ANNUAL REVIEWS

Annual Review of Ecology, Evolution, and Systematics

Terrestrial Phosphorus Cycling: Responses to Climatic Change

Duncan N.L. Menge,[1] Sian Kou-Giesbrecht,[2,3] Benton N. Taylor,[4,5] Palani R. Akana,[1] Ayanna Butler,[1] K.A. Carreras Pereira,[1] Savannah S. Cooley,[1] Vanessa M. Lau,[1] and Emma L. Lauterbach[1]

[1]Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, NY, USA; email: dm2972@columbia.edu

[2]Canadian Centre for Climate Modelling and Analysis, Environment and Climate Change Canada, Victoria, British Columbia, Canada

[3]Department of Earth and Environmental Sciences, Dalhousie University, Halifax, Nova Scotia, Canada

[4]Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, USA

[5]The Arnold Arboretum, Harvard University, Boston, Massachusetts, USA

Annu. Rev. Ecol. Evol. Syst. 2023. 54:429–49

First published as a Review in Advance on August 24, 2023

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

https://doi.org/10.1146/annurev-ecolsys-110421-102458

Keywords

forest, grassland, tundra, limitation, model, experiment

Abstract

Phosphorus (P) limits productivity in many ecosystems and has the potential to constrain the global carbon sink. The magnitude of these effects depends on how climate change and rising CO_2 affect P cycling. Some effects are well established. First, P limitation often constrains CO_2 fertilization, and rising CO_2 often exacerbates P limitation. Second, P limitation and P constraints to CO_2 fertilization are more common in warmer and wetter sites. Models that couple P cycling to vegetation generally capture these outcomes. However, due largely to differences between short-term and long-term dynamics, the patterns observed across climatic gradients do not necessarily indicate how climate change over years to decades will modify P limitation. These annual-to-decadal effects are not well understood. Furthermore, even for the well-understood patterns, much remains to be learned about the quantitative details, mechanisms, and drivers of variability. The interface between empirical and modeling work is particularly ripe for development.

INTRODUCTION

Phosphorus (P) is one of the most important nutrients in terrestrial ecosystems. It is essential to biology, from nucleic acids to cell walls to ATP (Smil 2000), and often limits primary productivity (Du et al. 2020). Unlike nitrogen (N), which has a functionally inexhaustible atmospheric pool, P primarily comes from rocks (Walker & Syers 1976), including the deposition of atmospheric dust. P also has more complex interactions with soil minerals (Weil & Brady 2017). Due to these and other differences, an independent consideration of the P cycle is critical for understanding how the terrestrial biosphere responds to a changing climate and elevated CO_2 (Reed et al. 2015). For example, CO_2 fertilization, in which rising atmospheric CO_2 stimulates plant growth, depends on sufficient P supply to support the increased growth (Wieder et al. 2015).

Historically, the paradigm has been that P limitation is most common in tropical regions. The reasoning was that more weathered soils have less P (Walker & Syers 1976, Crews et al. 1995), and more weathered soils are more common in the tropics (Vitousek 1984). However, many factors complicate this story. These factors include dust transport (which can replenish P supply) (Mahowald et al. 2008), plate tectonics and topography (which create newer soils) (Porder et al. 2007), wide variation in P content across rock types (Porder & Ramachandran 2013), and biological responses that mitigate P limitation (Treseder & Vitousek 2001, Vance et al. 2003, Lambers et al. 2012). There is increasingly clear evidence that P limitation is common in many tropical ecosystems (Cleveland et al. 2011, Quesada et al. 2012, Wright 2019, Cunha et al. 2022, Ellsworth et al. 2022), but P limitation also occurs in many extratropical regions (Fay et al. 2015, Ellsworth et al. 2017, Goswami et al. 2018). Overall, P limitation is globally relevant even if it is stronger at lower latitudes (Augusto et al. 2017, Du et al. 2020, Hou et al. 2021).

Any understanding of how P limitation might constrain future carbon (C) sequestration depends on understanding the effects of climate change and elevated CO_2 on the P cycle. If climate change and rising CO_2 increase P supply more than P demand, P limitation will be alleviated, facilitating future C capture in P-limited ecosystems. Alternatively, if P supply increases less than P demand, P limitation will constrain C sequestration. With the goal of understanding P constraints on future C sequestration, this review focuses on the effects of climatic change on P cycling in terrestrial ecosystems.

The scope of this review is as follows. We cover all terrestrial biomes except for agricultural systems, in which nutrient availability is often managed by humans. We consider all aspects of P cycling, from inputs to within-system cycling to losses, with an eye toward limitation. Climatic change involves many anthropogenic effects of interest, but we focus on the ones that are most directly related to CO_2 or climate and that have enough work to review: changing precipitation, rising temperature, and rising atmospheric CO_2 concentrations but not extreme weather events, N deposition (Peñuelas et al. 2013, Deng et al. 2017), land use change, changing biodiversity, or direct human effects on phosphorus cycling (Smil 2000). We recognize that rising CO_2 is not strictly a component of climate change, but we include it due to its critical role as a driver of climate change. We focus on single-direction effects of climate change and elevated CO_2 on P cycling, although we note that feedbacks are interesting and important. We direct interested readers elsewhere for reviews on CNP modeling (Achat et al. 2016) and the effects of climate change on P in agricultural ecosystems (Forber et al. 2018), which are important on a global scale (Lun et al. 2018).

We structure this review as follows. First, we describe epistemological issues that help make sense of the relevant research. Next, we delve into how climate change and elevated CO_2 affect P inputs, within-system P cycling, P losses, and P limitation, introducing each topic, reviewing evidence, and describing how well current models reflect empirical understanding. There are far

too many studies to cover completely, so we focus on particularly noteworthy studies that cover a variety of biomes and represent the dominant trends in the literature. To constrain our discussion of models, we focus on the six TRENDY terrestrial biosphere models (for descriptions and terminology for different types of models, see **Table 1** and Fisher et al. 2014) that include a P cycle. Many other types of models include interesting aspects of P cycling (see Achat et al. 2016, table 1), but we focus on the TRENDY models because they are the ones that contribute to the Global Carbon Budget (Friedlingstein et al. 2022) and thus that could be used to understand P constraints to CO_2 sequestration on a global scale. Finally, we conclude with critical unknowns and future directions.

EPISTEMOLOGICAL CHALLENGES

There are many ways to study how climate change affects P cycling. Consider the question, How does increasing precipitation affect P inputs from rock weathering? One way to address this question is with a manipulative experiment: manipulate precipitation, then measure P weathering. There are challenges to this approach, however. Importantly, the timescale over which P inputs change might be too slow. Another way to address this question is with observations across a natural gradient. One could establish sites that vary in precipitation but are otherwise similar, then measure P inputs across these sites. Here, we highlight the contrasting information provided by these approaches, specifically with regard to short-term versus long-term dynamics.

For processes with characteristic timescales longer than a typical experiment, which include many processes in the P cycle (Helfenstein et al. 2018), experiments give short-term answers, whereas observations across gradients give long-term answers. Annoyingly, short- versus long-term answers can be diametrically opposite. Consider again our question, How does increasing precipitation affect P inputs from rock weathering? An experimental manipulation might show that precipitation increases weathering P inputs, whereas an observational gradient might show a decrease. Why? The manipulation increases the weathering rate from a rock P pool that starts at the same size as the control, whereas along the gradient, past weathering in the wetter sites had already depleted the rock P pool.

It is easy to illustrate this concept with a simple model (adapted from Menge et al. 2012). Let the pool of weatherable P in rock at time t be $W(t)$, and let it be weathered at the rate constant ψ. The change in weatherable rock is $\mathrm{d}W(t)/\mathrm{d}t = -\psi W(t)$, and the P input flux from weathering is $I(t) = \psi W(t)$. Solving the differential equation shows that the P input flux from weathering is $I(t) = \psi W(0)e^{-\psi t}$, where $W(0)$ is the initial ($t = 0$) amount of P in the rock. This equation describes how rock P weathering changes over time. The P input declines over time, from a maximum of $\psi W(0)$ at $t = 0$ to zero as t approaches infinity (**Figure 1*b***).

How does precipitation affect these dynamics, and how do manipulations versus observations give different answers? Precipitation is unlikely to affect the starting rock P content, $W(0)$, but it is likely to increase the weathering rate constant ψ such that $\psi_{\mathrm{wet}} > \psi_{\mathrm{dry}}$. Therefore, an experimental increase in precipitation increases P inputs at $t = 0$, $I(0)$, given that $I(0) = \psi W(0)$ and $\psi_{\mathrm{wet}} W(0) > \psi_{\mathrm{dry}} W(0)$ (**Figure 1*a***, *red line*; **Figure 1*b***, *left*). However, as we intuited earlier, the weathering P input flux will eventually be higher in drier sites than wetter sites. We can formalize this by taking the derivative of P inputs with respect to the weathering rate constant, which varies with precipitation as follows: $\mathrm{d}I(t) = \mathrm{d}\psi = (1 - \psi t)W(0)e^{-\psi t}$. A positive derivative means that the weathering P input increases with precipitation, and vice versa. Given that the weathering rate constant ψ and time t appear in the equation together, we can think about this equation across a chronosequence (varying time) or a climosequence (varying precipitation, and thus ψ). As shown above, precipitation stimulates P weathering at the initial time ($t = 0$) or at low precipitation

Table 1 Subset of the epistemological approaches used to study effects of climate and CO_2 on P cycling

Approach	Relevant timescale	Relevant spatial scale	Pros	Cons	Key examples
Empirical: field experiment	Months–low decades	Individual sites	Ability to simulate global changes in real ecosystems and pinpoint mechanisms	Small spatial scale Expensive Hard	Ellsworth et al. (2017) found that Eucalyptus growth did not respond to free-air CO_2 enrichment but did respond to P fertilization, implying that P might have constrained CO_2 fertilization. McLaren & Buckeridge (2021) found that long-term warming of arctic tundra had small or no effects on soil P cycling.
Empirical: controlled environment experiment	Months–years	Greenhouse or chamber	Ability to simulate global changes in a controlled manner and pinpoint mechanisms	Typically limited to small organisms Short timescale Small spatial scale	Studies included in Jiang et al. (2020) that manipulated CO_2 and P in factorial combination and found that P constrained seedling growth response to elevated CO_2.
Empirical: observations along natural gradient	Centuries–longer	Individual sites	Observe long-term effects in real ecosystems	Wrong timescale for climate change (see **Figure 1**) Hard to pinpoint mechanisms	Helfenstein et al. (2018) found, among other things, that arid 150,000-year-old soils had primary mineral P remaining, whereas humid soils of the same age had none remaining.
Empirical: meta-analysis of experiments	Months–low decades for the experimental component Centuries–longer for climatic differences across sites	Few sites–global	Span large spatial scale Aggregate studies that can test mechanisms Cheap	Cannot control methods used by published studies Methods likely differ Gloss over important nuances	Terrer et al. (2019) found that the fertilization effect of elevated CO_2 increased in sites with higher soil P availability for ectomycorrhizal plants, though not for arbuscular mycorrhizal plants.
Empirical: meta-analysis of observations	Centuries–longer	Few sites–global	Span large spatial scale Aggregate studies, consider many factors Often high sample size Cheap	Cannot control methods used by published studies Methods likely differ Gloss over important nuances Wrong timescale for climate change (see **Figure 1**)	Hou et al. (2018) found that, despite substantial variation, wetter and warmer sites had lower primary mineral P and lower labile P in soils.

(*Continued*)

Table 1 (*Continued*)

Approach	Relevant timescale	Relevant spatial scale	Pros	Cons	Key examples
Modeling: general	Whatever you want! Typically years–millennia	Individual ecosystem–global	Can run model experiments at timescales and spatial scales unattainable with experiments Can conduct manipulations that are not possible logistically or ethically	Not real	See examples of specific models below
Modeling: ecosystem model	Years–millennia	Individual ecosystem	Simpler means easier to understand model mechanisms	Less realism No interaction with surrounding systems No feedback to climate	Menge et al. (2012) found that limitation by P and N depends on different processes at different timescales: Preferential mineralization of P over N facilitates N limitation over decades–centuries, whereas P weathering facilitates P limitation over millennia, except where dust deposition is substantial.
Modeling: TBM and land model	Years–millennia	Individual site–global	Faster and cheaper to run than ESMs Larger scale and more realism than ecosystem models	No feedback to climate Harder to understand mechanisms than in ecosystem models	Goll et al. (2012), an early effort to model P at this scale, used JSBACH to suggest that P limitation will constrain C sequestration by 16% by 2100, even affecting high latitudes. They also pointed out the lack of information needed to accurately model soil P sorption and P mineralization.
Modeling: ESM (land model coupled to ocean and atmosphere models)	Years–millennia	Global	Includes feedback to climate, atmosphere, oceans	Slower and more expensive to run than TBMs/land models and ecosystem models Most difficult to understand mechanisms because of complexity	No studies that include P have been published yet, to our knowledge
Modeling: model inter-comparison	Years–millennia	Individual site–global	Compares across different models	Runs risk of model herding Difficult to infer mechanisms	Fleischer et al. (2019) used six separate models to estimate that P limitation would reduce C storage in response to elevated CO_2 by 50% in Amazonian rainforests.

Abbreviations: ESM, Earth system model; TBM, terrestrial biosphere model.

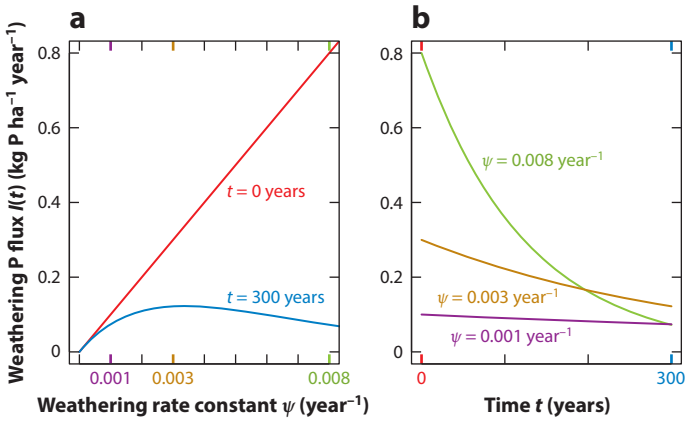


Figure 1

Heuristic example of short-term versus long-term effects of climate drivers. The curves are drawn from the equations for rock weathering in the section titled Epistemological Challenges and are based on the assumption that increasing moisture causes an increase in the rate constant of rock weathering (ψ, in units of year^{-1}). (*a*) Weathering P input flux [$I(t)$] as a function of the weathering rate constant ψ (and thus as a function of moisture), shown at two different times. (*b*) Weathering P input flux as a function of time, shown at three different weathering rate constants (moisture levels). An increase in moisture (further to the right in panel *a* or from *purple* to *gold* to *green* in panel *b*) leads to an increased weathering P input flux in the short term ($t = 0$ years; *red curve* in panel *a*, *left* side of panel *b*) but a hump-shaped response in the long-term ($t = 300$ years; *blue curve* in panel *a*, *right* side of panel *b*). The reason is that the weathering P input flux is the product of the weathering rate constant ψ and the amount of weatherable rock. In the short term, as in an experimental increase in moisture, the amount of weatherable rock is effectively constant. In the long term, past weathering has already depleted the amount of weatherable rock. Therefore, the highest weathering flux occurs at intermediate moisture (*blue curve* at $\psi = 0.003$ year^{-1} in panel *a*; *gold curve* at $t = 300$ years in panel *b*). Similar dynamics have been observed along climate gradients in Hawaii (e.g., Helfenstein et al. 2018).

($\psi = 0$), given that $\mathrm{d}I(t) = \mathrm{d}\psi|_{\psi t=0} = W(0)$, which is positive. This is what one would see in an experiment. However, the derivative becomes negative, and wetter sites have lower P weathering input fluxes, when enough time has elapsed or when precipitation becomes high enough, given that $\mathrm{d}I(t) = \mathrm{d}\psi < 0$ when $\psi t > 1$ (**Figure 1*a***, *blue line*; **Figure 1*b***, *right*). This is what one might see across a precipitation gradient.

This exact phenomenon occurs along a precipitation gradient in the Kohala mountains of Hawaii, USA, where weathering P input fluxes increased from near zero at the driest (275 mm year^{-1}) site to high rates at intermediate rainfall (~1,500 mm year^{-1}), then declined again to near zero at the wettest (3,125 mm year^{-1}) site (Helfenstein et al. 2018).

In places without such well-calibrated time–climate relationships, though, it might be difficult to interpret results from different approaches. If warmer sites have lower soil organic P pools than colder sites, does that mean that climate warming will deplete soil organic P over the next decade or century? Even if the direction of the effect is the same, is the magnitude informative? We are optimistic that a synthetic approach will uncover answers to these questions. Specifically, detailed understanding of processes from empirical work can combine with dynamic models to uncover these answers. Dynamic models specifically address the long-term versus short-term phenomena described above, but they depend on a deep empirical understanding.

We give preference to field experiments in this review, given the closer match of experimental timescales to the timescale of anthropogenic climate change and the increased realism in field

studies as opposed to pot, greenhouse, or laboratory studies, but we cover all methods to some degree (**Table 1**). We draw heavily on meta-analyses in this review, given their ability to synthesize across studies, but we urge the standard caution with interpreting aggregations of studies (**Table 1**).

We end this section with a note on terminology about pools, fluxes, and parameters. Empirically, it is common to measure P pools (amounts per area or volume), like the weatherable rock pool $W(t)$ above, and to a lesser extent P fluxes (changes in the pools over time), like the P input flux $I(t) = \psi W(t)$. Dynamic models link pools and fluxes via parameters, like the parameter ψ. The term rate can be ambiguous, as it can refer to a flux or a parameter; we use the terms flux and rate constant, respectively, even though many functions in models are more complicated than linear functions. Most of the empirical studies we discuss below measure how P pools or fluxes change with climate, whereas models typically assume that climate affects rate constants. In our example above, precipitation increases the weathering rate constant ψ, resulting in a decline in the pool $W(t)$, and an initial increase followed by an eventual decline in the weathering flux $\psi W(t)$.

PHOSPHORUS INPUTS

Inputs of P are typically low relative to within-system recycling, so changes in P inputs are likely to have consequences over longer timescales (decades to centuries to longer) (Newman 1995). There are two main natural inputs of P to most terrestrial ecosystems: atmospheric deposition and rock weathering (Newman 1995). Other P inputs are important in some systems, such as the release of organic P when permafrost thaws (Yang et al. 2021), the deposition of P during flooding (Kiedrzyńska et al. 2008), and transfers of P from aquatic systems [e.g., from bears eating salmon (Cederholm et al. 1999)]. For the sake of brevity, we limit our review of P inputs to atmospheric deposition and weathering.

Atmospheric Phosphorus Deposition

Atmospheric P comes primarily from the transport of dust (Hamilton et al. 2022), though in some cases biomass burning is also important (Barkley et al. 2019). Worldwide, approximately half of all dust originates in Northern Africa (Ginoux et al. 2001, Prospero et al. 2002). Prevailing winds carry dust within and across continents. Dust from Northern Africa, for instance, travels to other regions of Africa, the Caribbean, and the Americas (Swap et al. 1992, Prospero & Lamb 2003). This dust provides a large fraction of P inputs to ecosystems with old, P-depleted soils, such as the southeastern United States, the Amazon basin, and the Congo basin (Swap et al. 1992, Okin et al. 2004). Dust-derived P plays a large role in sustaining the productivity of these ecosystems (Okin et al. 2004, Goll et al. 2022). Therefore, climate-driven changes in dust transport are likely to influence these ecosystems over timescales of decades and longer.

Given that P deposition in dust is driven by atmospheric transport, it is not a surprise that it depends on climate. Precipitation has direct effects on dust emission and deposition: Drier conditions in the region of origin facilitate dust emission (Shao 2008), in part due to reduced vegetation cover (Cowie et al. 2013), and once dust is in the air, precipitation increases the rate of deposition (Swap et al. 1992). Drought has been linked with dust transport from Northern Africa to the Caribbean, with a ~three- to fourfold increase in dust from 1970 to 2000 driven by drought in the Sudano-Sahel (Prospero & Lamb 2003).

Climate can also have indirect effects on dust emissions. For instance, cooler temperatures in the tropical Indian Ocean during La Niña changed regional circulation and precipitation patterns, enhancing summer dust emissions in Saudi Arabia by decreasing rainfall (Yu et al. 2015). Another indirect effect on P deposition acts through fire. Warmer and drier conditions often promote

fires, though the effects are complex (Williams & Abatzoglou 2016), and biomass burning can contribute a large fraction of atmospheric P deposition (Barkley et al. 2019).

Weathering Input

Along with atmospheric deposition, chemical weathering, in which P is released from rocks by the chemical breakdown of P-containing primary minerals, is the dominant P input flux to ecosystems with younger, less-weathered soils (Newman 1995, Chadwick et al. 1999). The dominant P-containing primary mineral in rock is apatite, the same calcium phosphate mineral found in teeth and bones. Although it is possible to measure weathering P input fluxes directly, it is more common to infer P input fluxes from the pool of primary P remaining (Newman 1995). HCl-extractable inorganic P (P_i), which is the final extraction in the Hedley fractionation, is commonly interpreted as primary mineral P (Hou et al. 2018). Recent work with novel techniques indicates that HCl-extractable P includes more than apatite, including P that has been biologically cycled (Tamburini et al. 2012, Helfenstein et al. 2018). This finding clouds the interpretation of weathering P inputs from soil pool data, but hereafter we proceed with the interpretation that Hedley-derived HCl-P is primary mineral P, following the studies we cite.

As discussed above, the weathering rate constant should increase with precipitation and temperature (Jenny 1941). As expected from this effect, the P weathering flux varies unimodally with precipitation, as observed on the Kohala gradient (Helfenstein et al. 2018). Myriad studies have examined primary mineral P remaining in different ecosystems. A meta-analysis of these studies found that primary mineral P declined substantially across the global range of mean annual temperature and precipitation, with the warmest and wettest sites each having approximately 10% as much primary mineral P as the coldest and driest sites, after accounting for as many confounding variables as possible (Hou et al. 2018). All of these studies used observations rather than experiments, but the fact that they match with expectations and models (Goll et al. 2014) is encouraging. Soil pH was a key intermediate driver, according to the statistical analysis of Hou et al. (2018): Precipitation lowered pH, which lowered primary mineral P.

Model Treatment of Phosphorus Inputs

To capture these climate effects on P inputs in model simulations, models would need to represent P inputs in a way that has the capacity to respond to moisture or temperature. Three of the six TRENDY models [CASA-CNP (Wang et al. 2010), JSBACH (Goll et al. 2012), and ORCHIDEE-CNP (Goll et al. 2017, Sun et al. 2021)] include spatially gridded atmospheric P deposition, but to our knowledge, only one (ORCHIDEE-CNP) is capable of a dynamic climate response for P deposition. CLM-CNP (Yang et al. 2014) and DLEM-CNP (Wang et al. 2020) represent atmospheric P deposition but do not explain how, and JULES-CNP (Nakhavali et al. 2022) does not represent it (**Supplemental Table 1**).

Supplemental Material >

All TRENDY models include P weathering (**Supplemental Table 1**). CASA-CNP and JSBACH treat P weathering as a constant for each USDA soil order, and CLM-CNP and JULES-CNP treat it as a linear function of parent material. Thus, these four models do not currently allow for dynamic change with climate. DLEM-CNP and ORCHIDEE-CNP do, as they assume that P weathering increases with temperature and moisture (or runoff, for ORCHIDEE-CNP).

WITHIN-SYSTEM PHOSPHORUS CYCLING

On timescales of decades and shorter, P availability in terrestrial ecosystems is largely controlled by within-system P cycling (Cleveland et al. 2013). Within-system P cycling is more complex

than inputs and losses (Weil & Brady 2017). A simplified version, similar to many models, is that death, turnover, and excretion from organisms provide organic P to the soil, which can then be decomposed (mineralized) by microbes into labile P. Labile P can be taken up by plants and microbes, precipitated into secondary minerals or adsorbed to mineral surfaces, or lost. Phosphorus in or on secondary minerals can return to available P via dissolution or desorption, respectively, or it can become occluded, which means it is functionally lost. As with many nutrients, decomposition is a main driver of P availability (Chapin et al. 1978), but mineral sorption of P is also a main driver of P availability, often out-competing plants and microbes for available P (Sollins et al. 1988, Herndon et al. 2019). Unfortunately, these fluxes are rarely measured due to methodological challenges.

We organize this section by climatic driver. For each driver we discuss evidence from experimental field studies, observational studies along climate gradients, and meta-analyses, finishing with a section on model treatment of within-system P cycling.

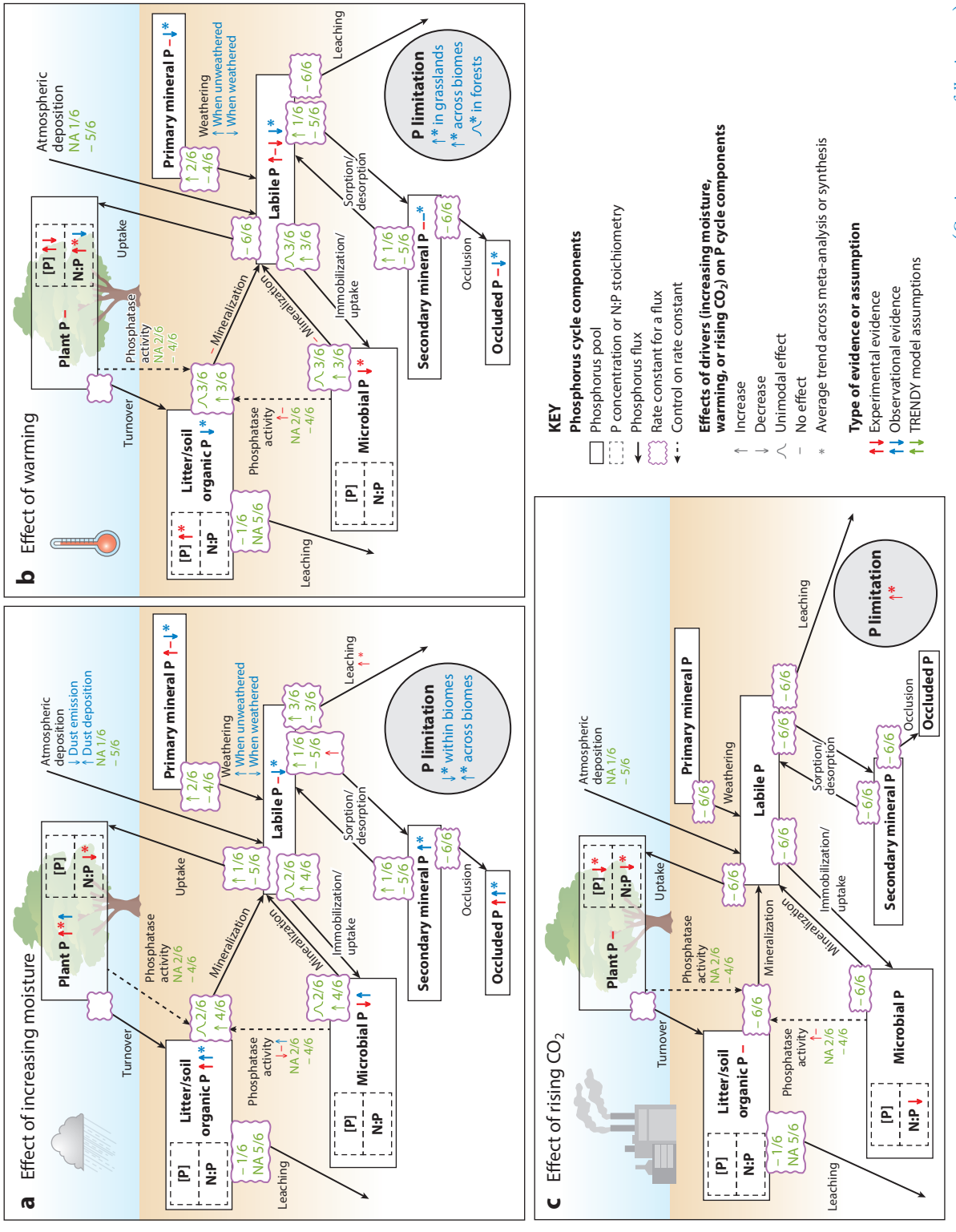
Precipitation and Within-System Phosphorus Cycling

In general, we expect increasing moisture to increase the rate constants of most processes in the P cycle, and to increase biotic P demand, but how these effects propagate to pool sizes is unclear. A number of field experiments spanning a wide range of biomes have manipulated precipitation and measured various aspects of P cycling. In a tropical forest in southern China with 1,400–1,700 mm rainfall year^{-1}, Sun et al. (2020) found that a 25% increase in annual rainfall for 7 years led to a decrease in microbial biomass P and alkaline phosphatase activity, along with increased P sorption capacity. Organic P and residual P also increased with rainfall, but the labile fractions did not change (Sun et al. 2020). In a Mediterranean shrubland in Catalonia, experimental drought had no effect on soil phosphatase activity or soil available P (Sardans et al. 2006). In an annual Mediterranean grassland in California, USA, a 50% experimental increase in precipitation caused decreased soil phosphatase activity and a slight decrease in senescent P in a common grass species (Henry et al. 2005, Menge & Field 2007), though the effects had disappeared a decade later (Mellett et al. 2018), suggesting that some aspects of within-system P cycling may acclimate to changing precipitation within a decade. Neither foliar P, foliar N:P, nor senescent N:P changed with precipitation at any time (Menge & Field 2007, Mellett et al. 2018).

Multiple studies have manipulated precipitation and monitored plant N:P stoichiometry. Synthesizing 15 rainfall addition studies and 6 drought studies, Yuan & Chen (2015) found that foliar N:P decreased with precipitation and increased with drought. Similarly, in a meta-analysis of 25 drought manipulations, He & Dijkstra (2014) found that drought decreased plant P by 9% and increased plant N:P by 7%.

A number of studies have examined P cycling along natural gradients of precipitation, including at multiple sites in Hawaii, USA (Austin & Vitousek 1998, Miller et al. 2001, Helfenstein et al. 2018, Bateman et al. 2019). The Kohala gradient (Chadwick et al. 2003, Vitousek & Chadwick 2013) revealed contrasts between findings from natural rainfall gradients and experimental water additions. Along the Kohala gradient, increasing rainfall led to increasing soil phosphatase activity, organic P, plant P, and microbial P and decreasing primary mineral P and available P (Helfenstein et al. 2018), many of which differed from experimental findings (**Figure 2*a***).

A primary study and a meta-analysis have been used to examine P cycling across ranges of moisture without holding other factors constant, both of which agreed with the gradient studies. In dryland sites across the globe, increasing aridity was associated with decreased soil phosphatase activity and slightly increased total soil P, but a stronger trend showed the decoupling of P from N due to changes in N (Delgado-Baquerizo et al. 2013). In a meta-analysis of 96 observational



(Caption appears on following page)

Figure 2 (*Figure appears on preceding page*)

Effects of climate and CO_2 on P cycling in terrestrial ecosystems. Pools (*black boxes*), stoichiometry (*dashed black boxes*), fluxes (*solid black arrows*), rate constants (*purple boxes*), and enzyme activity that influences rate constants (*dashed black arrows* pointing to *purple boxes*) are shown for a simplified terrestrial P cycle. Effects on P limitation are shown separately (*gray circles*). The general effects of (*a*) increasing moisture, (*b*) warming, and (*c*) rising CO_2 on P cycle components are shown for manipulative experiments (*red symbols* and *text*), observational studies along gradients (*blue symbols* and *text*), and model assumptions (*green symbols* and *text*). An up arrow means that (*a*) increasing moisture, (*b*) warming, or (*c*) rising CO_2 causes an increase, a down arrow indicates a decrease, and a bell curve indicates a unimodal response. Many of the responses are nonlinear, particularly across wide ranges of moisture and temperature. A dash symbol indicates evidence of no effect, whereas a lack of symbol indicates no evidence. An asterisk indicates an average trend across a meta-analysis or synthesis. Multiple symbols of the same color (evidence type) in the same panel without accompanying text mean that the effect varies across individual studies, but there has been no meta-analysis or synthesis to assess the general trend. Multiple symbols with accompanying text mean that the effect varies in the indicated way. Model assumptions are shown with how many of the six TRENDY models use each assumption. For model assumptions, NA indicates that the process is not represented in a model. Abbreviations: N, nitrogen; P, phosphorus.

studies that used Hedley fractionation, Hou et al. (2018) found that wetter sites had lower available P, lower primary mineral P, and higher organic P.

Overall, the average trends from observational studies are consistent with the expectation that wetter sites are more weathered (Walker & Syers 1976). Wetter sites had lower primary and labile P but higher secondary, occluded, microbial, and soil organic P (**Figure 2*a***). On the contrary, experimental studies often show different effects: Wetter treatments led to higher or similar primary and labile P and lower microbial P, for instance, as well as lower plant N:P, indicating a short-term increase in P relative to N (**Figure 2*a***). There are many potential reasons for the differences in results from observational versus experimental approaches, including sample size (there are more observational data, which means a greater ability to detect trends) and the wider range of moisture in observational studies. One key difference, though, is the timescale (**Figure 1**). Wetter sites along a gradient have been wetter for much longer than wetter treatments, so longer-term processes such as weathering have left an imprint along gradients.

Temperature and Within-System Phosphorus Cycling

Similar to precipitation, we expect warming to increase rate constants of most processes in the P cycle, though how those propagate to pool sizes is unclear. Warming field experiments offer useful insights. A variety of warming experiments in tundra ecosystems were reviewed by McLaren & Buckeridge (2021). Somewhat surprisingly, the majority of those studies found that warming had no effect on P cycling (soil labile P, soil total P, P mineralization, microbial P, phosphatase activity, or plant P). Some, though, found that warming increased some metrics (labile P, P mineralization, microbial P, phosphatase activity, and plant P), whereas others found that warming decreased a smaller set of metrics (microbial P, phosphatase activity, and plant P) (McLaren & Buckeridge 2021). In a Mediterranean shrubland in Catalonia, warming increased soil phosphatase activity and foliar [P] but decreased soil labile P (Sardans et al. 2006). In an annual grassland in California, USA, ~1°C of experimental warming had no effect on soil phosphatase activity or P content or the stoichiometry of a dominant plant species a few years after the manipulations (Henry et al. 2005, Menge & Field 2007) or a decade later (Mellett et al. 2018). Meta-analyses have found that experimental warming increased foliar N:P (Yuan & Chen 2015) and that, in grasslands, experimental warming increased litter %P but decreased soil labile P and microbial P (Hu et al. 2022).

Studies along natural temperature gradients, typically driven by elevation (Unger et al. 2010, Vincent et al. 2014), showed different results in different locations. In Ecuador, resin-extractable P increased tenfold from the lowest elevation (500 m, 22°C) to the highest elevation (2,000 m, ~14°C) sites (Unger et al. 2010), whereas in Abisko, Sweden, higher elevation (2.5–3°C cooler) sites had lower soil available P, though total P did not change (Vincent et al. 2014). A meta-analysis

across 96 studies found that warmer sites had lower soil available, organic, primary mineral, occluded (though with an R^2 of 0.01), and total P but similar secondary mineral P (Hou et al. 2018).

As was the case with precipitation, long-term (gradients and meta-analyses of observations) and short-term (experimental) responses to temperature sometimes differed. Sites that had been warmer for long periods of time had lower primary mineral P, as expected from more weathering, whereas experimental warming had no effect on primary mineral P, as expected for a slow process (**Figure 2*b***). Warmer sites had lower labile P, as expected if weathering-driven P depletion over long time periods causes P limitation, whereas experimental warming had variable effects on labile P (**Figure 2*b***), as expected if the near-term effects of warming act mainly through mineralization, sorption/desorption, and uptake, which interact in complex ways over short to intermediate timescales to determine available P.

Carbon Dioxide and Within-System Phosphorus Cycling

A number of field experiments have increased atmospheric CO_2 concentrations and measured one or more aspects of P cycling. In the California annual grasslands mentioned above, free-air CO_2 enrichment (FACE) had no effect on soil phosphatase activity, [P], or N:P stoichiometry in a dominant grass species (Menge & Field 2007, Mellett et al. 2018), though CO_2 did not stimulate production (Dukes et al. 2005). In a Swiss calcareous grassland, elevated CO_2 did stimulate biomass, but did not change biomass P (or N) in the field component of their study (Niklaus et al. 1998), despite increased phosphatase activity (Ebersberger et al. 2003). However, in a semiarid grassland in Wyoming, USA, elevated CO_2 lowered plant and microbial N:P, indicating relatively higher availability of P than N (Dijkstra et al. 2012). Elevated CO_2 decreased foliar [P] in a subtropical grassland in South Africa (Hattas et al. 2005). In tussock tundra in Alaska, USA, elevated CO_2 increased soil and root phosphatase activity (Moorhead & Linkins 1997). In a temperate coniferous forest in North Carolina, USA, elevated CO_2 had no short-term (2 year) effect on foliar or litter P, P resorption, foliar N:P ratios (Finzi et al. 2004), or soil phosphatase (Finzi et al. 2006).

There are few studies on natural gradients of CO_2. Peñuelas & Matamala (1993) found a decline in plant P concentrations in herbarium specimens over three centuries. This was not strictly a CO_2 gradient, as many other factors changed concurrently, but the authors' interpretation was that increasing CO_2 led to declining concentrations of P and other nutrients (Peñuelas & Matamala 1993).

Given the ease of measuring foliar stoichiometry, there are numerous studies of how elevated CO_2 affects foliar stoichiometry, which have been aggregated in meta-analyses. Sardans & Peñuelas (2012) found that elevated CO_2 decreased [P] in C_3 but not C_4 plants. In a meta-analysis of 46 field studies, elevated CO_2 lowered foliar [P] but lowered foliar N more, resulting in lower N:P (Huang et al. 2015). Du et al. (2019), studying 386 studies from a combination of FACE, open-top chambers, and controlled environments, found a similar answer: elevated CO_2 decreased foliar [P] by 3% and N:P by 7%. Overall, there is enough evidence to conclude that elevated CO_2 causes declining foliar [P] and N:P (**Figure 2*c***), but the effects of elevated CO_2 on other aspects of P cycling are not as well established.

Model Treatment of Within-System Phosphorus Cycling

Supplemental Material >

The TRENDY models vary substantially in the degree to which temperature and moisture affect within-system P cycling (**Figure 2**, **Supplemental Table 1**). One, DLEM-CNP, includes moisture control on root uptake capacity. All include moisture and temperature control on

decomposition, generally specifying that decomposition increases with or has a unimodal response to both moisture and temperature. Four of the six TRENDY models include explicit enzyme-driven mineralization of organic P (phosphatase activity), but phosphatase activity does not depend on temperature or moisture. There are examples of modeling soil enzyme activity as a function of temperature and moisture in ecosystem-scale models (e.g., Steinweg et al. 2012). Although all of the TRENDY models include a representation of the sorption–desorption of P_i, only DLEM-CNP allows it to depend explicitly on temperature and moisture. Phosphorus sorption is known to increase with temperature (Barrow 1983).

Models typically do not assume that elevated CO_2 affects parameters; rather, P cycling responses emerge from indirect effects. For example, in CLM-CNP, elevated CO_2 indirectly leads to higher phosphatase activity and P_i sorption (Yang et al. 2014).

PHOSPHORUS LOSSES

Similar to inputs, loss fluxes of P are typically small relative to internal recycling fluxes (Cleveland et al. 2013), so their effects emerge over longer timescales. A number of P loss pathways are important in terrestrial ecosystems. Leaching and runoff carry inorganic and organic P away hydrologically. Erosion from gravity and wind can cause significant P losses (Berhe et al. 2018). The occlusion of P in extremely recalcitrant soil minerals is sometimes considered a loss, though it might be available on longer timescales (Buendía et al. 2014).

Given the hydrological nature of P leaching, it is no surprise that it depends on moisture, but the details can depend on the range of moisture in a system. For example, P_i concentrations in stream leachate declined drastically from sites with less than 2,000 mm year^{-1} precipitation to wetter sites in New Zealand (McGroddy et al. 2008). Gao et al. (2020), in a meta-analysis of 79 experimental drying–rewetting studies, found that rewetting increased leaching fluxes of P_i more than N. Three of the TRENDY models (JSBACH, ORCHIDEE-CNP, and DLEM-CNP) treat P leaching as an increasing function of runoff, and thus moisture (**Figure 2*a***, **Supplemental Table 1**).

Supplemental Material >

Studying climate effects on erosion losses of P and P occlusion is not common, though increased aridity can increase wind erosion losses by decreasing plant cover (Cowie et al. 2013). The TRENDY models do not typically include erosion losses, though there are examples of how to do so (Berhe et al. 2018, Tan et al. 2021). All TRENDY models include P occlusion, though not as a function of climate (**Figure 2**, **Supplemental Table 1**).

PHOSPHORUS LIMITATION

The degree to which plant growth, productivity, and related processes are limited by P depends on all the fluxes and pools described above, along with the factors that control them, and thus has many potential connections to temperature, precipitation, and CO_2. Many of the studies cited above make inferences about potential P limitation from indicators such as plant investment in P acquisition or N:P stoichiometry. However, the gold standard for empirical studies of limitation is the response of plant growth to a change in P supply. We cover those studies here along with model treatments of P limitation.

Precipitation, Temperature, and Phosphorus Limitation

We are not aware of field studies that have manipulated precipitation or temperature along with P, but recent meta-analyses have analyzed how P limitation varies across natural ranges of precipitation and temperature (Du et al. 2020, Hou et al. 2021). Hou et al. (2021) studied the response of aboveground primary production or other correlated variables to P fertilization in 351 sites,

focusing on the magnitude of P limitation. Using a different approach, Du et al. (2020) studied the response of plant growth to P versus N fertilization in 53 sites, focusing on relative P versus N limitation. Overall, P limitation was stronger (Hou et al. 2021) and relatively more important than N limitation in warmer and wetter sites (Du et al. 2020). An important caveat for the strength of P limitation, though, was that part of the temperature trend and the entire precipitation trend emerged from a biome-related Simpson's paradox. Individually, forests and grasslands were less P limited in wetter sites, but because forests, compared to grasslands, were more common in wetter sites and more P limited, wetter sites were more P limited overall (Hou et al. 2021). The biome transition was not as strong a driver of the temperature trend, but it still appeared. Whereas grasslands were more P limited in warmer than colder sites, following the global trend, forests were most P limited at intermediate temperatures. As with the precipitation trend, the biome transition—forests were more common in warmer sites and were more P limited—played a major role in the global trend that P limitation was more common in warmer areas (Hou et al. 2021). Biome transitions are longer-term effects, which are less likely to emerge over the near term of a changing climate. Therefore, despite a good understanding of P limitation across broad climate gradients, we have little direct information to assess how climate change over years to decades will influence P limitation.

Carbon Dioxide and Phosphorus Limitation

Supplemental Material >

Effects of CO_2 on P limitation have been studied in a variety of ways. One approach is to manipulate CO_2 along with P (**Supplemental Figure 1**), whereas another is to manipulate CO_2 and study how its effects on productivity vary across a natural P gradient. As a side note, experiments in this subsection are typically framed as P limitation constraints to CO_2 fertilization, whereas our **Figure 2*c*** frames it as effects of elevated CO_2 on P limitation. For an ANOVA design where both factors have been manipulated, these are statistically identical (**Supplemental Figure 1**), but for some other statistical designs they are not. In our text we follow the phrasing of the studies we cite, but at risk of offending statistical sticklers, **Figure 2** retains the "effects of elevated CO_2 on P limitation" phrasing for consistency with temperature and precipitation.

Multi-factor field experiments that manipulate P along with climate or CO_2 are rare. We highlight one strong example (Ellsworth et al. 2017), a FACE experiment that also used P fertilization in a *Eucalyptus* stand grown on P-poor soil in Sydney, Australia. CO_2 enrichment over 3 years led to a 19% increase in photosynthesis, but unlike many FACE experiments, it did not enhance aboveground productivity or growth. Growth increased 35% with P fertilization, though, revealing P limitation. Because there was no combined $+CO_2$ +P treatment it was not possible to conclude whether P limited the response to elevated CO_2 (**Supplemental Figure 1**), though it was one of the possibilities that was consistent with their results.

Although field experiments that manipulate CO_2 and P are rare, there are many combined CO_2 and P manipulations in pots, many of which use factorial designs and can thus assess the effect of P limitation to CO_2 fertilization. Jiang et al. (2020) studied 45 of these in a meta-analysis. In these pot studies, low P reduced the photosynthetic response to elevated CO_2 by 25% and the biomass response by 12–15% (Jiang et al. 2020).

In a separate meta-analysis, Terrer et al. (2019) took the second approach mentioned above, analyzing how the effect of elevated CO_2 varied across a natural P gradient. Studying 138 elevated CO_2 experiments, they found that the elevated CO_2 effect was primarily driven by P for ectomycorrhizal vegetation (which comprise 25% of global vegetation) but not for arbuscular mycorrhizal vegetation. Specifically, the biomass response of ectomycorrhizal plants to elevated (+250 ppm) CO_2 rose from zero to a ~30% increase across the measured range of Bray-extractable P. Scaling across biomes, the biomass response to elevated CO_2 was +8–14%, which was only approximately

a third as large as the simulated response in models that did not include P (or N) (Terrer et al. 2019). This result was qualitatively the same as the result from the pot study meta-analysis of Jiang et al. (2020), except that Jiang et al. (2020) found P constraints to CO_2 fertilization for arbuscular mycorrhizal plants as well.

Models and Phosphorus Limitation

Model investigations of P limitation inherently depend on how P limitation can occur in the model. Some models use a Liebig's law–type formulation, which means that productivity [net primary production (NPP) or gross primary production] is limited by a nutrient when supply is less than demand (**Supplemental Table 2**). Another approach, exemplified by ORCHIDEE-CNP (**Supplemental Table 2**), is that photosynthetic parameters depend on leaf P. Recent evidence ties leaf P to photosynthetic parameters, paving the way to including these relationships in models (Walker et al. 2014, Lombardozzi et al. 2018, Ellsworth et al. 2022).

Supplemental Material >

Six of the TRENDY models now have versions with P cycles (**Supplemental Table 1, 2**), giving hope that these will soon be incorporated into Earth system models (ESMs). However, unlike the versions with N, the versions of these models with P were not used for the 2022 Global Carbon Project publication (Kou-Giesbrecht et al. 2023). Most terrestrial biosphere models that include P cycles suggest that P limitation constrains responses to elevated CO_2 (Goll et al. 2012; Peñuelas et al. 2013; Wieder et al. 2015; Yang et al. 2016, 2019; Sun et al. 2017, 2021; Nakhavali et al. 2022). For example, in ELM-ECA, P supply cannot keep up with increased demand, decreasing the CO_2 sink (Yang et al. 2019). In JULES-CNP, P availability limits the productivity and biomass responses to elevated CO_2, particularly in the Amazon (Nakhavali et al. 2022). The amounts are significant. In JULES-CNP, P limitation reduces NPP by 24% at current CO_2 and 46% at elevated CO_2 (Nakhavali et al. 2022).

Mechanistically, many factors feed into the P limitation effects on CO_2 fertilization. In a comparison of Coupled Model Intercomparison Project 5 ESMs, Sun et al. (2017) found that the discrepancy between inferred P demand and P availability depended on assumptions about the availability of different P forms. Miniscule changes in assumptions about the availability of large P pools had large effects on P limitation. Given the ongoing discussion about the availability of different measured P pools in empirical work (e.g., Helfenstein et al. 2018), this is clearly an area for future work at the interface of empirical and modeling studies. Another area of recent model development is the treatment of sorption and desorption of P_i. Using the QUINCY model, Yu et al. (2023) found that a change in formulation—assuming that sorbed P_i (secondary mineral P in **Figure 2**) exchanged with P_i in solution rather than with labile P_i directly—improved model fit substantially and reduced P limitation (Yu et al. 2023).

The Amazon region has been the focus of much interest in P limitation (Cleveland et al. 2011, Cunha et al. 2022). An ensemble of six terrestrial models that included P cycling (including stand-scale models and terrestrial biosphere models) simulated the effects of elevated CO_2 in the Amazon rainforest, finding that P limitation constrained C storage and NPP in response to elevated CO_2 by approximately 50% compared to models without P limitation (Fleischer et al. 2019).

CRITICAL UNKNOWNS AND CONCLUSIONS

Not surprisingly for such a complex topic, we could fill an entire book with critical unknowns, but we confine ourselves to a few brief points. One is a disconnect between models and empirical work. In reading this paper, readers might notice that the empirical and modeling sections often focus on different issues. That is not because we, the authors, are trying to obfuscate but rather because the different approaches have had different foci. Models need information on rate constants—their values and how they depend on temperature and moisture (Achat et al. 2016) (**Figure 2**)—whereas

most empirical studies focus on pools, enzyme activity, and to a lesser degree, fluxes (**Figure 2**). Pool and flux data are extremely useful for training and benchmarking models but are not ideal for parameterizing rate constants. Our hope is that the ever-expanding toolkit for measuring P cycling [e.g., ^{33}P isotope dilution with sterilization to probe fluxes, ^{18}O tracking of phosphate to probe biological activity, X-ray techniques to distinguish specific soil P chemistry (Helfenstein et al. 2018, Wanek et al. 2019)] will facilitate the measurements of rate constants as well as pools and fluxes. Moreover, we hope that efforts to bring modelers and empiricists together, such as GOLUM (Wang et al. 2018), INTERFACE (**https://www.bio.purdue.edu/INTERFACE/**), and INCyTE (**https://www.umt.edu/incyte/**), will catalyze work that benefits both approaches, and thus the field as a whole.

There is much more information about the effects of moisture and temperature from natural ranges of existing conditions than from manipulative experiments. Because of the long-term versus short-term dynamics described above, field experiments, and particularly long-term field experiments, are a better indicator of the effects of climate change over timescales of years to decades, and they are also better at targeting mechanisms. The problem is that field experiments are expensive and challenging. Our hope is that funding agencies will support the difficult and expensive—but essential—task of conducting long-term experiments.

Most existing work focuses on average climate trends. Climate extremes are important for carbon cycling (Frank et al. 2015) and likely are for P cycling as well. There is some work on how climate variability affects P cycling (e.g., Gao et al. 2020, 2021), but it is a complex issue.

As is common throughout ecology, many critical parts of the world, including much of the tropics and Africa in particular, are underrepresented in the studies we review herein. On the CO_2 side, there are a number of elevated CO_2 experiments but as yet no published studies from tropical forests, which are expected to be particularly subject to P limitation (Cunha et al. 2022). Therefore, we are excited about the upcoming work from AmazonFACE (**https://www.inpa.gov.br/amazonface/**), particularly that the experiment involved collaboration between empiricists and modelers from the outset (Fleischer et al. 2019).

Despite the need for future development in these and other areas, our review offers some answers. One clear answer is that P limitation often constrains CO_2 fertilization (and rising CO_2 exacerbates P limitation), though the magnitude varies across locations and conditions. Another answer that emerges is that, as Walker & Syers (1976) hypothesized long ago, pools over long time periods are largely driven by weathering, which increases with time, precipitation, and temperature. Consequently, P limitation is more pervasive in warmer, wetter areas, where it is more likely to constrain CO_2 fertilization. However, much of that trend is driven by long-term, cross-biome differences. The effects of climate change over years to decades are much less well understood and are not well informed by studies across natural gradients. The literature is not yet mature enough to draw conclusions about how and under what conditions climate change will modify P limitation, but we are optimistic that further collaboration between empiricists and modelers will lead to rapid progress.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We gratefully acknowledge the decades of excellent work that we review herein. We apologize to the myriad authors whose excellent work we did not have space to include. We also thank the reviewers for their time and suggestions.

LITERATURE CITED

Achat DL, Pousse N, Nicolas M, Brédoire F, Augusto L. 2016. Soil properties controlling inorganic phosphorus availability: general results from a national forest network and a global compilation of the literature. *Biogeochemistry* 127(2):255–72

Augusto L, Achat DL, Jonard M, Vidal D, Ringeval B. 2017. Soil parent material—a major driver of plant nutrient limitations in terrestrial ecosystems. *Glob. Chang. Biol.* 23(9):3808–24

Austin AT, Vitousek PM. 1998. Nutrient dynamics on a precipitation gradient in Hawai'i. *Oecologia* 113(4):519–29

Barkley AE, Prospero JM, Mahowald N, Hamilton DS, Popendorf KJ, et al. 2019. African biomass burning is a substantial source of phosphorus deposition to the Amazon, Tropical Atlantic Ocean, and Southern Ocean. *PNAS* 116(33):16216–21

Barrow N. 1983. A mechanistic model for describing the sorption and desorption of phosphate by soil. *J. Soil Sci.* 34:733–50

Bateman JB, Chadwick OA, Vitousek PM. 2019. Quantitative analysis of pedogenic thresholds and domains in volcanic soils. *Ecosystems* 22(7):1633–49

Berhe AA, Barnes RT, Six J, Marin-Spiotta E. 2018. Role of soil erosion in biogeochemical cycling of essential elements: carbon, nitrogen, and phosphorus. *Annu. Rev. Earth Planet Sci.* 46:521–48

Buendía C, Arens S, Hickler T, Higgins SI, Porada P, Kleidon A. 2014. On the potential vegetation feedbacks that enhance phosphorus availability – insights from a process-based model linking geological and ecological timescales. *Biogeosciences* 11:3661–83

Cederholm CJ, Kunze MD, Murota T, Sibatani A. 1999. Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries* 24(10):6–15

Chadwick OA, Derry LA, Vitousek PM, Huebert BJ, Hedin LO. 1999. Changing sources of nutrients during four million years of ecosystem development. *Nature* 397(6719):491–97

Chadwick OA, Gavenda RT, Kelly EF, Ziegler K, Olson CG, et al. 2003. The impact of climate on the biogeochemical functioning of volcanic soils. *Chem. Geol.* 202(3–4):195–223

Chapin FS III, Barsdate RJ, Barel D. 1978. Phosphorus cycling in Alaskan coastal tundra: a hypothesis for the regulation of nutrient cycling. *Oikos* 1:189–99

Cleveland CC, Houlton BZ, Smith WK, Marklein AR, Reed SC, et al. 2013. Patterns of new versus recycled primary production in the terrestrial biosphere. *PNAS* 110(31):12733–37

Cleveland CC, Townsend AR, Taylor P, Alvarez-Clare S, Bustamante MM, et al. 2011. Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. *Ecol. Lett.* 14(9):939–47

Cowie SM, Knippertz P, Marsham JH. 2013. Are vegetation-related roughness changes the cause of the recent decrease in dust emission from the Sahel? *Geophys. Res. Lett.* 40(9):1868–72

Crews TE, Kitayama K, Fownes JH, Riley RH, Herbert DA, et al. 1995. Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. *Ecology* 76(5):1407–24

Cunha HF, Andersen KM, Lugli LF, Santana FD, Aleixo IF, et al. 2022. Direct evidence for phosphorus limitation on Amazon forest productivity. *Nature* 608(7923):558–62

Delgado-Baquerizo M, Maestre FT, Gallardo A, Bowker MA, Wallenstein MD, et al. 2013. Decoupling of soil nutrient cycles as a function of aridity in global drylands. *Nature* 502(7473):672–76

Deng Q, Hui D, Dennis S, Reddy KC. 2017. Responses of terrestrial ecosystem phosphorus cycling to nitrogen addition: a meta-analysis. *Glob. Ecol. Biogeogr.* 26(6):713–28

Dijkstra FA, Pendall E, Morgan JA, Blumenthal DM, Carrillo Y, et al. 2012. Climate change alters stoichiometry of phosphorus and nitrogen in a semiarid grassland. *New Phytol.* 196(3):807–15

Du C, Wang X, Zhang M, Jing J, Gao Y. 2019. Effects of elevated CO_2 on plant CNP stoichiometry in terrestrial ecosystems: a meta-analysis. *Sci. Total Environ.* 650:697–708

Du E, Terrer C, Pellegrini AF, Ahlström A, van Lissa CJ, et al. 2020. Global patterns of terrestrial nitrogen and phosphorus limitation. *Nat. Geosci.* 13(3):221–26

Dukes JS, Chiariello NR, Cleland EE, Moore LA, Shaw MR, et al. 2005. Responses of grassland production to single and multiple global environmental changes. *PLOS Biol.* 3(10):e319

Meta-analysis and model analysis of how N and P limitation varies across climate.

Ebersberger D, Niklaus PA, Kandeler E. 2003. Long term CO_2 enrichment stimulates N-mineralisation and enzyme activities in calcareous grassland. *Soil Biol. Biochem.* 35(7):965–72

CO_2 fertilization and P fertilization field experiment in Eucalypt forest.

Ellsworth DS, Anderson IC, Crous KY, Cooke J, Drake JE, et al. 2017. Elevated CO_2 does not increase Eucalypt forest productivity on a low-phosphorus soil. *Nat. Clim. Chang.* 7(4):279–82

Ellsworth DS, Crous KY, De Kauwe MG, Verryckt LT, Goll D, et al. 2022. Convergence in phosphorus constraints to photosynthesis in forests around the world. *Nat. Commun.* 13(1):5005

Fay PA, Prober SM, Harpole WS, Knops JM, Bakker JD, et al. 2015. Grassland productivity limited by multiple nutrients. *Nat. Plants* 1(7):15080

Finzi AC, DeLucia EH, Schlesinger WH. 2004. Canopy N and P dynamics of a southeastern US pine forest under elevated CO_2. *Biogeochemistry* 69(3):363–78

Finzi AC, Sinsabaugh RL, Long TM, Osgood MP. 2006. Microbial community responses to atmospheric carbon dioxide enrichment in a warm-temperate forest. *Ecosystems* 9(2):215–26

Fisher JB, Huntzinger DN, Schwalm CR, Sitch S. 2014. Modeling the terrestrial biosphere. *Annu. Rev. Environ. Resour.* 39:91–123

Multi-model analysis of P constraints on CO_2 fertilization in Amazon forest; prelude to Amazon-FACE.

Fleischer K, Rammig A, De Kauwe MG, Walker AP, Domingues TF, et al. 2019. Amazon forest response to CO_2 fertilization dependent on plant phosphorus acquisition. *Nat. Geosci.* 12(9):736–41

Forber KJ, Withers PJ, Ockenden MC, Haygarth PM. 2018. The phosphorus transfer continuum: a framework for exploring effects of climate change. *Agric. Environ. Lett.* 3(1):180036

Frank D, Reichstein M, Bahn M, Thonicke K, Frank D, et al. 2015. Effects of climate extremes on the terrestrial carbon cycle: concepts, processes and potential future impacts. *Glob. Chang. Biol.* 21(8):2861–80

Friedlingstein P, O'Sullivan M, Jones MW, Andrew RM, Gregor L, et al. 2022. Global carbon budget 2022. *Earth Syst. Sci. Data* 14(1):4811–900

Gao D, Bai E, Li M, Zhao C, Yu K, Hagedorn F. 2020. Responses of soil nitrogen and phosphorus cycling to drying and rewetting cycles: a meta-analysis. *Soil Biol. Biochem.* 148:107896

Gao D, Bai E, Yang Y, Zong S, Hagedorn F. 2021. A global meta-analysis on freeze-thaw effects on soil carbon and phosphorus cycling. *Soil Biol. Biochem.* 159:108283

Ginoux P, Chin M, Tegen I, Prospero JM, Holben B, et al. 2001. Sources and distributions of dust aerosols simulated with the GOCART model. *J. Geophys. Res.* 106(D17):20255–73

Goll DS, Bauters M, Zhang H, Ciais P, Balkanski Y, et al. 2022. Atmospheric phosphorus deposition amplifies carbon sinks in simulations of a tropical forest in Central Africa. *New Phytol.* 237(6):2054–68

Goll DS, Brovkin V, Parida BR, Reick CH, Kattge J, et al. 2012. Nutrient limitation reduces land carbon uptake in simulations with a model of combined carbon, nitrogen and phosphorus cycling. *Biogeosciences* 9(9):3547–69

Goll DS, Moosdorf N, Hartmann J, Brovkin V. 2014. Climate-driven changes in chemical weathering and associated phosphorus release since 1850: implications for the land carbon balance. *Geophys. Res. Lett.* 41(10):3553–58

Goll DS, Vuichard N, Maignan F, Jornet-Puig A, Sardans J, et al. 2017. A representation of the phosphorus cycle for ORCHIDEE (revision 4520). *Geosci. Model Dev.* 10(10):3745–70

Goswami S, Fisk MC, Vadeboncoeur MA, Garrison-Johnston M, Yanai RD, Fahey TJ. 2018. Phosphorus limitation of aboveground production in northern hardwood forests. *Ecology* 99(2):438–49

Hamilton DS, Perron MMG, Bond TC, Bowie AR, Buchholz RR, et al. 2022. Earth, wind, fire and pollution: aerosol nutrient sources and impacts on ocean biogeochemistry. *Annu. Rev. Mar. Sci.* 14:303–30

Hattas D, Stock WD, Mabusela WT, Green IR. 2005. Phytochemical changes in leaves of subtropical grasses and fynbos shrubs at elevated atmospheric CO_2 concentrations. *Glob. Planet. Chang.* 47(2–4):181–92

He M, Dijkstra FA. 2014. Drought effect on plant nitrogen and phosphorus: a meta-analysis. *New Phytol.* 204(4):924–31

Novel multi-technique analysis of P cycling along a precipitation gradient; new insights into standard measurements.

Helfenstein J, Tamburini F, von Sperber C, Massey MS, Pistocchi C, et al. 2018. Combining spectroscopic and isotopic techniques gives a dynamic view of phosphorus cycling in soil. *Nat. Commun.* 9(1):3226

Henry HA, Juarez JD, Field CB, Vitousek PM. 2005. Interactive effects of elevated CO_2, N deposition and climate change on extracellular enzyme activity and soil density fractionation in a California annual grassland. *Glob. Chang. Biol.* 11(10):1808–15

Herndon EM, Kinsman-Costello L, Duroe KA, Mills J, Kane ES, et al. 2019. Iron (oxyhydr)oxides serve as phosphate traps in tundra and boreal peat soils. *J. Geophys. Res.* 124(2):227–46

Hou E, Chen C, Luo Y, Zhou G, Kuang Y, et al. 2018. Effects of climate on soil phosphorus cycle and availability in natural terrestrial ecosystems. *Glob. Chang. Biol.* 24(8):3344–56

Meta-analysis of temperature and precipitation effects on soil P cycling.

Hou E, Wen D, Jiang L, Luo X, Kuang Y, et al. 2021. Latitudinal patterns of terrestrial phosphorus limitation over the globe. *Ecol. Lett.* 24(7):1420–31

Hu W, Tan J, Shi X, Lock TR, Kallenbach RL, Yuan Z. 2022. Nutrient addition and warming alter the soil phosphorus cycle in grasslands: a global meta-analysis. *J. Soils Sediments* 22:2608–19

Huang W, Houlton BZ, Marklein AR, Liu J, Zhou G. 2015. Plant stoichiometric responses to elevated CO_2 vary with nitrogen and phosphorus inputs: evidence from a global-scale meta-analysis. *Sci. Rep.* 5(1):18225

Jenny H. 1941. *Factors of Soil Formation: A System of Pedology*. New York: Dover Publ. Inc.

Jiang M, Caldararu S, Zhang H, Fleischer K, Crous KY, et al. 2020. Low phosphorus supply constrains plant responses to elevated CO_2: a meta-analysis. *Glob. Chang. Biol.* 26(10):5856–73

Meta-analysis of combined CO_2 and P fertilization experiments in pots.

Kiedrzyńska E, Kiedrzyński M, Zalewski M. 2008. Flood sediment deposition and phosphorus retention in a lowland river floodplain: impact on water quality of a reservoir, Sulejów, Poland. *Ecohydrol. Hydrobiol.* 8(2–4):281–89

Kou-Giesbrecht S, Arora V, Seiler C, Arneth A, Falk S, et al. 2023. Evaluating nitrogen cycling in terrestrial biosphere models: a disconnect between the carbon and nitrogen cycles. *Earth Syst. Dynam.* 14(4):767–95

Lambers H, Bishop JG, Hopper SD, Laliberté E, Zúñiga-Feest A. 2012. Phosphorus-mobilization ecosystem engineering: the roles of cluster roots and carboxylate exudation in young P-limited ecosystems. *Ann. Bot.* 110(2):329–48

Lombardozzi DL, Smith NG, Cheng SJ, Dukes JS, Sharkey TD, et al. 2018. Triose phosphate limitation in photosynthesis models reduces leaf photosynthesis and global terrestrial carbon storage. *Environ. Res. Lett.* 13(7):074025

Lun F, Liu J, Ciais P, Nesme T, Chang J, et al. 2018. Global and regional phosphorus budgets in agricultural systems and their implications for phosphorus-use efficiency. *Earth Syst. Sci. Data* 10:1–18

Mahowald N, Jickells TD, Baker AR, Artaxo P, Benitez-Nelson CR, et al. 2008. Global distribution of atmospheric phosphorus sources, concentrations and deposition rates, and anthropogenic impacts. *Glob. Biogeochem. Cycles* 22(4):GB4026

McGroddy ME, Baisden WT, Hedin LO. 2008. Stoichiometry of hydrological C, N, and P losses across climate and geology: an environmental matrix approach across New Zealand primary forests. *Glob. Biogeochem. Cycles* 22(1):GB1026

McLaren JR, Buckeridge KM. 2021. Enhanced plant leaf P and unchanged soil P stocks after a quarter century of warming in the arctic tundra. *Ecosphere* 12(11):e03838

Plant and soil P responses to long-term warming of tundra.

Mellett T, Selvin C, Defforey D, Roberts K, Lecher AL, et al. 2018. Assessing cumulative effects of climate change manipulations on phosphorus limitation in a Californian grassland. *Environ. Sci. Technol.* 52(1):98–106

Menge DNL, Field CB. 2007. Simulated global changes alter phosphorus demand in annual grassland. *Glob. Chang. Biol.* 13(12):2582–91

Menge DNL, Hedin LO, Pacala SW. 2012. Nitrogen and phosphorus limitation over long-term ecosystem development in terrestrial ecosystems. *PLOS ONE* 7(8):e42045

Miller AJ, Schuur EA, Chadwick OA. 2001. Redox control of phosphorus pools in Hawaiian montane forest soils. *Geoderma* 102(3–4):219–37

Moorhead DL, Linkins AE. 1997. Elevated CO_2 alters belowground exoenzyme activities in tussock tundra. *Plant Soil* 189(2):321–29

Nakhavali MA, Mercado LM, Hartley IP, Sitch S, Cunha FV, et al. 2022. Representation of the phosphorus cycle in the Joint UK Land Environment Simulator (vn5. 5_JULES-CNP). *Geosci. Model Dev.* 15(13):5241–69

Newman EI. 1995. Phosphorus inputs to terrestrial ecosystems. *J. Ecol.* 1:713–26

Niklaus PA, Leadley PW, Stöcklin J, Körner C. 1998. Nutrient relations in calcareous grassland under elevated CO_2. *Oecologia* 116(1):67–75

Okin GS, Mahowald N, Chadwick OA, Artaxo P. 2004. Impact of desert dust on the biogeochemistry of phosphorus in terrestrial ecosystems. *Glob. Biogeochem. Cycles* 18(2):GB2005

Peñuelas J, Matamala R. 1993. Variations in the mineral composition of herbarium plant species collected during the last three centuries. *J. Exp. Bot.* 44(9):1523–25

Peñuelas J, Poulter B, Sardans J, Ciais P, Van Der Velde M, et al. 2013. Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. *Nat. Commun.* 4(1):2934

Porder S, Ramachandran S. 2013. The phosphorus concentration of common rocks—a potential driver of ecosystem P status. *Plant Soil* 367(1):41–55

Porder S, Vitousek PM, Chadwick OA, Chamberlain CP, Hilley GE. 2007. Uplift, erosion, and phosphorus limitation in terrestrial ecosystems. *Ecosystems* 10(1):159–71

Prospero JM, Ginoux P, Torres O, Nicholson SE, Gill TE. 2002. Environmental characterization of global sources of atmospheric soil dust identified with the Nimbus 7 Total Ozone Mapping Spectrometer (TOMS) absorbing aerosol product. *Rev. Geophys.* 40(1):1002

Prospero JM, Lamb PJ. 2003. African droughts and dust transport to the Caribbean: climate change implications. *Science* 302(5647):1024–27

Quesada CA, Phillips OL, Schwarz M, Czimczik CI, Baker TR, et al. 2012. Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences* 9(6):2203–46

Reed SC, Yang X, Thornton PE. 2015. Incorporating phosphorus cycling into global modeling efforts: a worthwhile, tractable endeavor. *New Phytol.* 208(2):324–29

Sardans J, Peñuelas J. 2012. The role of plants in the effects of global change on nutrient availability and stoichiometry in the plant-soil system. *Plant Physiol.* 160(4):1741–61

Sardans J, Peñuelas J, Estiarte M. 2006. Warming and drought alter soil phosphatase activity and soil P availability in a Mediterranean shrubland. *Plant Soil* 289:227–38

Shao Y. 2008. *Physics and Modelling of Wind Erosion*. Dordrecht, Neth.: Springer

Smil V. 2000. Phosphorus in the environment: natural flows and human interferences. *Annu. Rev. Energy Env.* 25:53–88

Sollins P, Robertson GP, Uehara G. 1988. Nutrient mobility in variable- and permanent-charge soils. *Biogeochemistry* 6(3):181–99

Steinweg JM, Dukes JS, Wallenstein MD. 2012. Modeling the effects of temperature and moisture on soil enzyme activity: linking laboratory assays to continuous field data. *Soil Biol. Biochem.* 55:85–92

Sun F, Song C, Wang M, Lai DY, Tariq A, et al. 2020. Long-term increase in rainfall decreases soil organic phosphorus decomposition in tropical forests. *Soil Biol. Biochem.* 151:108056

Sun Y, Goll DS, Chang J, Ciais P, Guenet B, et al. 2021. Global evaluation of the nutrient-enabled version of the land surface model ORCHIDEE-CNP v1.2 (r5986). *Geosci. Model Dev.* 14(4):1987–2010

Sun Y, Peng S, Goll DS, Ciais P, Guenet B, et al. 2017. Diagnosing phosphorus limitations in natural terrestrial ecosystems in carbon cycle models. *Earth's Futur.* 5(7):730–49

Swap R, Garstang M, Greco S, Talbot R, Kållberg P. 1992. Saharan dust in the Amazon Basin. *Tellus B* 44(2):133–49

Tamburini F, Pfahler V, Bünemann EK, Guelland K, Bernasconi SM, Frossard E. 2012. Oxygen isotopes unravel the role of microorganisms in phosphate cycling in soils. *Environ. Sci. Technol.* 45:5956–62

Tan Z, Leung LR, Li H-Y, Tesfa T, Zhu Q, et al. 2021. Increased extreme rains intensify erosional nitrogen and phosphorus fluxes to the northern Gulf of Mexico in recent decades. *Environ. Res. Lett.* 16:054080

Meta-analysis of N and P constraints to CO_2 fertilization.

Terrer C, Jackson RB, Prentice IC, Keenan TF, Kaiser C, et al. 2019. Nitrogen and phosphorus constrain the CO_2 fertilization of global plant biomass. *Nat. Clim. Chang.* 9(9):684–89

Treseder KK, Vitousek PM. 2001. Effects of soil nutrient availability on investment in acquisition of N and P in Hawaiian rain forests. *Ecology* 82(4):946–54

Unger M, Leuschner C, Homeier J. 2010. Variability of indices of macronutrient availability in soils at different spatial scales along an elevation transect in tropical moist forests (NE Ecuador). *Plant Soil* 336(1):443–58

Vance CP, Uhde-Stone C, Allan DL. 2003. Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. *New Phytol.* 157(3):423–47

Vincent AG, Sundqvist MK, Wardle DA, Giesler R. 2014. Bioavailable soil phosphorus decreases with increasing elevation in a subarctic tundra landscape. *PLOS ONE* 9(3):e92942

Vitousek PM. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65(1):285–98

Vitousek PM, Chadwick OA. 2013. Pedogenic thresholds and soil process domains in basalt-derived soils. *Ecosystems* 16(8):1379–95

Walker AP, Beckerman AP, Gu L, Kattge J, Cernusak LA, et al. 2014. The relationship of leaf photosynthetic traits – V_{cmax} and J_{max} – to leaf nitrogen, leaf phosphorus, and specific leaf area: a meta-analysis and modeling study. *BMC Ecol. Evol.* 4(16):3218–35

Walker TW, Syers JK. 1976. The fate of phosphorus during pedogenesis. *Geoderma* 15(1):1–9

Wanek W, Zezula D, Wasner D, Mooshammer M, Prommer J. 2019. A novel isotope pool dilution approach to quantify gross rates of key abiotic and biological processes in the soil phosphorus cycle. *Biogeosciences* 16(15):3047–68

Wang Y, Ciais P, Goll D, Huang Y, Luo Y, et al. 2018. GOLUM-CNP v1. 0: a data-driven modeling of carbon, nitrogen and phosphorus cycles in major terrestrial biomes. *Geosci. Model Dev.* 11(9):3903–28

Wang YP, Law RM, Pak B. 2010. A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere. *Biogeosciences* 7(7):2261–82

Wang Z, Tian H, Yang J, Shi H, Pan S, et al. 2020. Coupling of phosphorus processes with carbon and nitrogen cycles in the dynamic land ecosystem model: model structure, parameterization, and evaluation in tropical forests. *J. Adv. Model. Earth Syst.* 12(10):e2020MS002123

Weil RR, Brady NC. 2017. *The Nature and Property of Soils*. New York: Pearson. 15th ed.

Wieder WR, Cleveland CC, Smith WK, Todd-Brown K. 2015. Future productivity and carbon storage limited by terrestrial nutrient availability. *Nat. Geosci.* 8(6):441–44

Williams AP, Abatzoglou JT. 2016. Recent advances and remaining uncertainties in resolving past and future climate effects on global fire activity. *Curr. Clim. Chang. Rep.* 2(1):1–14

Wright SJ. 2019. Plant responses to nutrient addition experiments conducted in tropical forests. *Ecol. Monogr.* 89(4):e01382

Yang G, Peng Y, Abbott BW, Biasi C, Wei B, et al. 2021. Phosphorus rather than nitrogen regulates ecosystem carbon dynamics after permafrost thaw. *Glob. Chang. Biol.* 27(22):5818–30

Yang X, Ricciuto DM, Thornton PE, Shi X, Xu M, et al. 2019. The effects of phosphorus cycle dynamics on carbon sources and sinks in the Amazon region: a modeling study using ELM v1. *J. Geophys. Res. Biogeosci.* 124(12):3686–98

Yang X, Thornton PE, Ricciuto DM, Post WM. 2014. The role of phosphorus dynamics in tropical forests – a modeling study using CLM-CNP. *Biogeosciences* 11(6):1667–81

Yang X, Thornton PE, Ricciuto DM, Hoffman FM. 2016. Phosphorus feedbacks constraining tropical ecosystem responses to changes in atmospheric CO_2 and climate. *Geophys. Res. Lett.* 43(13):7205–14

Yu L, Caldararu S, Ahrens B, Wutzler T, Schrumpf M, et al. 2023. Improved representation of phosphorus exchange on soil mineral surfaces reduces estimates of phosphorus limitation in temperate forest ecosystems. *Biogeosciences* 20(1):57–73

Yu Y, Notaro M, Liu Z, Wang F, Alkolibi F, et al. 2015. Climatic controls on the interannual to decadal variability in Saudi Arabian dust activity: toward the development of a seasonal dust prediction model. *J. Geophys. Res.* 120(5):1739–58

Yuan ZY, Chen HY. 2015. Decoupling of nitrogen and phosphorus in terrestrial plants associated with global changes. *Nat. Clim. Chang.* 5(5):465–69