, doi:10.5194/bg-11-6725-2014, 2014.

Wieder, W. R., Grandy, A. S., Kallenbach, C. M. and Bonan, G. B.: Integrating microbial physiology and physio-chemical principles in soils with the MIMICS (MIMicrobial-MINeral Carbon Stabilization) model, *Biogeosciences*, 11(14), 3899–3917, doi:10.5194/bg-11-3899-2014, 2014.

1155 Williams, C. and Steinbergs, A.: Sulphur and phosphorus in some Eastern Australian soils, *Aust. J. Agric. Res.*, 9(4), 483–491, doi:10.1071/AR9580483, 1958.

Xu, X., Thornton, P. E. and Post, W. M.: A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems, *Glob. Ecol. Biogeogr.*, 22(6), 737–749, doi:10.1111/geb.12029, 2013.

1160 Yan, Y., Li, W., Yang, J., Zheng, A., Liu, F., Feng, X. and Sparks, D. L.: Mechanism of myo-inositol hexakisphosphate sorption on amorphous aluminum hydroxide: Spectroscopic evidence for rapid surface precipitation, *Environ. Sci. Technol.*, 48(12), 6735–6742, doi:10.1021/es500996p, 2014.

Yang, X. and Post, W. M.: Phosphorus transformations as a function of pedogenesis: A synthesis of soil phosphorus data using Hedley fractionation method, *Biogeosciences*, 8(10), 2907–2916, doi:10.5194/bg-8-2907-2011, 2011.

Yang, X., Thornton, P. E., Ricciuto, D. M. and Post, W. M.: The role of phosphorus dynamics in tropical forests – a modeling study using CLM-CNP, *Biogeosciences*, 11(6), 1667–1681, doi:10.5194/bg-11-1667-2014, 2014.

1165 Yu, L., Zanchi, G., Akselsson, C., Wallander, H. and Belyazid, S.: Modeling the forest phosphorus nutrition in a southwestern Swedish forest site, *Ecol. Modell.*, 369, 88–100, doi:10.1016/j.ecolmodel.2017.12.018, 2018.

Yu, L., Ahrens, B., Wutzler, T., Schrupf, M. and Zaehle, S.: Jena Soil Model (JSM v1.0; Revision 1934): A microbial soil organic carbon model integrated with nitrogen and phosphorus processes, *Geosci. Model Dev.*, 13(2), 783–803, doi:10.5194/gmd-13-783-2020, 2020.

1170 Zechmeister-Boltenstern, S., Keiblinger, K. M., Mooshammer, M., Peñuelas, J., Richter, A., Sardans, J. and Wanek, W.: The application of ecological stoichiometry to plant–microbial–soil organic matter transformations, *Ecol. Monogr.*, 85(2), 133–155, doi:10.1890/14-0777.1, 2015.

van der Zee, S. E. A. T. M. and van Riemsdijk, W. H.: Model for Long-term Phosphate Reaction Kinetics in Soil, *J. Environ. Qual.*, 17(1), 35–41, doi:10.2134/jeq1988.00472425001700010005x, 1988.

1175 Zhou, Y., Boutton, T. W. and Wu, X. Ben: Soil phosphorus does not keep pace with soil carbon and nitrogen accumulation following woody encroachment, *Glob. Chang. Biol.*, 24(5), 1992–2007, doi:10.1111/gcb.14048, 2018.

Zhu, Q., Riley, W. J., Tang, J., Collier, N., Hoffman, F. M., Yang, X. and Bisht, G.: Representing Nitrogen, Phosphorus, and Carbon Interactions in the E3SM Land Model: Development and Global Benchmarking, *J. Adv. Model. Earth Syst.*, 11(7), 2238–2258, doi:10.1029/2018MS001571, 2019.

1180 Zohar, I., Shaviv, A., Klass, T., Roberts, K. and Paytan, A.: Method for the Analysis of Oxygen Isotopic Composition of Soil

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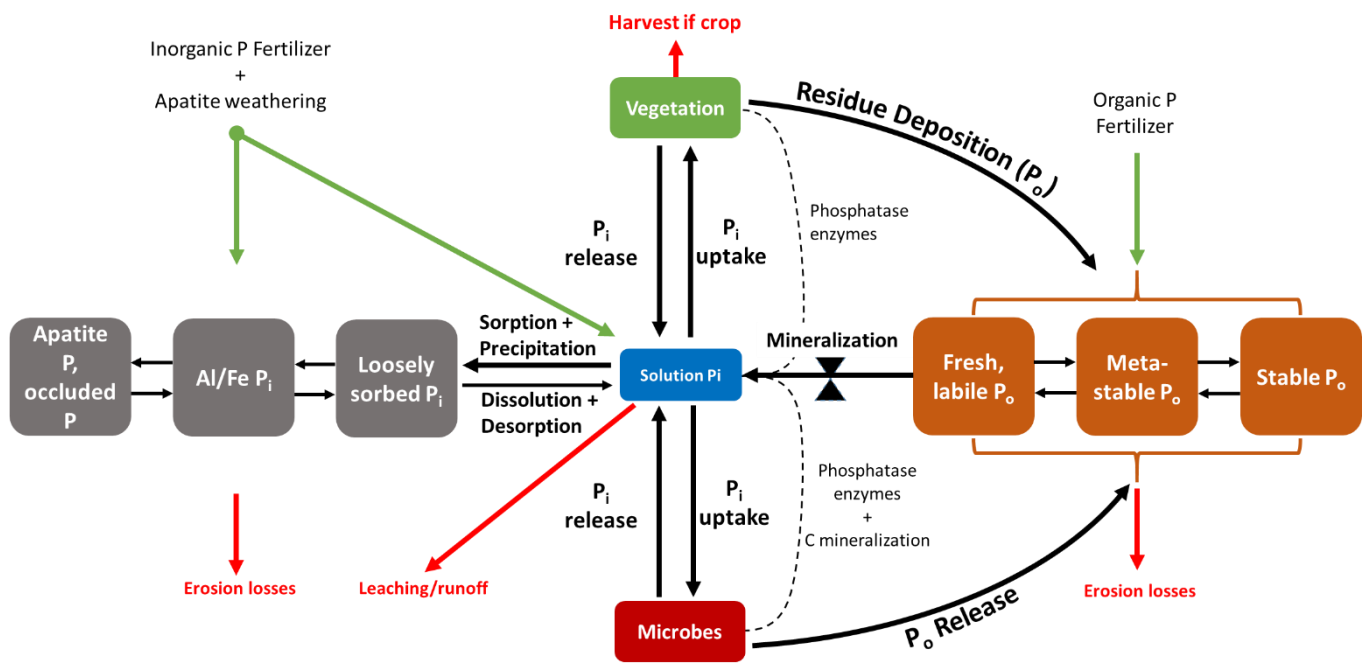
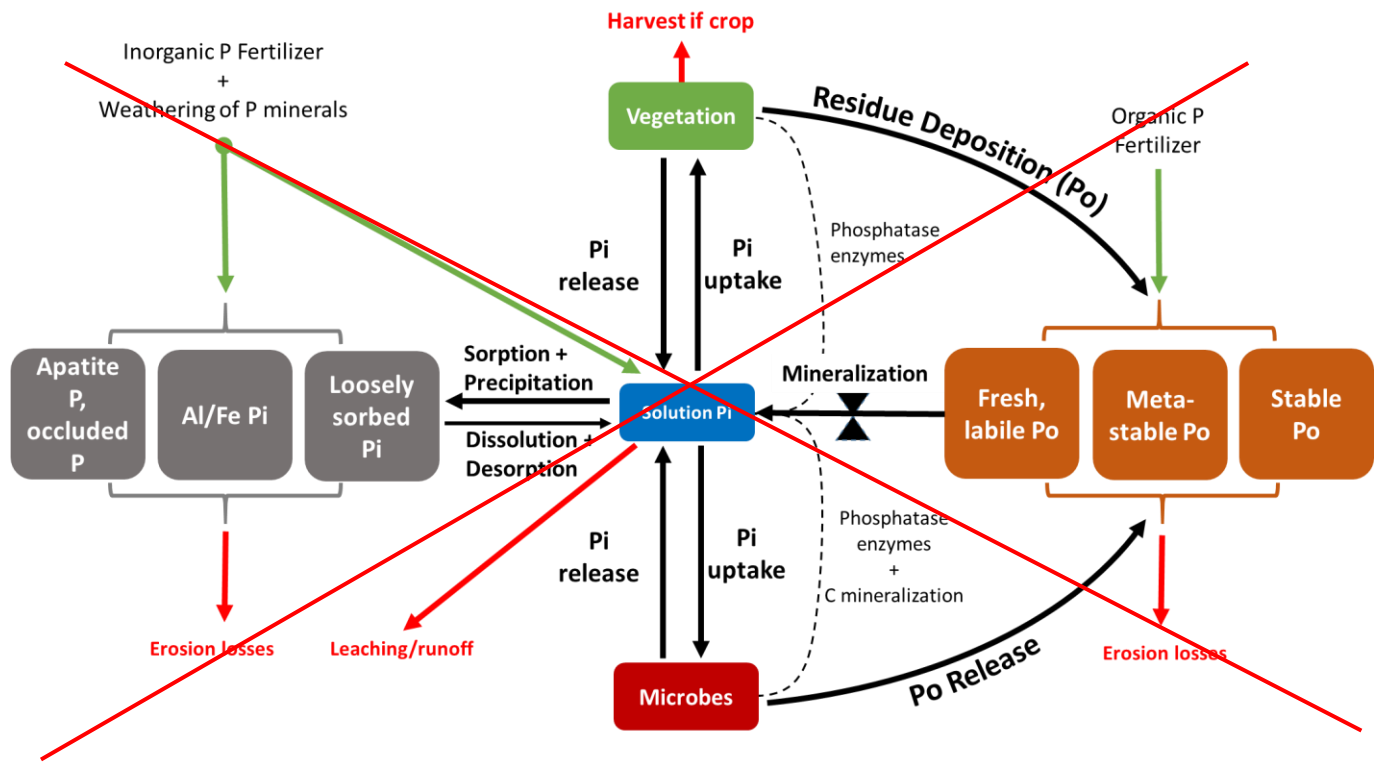


Figure 1. Conceptual diagram of the soil P cycle. P_i and P_o represent inorganic (gray) and organic (orange) phosphates, respectively. The P_i and P_o pools that are situated farthest from the depicted solution pool in this diagram are considered more stable. There are small amounts of organic P in 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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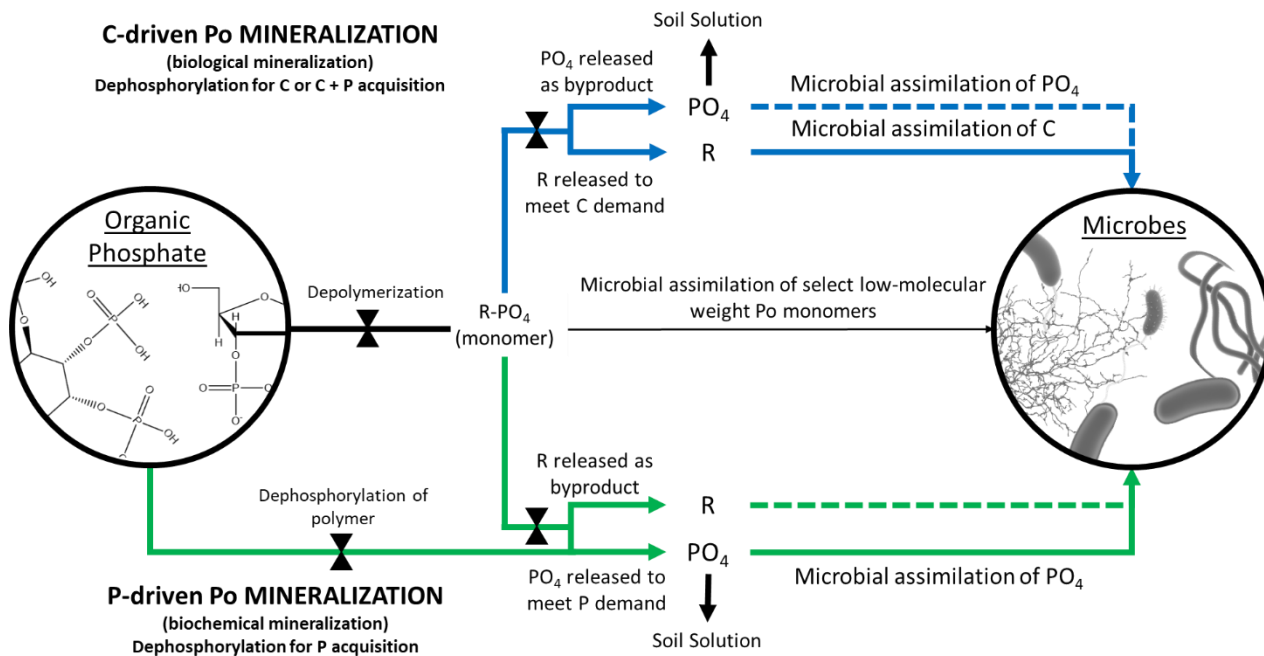


Figure 2. Conceptual diagram of C and P-driven Po mineralization. Because microorganisms can only directly uptake specific types of orthophosphate ester (Po) monomers directly (thin middle black arrow), the accessibility of Po is controlled by the action of phosphatase enzymes (indicated by bowties). 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 PO₄ 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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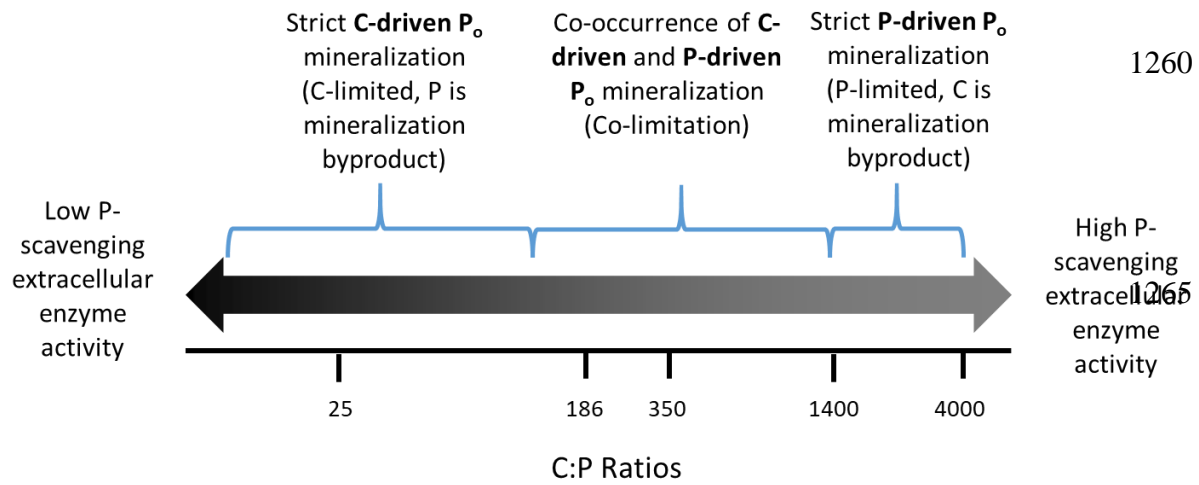
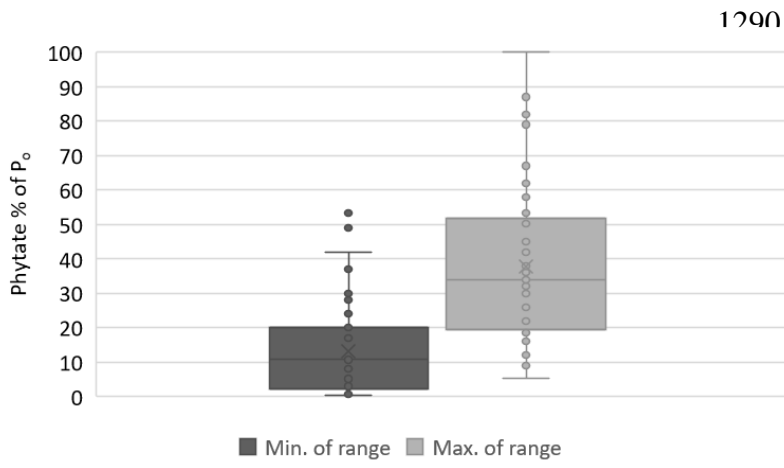


Figure 3. Hypothesis of stoichiometric controls on C-driven and P-driven P_o mineralization. The log-scaled numbers are C:P ratios taken from the literature that include stoichiometry of microbes, litter, soil, and critical ratios. The brackets represent where biological or biochemical mineralization 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-MB 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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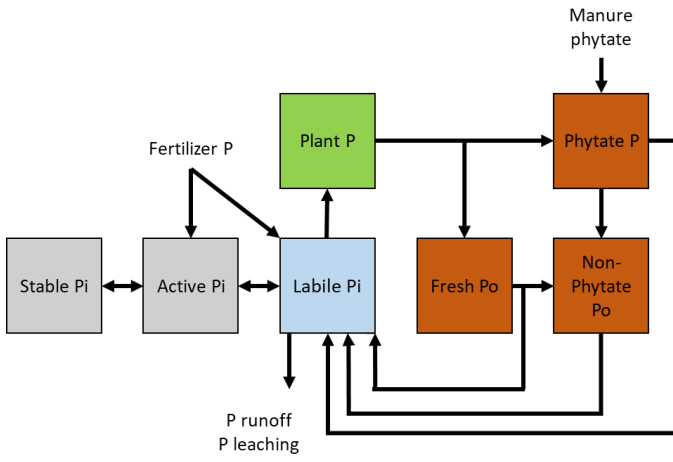


Figure 5: Simple conceptual diagram for modeling inorganic and organic phosphorus cycling, which includes an explicit phytate pool.

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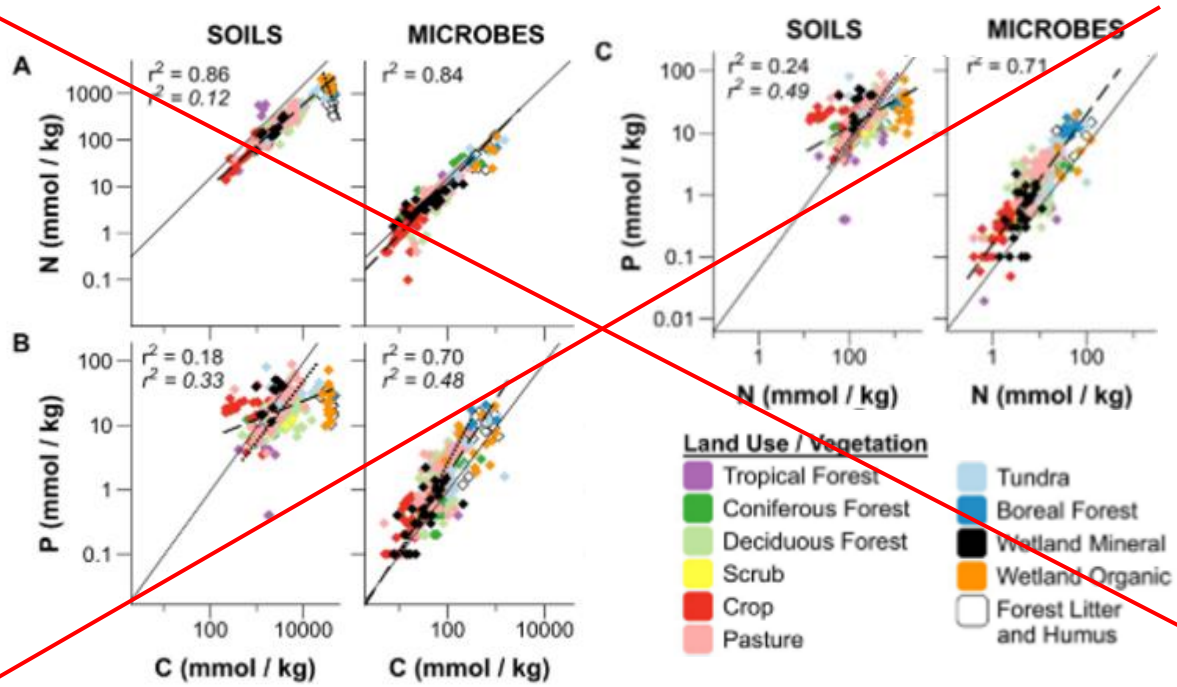


Figure 6. Regressions of C:N (A), C:P (B), and N:P (C) ratios in soils and the microbial biomass using a log₁₀ transformation. The dashed lines (standard font r²) represent the stoichiometric regressions for global soil or microbial biomass measurements, while the solid lines represent the Redfield (1958) ratio. Dotted lines are regressions (italicized r²) for specific habitats whose soil stoichiometry differed significantly from the others. Modified from Hartman and Richardson 2013.

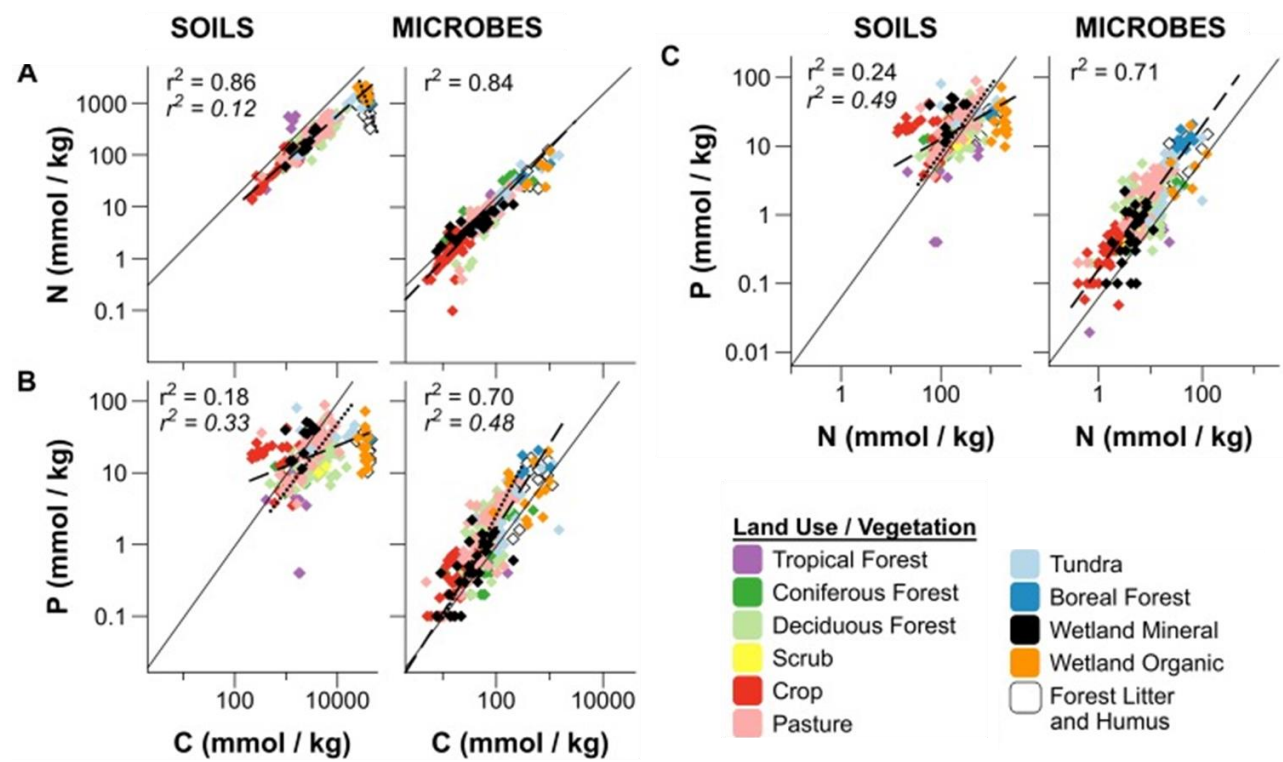


Figure 6. Regressions of C:N (A), C:P (B), and N:P (C) ratios in soils and the microbial biomass using a log₁₀ transformation. The dashed lines (standard font r²) represent the stoichiometric regressions for of global soil or microbial biomass stoichiometry measurements for all land use/vegetation types that do not differ significantly, while the solid lines represent the Redfield (1958) ratio. Dotted lines are regressions (italicized r²) for specific habitats whose soil stoichiometry differed significantly from the others. Modified from Hartman and Richardson 2013. 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	1405 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 1410

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 P_i 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 P_o would be included in the measurement, resulting in a higher % DPS than presented here.

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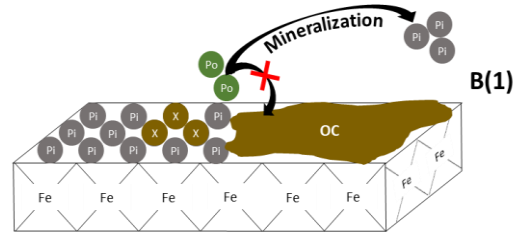
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C_o anion- P_i competitive sorption (A)



C_o saturation increases P_o mineralization (B)



Disparities in DPS (C)

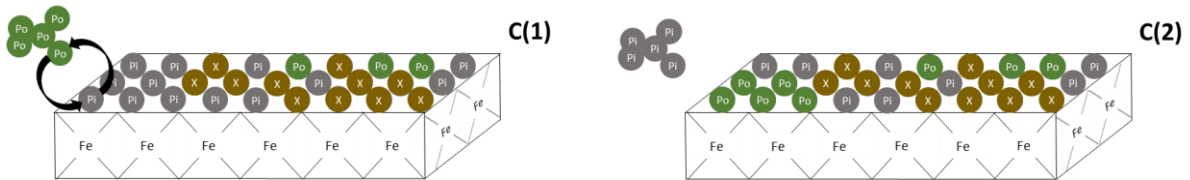


Figure 7. Conceptual depiction of P_i and P_o saturation dynamics. The green P_o bubbles are organic phosphate, the gray P_i bubbles are inorganic phosphate, and the brown “X” bubbles are non-P bearing organic and inorganic compounds. (A) represents the competitive sorption of non-P-bearing organic carbon (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 perceived 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	$\frac{C}{S} = \frac{C}{S_{max}} + \frac{1}{K_L \times S_{max}}$	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	$\frac{x}{m} = \frac{b_I K_I EPC}{1 + K_I EPC} + \frac{b_{II} K_{II} EPC}{1 + K_{II} EPC}$	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* CaCO₃ : calcium carbonate (%)
6	PSP: Slightly weathered soils	$PSP = -0.70 - 0.0043 * BS + 0.0034 * P_{il} + 0.11 * pH$	BS : base saturation (%) P_{il} : labile P (μg g ⁻¹ soil) pH
7	PSP: Highly weathered soils	$PSP = 0.038 - 0.047 * \ln\left(\frac{f_{clay}}{10}\right) + 0.045 * P_{il} - 0.053 * OC$	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)