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REGULAR ARTICLE

Organic phosphorus in the terrestrial environment: a perspective on the state of the art and future priorities

T. S. George · C. D. Giles · D. Menezes-Blackburn · L. M. Condron · A. C. Gama-Rodrigues · D. Jaisi · F. Lang · A. L. Neal · M. I. Stutter · D. S. Almeida · R. Bol · K. G. Cabugao · L. Celi · J. B. Cotner · G. Feng · D. S. Goll · M. Hallama · J. Krueger · C. Plassard · A. Rosling · T. Darch · T. Fraser · R. Giesler · A. E. Richardson · F. Tamburini · C. A. Shand · D. G. Lumsdon · H. Zhang · M. S. A. Blackwell · C. Wearing · M. M. Mezeli · Å. R. Almås · Y. Audette · I. Bertrand · E. Beyhaut · G. Boitt · N. Bradshaw · C. A. Brearley · T. W. Bruulsema · P. Ciais · V. Cozzolino · P. C. Duran · M. L. Mora · A. B. de Menezes · R. J. Dodd · K. Dunfield · C. Engl · J. J. Frazão · G. Garland · J. L. González Jiménez · J. Graca · S. J. Granger · A. F. Harrison · C. Heuck · E. Q. Hou · P. J. Johnes · K. Kaiser · H. A. Kjær · E. Klumpp · A. L. Lamb · K. A. Macintosh · E. B. Mackay · J. McGrath · C. McIntyre · T. McLaren · E. Mészáros · A. Missong · M. Mooshammer · C. P. Negrón · L. A. Nelson · V. Pfahler · P. Poblete-Grant · M. Randall · A. Seguel · K. Seth · A. C. Smith · M. M. Smits · J. A. Sobarzo · M. Spohn · K. Tawaraya · M. Tibbett · P. Voroney · H. Wallander · L. Wang · J. Wasaki · P. M. Haygarth

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Abstract
Background The dynamics of phosphorus (P) in the environment is important for regulating nutrient cycles in natural and managed ecosystems and an integral part in assessing biological resilience against environmental change. Organic P (P_o) compounds play key roles in biological and ecosystems function in the terrestrial environment being critical to cell function, growth and reproduction.
Scope We asked a group of experts to consider the global issues associated with P_o in the terrestrial

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Responsible Editor: Hans Lambers

T. S. George (✉) · C. D. Giles · M. M. Mezeli
The James Hutton Institute, Dundee DD2 5DA, UK
e-mail: tim.george@hutton.ac.uk

M. I. Stutter · C. A. Shand · D. G. Lumsdon
The James Hutton Institute, Aberdeen AB15 8QH, UK

D. Menezes-Blackburn · H. Zhang · C. Wearing · P. M. Haygarth
Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

L. M. Condron · G. Boitt · K. Seth
Lincoln University, Lincoln, Christchurch 7647, New Zealand

A. C. Gama-Rodrigues
Universidade Estadual do Norte Fluminense Darcy Ribeiro (UENF - Laboratório de Solos), Av. Alberto Lamego 2000, Campos dos Goytacazes, RJ, Brazil

D. Jaisi
Plant and Soil Sciences, University of Delaware, 160 Townsend Hall, Newark, DE 19716, USA

F. Lang · J. Krueger
Faculty of Environment and Natural Resources, Chair of Soil Ecology, University of Freiburg, Bertoldstraße 17, 79098 Freiburg, Germany

environment, methodological strengths and weaknesses, benefits to be gained from understanding the P_o cycle, and to set priorities for P_o research.

Conclusions We identified seven key opportunities for P_o research including: the need for integrated, quality controlled and functionally based methodologies; assessment of stoichiometry with other elements in organic matter; understanding the dynamics of P_o in natural and managed systems; the role of microorganisms in controlling P_o cycles; the implications of nanoparticles in the environment and the need for better modelling and communication of the research. Each priority is discussed and a statement of intent for the P_o research community is made that highlights there are key contributions to be made toward understanding biogeochemical cycles, dynamics and function of natural ecosystems and the management of agricultural systems.

Keywords Ecosystems services · Method development · Microbiome · Modelling · Organic phosphorus · Stoichiometry

Abbreviations

δ18OP	Oxygen-18 isotope ratio
16S rRNA	16S ribosomal Ribonucleic acid
Al	Aluminium
ATP	Adenosine triphosphate
C	Carbon
DNA	Deoxyribonucleic acid
Fe	Iron
N	Nitrogen
P	Phosphorus
Pho	Pho regulon transcription factors
P_i	Inorganic orthophosphate
P_o	Organic phosphorus compounds
S	Sulphur

The importance of phosphorus and organic phosphorus

The dynamics of phosphorus (P) in the terrestrial environment is critical for regulating nutrient cycling in both natural and managed ecosystems. Phosphorus compounds fundamentally contribute to life on earth: being essential to cellular organization as phospholipids, as chemical energy for metabolism in the form of ATP, genetic instructions for growth, development and cellular function as nucleic acids, and as intracellular signalling molecules (Butusov and Jernelöv 2013). Plant growth is limited by soil P availability, so turnover of

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A. L. Neal
Rothamsted Research, West Common, Harpenden,
Herts AL5 2JQ, UK

T. Darch · M. S. A. Blackwell · S. J. Granger · V. Pfahler
Rothamsted Research, West Common, Harpenden, North Wyke,
Okehampton, Devon EX20 2SB, UK

D. S. Almeida
College of Agricultural Sciences, Department of Crop Science, Sao
Paulo State University (UNESP), 1780, Jose Barbosa de Barros st,
Botucatu, Sao Paulo, Brazil

R. Bol · A. Missong · L. Wang
Institute of Bio- and Geosciences, IBG-3: Agrosphere,
Forschungszentrum Jülich GmbH, 52425 Jülich, Germany

K. G. Cabugao
Oak Ridge National Laboratory, P.O.Box 2008, Oak Ridge, TN
37831, USA

L. Celi
DISAFA, Soil Biogeochemistry, University of Turin, largo Braccini
2, 10095 Grugliasco (TORINO), Italy

J. B. Cotner
University of Minnesota-, Cities, 1479 Gortner Ave. Saint Paul,
Twin, MN 55108, USA

G. Feng
China Agricultural University, Beijing, China

D. S. Goll · P. Ciais
Le Laboratoire des Sciences du Climat et de l'Environnement,
IPSL-LSCE CEA/CNRS/UVSQ Saclay, Gif sur Yvette, France

M. Hallama
Institute of Soil Science, University of Hohenheim, Emil Wolff Str.
27, D-70599 Stuttgart, Germany

C. Plassard · I. Bertrand
INRA UMR ECO&SOLS, Montpellier, France

A. Rosling · E. Klumpp
Evolutionary Biology Centre, EBC, Kåbovägen 4, house 7, -752
36 Uppsala, SE, Sweden

T. Fraser · M. Tibbett
Centre for Agri-environmental Research, School of Agriculture
Policy and Development, University of Reading, Whiteknights, PO
Box 237, Reading RG6 6AR, UK

organic phosphorus (P_o) represents a source of P for ecosystem function and, critically, P supply affects crop production (Runge-Metzger 1995). Phosphorus deficiency constrains the accumulation and turnover of plant biomass and dictates community assemblages and biodiversity in a range of natural ecosystems (Attiwill and Adams 1993; McGill and Cole 1981).

Chemically, P is a complex nutrient that exists in many inorganic (P_i) and organic forms in the environment. Through the utilization of orthophosphate, plants and other organisms drive the conversion of P_i to P_o. Death, decay and herbivory facilitate the return of both P_o and P_i in plant materials to soil. Inputs of P to soil through these processes may contribute P_o directly to soil or indirectly, following decomposition, accumulation, and stabilization of P_o by microorganisms (Harrison 1982; Lang et al. 2016; Magid et al. 1996; McGill and Cole 1981; Stewart and Tiessen 1987; Tate and Salcedo 1988). In its simplest definition, P_o is any compound that contains an organic moiety in addition to P, while a wider definition would include phosphate which is associated with organic matter. Such discrete P_o compounds are categorized into similarly structured forms and these forms and their relative lability in soil is

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R. Giesler
Climate Impacts Research Centre, Dep. of Ecology and Environmental Science, Umeå University, 981 07 Abisko, Sweden

A. E. Richardson
CSIRO Agriculture & Food, Canberra, Australia

F. Tamburini · G. Garland · T. McLaren · E. Mészáros
D-USYS, ETH Zurich, Tannenstrasse 1, 8092 Zurich, Switzerland

Å. R. Almås
Department of Environmental Sciences, Norwegian University of Life Sciences, Post Box 5003, 1432 Ås, Norway

Y. Audette · K. Dunfield · P. Voroney
University of Guelph, 50 Stone Road East, Guelph, ON N1G 2W1, Canada

E. Beyhaut
National Institute of Agricultural Research of Uruguay, Montevideo, Uruguay

N. Bradshaw
Department of Chemical & Biological Engineering, The University of Sheffield, Mappin Street, S1 3JD, Sheffield, UK

C. A. Brearley
School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich, Norfolk NR4 7TJ, UK

T. W. Bruulsema
International Plant Nutrition Institute, 18 Maplewood Drive, Guelph, ON N1G 1L8, Canada

V. Cozzolino · M. L. Mora
Centro Interdipartimentale di Ricerca sulla Risonanza Magnetica Nucleare per l'Ambiente, l'Agro-Alimentare ed i Nuovi Materiali (CERMANU), Università di Napoli Federico II, Via Università 100, 80055 Portici, Italy

P. C. Duran · C. P. Negrón · P. Poblete-Grant · A. Seguel · J. A. Sobarzo
Universidad de La Frontera, Temuco, Chile

A. B. de Menezes
School of Environment and Life Sciences, University of Salford, Greater Manchester, The Crescent M5 4WT, UK

R. J. Dodd
School of the Environment, Natural Resources and Geography, Bangor University, Gwynedd LL57 2UW, UK

C. Engl · K. A. Macintosh · J. McGrath
School of Biological Sciences and Institute for Global Food Security, The Queen's University of Belfast, Medical Biology Centre, 97 Lisburn Road, Belfast, Northern Ireland BT9 7BL, UK

J. J. Frazão
CENA, University of Sao Paulo, Avenida Centenario, 303, Piracicaba, SP 13416-000, Brazil

J. L. González Jiménez · J. Graca
Teagasc, Environmental Research Centre, Johnstown Castle, Co. Wexford, Ireland

A. F. Harrison · E. B. Mackay
Centre for Ecology & Hydrology, Library Avenue, Bailrigg, Lancaster LA1 4AP, UK

C. Heuck · M. Spohn
Department of Soil Biogeochemistry, Bayreuth Center of Ecology and Environmental Research (BayCEER), University Bayreuth, Dr.-Hans-Frisch-Str. 1-3, 95448 Bayreuth, Germany

E. Q. Hou
Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, 723 Xingke Road, Tianhe District, Guangzhou 510650, China

P. J. Johnes · C. McIntyre
School of Geographical Sciences & School of Chemistry, University of Bristol, University Road, Bristol BS8 1SS, UK

K. Kaiser
Soil Science and Soil Protection, Martin Luther University Halle-Wittenberg, von-Seckendorff-Platz 3, 06120 Halle (Saale), Germany

shown in Fig. 1, taken from Darch et al. (2014). The P_o compounds, which are considered to be biologically relevant include monoesters, inositol phosphates, diesters and phosphonates. The relative lability and accumulation of these different groups varies in the environment, but overall the labile monoesters and diesters tend to be less prevalent and the inositol phosphates tend to be less labile and accumulate in the environment (Darch et al. 2014). In general, soil P_o forms have a smaller affinity to the soil solid phase than P_i forms and a large proportion of the P forms found in leachate are found to be in organic forms (Chardon and Oenema 1995; Chardon et al. 1997; Espinosa et al. 1999) and can therefore have large impacts on ecosystem function (Sharma et al. 2017; Toor et al. 2003). All P_o compounds have a range of chemical bonds, and all require specific catalytic enzymes to make them biologically available in the form of orthophosphate. The hydrolysis of P_o is mediated by the action of a suite of phosphatase enzymes which may have specificity for single compounds or broad specificity to a range of compounds (George et al. 2007). Unlike for organic nitrogen, there is no evidence for direct uptake of dissolved P_o compounds by biology, apart from the uptake of phosphonates by bacteria in marine systems (Dyhrman et al. 2006). Plants and microbes possess a range of phosphatases that are associated with various cellular functions, including; energy metabolism, nutrient transport, metabolic regulation and protein activation (Duff et al. 1994). However, it is the extracellular phosphatases released into the soil that are of particular importance for the mineralisation of soil P_o. Extracellular phosphatase activity is induced under conditions of P deficiency and is either associated with root cell walls or released directly into the rhizosphere (Richardson et al. 2009).

There have been a number of important advances in our understanding of P_o dynamics at the ecosystem and rhizosphere scale in the past decade, with particular advancement in understanding of plant-soil-microorganism interactions and concomitant advances in techniques used to assess these dynamics. It is now timely to start to consider how to integrate this information and extract further understanding of the dynamics of P_o in the managed and natural environment and this will have a number of potentially important impacts on how we tackle some of the most pressing global issues of today. Here we summarise the state of the art of P_o research and identify priorities for future research, which will help meet these goals.

Establishing priorities for organic phosphorus research

There has been a large increase in the number of publications in the P_o research field in the last two decades, with ~400 publications in 2016, compared to 150 in 2000. In September 2016 a workshop on Organic Phosphorus was held (https://op2016.com), gathering together 102 experts in the field of P_o research from 23 countries to identify research priorities. Contributors were asked, in five groups, to consider the global issues associated with P_o, methodological strengths

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H. A. Kjær
Centre for Ice and Climate, Niels Bohr Institute, University of Copenhagen, Copenhagen, Denmark

A. L. Lamb · A. C. Smith
NERC Isotope Geosciences Facility, British Geological Survey, Nottingham NG12 5GG, UK

M. Mooshammer
Department of Microbiology and Ecosystem Science, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria

L. A. Nelson
University of Northern British Columbia, 3333 University Way, Prince George, BC V2N 4Z9, Canada

M. Randall
Brigham Young University, Provo, UT 84602, USA

M. M. Smits
Centre for Environmental Sciences, Hasselt University Building D, Agoralaan, 3590 Diepenbeek, Belgium

K. Tawaraya
Yamagata University, Tsuruoka 997-8555, Japan

H. Wallander
Department of Biology, Lund University, Biology Building Sölvegatan 35, 223 62 Lund, Sweden

J. Wasaki
Assessment of Microbial Environment, Graduate School of Biosphere Science, Hiroshima University, Hiroshima, Japan

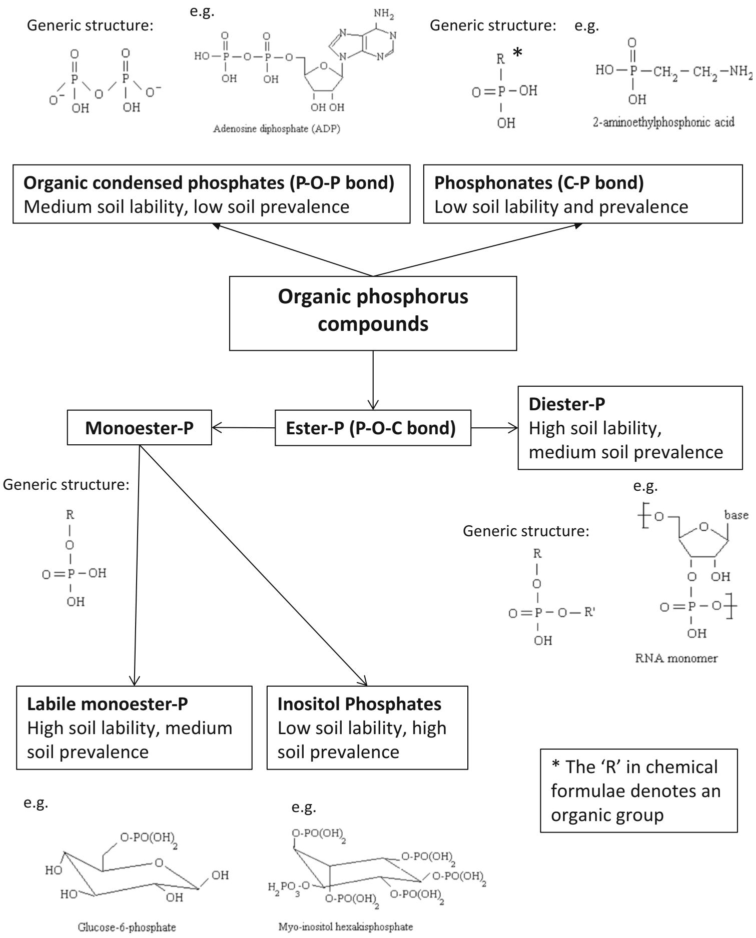

Fig. 1 Organic phosphorus forms with generic and example structures and information on the relative lability and prevalence in soil. (Adapted from Darch et al. (Darch et al. 2014))

and weaknesses, benefits to be gained from understanding the P_o cycle, and priorities for P_o research. The information from the five groups was collected and the concepts, where consensus between at least two of the groups was reached, are summarized in Table 1. It is clear from this that research into P_o has the potential to have impacts on global biogeochemical cycles of P both in natural and managed systems and will therefore potentially impact food security, agricultural sustainability, environmental pollution of both the aquatic and atmospheric environments and will be profoundly affected by environmental change both in geopolitical terms and through man-made climate change. We are well placed to tackle these as there are a number of strengths in the way the research is performed and the weaknesses are well understood. It was considered that P_o research will have a range of impactful outcomes on our understanding of how natural and agricultural systems work and has the potential to give society a number of important tools to help manage the environment more effectively to either prevent or mitigate against some of the major global threats. A number of research priorities were identified and grouped into specific opportunities which are detailed below. The key opportunities to improve the effectiveness of P_o research identified here are similar to those highlighted in Turner et al. (2005a, 2005b), although it is clear that some progress has been made since that set of recommendations were made. However, the similarities and consistency between the outcomes of these two studies suggests we still have some progress to make. A number of new priority areas were identified here that were not identified in Turner et al. (2005a, 2005b), including the need for greater understanding of the metagenomics and functional microbial genes involved in P_o turnover, greater understanding of the impact of nanoparticles in the environment on P_o turnover and the need to integrate the system more effectively in the form

Table 1 Synthesis of expert opinions on the global issues associated with organic phosphorus, how the research community can potentially contribute to solutions to such issues, and identification of opportunities for research to allow this to happen

What are the global issues associated with P_o?	What are the methodological strengths and weaknesses?	What are benefits of understanding dynamics of P_o?	What are the priorities for P_o research?	Opportunities in P_o research
Food Security and agricultural sustainability P_o has a role as a source of P for agricultural crops	**Strengths** Strong collection of well-developed methods Wide range of techniques Capacity for multi-disciplinarity	Management of plant P nutrition Assessment of soil P availability Understanding biological system function Input into climate and biogeochemical models Potential to close the P cycle	• Use existing datasets more effectively • Avoid repeating experiments by being aware of past research • Better access to shared facilities	General advances in the research model
Nutrient cycling in natural ecosystems P_o buffers ecosystem function with effects on ecosystem resilience and biodiversity	Strong international networks Potential for commercialisation of techniques Range of field based applications **Weaknesses** 'Snap-shot' rather than dynamic techniques	Manage ecosystem services and resilience Understand the role of soil biology – fungal vs bacterial dominated systems Assess stability of P forms in soil Identify mechanisms from natural systems that can be applied in managed systems	• Training programmes in P_o related techniques and concepts • Interdisciplinary and long term research • Link operationally-defined pools with biological processes	Opportunities in organic phosphorus analytical methodologies
Renewable resources Use of wastes containing P_o as fertilisers to close the loop	Operational methodologies lack biological relevance	Separate plant and microbial contributions to soil functions Develop indicators for tipping points in ecosystem function – identify conditions of resistance, resilience and "points of no return"	• Some standardisation of protocols • Development of in situ, non-destructive techniques for P_o • Develop a minimum dataset and an accessible database	
C storage in soils Utilisation of soil P_o may be counter to our need to store C in organic matter	Lack of standardisation and quality control	Allow scaling up in time and space through input to models	• Link the P_o cycle with other biogeochemical cycles	Opportunities from understanding stoichiometry – interactions with other element cycles
Environmental pollution Need to manage the balance of food security vs environmental P pollution	Methodological limitations (matrix issues)	Extend our understanding of global nutrient dynamics beyond what can be ascertained empirically	• Optimise stoichiometry between P_o and other elements for system function • Integrate soil physics, chemistry and biology to understand P_o and how it fits with wider soil fertility	
Environmental change Warmer temperatures will shift the biogeochemical cycle of P_o	Loss of training/education in soil science Lack of replication and appropriate statistical approaches		• Design tailored systems for specific managed environments that optimise use of P_o • Optimise P_o utilisation over loss	Opportunities from understanding interactions with land management
Biogeochemical cycling from global to cellular scales P_o compounds are vital for cell function and are moved globally as part of biogeochemical cycles and in the food chain	Limited access to advanced techniques for all		• Improve soil P testing • Develop a P credits system • Utilise P_o more effectively by using what's in soil, what's added to soil and what's lost	
Geopolitical stability P_o as an alternative to mined P resources			• Understand which genes and transcripts control the microbial response to P_o • Understand microbial impacts on P_o cycles • Understand the P limits to plants and microbes	Opportunities from understanding Microbial Po: Function and dynamics

Table 1 (continued)

What are the global issues associated with P_o?	What are the methodological strengths and weaknesses?	What are benefits of understanding dynamics of P_o?	What are the priorities for P_o research?	Opportunities in P_o research
			• Produce a molecular toolkit for studying microbial structure and function	
			• Understand P_o interaction with natural and manmade nanoparticles • Assess the utility of nanoparticles to help manage the system	Opportunities from interactions with nanoparticles
			• Model P dynamics in the environment • Develop conceptual models of cycling at a range of scales • Build empirical models using existing data • Produce a life cycle analysis of P_o	Opportunities to use modelling of Po in soil and ecosystems
			• Promote discussion of P_o within the scientific community • Better communication with stakeholders and the public on the importance of P_o • Develop a central platform for knowledge exchange • Understand the needs and motivations of land managers and policy makers with respect to P_o • Emphasise educating the public in issues associated with P_o • Understand the socio-economic factors influencing P_o dynamics • Improve the translation of research in P_o to impactful outcomes	Opportunities to better communicate and translate research

of models. It is clear that P_o research field is evolving, but some of the issues of a decade ago still persist.

Opportunities in organic phosphorus analytical methodologies

The core analytical tools for the P_o discipline are ^{31}P NMR spectroscopy (Cade-Menun and Liu 2014; Cade-Menun 2005; Cade-Menun et al. 2005; Turner et al. 2005a, 2005b), which is used to identify P_o compounds in several environmental matrices, along with more traditional soil extraction methods, such as those to measure total P_o and the fractionation method developed by Hedley et al. (Condron and Newman 2011; Hedley et al. 1982; Negassa and Leinweber 2009). There is discussion and debate focused around the suitability of these analytical methodologies for characterizing P_o in soil and terrestrial systems (Liu et al. 2014; Doolette and Smernik 2011) and this debate revolves around the identity of the broad base of the inositol hexaphosphate peak on NMR spectra, which some contest is resolved and other suggest is unidentified (Jarosch et al. 2015). Despite this, research into P_o is still limited methodologically and many methods are operationally-defined. Importantly, there is a need to link the results from these methods to biological and biogeochemical processes in the environment. In the process of achieving this, there is debate over the benefits of (i) standardization or homogenization of analytical methods, versus the merits of (ii) promoting diversity of analytical procedures.

It is critical to develop non-destructive methods to analyse soil pools and their dynamics without the need for extraction. Some solid-state methods, such as solid-state NMR or P-XANES (X-ray Adsorptive Near Edge Structure) spectroscopy are limited by the naturally low concentrations of P_o forms in soils (Liu et al. 2013, 2014, 2015). Visible Near-Infrared Reflectance Spectroscopy (VNIRS) has shown some promise for determining total P_o in soils (Abdi et al. 2016), but further testing is needed. Another priority for P_o methodologies is the development of standard analytical quality controls through the use of standardized reference materials for cross-comparison and checks on analytical methods. These standardized reference materials will include reference soils and chemicals. There is a need for the community to identify standardized natural reference materials such as soils and manures, but a large amount of effort would be needed to put together a collection of appropriate materials as well as a means to share them internationally. Standardization of P_o compounds could be achieved through the use of simple, relatively pure, and inexpensive P_o compounds (e.g. Na-phytate, glucose 1-P) purchased from a single supplier operating in many countries with a guaranteed long-term production commitment. And there is a need to develop a commercial supply of other commonly identified P_o compounds in soils, such as scyllo-inositol hexakisphosphate, to allow the use of appropriate substrates for research to fully understand the biological and chemical processes controlling the behaviour of this and other P_o compounds in the environment. It is a priority for researchers to further develop methods, while also refining existing P_o methods and standards, to generate useful and comparable datasets and to build a consensus with respect to P_o dynamics and function in agricultural and natural ecosystems.

Opportunities from understanding stoichiometry – Interactions of organic phosphorus with other element cycles

Comparing element ratios of living organisms and their non-living environment has been at the centre of scientific debate for many years. In oceans, planktonic biomass is characterized by similar C:N:P ratios as marine water (106:16:1) (Redfield 1958). While similar characteristic element ratios also exist for terrestrial ecosystems with much greater heterogeneity across a range of spatial scales (Cleveland and Liptzin 2007). The comparison of C:N:P ratios in the microbial biomass of soils with that of soil organic matter (SOM) may therefore help to identify the nutrient status of the soil (Redfield 1958). Following this concept, the stoichiometric ratios of resources (e.g., SOM) over the microbial biomass has been calculated as a proxy for nutrient imbalances (Cleveland and Liptzin 2007). An understanding of stoichiometric ratios in soils and their relationship to those in crop plants and for the decomposition of litter and SOM will provide an important indicator of nutrient status in terrestrial ecosystems and better management of systems.

Until now, the large temporal and spatial heterogeneity of soil systems and the heterogeneous distribution of SOM constituents have made the analysis and interpretation of ecosystem stoichiometry a challenge because for microbial decomposers the elemental composition of micro-sites in soils might be more relevant than the overall element ratio of the soil. For example, by analysing the C:N:P ratio of bulk soils only, information on relevant and spatially-dependent processes may be lost (e.g., rhizosphere, soil horizons). The most obvious reason for soil-specificity and heterogeneity among stoichiometric ratios is that part of the SOM is separated from microorganisms and roots via physical and physicochemical barriers. By re-analysing the results of C:N:P:Sulphur (S) analyses of SOM obtained from 2000 globally distributed soil samples, Tipping et al. (2016) demonstrated that there is both nutrient-poor and nutrient-rich SOM, with the latter being strongly sorbed by soil minerals (Tipping et al. 2016). This may be explained by the incorporation of SOM into aggregates (Stewart and Tiessen 1987) or the adsorption of P-containing organic and inorganic molecules to mineral surfaces (Celi et al. 2003; Giaveno et al. 2010). Clay and metal (oxy)hydroxide minerals can sequester P_o and P_i released by microbial- or plant-driven processes and/or affect enzyme activities, while limiting P biocycling (Celi and Barberis 2005). This highlights the need to understand the tight interrelationship between chemical, physical and biological processes and the potential for stoichiometric assessment as an indicator of P and organic matter availability in soils. Modern analytical techniques which enable to analyse the stoichiometry of the soil constituents at a high resolution might help provide this knowledge (Mueller et al. 2012).

There are many known mechanisms by which organisms can improve access to P_o (Richardson et al. 2011), but there are several novel mechanisms being identified that target key components of SOM, such as polyphenols and tannins, to mobilise P (Kohlen et al. 2011). A priority will be to understand the plant and microbial mechanisms involved in the accumulation and mobilization of P from organic matter. It is important to attempt to determine the optimal stoichiometry between C:N:P, and understand the role P_o plays in this, to allow sustainable management of P in arable soils and to identify anthropogenic nutrient imbalances in natural, agricultural and forest ecosystems (Frossard et al. 2015).

Opportunities from understanding interactions of organic phosphorus with land management

An ability to utilise P_o to sustain agronomic productivity with declining conventional fertiliser inputs drives research into interactions among P_o, land use and management (Nash et al. 2014; Stutter et al. 2012). The conditions to better utilise P_o may bring benefits for other soil quality factors (e.g., SOM status and microbial cycling), but may require management of potentially adverse effects on wider biological cycles and water quality (Dodd and Sharpley 2015). Societal drivers for food and timber production underpin much of the research into P_o speciation, biological turnover and integration with agronomic systems. Numerous studies have reported P_o stocks and changes associated with management; fewer have studied the time-course of transformations and turnover with management change, linked with soil chemical and biological processes. The interactions between P speciation, (bio)availability and SOM are of prime importance since land management greatly affects SOM in space and time (in beneficial or detrimental ways) and exert strong geochemical and microbial controls on P_o cycling.

The interactions of land cover, use and management are important for understanding the role of P_o across ecosystems. In agricultural systems, the information on soil P_o stocks is well represented and have been quantified by numerous studies in North America (Abdi et al. 2014; Cade-Menun et al. 2015; Liu et al. 2015; Schneider et al. 2016), Europe (Ahlgren et al. 2013; Annaheim et al. 2015; Keller et al. 2012; Stutter et al. 2015), China (Liu et al. 2013), South America (de Oliveira et al. 2015), and Australia (Adeloju et al. 2016). In forestry, such information is available in tropical (Zaia et al. 2012) and temperate systems (Slazak et al. 2010) and orchards (Cui et al. 2015). However, an important improvement will be to better understand the reasons as to why particular stocks exist under certain geoclimatic-land cover combinations. Key opportunities exist to understand P_o dynamics for sustainable P use in tropical systems and for forests growing on marginal soils, both of which depend on effective management of P_o resources.

It is known that both land cover and management factors (tillage, fertilizer type, application rate and timing) interact with abiotic factors in controlling P_o stocks and cycling, such as SOM, stabilizing surfaces [e.g., Fe- and aluminium (Al)-oxides, calcium (Ca) forms, clays] and soil moisture, (Adeloju et al. 2016; Cade-Menun et al. 2015; Stutter et al. 2015). Chemical fractionation studies of P_o stocks provide a snap-shot in time, missing temporal aspects of cycling associated with management-induced change at seasonal or to longer term management. As a result, short periods of rapid change in P speciation and turnover may not be appreciated. The utilization of 'legacy P' (Haygarth et al.

2014; Powers et al. 2016), following declining fertiliser inputs or altered cropping practices, has been studied following long-duration manipulations. Often these look at the end point of change (Cade-Menun et al. 2015), but have not 'followed' the dynamic. Although powerful methods for P_o assessment are developing rapidly, studies that preceded these have the opportunity to incorporate them with archived samples or control soils (Keller et al. 2012; Liu et al. 2015). Long-term understanding of P_o dynamics in management systems should be pursued, while short-term seasonal observations (for example Ebuele et al. 2016) will be needed to understand the influence of microbial dynamics on P speciation and turnover under various land-use and management scenarios. If studies of short-term peturbations (via management, climate etc) can show benefits for providing greater P_o resources into available pools then these processes may be beneficially incorporated in future land management.

'Organic' farming brings a commercial stimulus to substitute agro-chemicals (including chemical P fertilisers) with sustainable management, such as use of organic amendments, for example enhancing soil P cycling with the aim of better utilizing P already present and moving towards a 'closed' system (Annaheim et al. 2015; Gaind and Singh 2016; Schneider et al. 2016). The same approaches can be applied to less intensive, or developing, agricultural systems. Canadian pastures managed under an organic regime, had a greater abundance of P_o (65% vs 52% of total P) compared to conventional pastures and were able to maintain yield without inorganic fertilisers (Schneider et al. 2016). These authors concluded that plants were using P_i rather than P_o and supported by other studies showing no indication that the greater microbial activity under organic farming caused utilization of stabilized P_o forms (Keller et al. 2012). Therefore, the management conditions and actions required to promote better acquisition of P_o pools remain elusive.

The consensus is that a key question remains: How long could the turnover of P_o sustain crop yields under scenarios of reduced P inputs and maintained or increased outputs and thus contribute to agricultural production and feed supplies? The mechanistic understanding required to answer this question lies in the role of biota (in the context of their abiotic setting) in P_o turnover and the potential pathways of P_o loss to be managed (e.g. runoff). In order to progress, a systems approach is needed to fully assess the opportunities and role of P_o, as well as the interactions of soil chemical, physical and biological processes and impacts of land use change that control P availability.

Opportunities from understanding microbial P_o: Functional genes and metagenomics

As our abilities to analyse and interpret the complexity inherent in the soil microbiome improves, interest is burgeoning around the functional ecology of microorganisms. Organic P dynamics across ecosystems, along with development of many techniques that will aid in this understanding, are beginning to emerge. Scavenging of P from P-containing organic compounds by soil microbes is tightly controlled by intracellular P availability through the Pho pathway in yeast (Secco et al. 2012) and the Pho regulon in bacteria. In both cases, transcription of phosphatase and phytase, which act to release orthophosphate from phosphate esters, and high affinity transporters which transport P_i into the cell, are up-regulated under P_i limitation, affecting the organisms' ability to utilise P_o. The Pho regulon also acts as a major regulator of other cellular processes, including N assimilation and ammonium uptake (Santos-Beneit 2015). The C:N:P elemental ratios of the soil bacterium *Bacillus subtilis* range between $C_{53–125}$:$N_{12–29}$:P_1 under N- and P-limited culture conditions (Dauner et al. 2001), although environmental assemblages may exhibit greater stoichiometric flexibility (Godwin and Cotner 2015). Given this regulatory cross-talk, nutrient stoichiometry will be important to cellular and community metabolism meaning that the cycling of P must be considered within the context of other biogeochemical cycles, as highlighted earlier.

Soil type, nutrient inputs, and plant species have been shown to determine microbiota species composition and function (Alegria-Terrazas et al. 2016). However, plant root exudation drives recruitment of specific microbes and microbial consortia to the rhizosphere and may outweigh the impacts of soil and its management in shaping community composition and function (Tkacz et al. 2015). As yet, there is only limited understanding of how specific root exudates affect microbial recruitment (Neal et al. 2012), let alone specific microbiota responsible for phosphatase expression and production. A better understanding of interactions between plants and microbes would facilitate identification of functional redundancy among them, which could ultimately help manage the availability of P in soils and sediments by selection of the optimal plant rhizosphere compliment.

Alkaline phosphatase and phytase genes are distributed across a broad phylogenetic range and display a high degree of microdiversity (Jaspers and Overmann 2004; Lim et al. 2007; Zimmerman et al. 2013), where closely related organisms exhibit different metabolic activities. It is therefore not possible to determine community functional potential from 16S rRNA gene abundance – functional gene abundance information is required and this can be provided by employing sequencing techniques to assess the soil metagenome. In marine systems, there is evidence from metagenomic sequencing of environmental DNA that alkaline phosphatase genes phoD and phoX are more abundant than phoA (Luo et al. 2009; Sebastian and Ammerman 2009) and the β-propeller phytase is the most abundant phytase gene (Lim et al. 2007). The dominant alkaline phosphatase gene in terrestrial ecosystems is also phoD (Tan et al. 2013), which is more abundant in soils than other environments (Courty et al. 2010; Ragot et al. 2015; Fraser et al. 2017). From a functional standpoint, abundance of phoD-like sequences correlate well with estimates of potential alkaline phosphatase activity (Fraser et al. 2015), although this is not always the case (Ragot et al. 2015). Moreover, in soils there is little information regarding other phosphatases and little is known about the distribution and abundance of bacterial acid phosphatases, but there is some information related to phoX (Ragot et al. 2016). In contrast, fungi are well known for their capacity to secrete acid phosphatases (Plassard et al. 2011; Rosling et al. 2016), especially ectomycorrhizal fungi. Since only a small percentage of soil microorganisms are cultivable, research will need to rely upon culture-independent approaches to generate a thorough understanding of the abundance and diversity of genes associated with P_o turnover. Environmental metagenomic sequencing can form the basis of an efficient molecular toolkit for studying microbial gene dynamics and processes relevant to P_o mineralization (Neal et al. 2017). Such an approach will need to prioritize generating comprehensive understanding of the distribution of alkaline and acid phosphatase and phytase genes within soils, coupled with activity measurements, and an assessment of their relative sensitivities to edaphic factors. This will allow explicit incorporation of microbial P_o turnover in the new generation of soil models, as well as allowing rapid assessment of a soil's capabilities for P_o cycling. Improved knowledge will allow the exploitation of microbial activity to sustain and improve soil fertility and allow the tailoring of new fertilizers based upon the capacity of microbes to exploit P_o.

Opportunities from understanding microbial P_o: Measuring stocks, mineralisation and dynamics of turnover

The apparently large diversity of genes associated with P_o-hydrolysing enzymes suggests that changes in community composition are unlikely to result in a loss of ecosystem function. This confers resilience to P-cycling processes, although many of these genes have very specific functions intracellularly. However, trait differences are likely to have significant implications for community function in soils, e.g., the contrasting effects of arbuscular and ectomycorrhizal fungi upon the cycling of P in forest soils, where it has been shown that P_o is more labile in ectomycorrhizal dominated systems than arbuscular mycorrhizal systems (Rosling et al. 2016). The fact that enzyme activity in soil appears to be disconnected from soil P status is at odds with the apparent influence of the Pho regulon or pathway upon gene expression and indicates that much of the observed activity derives from multiple enzyme sources, which have been stabilised by soil colloids (Nannipieri et al. 2011). This also suggests that soil enzyme activity does not directly represent microbial activity or simply reflects the complexity in current P requirements of different microbial species. However, visualization of acid and alkaline phosphatase activity associated with roots by zymography (Spohn and Kuzyakov 2013) does provide an exciting means to determine regulation of soil phosphatase activity with P availability and illustrates the clear spatial separation among the activities of physiologically different enzymes. It is a priority to develop and couple techniques that resolve the distribution of active enzymes in soil with estimates of gene expression derived from functional genes or meta-transcriptomic studies.

The stock of microbial P is an easy-to-determine component in soils, which is widely used to characterize the P status of microbial communities and ecosystems (Brookes et al. 1982, 1984). Nevertheless, its analysis relies on many different protocols (Bergkemper et al. 2016). Building on the previous work, further insights into both microbial-mediated and enzyme-mediated P transformations in soils may now be gained from measurement of the isotopic composition of oxygen associated with phosphate (δ^{18}OP) (Tamburini et al. 2014; von Sperber et al. 2014) and the use of radiolabelled (^{32}P or ^{33}P) P_o compounds to measure mineralisation and immobilisation rates directly (Harrison 1982). A powerful tool for quantifying soil P pools and transformation rates is the isotope dilution technique [reviewed in Bünemann 2015; Di et al. 2000; Frossard et al. 2011]. The decrease in radioactivity with time is caused by the exchange of the added radiolabelled P (either ^{32}P or ^{33}P) with ^{31}P from the sorbed/solid phase and by the release of inorganic ^{31}P from the organic pool via hydrolysing enzymes (Bünemann 2015). Determination of gross P_o mineralization rates from P_o to P_i remains a critical approach, helping understand the processes and rates of P cycling in different soils and under different environmental conditions (Frossard et al. 2011). These techniques present new opportunities to link P cycling to other biogeochemical cycles, such as C and N.

Opportunities in the emerging area of interactions between P_o dynamics and nanoparticles

Reactive nanoparticles can take the form of natural soil colloids or man-made particles and are potential P_o carriers, sources and sinks in ecosystems. Up to 90% of P in stream water and runoff is present in nano- and colloidal sized materials (Borda et al. 2011; Gottselig et al. 2014; Uusitalo et al. 2003; Withers et al. 2009). Colloidal P may comprise nano-sized aggregates (Jiang et al. 2015) bound to Fe, Al and SOM (Celi and Barberis 2005; Celi and Barberis 2007), including inositol phosphates. However, the influence of nanoparticles on the dynamics and bioavailability of P in soil-plant systems is unclear (Bol et al. 2016). Nanoparticles such as C-magnetite, which adsorb and retain P_i and P_o, are used to enhance the recovery and recycling of P from P-rich wastes (Magnacca et al. 2014; Nisticò et al. 2016). It may also be possible to enhance soil enzyme activity with amendments containing mesoporous nanoparticle materials (Zhou and Hartmann 2012). Phytase encapsulated in nanoparticles was shown to be resistant to inhibitors and proteases and to promote the hydrolysis of phytate for P uptake by *Medicago truncatula* (Trouillefou et al. 2015). Nanotechnology has also been used to develop new fertilizers and plant-growth-enhancing materials (Liu and Lal 2015), representing one potentially effective option for enhancing global food production. A better understanding of the P_o nanoparticle interaction may improve our understanding of P fluxes in natural and agricultural systems, and provide innovative technologies for fertilizer production and environmental remediation.

Opportunities to use modelling of P_o in soil and ecosystems

The use of all types of modelling approaches to study P_o is generally overlooked and there is a dearth of P_o based models, but development of such models would be extremely beneficial. Modelling should facilitate the development of a systems-based perspective and help to identify knowledge gaps in the current understanding of P_o. Models of all types are needed including those that are conceptual, mechanistic or empirical in nature and in general there is a lack of focus on all the types of models that exist for P_o. The potential benefits of advances in modelling for P_o include:

- Prediction of the relationship between soil P_o and plant uptake, which should be developed in both conceptual and mechanistic models of P dynamics in the environment.
- Application at different scales to determine the relationship between P_o with land use and management should be possible by building empirical models based on existing data.
- Application of modelling to help understand the role of microbial traits in soil (Wieder et al. 2015), which may determine the effects of gene expression, enzyme activities and the stoichiometric ratio of C:N:P in the microbial biomass relative to that of SOM
- Application of complete Life-Cycle Analysis for relying of the run-down of soil P_o as a replacement to inorganic fertilisers will help us develop adequate conceptual models for management of the system.
- Modelling could also be used to help in the quantification of soil P pools for estimating flow among P_o pools.

In general, there is a great opportunity for the development of modelling in all areas of P_o research and this will be of considerable benefit to the subject if this can be developed and integrated with all areas. The cooperation of modellers and empiricists is essential for building models with great potential use to predict changes in P_o bioavailability due to land-use and management change and to infer the sustainability of the system as a whole.

Opportunities to better communicate and translate research

Organic P represents a small, albeit critical component of biogeochemical research. The marginal nature of the subject to date creates a need to communicate the importance of this science for the future of P sustainability. As for other scientific disciplines, communication priorities include (1) strengthening communication among scientists within and outside of the P_o research community; (2) engagement with stakeholders; and (3) dissemination of knowledge to the public and specific end-users.

Conferences and workshops on the topic of organic P promote the exchange of ideas and forging of new research partnerships (Sharpley et al. 2015; Turner et al. 2015). Online platforms are also powerful tools to connect researchers and stakeholders on issues of global P sustainability (e.g., European Sustainable Phosphorus Platform, www.phosphorusplatform.eu, North America Partnership for Phosphorus Sustainability) (Rosemarin and Ekane 2015). The 'Soil Phosphorus Forum' (www.soilpforum.com) provides a platform for the exchange of information relating to P_o. Specific protocols and conference presentations are also featured in archived YouTube channels (https://www.youtube.com/channel/UCtGI3eUZscCgByewafsQKdw). A central platform for P_o research and communications is still needed, to connect existing forums to global research networks and would include features such as researcher membership, methodological resources, links to relevant organizations and platforms, and a clearing house of P_o data for future meta-analysis and modelling efforts.

Key stakeholder groups such as land managers, farmers and extension services are a natural link between industry, government, and academia (FAO 2016). These key groups hold traditional knowledge on sustainable farming techniques, which serve as a potential basis for future P_o research. Industry initiatives such as the 4R Nutrient Stewardship framework provide feedback from end users and practitioners on research priorities associated with the management of agricultural nutrients (Vollmer-Sanders et al. 2016). The engagement of P_o researchers with existing nutrient initiatives such as these will be critical for bolstering public understanding of P_o and its important role in global P dynamics.

Conclusion - statement of intent for the P_o research community

Organic P research has a critical role to play in tackling a number of important global challenges and there are key contributions to be made toward understanding biogeochemical cycles, dynamics and function of natural ecosystems and the management of agricultural systems. In particular, we must reduce our reliance on inorganic P fertilisers and strategies to do this will increase the relevance of soil P_o for plant nutrition. Secondly, there is a need to develop a circular P economy and close the P cycle which will likely lead to an increase in the amounts of organic P "waste" products being recycled to land shifting the P_o/P_i balance in the soil. To address these global environmental changes and challenges, we should concentrate our efforts on understanding the biological significance of P_o by considering its interactions with other elements in SOM, soil microorganisms and active soil surfaces. We should consider these interactions with respect to changes in land use and management and as a function of geochemical conditions in the wider biophysical and socio-economic environment. We need to integrate this understanding through the production of models for P_o, which capture both whole systems and fine-scale mechanisms. In addition, we need to develop novel and standardised methodologies that can integrate the dynamics and function of P_o on appropriate scales in a non-invasive manner. To achieve a step-change in the impact of P_o research, we need to engage with researchers outside of the discipline, align the research with pressing societal issues, and become more global, collaborative, inclusive, interdisciplinary, and longer-term in nature. The key to fostering this change will depend on logically communicating the importance of P_o to society at large, engaging with stakeholders on important global issues, and ultimately pushing this important area of research up the agenda of policy makers and funding bodies on a global scale.

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