



Global Phosphorus Dynamics

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Introduction

Phosphorus (P) is an essential element for both plant and animal life. It provides energy to cells in the form of adenosine triphosphate (ATP), and is a structural component of cell walls (phospholipids) and of nucleic acids (phosphate backbone of DNA and RNA). Biological productivity is heavily reliant on P availability to photosynthetic organisms, which constitute the base of the food chain in both terrestrial and aquatic ecosystems and hence used as a fertilizer to increase crop yield. The biogeochemical processes governing P availability and dynamics in the environment are complex, and vary widely from one ecosystem to another, thus requiring a highly interdisciplinary approach to research.

General Overviews and Textbooks

Unlike other major biogeochemical elements, the global P cycle is unique in that it does not have a significant gaseous component, as phosphine requires a highly reduced environment to be stable. The majority of terrestrial reactive P is originally derived from the weathering of calcium phosphate (e.g., apatite) and other minerals and the conversion of mineral P to dissolved forms. Since P content in rocks is generally low, microbial recycling of organic P forms plays an important role in supporting primary production and controlling ecosystem structure. Overall, the global P cycle has five main components: (1) tectonic uplift of P-bearing rocks (e.g., phosphorite); (2) physical and chemical weathering of rocks and minerals, generating soils as well as particulate and dissolved P forms; (3) P transport to water bodies via rivers, streams, groundwater, and aerosols; (4) P transport to the deep ocean via sedimentation of mineral P and particulate organic matter (marine snow); and (5) P burial in marine sediments and transformations and lithification after burial. The textbooks included below provide overviews of specific components of the P cycle. Schlesinger and Bernhardt 2013 is a comprehensive textbook dedicated to biogeochemistry, with insights into global biogeochemical cycles, including that of P cycle. Libes 1992 and Hansell and Carlson 2002 focus on marine biogeochemistry, with the former including an overview of the marine P cycle and the latter focusing on dissolved organic matter and the dynamics of dissolved organic P. Turner, et al. 2005 focuses on organic P in the environment, from its characterization to the biotic and abiotic processes controlling its reactivity in the environment. Selim 2015 is a compilation of studies examining the role P plays in enhancing or reducing the mobility of heavy metals in soil and the soil-water-plant environment. Nriagu and Moore 1984 is dedicated to P mineralogy, while Shergold and Cook 2005; Notholt, et al. 2005; and Burnett and Riggs 2006 focus on phosphorite deposits across geologic time. Lastly, Zapata and Roy 2004 combines research on the application of phosphate rocks in agriculture.

Burnett, W. C., and S. R. Riggs. 2006. *Phosphate deposits of the world. Vol. 3, Neogene to modern phosphorites*. Cambridge, UK: Cambridge Univ. Press.

This volume investigates the environmental setting and resulting phosphorus that formed during the Miocene, a recent major phosphogenic period.

Hansell, D. A., and C. A. Carlson. 2002. *Biogeochemistry of marine dissolved organic matter*. San Diego, CA: Elsevier.

This text focuses on marine dissolved organic matter (DOM) and presents analytic methods for different DOM pools in addition to insights into the processes controlling DOM reactivity, composition, and transformations.

Libes, Susan M. 1992. *An introduction to marine biogeochemistry*. 2d ed. Burlington, MA: Elsevier.

This book examines the physical and redox chemistry of seawater and marine sediments, as well as marine organic biogeochemistry and the issues of marine pollution.

Notholt, A. J. G., R. P. Sheldon, and D. F. Davidson. 2005. *Phosphate deposits of the world*. Vol. 2, *phosphate rock resources*. Cambridge, UK: Cambridge Univ. Press.

This book details most major individual deposits or phosphate fields of the world, both of igneous and sedimentary origin.

Nriagu, J. O., and P. H. Moore. 1984. *Phosphate minerals*. Berlin: Springer.

This mineralogy text is dedicated to phosphate minerals or their synthetic equivalents.

Schlesinger, W. H., and E. S. Bernhardt. 2013. *Biogeochemistry: An analysis of global change*. 3d ed. Amsterdam: Elsevier.

This book provides in-depth coverage of biogeochemical processes in terrestrial, freshwater, and marine ecosystems along with a synthesis of the major biogeochemical cycles.

Selim, H. M. 2015. *Phosphate in soils: Interaction with micronutrients, radionuclides and heavy metals*. Boca Raton, FL: Taylor & Francis.

This text brings together the latest research to highlight the role phosphate plays in enhancing or reducing the mobility of heavy metals in soil and the soil-water-plant environment.

Shergold, J. H., and P. J. Cook. 2005. *Phosphate deposits of the world*. Vol. 1, *Proterozoic and Cambrian phosphorites*. Cambridge, UK: Cambridge Univ. Press.

This text describes almost one hundred Precambrian or Cambrian phosphorite deposits around the world, detailing their distribution, nature, and origin.

Turner, B. L., E. Frossard, and D. S. Baldwin. 2005. *Organic phosphorus in the environment*. Cambridge, MA: CABI.

This book details the various approaches available for characterizing the chemical structure of organic P, as well as the processes controlling the dynamics of organic P in the environment. These include the abiotic stabilization and degradation of organic P, microbial processes, enzymatic hydrolysis, as well as P utilization by higher plants.

Zapata, F., and R. N. Roy. 2004. *Use of phosphate rocks for sustainable agriculture*. Rome: Food and Agriculture Organization of the United Nations.

This book is dedicated to research on the application of phosphate rock sources to agriculture.

Journals and Meetings

Phosphorus studies related to the environment are published in many different journals due to the interdisciplinary nature of this type of research. Some journals specialize in terrestrial research (e.g., *Geoderma*, *Soil Biology and Biochemistry*), aquatic systems (e.g., *Limnology and Oceanography*, *Marine Chemistry*, *Aquatic Geochemistry*), or agriculture systems (e.g., *Agricultural, Ecosystems & Environment*, *Agriculture Systems*) and others that are more general (e.g., *Geochimica et Cosmochimica Acta*, *Global Biogeochemical Cycles*, *Biogeochemistry*, *Environmental Science & Technology*, *Science of the Total Environment*, *Journal of Geophysical Research: Biogeosciences*). Some important work in P research can also be found in higher-impact journals such as *Science* and *Nature*. Relevant meetings for P research include the American Geophysical Union Meetings, the European Geophysical Union General Assembly, the Ocean Sciences meeting, the Goldschmidt Conference (the foremost international conference dedicated to geochemistry), and specialized workshops (e.g. Organic Phosphorus workshop).

***Aquatic Geochemistry*. 1995–.**

A journal published by Springer containing studies relating to aqueous geochemistry and the interactions of water with rocks and minerals on Earth's surface.

***Agriculture, Ecosystems & Environment*. 1974–.**

A journal published by Elsevier with a focus on research dedicated to the interactions between agroecosystems and the environment.

***Agricultural Systems*. 1976–.**

A journal published by Elsevier with studies focusing on interactions among the components of agricultural systems.

***Biogeochemistry*. 1984–.**

A journal published by Springer dealing with biotic controls on the chemistry of the environment, or with the geochemical control of the structure and function of ecosystems.

***Environmental Science & Technology*. 1967–.**

A journal published by the American Chemical Society that contains interdisciplinary studies focusing on environmental science.

***Geochimica et Cosmochimica Acta*. 1950–.**

A journal published by Elsevier that contains a wide range of studies focusing on isotope geochemistry and chemical processes in the atmosphere, hydrosphere, biosphere, and lithosphere.

***Geoderma*. 1967–.**

A journal published by Elsevier that contains interdisciplinary studies investigating soil processes.

***Global Biogeochemical Cycles*. 1980–.**

A journal published by the American Geophysical Union that contains studies centered on biogeochemical interactions, including local, regional, and global studies.

Journal of Geophysical Research: Biogeosciences. 2000–.

A journal published by the American Geophysical Union focusing on biogeosciences of the Earth system through time, and the extension of this research to planetary studies.

Limnology and Oceanography. 1950–.

A journal published by the Association for the Sciences of Limnology and Oceanography. It contains studies focusing on aquatic systems.

Marine Chemistry. 1972–.

A journal published by Elsevier containing studies dedicated to improving our understanding of chemical processes in the marine environment.

Science of the Total Environment. 1972–.

A journal published by Elsevier that contains interdisciplinary research investigating processes in the atmosphere, hydrosphere, biosphere, lithosphere, and anthroposphere.

Soil Biology and Biochemistry. 1969–.

A journal published by Elsevier that contains studies focusing on biological processes affecting nutrient cycling in soils and sediments.

Phosphorus Cycling in Terrestrial Environments

The weathering of bedrock on continents, specifically that of rocks containing P-bearing minerals like carbonate fluorapatite, is the main source of biologically available P to soils, groundwater, and surface water and in turn to terrestrial vegetation. In soils, P is subject to a number of biotic (e.g., mediated by enzymatic activity) and abiotic (e.g., sorption, desorption) processes that control the relative reactivity and bioavailability of a given P pool. Plants have developed efficient P scavenging mechanisms to optimize P uptake from soils despite low phosphate content in soil solution. A number of in-depth reviews have been published detailing the global P cycle (Ruttenberg 2014), including its changes over time as a result of anthropogenic activity (Filippelli 2008) and insights into terrestrial P stoichiometry and cycling dynamics (Elser, et al. 2000; Schlesinger and Bernhardt 2013, cited under General Overviews and Textbooks).

Elser, J. J., W. F. Fagan, R. F. Denno, et al. 2000. Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408:578–580.

A study investigating the ecological stoichiometry of terrestrial habitats, specifically the carbon, nitrogen, and phosphorus ratios of primary producers and primary consumers.

Filippelli, G. M. 2008. The global phosphorus cycle: Past, present, and future. *Elements* 4:89–95.

A review of the global biogeochemical P cycle through time.

Ruttenberg, K. C. 2014. The global phosphorus cycle. In *Treatise on geochemistry*. 2d ed. Vol. 10. Edited by Heinrich Holland and Karl Turekian, 499–558. Amsterdam: Elsevier.

A review of the global biogeochemical P cycle, including terrestrial and marine environments.

Soil Phosphorus Cycling

Most of soil P is present in the form of orthophosphate (PO_4^{3-}) compounds, both organic and inorganic in nature (Frossard, et al. 2000). The main abiotic processes involved in soil P transformations are precipitation-dissolution and adsorption-desorption reactions that control the transfer between solid-phase P and soil solution (Frossard, et al. 2000). Biotic processes in soils involve microbial P stabilization and remineralization and control the transfer of P between organic and inorganic forms (Richardson and Simpson 2011). The amount and chemical forms of P change substantially during soil development. The overall bioavailable P decreases over time due to soil leaching, the transformation of primary mineral phosphate into secondary minerals, and P occlusion in organic compounds (Walker and Syers 1976; Turner, et al. 2013; Roberts, et al. 2015). These changes lead to P depletion in old soils, and a reduction in vegetation productivity (Vitousek, et al. 2010). A wide array of analytical methods exists to study soil P cycling. These include colorimetric and fluorescent methods, X-ray spectroscopy, ^{31}P nuclear magnetic resonance spectroscopy (^{31}P NMR), compound-specific analyses, and soil fractionation schemes like the Hedley procedure, which is a widely used approach that separates operationally defined P pools based on chemical solubility (Hedley, et al. 1982). Recently, the use of tracers such as radioisotopes (^{32}P and ^{33}P) and stable oxygen isotopes in phosphate have enabled studies to elucidate P cycling dynamics and better constrain the rates of P transformations in soils (Frossard, et al. 2011; Roberts, et al. 2015).

Frossard, E., D. L. Achat, S. M. Bernasconi, et al. 2011. The use of tracers to investigate phosphate cycling in soil-plant systems. In *Phosphorus in Action*. Vol. 26. Edited by Else Bünemann, Astrid Oberson, and Emmanuel Frossard, 59–91. Berlin: Springer.

A review dedicated to the use of P radioisotopes and stable oxygen isotopes as tracers for studying the soil-plant system.

Frossard, E., L. M. Condron, S. Sinaj, and J. C. Fardeau. 2000. Processes governing phosphorus availability in temperate soils. *Journal of Environmental Quality* 29:15–23.

An overview of the biotic and abiotic factors controlling soil P cycling.

Hedley, M. J., J. W. B. Stewart, and B. S. Chauhan. 1982. Changes in inorganic and organic soil phosphorus fractions induced by cultivation practices and by laboratory incubations. *Soil Science Society of America Journal* 46:970–976.

A method paper presenting the Hedley soil fractionation scheme, a widely used method for studying soil P cycling.

Richardson, A. E., and R. J. Simpson. 2011. Soil Microorganisms Mediating Phosphorus Availability. *Plant Physiology* 156:989–996.

An overview of the microbial mechanisms enhancing P availability in soils.

Roberts, K., D. Defforey, B. L. Turner, et al. 2015. Oxygen isotopes of phosphate and soil phosphorus cycling across a 6500 year chronosequence under lowland temperate rainforest. *Geoderma* 257–258:14–21.

A study that focuses on P cycling along a 6,500-year chronosequence.

Turner, B. L., H. Lambers, M. D. Cramer, J. R. Leake, A. E. Richardson, and S. E. Smith. 2013. Soil microbial biomass and the fate of phosphorus during long-term ecosystem development. *Plant and Soil* 367:225–234.

A study investigating soil P availability in a 120,000-year chronosequence and the role of microbial biomass in determining P availability as ecosystems mature.

Vitousek, P. M., S. Porder, B. Z. Houlton, and O. A. Chadwick. 2010. Terrestrial phosphorus limitation: Mechanisms, implications, and nitrogen-phosphorus interactions. *Ecological Applications* 20:5–15.

A review of the processes leading to P limitation in terrestrial ecosystems.

Walker, T. W., and J. K. Syers. 1976. The fate of phosphorus during pedogenesis. *Geoderma* 15:1–19.

A study investigating soil P transformations during pedogenesis across a range of soil sequences in New Zealand.

Phosphorus in Terrestrial Vegetation

Phosphorus is an important macronutrient for plants, and P bioavailability is limited since inorganic P (orthophosphate) content in soil solutions is low while plant requirements are high (Bielecki 1973; Schachtman, et al. 1998). To counter this, plants rely on specialized transporters at the root-soil interface to optimize P extraction from soil solutions and mechanisms for inorganic P transport across membranes allowing intracellular inorganic P content to be up to three orders of magnitude larger than that in soil solution (Schachtman, et al. 1998). In addition, the physical, chemical, and biological properties and interactions of the rhizosphere and the structural and functional structure of roots play an important role in nutrient acquisition (Richardson, et al. 2009). Research in the field of P uptake by plants is particularly relevant for agricultural, economic, and environmental conservation, since P is frequently a limiting nutrient for plant growth and development, and the application of P fertilizers results in runoff from P-loaded soils, contributing to eutrophication and hypoxia in lakes, estuaries, and the coastal ocean (Vance, et al. 2003). For these reasons, there is a growing interest in developing P-efficient plants to minimize fertilizer P inputs and reduce the potential for P loss to the environment (Richardson, et al. 2011). Another growing area of research focuses on the effects of simulated global climate change on plant P stoichiometry, as well as P cycling and demand (Menge and Field 2007; Yuan and Chen 2015; Mellett, et al. 2017). As with soil P studies, radioisotopes, ^{31}P NMR, as well as ratios of P to carbon and nitrogen and molecular analyses are used to study P processes within plants (Bielecki 1973; Schachtman, et al. 1998). In addition, stable oxygen isotopes in phosphate are also becoming a tool to trace biological transformations of P in plants (Pfahler, et al. 2012) and will substantially enhance our understanding of the controls of P transformations in vascular plants.

Bielecki, R. 1973. Phosphate pools, phosphate transport, and phosphate availability. *Annual Review of Plant Physiology* 24:225–252.

A review of P uptake, transport, transformations, and storage in plants.

Mellett, T., C. Selvin, D. Defforey, et al. 2017. Assessing cumulative effects of climate change manipulations on phosphorus limitation in a Californian grassland. *Environmental Science and Technology* 52:98–106.

A follow-up study to Menge and Field 2007 to assess changes and progression of P status with time in an annual grassland under simulated climate change conditions.

Menge, D. L., and C. B. Field. 2007. Simulated global changes alter phosphorus demand in an annual grassland. *Global Change Biology* 13:2582–2591.

A study investigating the changes in P cycling in an annual grassland under simulated climate change conditions.

Pfahler, V. T. Dürr-Auster, F. Tamburini, S. M. Bernasconi, and E. Frossard. 2012. ^{18}O enrichment in phosphorus pools extracted from soybean leaves. *New Phytologist* 197:186–193.

This study investigates the isotopic composition of oxygen in phosphate in different P pools in plant leaves.

Richardson, A. E., J. -M. Barea, A. M. McNeill, and C. Prigent-Combaret. 2009. Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. *Plant and Soil* 321:305–339.

An overview of nutrient uptake in the rhizosphere and the role of soil microorganisms in enhancing nutrient uptake.

Richardson, A. E., J. P. Lynch, P. R. Ryan, et al. 2011. Plant and microbial strategies to improve the phosphorus efficiency of agriculture. *Plant and Soil* 349:121–156.

A study assessing plant strategies for efficient P uptake.

Schachtman, D. P., R. J. Reid, and S. M. Ayling. 1998. Phosphorus uptake by plants: From soil to cell. *Plant Physiology* 116:447–453.

An article reviewing P acquisition, transport, and metabolism in plants.

Vance, C. P., C. Uhde-Stone, and D. L. Allan. 2003. Phosphorus acquisition and use: Critical adaptations by plants for securing a nonrenewable resource. *New Phytologist* 157:423–447.

An overview of P uptake by plants and their physiological adaptations to P deficiencies.

Yuan, Z. Y., and H. Y. H. Chen. 2015. Decoupling of nitrogen and phosphorus in terrestrial plants associated with global changes. *Nature Climate Change* 5:465–469.

A meta-analysis of 1,418 studies demonstrating changes in plant stoichiometry in response to simulated global change conditions.

Phosphorus in Rivers, Streams, and Lakes

Rivers and streams act as the main pathway for transporting P, in both particulate and dissolved forms, to lakes, wetlands, and the coastal ocean. During transport, P is exposed to a number of processes that alter its chemical reactivity. Those processes involve P assimilation and retention by macrophytes, periphyton, and microorganisms, P retention and release by soils and sediments, sorption-desorption reactions, advection and diffusion, and mineral precipitation-dissolution in the water column (Reddy, et al. 1999; Withers and Jarvie 2008). P sources to this system are varied and involve natural and anthropogenic sources, the latter including (1) wastewaters, (2) runoff from impervious surfaces (atmospheric deposition, runoff from roads, roofs), and (3) runoff from pervious surfaces, which include forests and agricultural lands (Withers and Jarvie 2008). These sources may be constrained through the use of oxygen isotopes in phosphate, which may reflect the source of phosphate when not in equilibrium with ambient water (Young, et al. 2009). Rivers deliver P to lakes, where organic and inorganic forms in the water column are subject to similar transformations as in rivers and lead to an increase in primary production in P limited systems (Elser, et al. 2007). Phytoplankton and particulate forms sinking to lake sediments can be characterized with ³¹P NMR (Reitzel, et al. 2007). Dissolved organic P can be analyzed with ³¹P NMR as well, but require pre-concentration prior to analysis. One means of doing so without the use of reverse osmosis involves co-precipitating nonreactive P with aluminum. This process has been used for revealing the prevalence of orthophosphate monoesters and diesters in dissolved organic P in lakes (Reitzel, et al. 2009). P forms in lake sediments are degraded at varying rates, with orthophosphate monoesters and teichoic acids being remineralized more slowly than DNA-P, polyphosphates, and phospholipids (Reitzel, et al. 2007). Lake sediments can also act as a source of P to the water column, as a number of mechanisms can lead to the release of P: redox conditions, microbial activity/remineralization, resuspension, temperature, pH, iron:phosphorus ratio, chemical diffusion and bioturbation and, in shallow lakes, submerged macrophytes (Søndergaard, et al. 2003). Because of this, internal P loading from sediments may hinder mitigation efforts to improve lake water quality (Paytan, et al., 2017).

Elser, J. J., M. E. S. Bracken, E. E. Cleland, et al. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* 10:1135–1142.

A meta-analysis of global freshwater, marine, and terrestrial experiments comparing growth responses across aquatic and terrestrial realms.

Paytan, A., K. Roberts, S. Watson, et al. 2017. Internal loading of phosphate in Lake Erie Central Basin. *Science of the Total Environment* 579:1356–1365.

A study examining P fluxes from sediments into the water column at Lake Erie, the shallowest of the Great Lakes, suffering from large algal blooms and anoxic events.

Reddy, K. R., R. H. Kadlec, E. Flaig, and P. M. Gale. 1999. Phosphorus retention in streams and wetlands: A review. *Critical Reviews in Environmental Science and Technology* 29:83–146.

An overview of the processes controlling P retention and cycling in streams and wetlands.

Reitzel, K., J. Ahlgren, H. DeBrabandere, et al. 2007. Degradation rates of organic phosphorus in lake sediment. *Biogeochemistry* 82:15–28.

A study investigating the nature of organic P in phytoplankton, sinking particulates, and sediments from the Swedish mesotrophic Lake Erken using ³¹P NMR.

Reitzel, K., H. S. Jensen, M. Flindt, and F. Ø. Andersen. 2009. Identification of dissolved nonreactive phosphorus in freshwater by precipitation with aluminium and subsequent ³¹P NMR analysis. *Environmental Science & Technology* 43:5391–5397.

A new method enhancing the use of ³¹P nuclear magnetic resonance spectroscopy to study dissolved nonreactive P in lakes.

Søndergaard, M., J. P. Jensen, and E. Jeppesen. 2003. Role of sediment and internal loading of phosphorus in shallow lakes. *Hydrobiologia* 506:135–145.

A review of controls of P retention and release from lake sediments.

Withers, P. J. A., and H. P. Jarvie. 2008. Delivery and cycling of phosphorus in rivers: A review. *Science of the Total Environment* 400:379–395.

A review investigating P dynamics in riverine systems.

Young, M. B., C. Kendall, W. Stringfellow, et al. 2009. Characterizing the oxygen isotopic composition of phosphate sources to aquatic ecosystems. *Environmental Science & Technology* 43:5190–5196.

A study that uses oxygen isotopes in phosphate as a tracer for P sources to aquatic systems.

Phosphorus in Wetlands

Wetlands are hotspots of biogeochemical activity and encompass a broad number of ecosystems, including swamps, marshes, fens, peatlands, bogs, potholes, bays, riparian zones, floodplains, and other shallow flooded areas (Reddy, et al. 2000). P inputs to these

ecosystems can include rivers, streams, groundwater, and/or aerosol deposition. As with other freshwater bodies, P is present in wetlands in varying proportions of organic and inorganic forms depending on the characteristics of the surrounding watershed (Dunne and Reddy 2005). These are subject to biotic and abiotic processes in the water column as described in the previous section. P forms are also deposited in the underlying soil via sedimentation, adsorbed, precipitated and/or exchanged between soil and the overlying water (Dunne and Reddy 2005). Given their prolonged saturation, wetland soils (organic or mineral) have unique physical, chemical (including redox conditions, metal content and pH), biological, and morphological characteristics compared to their upland counterparts (Reddy, et al. 2000). A number of studies have focused on the biotic and abiotic controls of P retention in wetlands with varying nutrient levels, including ombrotrophic peatlands, and on the nature of organic P in these ecosystems (Kellogg and Bridgman 2003; Turner and Newman 2005; Dunne and Reddy 2005; Cheesman, et al. 2010; Sjögersten, et al. 2011). While anthropogenic impacts on P cycling in natural wetlands have been well documented (Dunne and Reddy 2005; Verhoeven, et al. 2006), long-term trends of P in these ecosystems throughout the Holocene, however, remain poorly constrained.

Cheesman, A. W., E. J. Dunne, B. L. Turner, and K. R. Reddy. 2010. Soil phosphorus forms in hydrologically isolated wetlands and surrounding pasture uplands. *Journal of Environmental Quality* 39:1517–1525.

A study comparing P forms in wetland and surrounding upland pasture soils.

Dunne, E. J., and K. R. Reddy. 2005. Phosphorus biogeochemistry of wetlands in agricultural watersheds. In *Nutrient management in agricultural watersheds: A wetlands solution*. Edited by E. J. Dunne, K. R. Reddy, and O. T. Carton, 105–119. Wageningen, The Netherlands: Wageningen Academic.

A chapter on P biogeochemistry in wetlands located within agricultural watersheds.

Kellogg, L. E., and S. D. Bridgman. 2003. Phosphorus retention and movement across an ombrotrophic-minerotrophic peatland gradient. *Biogeochemistry* 63:299–315.

A study of the mechanisms underlying P retention and movement along a hydrologic and pH gradient in northern peatlands.

Reddy, K. R., E. M. D'Angelo, and W. G. Harris. 2000. Biogeochemistry of wetlands. In *Handbook of soil science*. Edited by Malcolm E. Sumner, G89–G119. Boca Raton, FL: CRC Press.

A chapter dedicated to wetlands and associated biogeochemical processes.

Sjögersten, S., A. W. Cheesman, O. Lopez, and B. L. Turner. 2011. Biogeochemical processes along a nutrient gradient in a tropical ombrotrophic peatland. *Biogeochemistry* 104:147–163.

A study of P biogeochemical processes along a strong nutrient gradient in a tropical ombrotrophic peatland.

Turner, B. L., and S. Newman. 2005. Phosphorus cycling in wetland soils: The importance of phosphate diesters. *Journal of Environmental Quality* 34:1921–1929.

A study that uses solution ³¹P NMR to quantify organic and inorganic phosphates in the northern Florida Everglades (USA).

Verhoeven, J. T. A., B. Arheimer, C. Yin, and M. M. Hefting. 2006. Regional and global concerns over wetlands and water quality. *TRENDS in Ecology and Evolution* 21:96–103.

A review of the practice of using wetlands to manage water quality in catchments impacted by agricultural activity.

Atmospheric Transport and Deposition of Phosphorus

Unlike carbon and nitrogen, P does not have a stable gaseous phase; therefore atmospheric transport of P is mainly restricted to particulate aerosols. The largest sources of atmospheric P (>10 µm in size) are mineral dust and primary biogenic particles (e.g., spores), and other important sources include biomass burning, fossil fuels, biofuels, volcanic activity, and sea salts (Mahowald, et al. 2008). A recent study has shown that the perturbation of the atmospheric P cycle due to anthropogenic emissions is larger than previously believed and that combustion-related emissions represent over 50 percent of global atmospheric sources of phosphorus (Wang, et al. 2015). Atmospheric P occurs in particulate and dissolved (in rain and fog) forms and can include a broad array of inorganic and organic P forms depending on its source. Chemical transformations during atmospheric transport, such as atmospheric acidification of aerosols, can produce soluble, more bioavailable P forms from soil-derived minerals (Nenes, et al. 2011). This is an important process since P aerosols from natural sources are less soluble and bioavailable than P aerosols from anthropogenic sources (Anderson, et al. 2010). The distance over which P-bearing aerosols travel depends in part on the size of particles, with larger particles being deposited closer to their source and long-range transport mainly involving fine dust and small particulates (Tipping, et al. 2014). The deposition of P aerosols (including wet and dry deposition) can lead to changes in nutrient stoichiometry and primary productivity, particularly in oligotrophic lakes and ombrotrophic peatlands (Brahney, et al. 2015; Tipping, et al. 2014). Such effects are also observed in the marine environment where P co-limitation can occur, for example in the North Atlantic (Mills, et al. 2004) and this input can influence ecosystem dynamics in the surface ocean (Chien, et al. 2016).

Anderson, L. D., K. L. Faul, and A. Paytan. 2010. Phosphorus associations in aerosols: What can they tell us about P bioavailability? *Marine Chemistry* 120:44–56.

A study investigating the solubility and bioavailability of P in aerosols collected in the Gulf of Aqaba.

Brahney, J., N. Mahowald, D. S. Ward, A. P. Ballantyne, and J. C. Neff. 2015. Is atmospheric phosphorus pollution altering global alpine lake stoichiometry? *Global Biogeochemical Cycles* 29:1369–1383.

A study assessing the impacts of anthropogenic activities on the chemistry of wet deposition and on the water chemistry of alpine lakes.

Chien, C. T., K. R. M. Mackey, S. Dutkiewicz, N. M. Mahowald, J. M. Prospero, and A. Paytan. 2016. Effects of African dust deposition on phytoplankton in the western tropical Atlantic Ocean off Barbados. *Global Biogeochemical Cycles* 30:716–734.

A study demonstrating the impacts of atmospheric P deposition on phytoplankton distribution in the surface ocean.

Mahowald, N., T. D. Jickells, A. R. Baker, et al. 2008. Global distribution of atmospheric phosphorus sources, concentrations and deposition rates, and anthropogenic impacts. *Global Biogeochemical Cycles* 22:GB4026.

This study combines global atmospheric P concentrations, deposition flux observations, and transport model simulations to assess global P sources to the atmosphere and P deposition rates.

Mills, M. M., C. Ridame, M. Davey, J. La Roche, and R. J. Geider. 2004. Iron and phosphorus co-limit nitrogen fixation in the eastern tropical North Atlantic. *Nature* 429:292–294.

A study investigating the impacts of aerosol deposition on primary productivity using incubation experiments of samples collected in the North Atlantic.

Nenes, A., M. D. Krom, N. Mihalopoulos, et al. 2011. Atmospheric acidification of mineral aerosols: A source of bioavailable phosphorus for the oceans. *Atmospheric Chemistry and Physics* 11:6265–6272.

A study that combines aerosol measurements and thermodynamic modeling to show that acid processing of mineral aerosols is an important pathway of water soluble P in the atmosphere.

Tipping, E., S. Benham, J. F. Boyle, et al. 2014. Atmospheric deposition of phosphorus to land and freshwater. *Environmental Science: Processes & Impacts* 16:1608–1617.

A compilation of measurements of global P atmospheric deposition rates.

Wang, R., Y. Balkanski, O. Boucher, P. Ciais, J. Peñuelas, and S. Tao. 2015. Significant contribution of combustion-related emissions to the atmospheric phosphorus budget. *Nature Geoscience* 8:48–54.

This study uses measurements of P in fuels and a global transport model to determine the contribution of combustion-related emissions to the atmospheric P budget.

Phosphorus in the Marine Environment

The main source of P to the ocean is via continental weathering, and is primarily transported in dissolved and particulate forms via riverine fluxes (Benitez-Nelson 2000; Paytan and McLaughlin 2007). As detailed in the previous section, atmospheric deposition of aerosols, volcanic ash, and mineral dust can also be an important source of P, particularly in the subtropical gyres (Paytan and McLaughlin 2007). These fluxes have been altered by anthropogenic activity, and indicate that the oceanic P budget is unbalanced since P sinks in the ocean (burial in sediments) exceed continental inputs in the form of particulate and dissolved P (Wallman 2010). A number of in-depth reviews have focused on the marine P cycle and the many P transformations in the oceanic water column (Paytan and McLaughlin 2007) and marine sediments (Defforey and Paytan 2018), with several dedicated to the role of microorganisms in marine P cycling (Dyhrman, et al. 2007; Karl 2014).

Benitez-Nelson, C. R. 2000. The biogeochemical cycling of phosphorus in marine systems. *Earth-Science Reviews* 51:109–135.

An overview of P cycling in the marine environment.

Defforey, D., and A. Paytan. 2018. Phosphorus cycling in marine sediments: Advances and challenges. *Chemical Geology* 477:1–11.

A review of the advances made in our understanding of phosphorus cycling in marine sediments and of the methods used in this field.

Dyhrman, S. T., J. W. Ammerman, and B. A. S. Van Mooy. 2007. Microbes and the marine phosphorus cycle. *Oceanography* 20:110–116.

This is an overview of the role microorganisms play in transforming P in the marine environment, specifically dissolved organic P.

Karl, D. M. 2014. Microbially mediated transformations of phosphorus in the sea: New views of an old cycle. *Annual Review of Marine Science* 6:279–337.

A thorough review of microbially mediated processes impacting P cycling in the marine environment.

Paytan, A., and K. McLaughlin. 2007. The oceanic phosphorus cycle. *Chemical Reviews* 107:563–576.

A review of P cycling in the marine environment, including P sources, sinks, forms, and transformations in the water column and sediments, as well as the impact of microbial processes on P cycling.

Wallman, K. 2010. Phosphorus imbalance in the global ocean? *Global Biogeochemical Cycles* 24:GB4030.

A review of the imbalances in the marine P cycle due to anthropogenic activity.

Phosphorus Dynamics in the Marine Water Column

Phosphorus in the marine environment exists in dissolved and particulate phases throughout the water column, both containing inorganic P (orthophosphate, pyrophosphate, polyphosphate, and phosphate-bearing minerals) and organic P (orthophosphate monoesters, diesters and phosphonates) forms. Both particulate and dissolved organic matter (DOM) are continuously produced and remineralized in the water column, with the latter representing the dominant form of OM in the oceans (Sannigrahi, et al. 2006). This DOM pool is distinct chemically from the particulate organic matter (POM) pool, suggesting it does not originate from a simple solubilization of POM (Paytan, et al. 2003; Sannigrahi, et al. 2006). It is dominated by orthophosphate monoesters (80–85 percent), but also contains phosphonates (5–10 percent) and polyphosphates (8–13 percent; Young and Ingall 2010). Dissolved inorganic P (DIP) is rapidly assimilated by phytoplankton and autotrophic bacteria in the photic zone and modified into organic compounds (Paytan and McLaughlin 2007, cited under Phosphorus in the Marine Environment). In oligotrophic regions of the ocean where DIP is scarce (e.g., the Sargasso Sea), dissolved organic P (DOP) remineralization in the photic zone can account for as much as 82 percent of P utilized by phytoplankton (Lomas, et al. 2010; McLaughlin, et al. 2013). Furthermore, recent work has shown that phytoplankton may reduce their cellular P requirements by substituting non-P membrane lipids for phospholipids, and also use reduced P compounds (phosphonates and/or phosphite) as a P source suggesting the existence of a vast P redox cycle (Van Mooy, et al. 2009; Van Mooy, et al. 2015). DIP and DOP are released by zooplankton excretion, and phytoplankton cell lysis, and subject to sorption-desorption processes with sinking POM (Paytan and McLaughlin 2007). A number of studies have investigated the chemical forms of particulates exported to the deep ocean using sediment traps, sequential extractions, and ³¹P NMR analyses (Paytan, et al. 2003; Faul, et al. 2005). They reveal that sinking particulates are mainly composed of reactive components that include acid-insoluble organic P (~40 percent), authigenic apatite (~25 percent) and oxide-associated and labile P (~21 percent), with small proportions of unreactive detrital apatite (13 percent; Faul, et al. 2005). They further demonstrate that POM is continuously remineralized as particulates are exported to the deep ocean.

Faul, K. L., A. Paytan, and M. L. Delaney. 2005. Phosphorus distribution in sinking oceanic particulate matter. *Marine Chemistry* 97:307–333.

This study assesses the different P forms in sinking marine particulates using a sequential extraction scheme.

Lomas, M. W., A. L. Burke, D. A. Lomas, et al. 2010. Sargasso Sea phosphorus biogeochemistry: An important role for dissolved organic phosphorus (DOP). *Biogeosciences* 7:695–710.

This study examines the role of dissolved organic P in fueling production in the Sargasso Sea, where primary production is limited by inorganic P.

McLaughlin, K., J. A. Sohm, G. A. Cutter, M. W. Lomas, and A. Paytan. 2013. Phosphorus cycling in the Sargasso Sea: Investigation using the oxygen isotopic composition of phosphate, enzyme-labeled fluorescence, and turnover times. *Global Biogeochemical Cycles* 27:375–387.

This study investigates P cycling in the photic zone of the oligotrophic, P-limited Sargasso Sea using a combination of stable isotopes, enzyme-labeled fluorescence and ³³P-labeled DIP turnover time estimates.

Paytan, A., B. J. Cade-Menun, K. McLaughlin, and K. L. Faul. 2003. Selective phosphorus regeneration of sinking marine particles: Evidence from ^{31}P -NMR. *Marine Chemistry* 82:55–70.

A study focusing on the transformations of P in sinking marine particulates using ^{31}P nuclear magnetic resonance spectroscopy.

Sannigrahi, P., E. D. Ingall, and R. Benner. 2006. Nature and dynamics of phosphorus-containing components of marine dissolved and particulate organic matter. *Geochimica et Cosmochimica Acta* 70:5868–5882.

A study investigating the nature of organic P in marine dissolved and particulate organic matter using ^{13}C and ^{31}P nuclear magnetic resonance spectroscopy.

Van Mooy, B. A. S., H. F., Fredricks, B. E., Pedler, et al. 2009. Phytoplankton in the ocean substitute lipids in response to phosphorus scarcity. *Nature* 458:69–72.

This study demonstrates how phytoplankton combat low P availability by lowering the P-lipids content in their cells.

Van Mooy, B. A. S., A. Krupke, S. T. Dyrman, et al. 2015. Major role of planktonic phosphate reduction in the marine phosphorus redox cycle. *Science* 348:783–785.

This study presents evidence suggesting the existence of a vast oceanic redox phosphorus cycle.

Young, C. L., and E. D. Ingall. 2010. Marine dissolved organic phosphorus composition: Insights from samples recovered using combined electro dialysis/reverse osmosis. *Aquatic Geochemistry* 16:563–574.

This study uses electro dialysis and reverse osmosis to concentrate dissolved organic matter for thirty-one P nuclear magnetic resonance spectroscopy analyses in order to investigate P compounds in this pool.

Sedimentary Phosphorus Cycling

Sediments are the main P sink in the marine P cycle, and the specific association of P with various sediment components after burial depends on sedimentary redox conditions. P is exported to the seafloor in the form of inorganic and organic particulates. Upon reaching the seawater-sediment interface, reactive P forms are subject to a number of abiotic and biological transformations, while unreactive (detrital) phases are passively buried. Reactive P can be quantified using sequential extraction schemes (e.g., SEDEX) and is made up of easily exchangeable P, oxide associated-P, authigenic and biogenic apatite, calcium carbonate-bound P, and organic P (Ruttenberg 1992). Such extractions have enabled detailed studies on the controls of P accumulation and concentrations in marine sediments (Filippelli 1997). Studying the chemical structure of P in marine sediments is difficult due to low P concentrations, but ^{31}P NMR and X-ray fluorescence spectromicroscopy have been successfully applied to study the nature of organic P and P-bearing minerals (Ingall, et al. 1990; Carman, et al. 2000; Brandes, et al. 2007). The dynamics of sedimentary P are complex, with diagenesis leading to a redistribution of P between phases as a function of changing redox conditions and microbial activity. Such transformations can be studied using radioisotopes (^{33}P), which yield valuable insights into microbial inorganic P cycling by tracing microbial P uptake and inorganic P turnover (Goldhammer, et al. 2010). Biotic and abiotic sedimentary P processes can be further traced and P turnover rates estimated using stable oxygen isotopes in phosphate in porewater and in solid-phase P phases (Jaisi and Blake 2010; Goldhammer, et al. 2011). The advent of such methods has substantially improved our understanding of P dynamics in marine sediments and will continue to answer longstanding questions regarding the fate of P after burial.

Brandes, J. A., E. D. Ingall, and D. Patterson. 2007. Characterization of minerals and organic phosphorus species in marine sediments using soft X-ray fluorescence spectromicroscopy. *Marine Chemistry* 103:250–265.

This study uses P near-edge x-ray fluorescence spectroscopy to assess inorganic and organic sedimentary P forms.

Carman, R., G. Edlund, and C. Damberg. 2000. Distribution of organic and inorganic phosphorus compounds in marine and lacustrine sediments: A ^{31}P NMR study. *Chemical Geology* 163:101–114.

A study determining the organic P forms in marine and lacustrine sediments with varying redox conditions using ^{31}P nuclear magnetic resonance spectroscopy.

Filippelli, G. M. 1997. Controls on phosphorus concentration and accumulation in oceanic sediments. *Geochimica et Cosmochimica Acta* 60:1479–1495.

This study compiles sedimentary P geochemistry data from the world's oceans and assesses the factors controlling P accumulation in marine sediments.

Goldhammer, T., V. Brüchert, T. G. Ferdelman. 2010. Microbial sequestration of phosphorus in anoxic upwelling sediments. *Nature Geoscience* 3:557–561.

In this study, ^{33}P radiotracers are used to study bacterial apatite formation in anoxic marine sediments.

Goldhammer, T., B. Brunner, S. M. Bernasconi, T. G. Ferdelman, and M. Zabel. 2011. Phosphate oxygen isotopes: Insights into sedimentary phosphorus cycling from the Benguela upwelling system. *Geochimica et Cosmochimica Acta* 75:3741–3756.

This study uses oxygen isotope ratios in porewater phosphate to investigate P cycling in marine sediments on the Namibian continental shelf.

Ingall, E. D., P. A. Schroeder, and R. A. Berner. 1990. The nature of organic phosphorus in marine sediments: New insights from ^{31}P NMR. *Geochimica et Cosmochimica Acta* 54:2617–2620.

This study assesses the nature of organic P in marine sediments (continental shelf, lower slope, and pelagic sediments) using solution and solid-state ^{31}P nuclear magnetic resonance spectroscopy.

Jaisi, D., and R. E. Blake. 2010. Tracing sources and cycling of phosphorus in Peru Margin sediments using oxygen isotopes in authigenic and detrital phosphates. *Geochimica et Cosmochimica Acta* 74:3199–3212.

This study uses sequential sediment extractions and oxygen isotope ratios in solid-phase phosphate to characterize P sources and transformations in marine sediments.

Ruttenberg, K. C. 1992. Development of a sequential extraction method for different forms of phosphorus in marine sediments. *Limnology and Oceanography* 37:1460–1482.

This study presents a sequential extraction method for marine sediments (SEDEX) that is widely used in the field of sedimentary P research.

Phosphorite Deposits and Mineral P Inventory

Phosphorites are authigenic deposits of which the main mineralogical constituent is carbonate fluorapatite (Kolodny 2009). They constitute the main source of phosphate rock for P fertilizers used in agriculture and current global reserves may be depleted in fifty to one hundred years (Cordell, et al. 2009). For this reason, current efforts are focusing on minimizing P runoff from agricultural soils, optimizing plant P uptake, and encouraging P recycling (Koppelaar and Weikard 2013). Phosphorite deposits are derived from the microbial respiration of organic matter and by iron and manganese redox cycles (Föllmi 1996). Both processes release dissolved inorganic P in marine sediment porewater, which reacts with calcium ions to form insoluble calcium phosphate compounds such as carbonate fluorapatite. Modern sites of phosphorite formation are mainly located in high primary productivity regions of the world's oceans characterized by the occurrence of pronounced oxygen-minimum zones and the development of laminated sediments, such as upwelling areas (Föllmi 1996). At present, phosphorite formation is not widespread and has been reported on the Namibian shelf, the continental margin of Peru and Mexico, the eastern Australian margin, and the Oman margin (Schenau, et al. 2000, Ruttenberg 2014).

Cordell, D., J. -O. Drangert, and S. White. 2009. The story of phosphorus: Global food security and food for thought. *Global Environmental Change* 19:292–305.

This study emphasizes the importance of including long-term phosphorus scarcity on the priority agenda for global food security given that phosphate rocks are a non-renewable source of P.

Föllmi, K. B. 1996. The phosphorus cycle, phosphogenesis and marine phosphate-rich deposits. *Earth-Science Reviews* 40:55–124.

An overview of the global P cycle, along with the formation mechanisms of phosphate-rich deposits.

Kolodny, Y. 2009. Phosphorite. In *Encyclopedia of Paleoclimatology and Ancient Environments*. Edited by Vivien Gornitz, 775–780. Dordrecht, The Netherlands: Springer.

An overview of phosphorites and the use of phosphate-rich rocks for agriculture.

Koppelaar, R. H. E. M., and H. P. Weikard. 2013. Assessing phosphate rock depletion and phosphorus recycling options. *Global Environmental Change* 23:1454–1466.

An assessment of P flows and phosphate rock availability for fertilizer use in 2009, along with a quantification of the costs and benefits of P use reduction and recycling.

Ruttenberg, K. C. 2014. The global phosphorus cycle. In *Treatise on Geochemistry*. 2d ed. Vol. 10. Edited by Heinrich Holland and Karl Turekian, 499–558. Amsterdam: Elsevier.

A review of the global biogeochemical P cycle, including terrestrial and marine environments.

Schenau S., C. P. Slomp, and G. J. DeLange. 2000. Phosphogenesis and active phosphorite formation in sediments from the Arabian Sea oxygen minimum zone. *Marine Geology* 169:1–20.

A study combining porewater chemistry, solid-phase analysis, and microscopic observations to demonstrate the present-day formation of phosphorites in the Arabian Sea oxygen minimum zone.

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