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Phosphorus: a limiting nutrient for humanity?

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Phosphorus is a chemical element that is essential to life because of its role in numerous key molecules, including DNA and RNA; indeed, organisms require large amounts of P to grow rapidly. However, the supply of P from the environment is often limiting to production, including to crops. Thus, large amounts of P are mined annually to produce fertilizer that is applied in support of the 'Green Revolution.' However, much of this fertilizer eventually ends up in rivers, lakes and oceans where it causes costly eutrophication. Furthermore, given increasing human population, expanding meat consumption, and proliferating bioenergy pressures, concerns have recently been raised about the long-term geological, economic, and geopolitical viability of mined P for fertilizer production. Together, these issues highlight the non-sustainable nature of current human P use. To achieve P sustainability, farms need to become more efficient in how they use P while society as a whole must develop technologies and practices to recycle P from the food chain. Such large-scale changes will probably require a radical restructuring of the entire food system, highlighting the need for prompt but sustained action.

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Introduction

Many chemical elements are essential for living things – the list includes at least several dozen that are used for a variety of structural, catalytic, and electron-transport purposes [1]. However, not all elements are created equal. Some, such as carbon, are ubiquitous for all life and connected to nearly all molecules and metabolic transformations. Others have only very rarefied and esoteric functions for some groups. For example, nickel is used by some microorganisms in cofactors associated with oxidation of molecular hydrogen or with methanogenesis. Furthermore, not all elements are created equal in the sense that some (such as hydrogen) are so abundant in the environment that they rarely become limiting for growth and production and thus do not present a strong selective force for evolution.

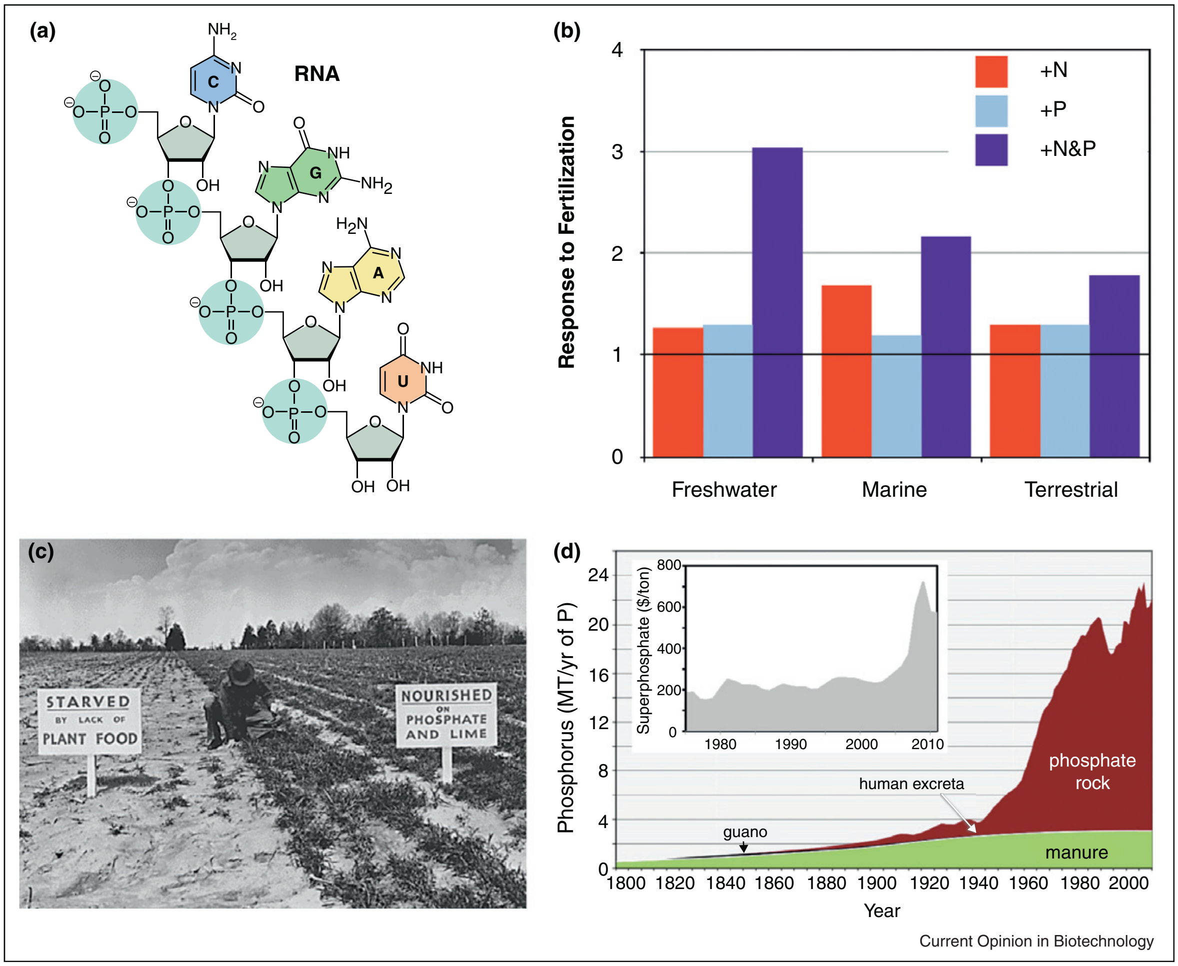
In this regard, phosphorus (P) is far more equal than the other elements involved in living systems, both in terms of its role in biology and its importance as an ecological and evolutionary factor. In this paper I will provide a broad and brief overview of the many dimensions of P to provide context for the papers that follow in this volume. My overview will include a look at P's central role in life's structures and metabolic pathways, its biogeochemical scarcity, its impacts on ecosystems, and finally its role as mined fertilizer in agriculture and thus its position as a key, and increasingly tenuous, pillar supporting the human enterprise. Phosphorus is 'hot' – the subject of two special journal issues during 2011 alone ([2•] and papers therein; [3•] and papers therein). This overview and the papers that follow seek to call attention to yet further dimensions of P that have brought such intense focus on element #15.

P is essential

Almost everywhere you look in a cell you find P. Indeed, in a paper elegantly titled ''Why Nature Chose Phosphates,'' biochemist Frank Westheimer wrote: ''Granted that the phosphates are ubiquitous in biochemistry, what do they do? The answer is that they can do almost everything'' [4]. Starting in the cell membrane itself, P is found in the functional moieties of phospholipid molecules, where the negative charges of the molecule's phosphate groups contribute to the repulsive forces that self-organize the lipid bilayer. Phospholipid molecules contain ~4% P by mass and contribute 5–10% of cellular biomass in most situations [5]. Further inside the cell we can find P connected the most fundamental processes of cellular bioenergetics in the adenylate molecules ATP, ADP, and AMP. While these molecules are extremely P-rich (ATP is 18% P by mass), the contribution of ATP/ADP/AMP to overall cellular biomass is relatively minor (~0.1%). Nevertheless, a continuous supply of PO_4 to 'recharge' AMP to ADP to ATP is clearly essential in maintaining the vitality of any living thing. Many microorganisms also rely on PO_4 in other aspects of energetic metabolism when they store energy (and P) in the form of long phosphate polymers ('polyphosphates'); these play an important role in understanding how microbes trap P during wastewater treatment.

Phosphorus is also at the heart of the storage and processing of genetic information, as P atoms contribute ~9% of the mass of nucleic acids (DNA and RNA; see Figure 1a).

Figure 1



(a) P is essential in a variety of key biological molecules. The structure of a section of single-stranded RNA is shown; the phosphates are indicated by the greenish circles. (*Source*: http://commons.wikimedia.org/wiki/File:RNA-Nucleobases.svg.) **(b)** P is limiting in diverse nature habitats in freshwater, marine, and terrestrial biomes and produces significant increases in growth of algae and plants, especially when added in combination with nitrogen (in the figure, a value of 1.0 indicates no response to fertilization; figure based on data from [13•]). **(c)** P is limiting in agriculture, as illustrated by this historical photograph (ca. 1935) from the Tennessee Valley Authority, USA. (*Source*: Wikimedia Commons.) **(d)** Fossil P is being increasingly exploited for use in fertilizer production (red area of figure; from [14•]) while in recent years increasing demands coupled to restricted supplies has led to increasing prices for phosphate fertilizers (inset; 2-year running average of USA superphosphate price.
Data source: Agricultural Prices, National Agricultural Statistics Service, USDA).

Since RNA/DNA ratios usually range from 2:1 to 20:1 and since the great majority (>80%) of cellular RNA is ribosomal RNA [5], most of the P involved in genetic transactions is associated with ribosomes. Indeed, this association led to the proposal of the 'Growth Rate Hypothesis' (GRH; [6•,7]), which suggests that variability in the P content of living things reflects growth-related demand for construction of ribosomal RNA. This idea has received empirical support in data generated for heterotrophic microorganisms and small invertebrates (e.g. zooplankton, larval *Drosophila*, *E. coli*) in which it was seen that overall cellular (or body) RNA contents often contributed 75–90% of the overall P contents [8]. This GRH has been extended to vascular plants ([9] but see [10]) and even to human cancer [11]. However, its usefulness in understanding whole-organism P content for larger (vertebrate) animals is limited because, in vertebrates, bone is the dominant pool of P, not ribosomal RNA [6•]. Bone is a tissue based on the mineral apatite ($Ca_{10}(PO_4)_6(OH)_2$; 18% P by mass) and in most vertebrate animals the skeleton (~12% P) makes up 5–15% of body dry mass. Thus, the GRH has greatest utility for small organisms (smaller than a fruit fly; [12]). Fundamentally, then, the GRH highlights an important feature of P in biology: rapid growth and high productivity, such as desired in agricultural crops, appears to inherently require disproportionately large amounts of phosphorus, in order to make ribosomes. This biological reality may ultimately place a inexorable molecular boundary on how much efficiency in P use we might be able to achieve in crops. Most importantly, the key insight from our understanding of P's central role in biology is that there is no substitute: unlike other elements of relevance to the human enterprise (e.g. the headline-grabbing 'rare earth elements' or other industrial commodities), one cannot swap another element in place of P if and when P becomes scarce and expensive.

P is limiting

The importance of an element in affecting ecological dynamics comes not only from its predominance in cells but also from its relative abundance in the environment. That is, limitation by a nutrient element is a matter of demand (set by the biological requirements of proliferating biota) and supply (set by the geological and physicochemical context). On first glance, P is relatively abundant: having a relatively low atomic number, it is the 13th most abundant element in the Universe. However, its abundance in the Earth's crust is relatively low (crustal rocks being dominated by Si, O, Al, Ca, Fe, Na, etc.) and, more importantly, the release of P trapped in rocks (and thus the ultimate supply to ecosystems) depends heavily on relatively slow rates of rock weathering. As a result, the biomass and productivity of primary producers (cyanobacteria, algae, vascular plants) in ecosystems is frequently limited by the supply of P. Indeed, a survey of published fertilization experiments [13•] has shown that the frequency and relative magnitude of P and nitrogen (N) limitation of primary production are approximately equal in freshwater and terrestrial ecosystems (Figure 1b). (In marine ecosystems, P is also of considerable importance although N limitation predominates.) In terrestrial systems, P limitation often arises because much soil P is actually unavailable to most plants: depending on pH, the P is bound into chemical complexes with aluminum or calcium.

The implications of widespread P limitation for ecosystem management and conservation are discussed below but the deficiencies of P in agricultural soils have long been recognized by agronomists, emphasizing the need to replenish soil P in order to enhance and maintain productivity (Figure 1c). As a result, during the past century humanity has massively mobilized P from geological sources for fertilizer production (Figure 1d from [14•]), adding it to fields along with N (from the Haber–Bosch reaction) in support of the 'Green Revolution.' Indeed, Falkowski *et al.* [15] estimated that human activities have amplified rates of P cycling globally by ~400% relative to pre-industrial times, far more than for carbon (~13%) or even nitrogen (~100%). The long-term sustainability of this practice will be discussed next.

P is a pollutant

One test of the sustainability of a human activity is to evaluate if it currently impairs important ecosystem services. This is clearly the case for human P use, as inputs of P from point sources (e.g. sewage outfalls) and non-point sources (e.g. leaching from agricultural fields) result in excessive algal growth in lakes and rivers, reducing their suitability for recreation use and for drinking water and requiring expensive treatment processes [16••]. This 'eutrophication' problem has been the focus of considerable scientific work and regulatory actions for many decades. These include the imposition, in the developed world, of advanced treatment facilities that not only break down organic wastes in wastewater but which also remove P before discharging treated waters. However, even in developed European countries the percentage of wastewater subjected to advanced wastewater treatment with P removal varies considerably, from <4% in Turkey to >97% in the Netherlands [17] while non-point sources increasingly contribute excess nutrients and impair water quality. In the developing world P inputs from sewage and agricultural runoff also continue to impair water supplies. These effects are costly. For example, in the USA alone, Dodds *et al.* [18•] estimated conservatively that eutrophication of inland waters imposed ~$2.7 billion of economic costs annually (in 2010 US dollars), by impairing recreational water usage and waterfront real estate values and by the expenses incurred for recovery of threatened and endangered species and drinking water treatment. The eutrophying effects of P runoff extend beyond inland waters. Agricultural and urban runoff of N and P is associated with increasing frequency and spatial extent of coastal ocean regions that are depleted in oxygen ('hypoxic zones') owing to decomposition of dead algal biomass [19]. These also have major economic impacts, including on valuable marine fisheries. These impacts led Carpenter and Bennett [16••] to conclude that current human use of P lies well beyond upper tolerable limits (e.g. 'planetary boundaries,' *sensu* [20]) for the inland waters upon which humans strongly depend for drinking water.

P is 'scarce'

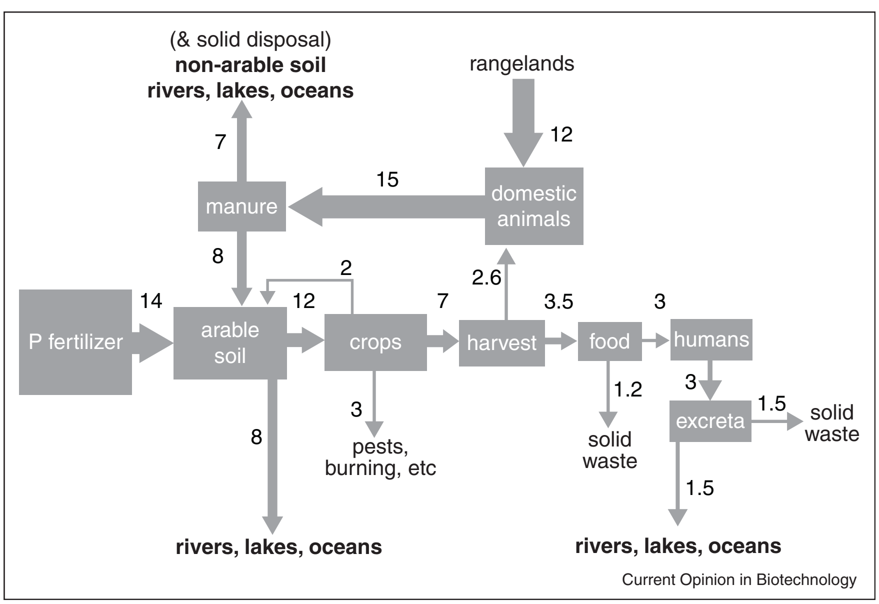
While increasing amounts of P leave the human system to impair water quality, paradoxically, concerns have begun to rise about the specter of P scarcity, or 'peak phosphorus' [21••]. These concerns reflect the fact that, in current approaches, P fertilizer is produced from a non-renewable resource – P-rich geological deposits localized in just a few countries around the globe (Morocco, China, USA, Jordan, and Tunisia are the five leaders for P reserves). Based on patterns of consumption and reserve estimates from ~2005, Cordell and colleagues used a Hubbert-type 'peak oil' analysis to estimate that peak global production of P from mines would occur in ~2035 [21••], an analysis that was particularly alarming given its temporal coincidence with 2007's global spikes in the prices of fertilizer (phosphate rock prices increased ~700% in one year; Figure 1d) and food. Subsequently, Van Kauwenbergh [22•] re-analyzed global P information sources and released an ~10-fold upward revision of the P reserves for Morocco, resulting in an ~4-fold increase in total global P reserves; this revision has been accepted by the United States Geological Survey but lacks independent confirmation [14•]. Regardless, Cordell *et al.* [14•] argue that the new reserve estimate only delays the timing of 'peak phosphorus' by several decades while Elser and Bennett [23•] note that the rarefaction of essential P supplies in a single country establishes the potential for monopoly pricing as well as uncertainty given the volatile political environment of northern Africa. Soil fertility has been identified as one of the most significant challenges in achieving food security in the developing world but developing world farmers cannot afford P fertilizer even at current, non-monopoly, prices. Thus, achieving global food security with the current, fossil fertilizer-based, agricultural system seems highly problematic. These difficulties appear even more acute when one considers upward pressures on P fertilizer demand owing to expanding human population size, increased meat consumption (especially in increasingly affluent China), and a burgeoning bioenergy sector.

What to do?

The two-sided challenge of P sustainability (pollution on the one hand, scarcity on the other) provides an open playing field for improved technologies and practices to 'close the human P cycle' (*sensu* [24•]). Figure 2 (based on [21••]) provides a rough picture of global P flows as of the mid-2000s and can help in targeting future efforts. One thing that is clear in Figure 2 is that much P is lost at the field itself via erosion and leaching. 'Best practices' for fertilizer application combined with no-till cultivation may help considerably in reducing erosion losses but it would also help if crops were more efficient in exploiting the soil volume and in extracting P from 'unavailable' chemical pools in the soil. Some new bioengineering approaches may help in this regard; for example, enhanced expression of a proton pyrophosphatase (AVP1) leads to a variety of phenotypic effects [25•], such as increased root production and rhizosphere soil acidification, allowing the plants to maintain yield on low fertilizer inputs. Much P is also lost in production of domestic animals (Figure 2), including P added as nutritional supplements for non-gastric animals (e.g. pigs) that are unable to digest the phytate-bound P in many feed grains. In another example of a biotechnology approach to P sustainability, a line of pigs has been bioengineered to produce the phytate-degrading enzyme phytase in their salivary glands [26]; these pigs do not require supplemental P for healthy growth and produce considerably less P in their manure.

As emphasized in the new analysis of Cordell *et al.* [14•], improvements in the overall P efficiency of agriculture will be insufficient on their own to achieve a sustainable P system – such as system needs to shift from mined sources of P towards a primary reliance on P fertilizers produced from sources recycled from within the human food chain.

Figure 2



A simplified material flow diagram of the global P system (modified from [21••]). The size of boxes is meant to (roughly) indicate the relative importance of different pools of P while the thickness of arrows is (roughly) proportional to the size of the fluxes (in units of MT $year^{-1}$). Only fluxes greater than 1 MT are shown; thus, inputs and outputs to a given pool will not necessarily balance. Values of P in manure differ somewhat from those in Figure 1 because of differences in accounting for P in manure used overall in the agriculture system and overall manure P used but excluding that recirculating in pastures. Importantly, note the almost complete absence of recycling pathways >1 MT that return P to arable land and that the largest losses are associated with crop and livestock production.

Figure 2 helps identify possible targets for this. It's important to note that technologies to recapture P from human excreta in sewage treatment plants are already relatively well-developed [27] but, as Figure 2 illustrates, even if *all* human excreta were somehow returned to agriculture only ~20% of current P fertilizer use could be satisfied. Other large targets include losses from livestock rearing and dairy operations, post-harvest crop losses, and waste of finished food products (40–50% of food is wasted in both the developed and developing world, but for different reasons; see [28•]). Various technologies for processing of large-volume organic waste streams for nutrient recapture are under development and some are in early deployment (reviewed by [29•]); some involve microbial bioreactors that are also coupled to bioenergy production and hold the promise of generating, from 'waste,' two new income streams: fertilizer and energy. All such systems will benefit from biotechnology innovation in fine-tuning the relevant microorganisms for each recycling task.

While innovations for improved agricultural efficiency and for new P recycling pathways, including those involving new forms of biotechnology, can contribute much to achievement of P sustainability, it is unlikely that technological innovation alone can be the whole answer. Instead, deeper, systems-level changes will almost certainly also be needed. These changes may need to involve human diet preferences (e.g. less meat in the diet would reduce the total P footprint of food production), attitudes (e.g. overcoming aversion to use of fertilizers produced by recycling of human waste), civil infrastructure (e.g. urban design to facilitate P recycling in the food chain), regulatory frameworks (e.g. legal obstacles that slow the evaluation of, and potential adoption of, genetically modified crops, animals, and microbes), and institutions (e.g. development of governing structures for P that cross food production and sanitation domains). These added societal dimensions imply that achieving P sustainability will be a slow process, as it will probably need to entail a 'radical redesign of agriculture' (as called for by [30••]). Indeed, I would argue that actually it will require a radical redesign of the *food system*.

In 2050, there will be ~9 billion humans on Earth but our planet will have pretty much the same number of P atoms it has had since life first emerged eons ago. In much the same way that a germinating seed relies on internal stores, we have built this population to such unprecedented levels by expending various forms of stored capital, including the highly concentrated P deposits that were put away in shallow seas over millions of years. A key ecological question for a seedling is whether it can access new sources of P to sustain itself as it transitions to a mature plant. Humanity now can contemplate much the same dilemma: can our species switch from its dependence on fossil phosphorus to reliance on stable, sustainable sources of this essential nutrient? Or will humanity itself face a P-limited collapse, having failed to develop and implement viable pathways to P sustainability? Given the scale and scope of the needed changes in coming decades, concerted efforts in research, technology transfer, and regulatory and institutional innovation should already be well underway. I end this piece by expressing my concern that they are not.

Acknowledgements

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

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This article introduces a series of 16 papers in a special issue on the phosphorus cycle in the journal *Chemosphere*. The articles in this issue deal with various dimensions of the P sustainability challenge, including genetic engineering strategies, waste P recovery, systems-level sustainability scenarios, geological assessments, material flow analyses, plant nutrition, and farm practices.

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13. • Elser JJ, Bracken MES, Cleland EE, Gruner DS, Harpole WS, Hillebrand H, Ngai JT, Seabloom EW, Shurin JB, Smith JE: **Global analysis of nitrogen and phosphorus limitation of primary production in freshwater, marine, and terrestrial ecosystems**. *Ecology Letters* 2007, **10**:1135-1142.

This paper involves a meta-analysis of more than 1000 fertilization experiments that manipulated nitrogen and phosphorus supplies in marine, freshwater, and terrestrial ecosystems. The data show a significant role of P in limiting production in all major ecosystem types, including terrestrial ecosytems, and a strong interaction with N in leading to enhanced production.

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This paper updates the analysis of Cordell *et al.* (2009) and presents a prospective look at the combination of measures to increase agricultural P efficiency, to lower P demand, and to recycle P needed to achieve a closed and sustainable P system.

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This paper reconsiders the ‘planetary boundaries’ analysis of Rockstrom *et al.* (2011), which neglected to consider inland waters in its analysis. The authors estimate that current anthropogenic impacts on freshwaters greatly exceed conservative planetary boundaries and recommend reduced P use in areas of overapplication with transfers to regions currently deficient in P.

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This paper integrates diverse information on human P use, both in current scenarios and over time. It includes one of the first global mass flow analyses for P as well as expressions of concern about the possibility of ‘peak phosphorus’ within decades, based on information available at that time.

22. • Van Kauwenbergh SJ: **World phosphate rock reserves and resources**. *Technical Bulletin IFDC-T-75*. Muscle Shoals, AL: International Fertilizer Development Center; 2010.

This self-produced report from the International Fertilizer Development Center (IFDC) revises the global phosphate reserve estimate, adjusting primarily the data for Morocco. The adjustment was based largely on inclusion of a previously overlooked geological report from the 1980s.

23. • Elser JJ, Bennett E: **A broken biogeochemical cycle**. *Nature* 2011, **478**:29-31.

This paper reflects on the (then) current state of the P sustainability situation and calls for more comprehensive treatment of the currently disjunct state of P research, planning, and regulation.

24. • Childers DL, Corman J, Edwards M, Elser JJ: **Sustainability challenges of phosphorus and food: solutions from closing the human phosphorus cycle**. *Bioscience* 2011, **61**:117-124.

This paper compares and integrates previous studies on mass flow of P in the human system and points out substantial discrepancies among reported data for major flow paths. The authors also note the highly linear nature of the flow of P in human society and call for a ‘close human P cycle’ by establishment of recycling pathways.

25. • Gaxiola R, Edwards M, Elser JJ: **A transgenic approach to enhance phosphorus use efficiency in crops as part of a comprehensive strategy for sustainable agriculture**. *Chemosphere* 2011, **84**:840-845.

This article notes that ‘wild plants’ have a suite of metabolic, physiological, and morphological strategies to deal with P limitation. They review development of some new genetic technologies that have strong potential to instill such strategies in agriculturally important plants and thus improve P use efficiency on the farm.

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This paper compiles diverse information from a wide range of sources to estimate that in the developed and developing world both, considerable amounts of food are wasted before consumption. In both the developed and developing world, considerable waste of perishable food occurs owing to improper refrigeration or shipping conditions, while post-harvest waste of crops is also a major (but poorly quantified) problem in the developing world. In the developed world, the majority of food waste occurs at the post-consumer stage (e.g. in the household).

29. • Rittmann BE, Mayer B, Westerhoff P, Edwards M: **Capturing the lost phosphorus**. *Chemosphere* 2011, **84**:846-853.

This paper describes a number of emerging technologies for recapturing the P present in various solid waste forms, including animal manure, crop wastes, and food waste captured at different sources. Several of these are connected to bioenergy production strategies.

30. •• Fedoroff NV, Battisti DS, Beachy RN, Cooper PJM, Fischhoff DA, Hodges CN, Knauf VC, Lobell D, Mazur BJ, Molden D *et al.*: **Radically rethinking agriculture for the 21st century**. *Science* 2011, **327**:833-834.

These authors note the inherently unsustainable nature of the current global agricultural system and the challenges for meeting future food demands while protecting the environment. They call for increased adoption of genetically engineered organisms, as appropriate, as well as for integrating nutrient flows to reduce environmental impacts.