Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions

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Abstract. Nutrient limitation to primary productivity and other biological processes is widespread in terrestrial ecosystems, and nitrogen (N) and phosphorus (P) are the most common limiting elements, both individually and in combination. Mechanisms that drive P limitation, and their interactions with the N cycle, have received less attention than mechanisms causing N limitation. We identify and discuss six mechanisms that could drive P limitation in terrestrial ecosystems. The best known of these is depletion-driven limitation, in which accumulated P losses during long-term soil and ecosystem development contribute to what Walker and Syers termed a "terminal steady state" of profound P depletion and limitation. The other mechanisms are soil barriers that prevent access to P; transactional limitation, in which weathering of P-containing minerals does not keep pace with the supply of other resources; low-P parent materials; P sinks; and anthropogenic changes that increase the supply of other resources (often N) relative to P. We distinguish proximate nutrient limitation (which occurs where additions of a nutrient stimulate biological processes, especially productivity) from ultimate nutrient limitation (where additions of a nutrient can transform ecosystems). Of the mechanisms that drive P limitation, we suggest that depletion, soil barriers, and low-P parent material often cause ultimate limitation because they control the ecosystem mass balance of P. Similarly, demand-independent losses and constraints to N fixation can control the ecosystem-level mass balance of N and cause it to be an ultimate limiting nutrient.

Key words: biogeochemistry; chronosequence; nitrogen; nutrient limitation; phosphorus; proximate vs. ultimate.

Introduction

The importance of phosphorus (P) and nitrogen (N) limitation to primary production and other ecosystem processes has been demonstrated in a wide variety of terrestrial ecosystems. Much of the conceptual framework for terrestrial nutrient limitation was synthesized by Walker and Syers (1976), who suggested that because P is derived primarily from rock weathering, ecosystems begin their existence with a fixed complement of P from which even very small losses can not readily be replenished. Consequently, ecosystems with very old soils can become depleted in P. Walker and Syers measured total soil P and some of its chemical forms in a number of New Zealand chronosequences (substrate age gradients), and demonstrated a pattern of lower total P and an increased fraction of recalcitrant P in older substrates; they suggested these old sites represent a "terminal steady state" of P depletion and biological limitation.

In contrast, combined N is nearly absent from most igneous and metamorphic rocks; outside of ecosystems underlain by certain sedimentary and meta-sedimentary rocks (Dahlgren 1994, Holloway and Dahlgren 2002), most terrestrial ecosystems are largely devoid of N as they begin their development (Walker and Syers 1976). Unlike P, N is accumulated from the atmosphere rapidly via biological N fixation, where symbiotic N fixers dominate an early stage of ecosystem development, or more slowly via atmospheric deposition and dispersed sources of biological fixation. Accordingly, biological processes in many ecosystems on young soils may be limited by low supplies of N.

This temporal pattern in P vs. N limitation gives rise to a geographical one (Vitousek and Sanford 1986), because over the last several million years high-latitude systems have been systematically and cyclically influenced by glaciation and related processes (such as loess deposition) that rejuvenate their supply of P and other

rock-derived nutrients and can remove their stocks of N. In contrast, no glaciers have existed in the lowland tropics for hundreds of millions of years, and so a larger fraction of tropical sites could approach Walker and Syers' terminal steady state of P depletion and limitation.

While developmental and latitudinal gradients in N vs. P limitation are supported by many observations and make sense logically, a number of studies have reported patterns of P and N limitation that differ from these expectations, suggesting that additional or alternative mechanisms could underlie P limitation. Wardle et al. (2004) evaluated six well-studied chronosequences that ranged from ~20° to ~65° in latitude, in which the oldest sites were lower in biomass and/or productivity than intermediate-aged sites. Wardle et al. (2004) concluded that this decrease was associated with a lower availability of P relative to N, in comparison with younger sites on each sequence, although evidence that changes in P caused changes in biomass/productivity was sparse for several sequences. Because of glacial processes, the oldest sites in their two high-latitude chronosequences originated in the Holocene (<15 kyr ago [1 kyr = 1000 yr], making them younger than the fertile "intermediate" aged sites in their two tropical/subtropical sequences, in which the oldest, P-poor sites are 600 and 4100 kyr old. It seems unlikely that ecosystem development proceeds to P depletion orders of magnitude more rapidly in boreal than in tropical environments; more likely the low P status of the older high-latitude sites is driven by different processes than in the tropical sites.

Evidence for widespread P limitation in terrestrial ecosystems outside the tropics has not been drawn solely from chronosequences. For example, Wassen et al. (2005) evaluated the distribution of endangered plants in putatively N- vs. P-limited sites across a long Eurasian transect, and concluded that many are confined to sites where foliar analyses suggest that the main limiting nutrient is P, not N. More directly, a recent meta-analysis by Elser et al. (2007) summarized patterns of N vs. P limitation from fertilization experiments conducted in 1079 sites in marine (243 sites), freshwater (653), and terrestrial (173) ecosystems. Contrary to expectations that N supply typically limits plant growth in temperate forests, grasslands, and the coastal ocean while P limits freshwater ecosystems and tropical forests (Schindler 1977, Vitousek and Howarth 1991, Howarth and Marino 2006), they found the mean effect of P (when added alone) to be substantial—similar to that of N added alone—across terrestrial ecosystems. Mean responses to N plus P additions were even greater. Further, they found little evidence for latitudinal or growth-form (e.g., grassland, shrubland, forest) differences in the mean responsiveness of plant growth to N vs. P, although the few tropical forest experiments they summarized reported more limitation by P than by N. Another recent meta-analysis (LeBauer and Treseder

2008) focused on N in terrestrial ecosystems; they too found no significant relationship between the extent of N limitation and latitude, when similar sites were compared. Elser et al. (2007) concluded that many ecosystems are poised near the point where N and P are equally limiting to the growth of plants. Consequently, they suggested that the identity of limiting nutrients in terrestrial environments should not be assumed, and that both science and management should recognize that ongoing human-caused alterations in the cycles of either N or P (Vitousek et al. 1997, Bennett et al. 2001, Galloway et al. 2008), and particularly of both together, have the potential to alter the dynamics of many ecosystems.

In this paper, we seek to identify and evaluate the mechanisms underlying global patterns in nutrient limitation. Earlier work by Vitousek and Howarth (1991; see also Vitousek and Field 1999, Vitousek et al. 2002) sought to explain the variety of mechanisms that drive N limitation, addressing in particular the conundrum of the co-occurrence of widespread N limitation to primary production and the ubiquitous occurrence of organisms with the capacity to fix N biologically from the unlimited supply of N_2 in the atmosphere. Accordingly, here we focus on the mechanisms that could cause or contribute to P limitation, and explore how the mechanisms driving P limitation relate to and interact with those driving N limitation.

Nutrient Limitation Concepts

Before addressing the mechanisms underlying P limitation in particular, we discuss a conceptual framework for nutrient limitation in general. At one level, the concept is straightforward: nutrient limitation occurs when meaningful additions of an essential element in biologically available forms cause an increase in the rate of a biological process (such as primary productivity) and/or in the size of an important ecosystem compartment (such as biomass). Nutrient limitation may be inferred by indirect measurements, of which the most common include (1) nutrient availability in soil (Powers 1980); (2) plant investments in acquiring particular nutrients (Harrison and Helliwell 1979); and (3) tissue concentrations or ratios of elements (van den Driessche 1974, Koerselman and Meuleman 1996). The last of these is now the most widely used; it provided the basis for both Wardle et al.'s (2004) and Wassen et al.'s (2005) identification of P-limited ecosystems. Inferring nutrient limitation in this way, particularly identifying the more-limiting nutrient, of N and P, should be robust when studies are carried out within a defined group of plants and ecosystems, and when they are calibrated with fertilization studies (Koerselman and Meuleman 1996). The approach can break down when applied across wide differences in phylogeny or climate; species (and regions) differ in their underlying N:P stoichiometry (for example, legumes are rich in N whether or not they actively fix N (McKey 1994)). In the end, nutrient

limitation is defined operationally: by how primary production and other biological processes respond to added nutrients, as in the studies summarized by Elser et al. (2007) and LeBauer and Treseder (2008).

Our ability to understand nutrient limitation is complicated in practice by the pervasiveness of multiple resource limitation (MRL), which occurs when the addition of any one of several resources causes an increase in production and/or biomass. MRL can arise in a variety of ways, including physiological processes within plants, positive interactions in resource supply, and limitation of different species or functional groups within an ecosystem by different resources. On the physiological level, MRL probably represents the normal situation for terrestrial plants (Bloom et al. 1985, Field et al. 1992); indeed theoretical analyses suggest that to the extent possible, plants should adjust their physiology and morphology (through root–shoot allocation and reciprocal changes in resource use efficiency) such that they are limited simultaneously by multiple resources (Field et al. 1992, Rastetter et al. 1997).

MRL on the physiological/morphological level applies most clearly to resources that are acquired by distinct pathways, like light, carbon dioxide, and water or nutrients (Field et al. 1992). However, MRL arising from positive interactions in resource supply clearly applies to nutrients like N and P that most plants obtain from soil through roots and mycorrhizae. The supply of P constrains rates of N fixation in many ecosystems, such that additions of P can increase the inputs and ultimately the availability of N in both aquatic (e.g., Schindler 1977) and terrestrial (e.g., Eisele et al. 1989, Crews et al. 2000) ecosystems. Conversely, additions of N can allow organisms to produce more extracellular phosphatase enzymes that cleave ester-P bonds in soil organic matter (McGill and Cole 1981, Olander and Vitousek 2000, Treseder and Vitousek 2001, Wang et al. 2007), increasing local availability of P. These interactions are not fully symmetrical; by affecting N fixation, P supply affects the quantity of N within ecosystems, while additional phosphatase enzymes affect the rate of cycling but not the quantity of P within ecosystems. However, within limits these and other interactions can allow the supply of biologically available N and P to equilibrate, yielding many ecosystems in which plants are poised near the point where N and P are equally limiting, as illustrated by the summary in Elser et al. (2007).

Finally, MRL in diverse ecosystems can arise because increases in productivity or biomass stimulated by added nutrients may be unevenly distributed across plant species and functional groups. Species that have evolved toward different resource requirements may simultaneously be limited by and respond to different resources in a common environment, a situation that in the aggregate represents MRL (Gleeson and Tilman 1992).

Another challenge in applying the concepts underlying nutrient limitation is the distinction between proximate and ultimate limiting resources. We define a proximate limiting nutrient as one for which additions stimulate biological processes or pools directly, while an ultimate limiting nutrient is one capable of transforming ecosystems, typically by driving a substantial and persistent change in ecosystem structure and/or species composition as well as increasing the rates of biological processes. Studies of lake eutrophication by David Schindler and colleagues (Schindler 1971, 1977) illustrate this distinction as we define it (a different definition is current in marine biogeochemistry). Several decades ago, there was considerable controversy surrounding the components of human activity that cause lake eutrophication. Was it due to anthropogenic inputs of C? Of N? Of P? Each of those elements gets into lakes by different pathways, and experiments based on bioassays (in which these elements were added one at a time or in combination to bottles or microcosms containing lake water) found that each of them alone could stimulate primary productivity and algal growth in soft-water lakes. Consequently, all could be considered proximate limiting nutrients, and the lake water exhibited multiple resource limitation. However, longer-term whole lake experiments (summarized in Schindler 1977) demonstrated that only additions of P had the potential to convert many oligotrophic lakes into eutrophic ones. Phosphorus is an ultimate limiting nutrient here because additions of P cause inputs of N (by biological N fixation) and C (by enhancing CO_2 diffusion into lakes); together, these inputs of P, N, and C transform oligotrophic lakes into eutrophic ones. In contrast, N and C are not ultimate limiting nutrients because adding them does not increase the input of P, and lakes remain oligotrophic.

Because primary producers are relatively long lived in terrestrial ecosystems, ultimate limiting nutrients are difficult to identify on the timescale of fertilization experiments, even though both science and management may be more concerned with ecosystem transformation than with bounded increases in productivity. We believe one well-characterized example of ultimate limitation in terrestrial ecosystems is the transformation of many northwestern European heathlands to productive grasslands, as a consequence of anthropogenically enhanced atmospheric deposition of N over a period of decades (Berendse et al. 1993). More generally, a combination of sustained whole-system experiments like those summarized by Schindler (1977, Schindler et al. 2008), long-term observational studies (including chronosequences), and fundamental understanding of the biogeochemical mechanisms that drive nutrient limitation can allow ultimate limiting nutrients to be identified and characterized.

Mechanisms Underlying Phosphorus Limitation

We recognize six mechanisms that can cause P limitation to terrestrial ecosystems: P depletion, soil barriers, transactional, low-P parent materials, P sinks, and anthropogenic forcings (Table 1). These mechanisms are not alternative hypotheses; rather, multiple mecha-

TABLE 1. Pathways, mechanisms, and timescales of P limitation to primary production in terrestrial ecosystems.

Pathway	Mechanism	Timescale
Depletion driven	loss of inorganic and dissolved organic P via leaching; exhaustion of primary minerals in soil	millions of years
Soil barrier	formation of soil layers that physically prevent/inhibit access by roots to potentially available P	hundreds to tens of thousands of years
Transactional	slow release of P from mineral forms, relative to the supply of other resources	decades to centuries
Low-P parent material	low inputs of P via weathering due to low concentrations of P in rock	all; develops quickly and persists
Sink driven	sequestration of available P in an accumulating pool within ecosystems	decades to millenia
Anthropogenic	enhanced supply of other resources (especially N) causes P limitation	years to decades

nisms can and do affect particular ecosystems both individually and interactively. To evaluate these mechanisms, and to determine the circumstances in which P can be an ultimate limiting resource, we consider the dynamics of N and P simultaneously. While the limits within which N and P can equilibrate are constrained by their different sources, cycles, and dynamics, any process that increases the availability of either N or P makes it more likely that the other element will become limiting.

Throughout our exploration of mechanisms driving P limitation, we make use of the chronosequences summarized by Wardle et al. (2004); the use of chronosequences forces a long time perspective that is consistent with detecting and characterizing ultimate limiting nutrients. Moreover, the particular chronosequences they discuss can be used to illustrate several of the mechanisms we review here.

Depletion-driven P limitation

Perhaps the best-recognized cause of P limitation to terrestrial ecosystems is the progressive loss of P that can occur during long term soil and ecosystem development. We term this mechanism depletion-driven P limitation; together with soil sinks for P, it is a major component of the Walker and Syers (1976) model (Fig. 1). Depletion of P is evident in a chronosequence across the Hawaiian archipelago; by the oldest site on the sequence (4.1 million years), 90% of the P from parent material has been lost (Chadwick et al. 1999, Vitousek 2004), much of it via leaching of dissolved organic P (Hedin et al. 2003). A long-term fertilizer experiment demonstrated that P supply limits both plant production and litter decomposition (Herbert and Fownes 1995, Hobbie and Vitousek 2000) in the oldest site, in contrast to younger sites on the sequence (Vitousek and Farrington 1997). After several years of fertilization, P additions induced secondary N limitation to plant growth in the oldest site (Harrington et al. 2001) and later still, the excess of P and relative dearth of N in P-fertilized plots led to a spectacular bloom of N-fixing cyanolichens on trunks and in the canopy of this forest (Benner and Vitousek 2007).

In contrast to tropical areas, Pleistocene glaciations have ensured that few cold-temperate or high-latitude sites reach soil ages of 40 000 years, much less 4 million years, without having their parent material P rejuvenated or subsidized by glacial or periglacial processes. Consistent with this suggested geographical pattern, P limitation plays a more prominent role in tropical than in temperate agriculture (Sanchez 1976), and a substantial subset of lowland tropical forests have lower tissue P concentrations and much wider N:P ratios than do any temperate forests (Vitousek 1984, McGroddy et al. 2004). However, P depletion is not a feature of all tropical soils—volcanism, tectonic uplift, erosion, and other disturbances (besides glaciation) that can rejuvenate the supply of P from rock are as frequent in the tropics as the temperate zone (Bern et al. 2005, Porder et al. 2005a, b, 2007), and so many tropical soils are relatively young and rich in P (Vitousek and Sanford 1986).

Phosphorus limitation caused by the development of soil barriers

Soil developmental processes other than depletion can contribute to P limitation by making portions of soils inaccessible or inhospitable to roots and thereby physi-
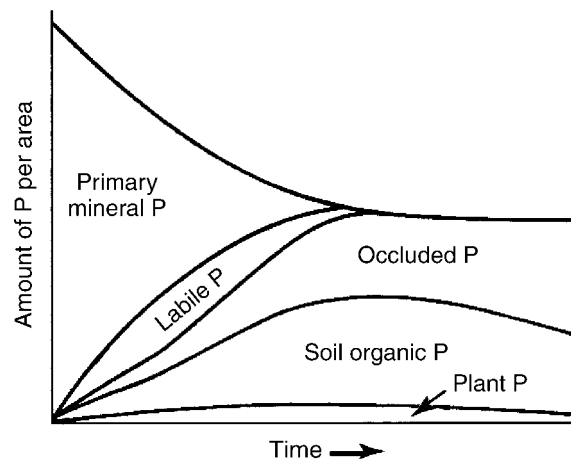

FIG. 1. Changes in the pools and overall quantity of P in ecosystems over the course of soil development, based on Walker and Syers (1976).

cally separating biota from P and P-bearing minerals. We term this class of mechanisms soil barrier-driven P limitation. A clear example occurs on chronosequences in permafrost-dominated regions; shade, organic soil horizons, and moss progressively insulate soils and allow permafrost to develop after several hundred years (Viereck et al. 1983), isolating plants from deeper portions of the soil profile.

Other pedogenic soil barriers can influence P availability and limitation. Iron pans (placic horizons) that form in high-rainfall regions can constrain root access to deeper parts of soil profiles and restrict drainage, routing water horizontally rather than vertically through soils and in high-rainfall sites causing soil saturation and anaerobiosis (McKeague et al. 1983, Kitayama et al. 1997). The development of clay-rich soil horizons can have similar consequences; Lohse and Dietrich (2005) demonstrated that a textural discontinuity associated with such a horizon routed most water horizontally in the P-limited oldest site of the Hawaiian chronosequences, and most roots in the site explore the area above that discontinuity (Ostertag 2001). Finally, acidic, high-aluminum subsoils that form in many high-rainfall environments may permit water flow but serve as a barrier to the growth of roots towards deeper, more P-rich portions of soil profiles (Soethe et al. 2006).

By blocking root access to deeper soil horizons with P-containing minerals, barriers can have a greater effect on the supply of P than N, making limitation by P more likely. Additionally, anaerobiosis resulting from soil barriers slows decomposition and element cycling and organic N and P can accumulate (Ugolini and Mann 1979), causing sink-driven limitation. P is relatively mobile in anaerobic soils, because the ferric iron that forms insoluble complexes with P under aerobic conditions is reduced to soluble ferrous iron, potentially increasing the availability of P in the short run, but at the same time greatly increasing rates of P depletion (Miller et al. 2001, Thompson et al. 2006). To the extent that soil barriers promote shallow flow paths through organic soils and high DON losses, N limitation may also be reinforced by barriers.

Overall, pedogenic barriers can cause rapid (hundreds to thousands of years) or slow (millions of years) reductions in the stature of vegetation (Simard et al. 2007). Soil barriers contribute to the low-stature, nutrient-limited vegetation observed on older marine terraces of the Mendocino chronosequence in California (Jenny et al. 1969; see Plate 1), and probably also to low nutrient availability in older muskeg sites of the Glacier Bay chronosequence summarized by Wardle et al. (2004).

Transactional P limitation

Early in soil development, most P remains in primary minerals and P availability in soil may be low (Crews et al. 1995). Where biological N fixers are sparse and other N inputs are small, N availability will generally be even lower than that of P—and N supply is likely to limit plant growth, as is observed in young sites on the Hawaiian chronosequence (Harrington et al. 2001, Vitousek 2004). However, where N fixers are abundant early in ecosystem development, as in the Glacier Bay chronosequence and many others, the resultant high N:P ratio of inputs can cause P limitation in young soils (Chapin et al. 1994). We term this mechanism transactional P limitation: abundant P is present in parent material, but it weathers slowly enough (and N and other resources are abundant enough) that P supply constrains plant growth. Transactional P limitation might be considerably more widespread were plants and mycorrhizae not able to increase the availability of P in soils by enhancing weathering rates (Blum et al. 2002, Hoffland et al. 2002) and by other pathways (Lambers et al. 2008). The potential importance of transactional P limitation is not confined to early soil development; as discussed below, either anthropogenic enrichment by N or very high rates of geological uplift and erosion can lead to transactional P limitation.

Parent-material-based P limitation

The P content of different parent materials can differ by over two orders of magnitude (McBirney 1993). At the low end of this range, the quantity of P present in parent material as soils begin to develop can constrain plant growth and other ecosystem processes, a situation that we characterize as parent material based P limitation. A clear illustration can be drawn from the quartzite sandstone rocks of the Cape Province, South Africa, that underlie portions of the notoriously P-poor fynbos biome; they contain less than 40 ppm total P (Soderberg and Compton 2007), vs. 700 ppm in average continental crust and 3000 ppm in particularly rich oceanic basalt (Taylor and McClennan 1985, McBirney 1993). Parent material differences can be accentuated during soil development, in that basaltic soils tend to collapse over time and concentrate remaining elements whereas quartz-rich soils lose mass (and elements) from other constituent minerals but tend to retain their original volume because quartz weathers so slowly (White 1995). The Cooloola chronosequence summarized by Wardle et al. (2004) developed in quartz sand; its P dynamics likely reflect both parent material based and depletion driven P limitation (Walker et al. 1983).

The texture of parent material also can play an important role, one that fits between parent material based and transactional P limitation. Weathering is a surface-area-dependent phenomenon, and massive surfaces (rock faces) weather much more slowly than fine particles. Raich et al. (1996) contrasted the response of native vegetation to N vs. P additions in three volcanic sites in Hawaii: one underlain by massive pahoehoe lava, one by rough cobbles of a'a lava, and the third by much finer particles of volcanic cinder. All three were on young substrates and supported few N fixers, and all were limited by N more than by P. However, their
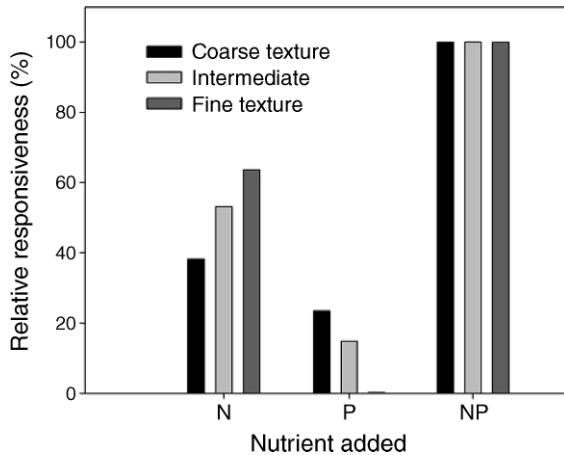
FIG. 2. The effect of the texture of parent material on the extent of P limitation to plant growth in young volcanic sites in Hawaii. Forests on coarse pahoehoe lava, intermediate-texture a'a lava, and fine volcanic cinder all respond most strongly to additions of N plus P, but the effect of added P (alone) is strongest in the coarse-textured site, where low surface area slows weathering; the effect of P is intermediate on the intermediate parent material texture, and absent in the finest-textured substrate. The fine-textured substrate supports the greatest particle surface area where weathering can take place. The figure is based on data in Raich et al. (1996).

response to P additions matched their parent material texture; tree growth following P addition was 62% of that following N addition in the low-surface-area pahoehoe site, 28% of the N response in the intermediate-texture a'a site, and there was no effect of added P in the high surface area cinder site (Fig. 2).

Sink-driven P limitation

The accumulation of meaningful quantities of an essential element into a growing pool within an ecosystem represents a withdrawal of that element from circulation, making limitation by that element more likely. We term this process sink-driven P limitation. The Walker and Syers model (Fig. 1) proposes that P limitation in ecosystems on old soils is caused by both depletion and sinks; they suggest that an increasing fraction of the P that remains within ancient soils is bound in occluded (insoluble and/or physically protected) forms that are not accessible to organisms. In the Hawaii chronosequence, 90% of parent material P had been lost, and about half of the remaining P in the oldest site was found in occluded forms (Crews et al. 1995, Chadwick et al. 1999, Vitousek 2004).

The importance of sinks for P vs. N limitation depends on the nature of the sinks. Strong adsorption of P on colloids and its precipitation with iron, aluminum, manganese, or calcium represent substantial sinks for P, and not N, in many soils. This adsorption and precipitation of P could compete with organisms for available P in the short term (Olander and Vitousek 2004), and represent an accumulating sink of P in the longer term. Such inorganic sinks drive biological processes toward P

limitation in a wide variety of soils, though by differing pathways: for example, by precipitation with Ca in aridland soils or with free iron and aluminum in podsols, or by adsorption onto allophane or sequioxides in many tropical soils (Uehara and Gillman 1981).

Where living biomass represents an accumulating sink (Miller 1981, Rothstein et al. 2004), its N:P stoichiometry should be similar to that of organisms' requirements. However, where the sink is litter or soil organic matter, biochemical (phosphatase-mediated) mineralization of P (McGill and Cole 1981) could regenerate P more rapidly than decomposition can regenerate N and so, all else being equal, a soil organic matter sink could drive systems toward N limitation. In high-rainfall areas where accumulated soil organic matter increases water holding capacity and slows drainage, the consequent soil saturation and anaerobiosis can feed back to enhance organic matter accumulation (van Breemen 1995). This feedback increases the sink, but it could also bring other processes to bear, including enhanced mobility of P and N, and potentially loss of contact with underlying mineral-soil horizons.

Anthropogenic P limitation

Just as human activity can transform P-limited ecosystems by adding P (Schindler 1977), human activity can induce P limitation by purposely or inadvertently affecting the supply of other resources, most often N. We call this mechanism anthropogenic P limitation. For example, extraordinarily high levels of atmospheric N deposition in northwestern Europe have overwhelmed N limitation in many sites (Berendse et al. 1993, Stevens et al. 2004), and many of the altered systems are now limited primarily by P (Fig. 3; Verhoeven and Schmitz 1991, Aerts et al. 1992). Similar results have been obtained in controlled experimental settings in North America (Tilman 1987, Huenneke et al. 1990, Suding et al. 2005). Fertilization experiments further demonstrate that adding N can increase the rate at which P cycles, by allowing organisms to produce more extracellular phosphatase enzyme and thereby release phosphate from soil organic matter (Olander and Vitousek 2000, Treseder and Vitousek 2001); a similar stimulation of P cycling occurs in areas receiving high levels of anthropogenic N deposition (Gress et al. 2007). However, the increase in P cycling observed in N-fertilized sites typically is insufficient to balance the increased rate of N inputs, and P often becomes limiting.

Human-enhanced N deposition now is concentrated in Europe, central and eastern North America, east Asia, and peri-urban areas elsewhere (Galloway and Cowling 2002). Ecological experiments (and ecologists) are concentrated in the same areas, and it is possible that much of the P limitation summarized in the meta-analysis by Elser et al. (2007) reflects anthropogenic P limitation secondary to human alteration of the N cycle. Conversely, human alterations of the global P cycle
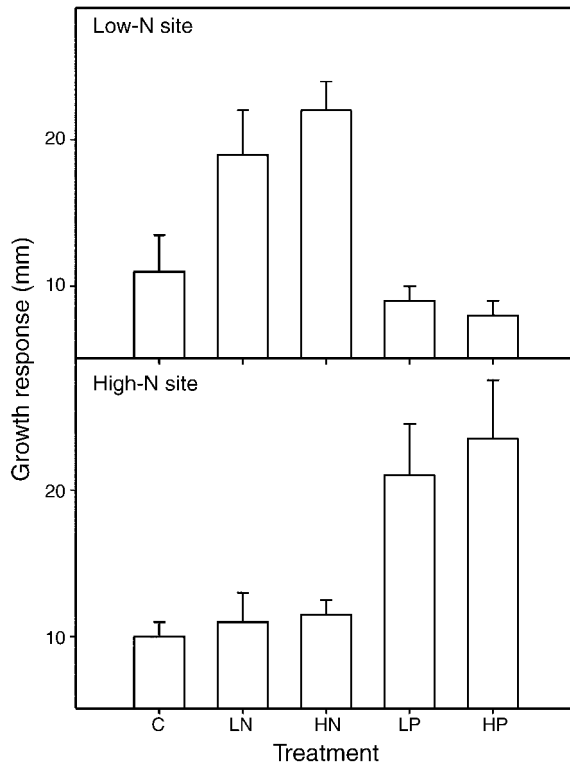
Fig. 3. Response of *Sphagnum* growth (mean + SE) to additions of two levels (low and high) of N and P in a bog in southern Sweden that received high levels of anthropogenic N deposition (high-N site), and one in northern Sweden that received little anthropogenic N. Treatments are: C, control; LN, low N addition; HN, high N addition; LP, low P addition; HP, high P addition. The figure is redrawn from Aerts et al. (1992).

could cause anthropogenic N limitation, certainly in P-fertilized ecosystems where N fixation is constrained, possibly where land use causes widespread increases in the long-distance transport of atmospheric dust (Okin et al. 2004, Tegen et al. 2004). The greater mobility and biological availability of combined N in the atmosphere implies that anthropogenic P limitation should be much more widespread (if perhaps less persistent) than anthropogenic N limitation.

DISCUSSION

The mechanisms that individually and interactively drive P limitation, together with those driving N limitation, which are summarized in Table 2, could contribute to our understanding of N and P dynamics in terrestrial ecosystems in two ways. First, we are concerned with nutrient limitation (both proximate and ultimate) to many more ecosystems than we will be able to test empirically with fertilization. Indirect measures like element ratios in foliage can be useful predictors of which nutrient is likely to limit particular sites, and so to which anthropogenic changes particular systems are likely to prove most vulnerable. However, the inferences derived from such indices will be much stronger if they are coupled to mechanism-based understanding of why those particular nutrients are limiting to particular ecosystems.

Second, identifying ultimate limiting nutrients is important, because alterations in their supply have the capacity to transform the structure and functioning of ecosystems. The long-term, well-controlled, whole-system experiments that are necessary to establish ultimate vs. proximate limitation (Schindler et al. 2008) will always be sparse, particularly in terrestrial ecosystems with perennial vegetation. It will be largely through the understanding of mechanisms that we can build upon those few experiments to determine where particular nutrients are likely to represent ultimate limiting resources, and why.

Which of the mechanisms driving P limitation are capable of causing ultimate P limitation? Clearly, P depletion in ancient, deeply leached soils can drive ultimate P limitation, just as Walker and Syers (1976) implied when they described such soils as being a "terminal steady state" of profound P limitation, from which there is no exit other than geological disturbance or human fertilization that can rejuvenate soils. Parent-material-based P limitation also can be deep and sustained. Where soil barriers develop into permanent features of soils (permafrost prior to rapid global warming; massive placic horizons in some tropical soils), they too could drive ultimate P limitation by physically

TABLE 2. Pathways, mechanisms, and timescales of N limitation to primary production in terrestrial ecosystems.

Pathway	Mechanism	Timescale
Demand-independent losses	losses of combined N that organisms cannot prevent, including leaching of DON, post- disturbance losses, some gaseous pathways	decades to centuries; depends on loss pathway
Constraints to biological N fixation	biological N fixation is slow or absent even when N is limiting; could be due to energetic costs, differential grazing, demands for P, Mo, or other essential elements	decades to centuries
Transactional	slow release of N from complex organic into soluble forms, relative to the supply of other resources	years to centuries
Sink driven	sequestration of available N in an accumulating pool within ecosystems	decades to millenia

Sources: Vitousek and Howarth (1991), Vitousek and Field (1999), and Vitousek (2004).

PLATE 1. Ecosystems of the Mendocino Terraces chronosequence, California, USA. The upper photo shows a large-statured coniferous forest on terrace 2, supported by deep and relatively fertile soils. The lower photo shows a very small-statured pygmy forest ecosystem on terrace 5; the development of a pedogenic barrier to water movement and root penetration and depletion of nutrients in the soil above that barrier contribute to profound nutrient limitation to vegetation on this older terrace (Jenny et al. 1969). Photo credits: B. Z. Houlton.

constraining the volume of the biologically accessible portion of the ecosystem.

In contrast, most forms of sink-driven P limitation are transitory, leading to proximate limitation; sooner or later most sinks become saturated, unless another process removes P from the system. The occluded P accumulated in ancient soils (Fig. 1; Walker and Syers 1976) may be an exception, although recent evidence suggests that much of that pool is dynamic on decadal timescales (e.g., Richter et al. 2004). Most often, transactional P limitation is similarly transitory; generally it occurs when other resources (particularly N) are supplied rapidly enough that even though P is present in primary minerals, its supply via weathering cannot keep up. Except where erosion is extremely rapid, P supplied via weathering should accumulate in biologically-available pools and eventually bring the supply of P more or less into alignment with other limiting resources. Anthropogenic

P limitation should behave similarly to transactional limitation; in many (not all) situations, it is a special case of transactional limitation.

We conclude that the most important mechanisms causing ultimate P limitation are those that affect the ecosystem-level mass balance of P. No terrestrial ecosystem is closed, even for a relatively immobile element like P, so an essential component of the maintenance of any low-P terminal steady state is losses of P. Mechanisms involving depletion, physical barriers, and low-P parent material all depend on the existence of pathways of P loss that continue even where P is limiting to organisms, and which thereby prevent accumulation of biologically available P from very small inputs via continued weathering or dust fluxes (Chadwick et al. 1999, Okin et al. 2004, Soderberg and Compton 2007). Losses via dissolved organic P could fulfill this condition (Hedin et al. 2003). In effect, the depletion-driven mechanism summarizes the situation during soil development in which losses of P are greater than inputs via weathering and other pathways—until the terminal steady state is reached, and inputs and outputs are both very small. Limitation based on soil barriers works similarly but can develop more rapidly; only processes occurring in the constrained space above the barrier are relevant to terrestrial biota, and these can come to a terminal steady state more rapidly. In parent-material-based limitation, inputs of P are low from the very early stages of soil development onward, and even very small losses of P can offset weathering.

An ecosystem-level steady state in P need not be the terminal steady state described by Walker and Syers (1976). The uplift/erosion model of ecosystem P balances by Porder et al. (2007) showed that moderate rates of uplift and erosion (typical of much of Earth's surface) should yield inputs of P via uplift and losses via erosion and other pathways that are more or less in balance, under circumstances that (for most parent material P contents) should provide a sufficient supply of P to terrestrial ecosystems. Ultimate limitation by P generally arises with very slow rates of erosion, which make depletion-driven and soil barrier limitation possible. On the other hand, very rapid uplift and erosion could cause losses via erosion to occur before much weathering of primary minerals can take place, preventing the accumulation of a biologically available pool and thereby allowing transactional P limitation to cause ultimate limitation.

We have focused on the mechanisms driving P limitation here, but N limitation could be proximate or ultimate as well. Without using this terminology, Vitousek and Field (1999) suggested that limitation by N could be an ultimate control over primary productivity only when each of two ecosystem mass balance conditions is met. First, there must be a pathway of N loss that cannot be controlled by biological activity, even when N is in short supply. Persistent losses of dissolved organic N from undisturbed ecosystems can satisfy this condition (Hedin et al. 1995, Perakis and

Hedin 2001), as can losses associated with frequent disturbance (Houlton et al. 2003, Vitousek 2004). These disturbance-associated losses should play a larger part in the development of N than of P limitation, because the high mobility of N means that N losses can be substantial whenever the supply of biologically available N exceeds demand, even briefly. Indeed, Davidson et al. (2007) recently demonstrated that N losses associated with human disturbances to putatively P-limited Amazonian ecosystems altered their N/P stoichiometry sufficiently to induce limitation by N in secondary forests. Where fire is an important agent of disturbance, it reinforces the likelihood of N limitation; fire in particular volatilizes much more N than it does P.

Second, for N to be an ultimate limiting nutrient there also must be constraints to biological N fixation that cannot be overcome even when N is limiting to primary production. Major constraints that have been identified include the energetic cost of fixing N (especially under a plant canopy), differential grazing on protein-rich N fixers, the supply of P and of trace elements associated with the biochemistry of N fixation (Vitousek and Howarth 1991, Vitousek and Field 1999), and low temperatures (Houlton et al. 2008). Where the supply of P is a major constraint to N fixation, proximate limitation by N can be a manifestation of ultimate limitation by P.

For both N and P, understanding the controls of ecosystem mass balances is crucial to identifying and characterizing ultimate limiting nutrients, as Schindler's studies of lake eutrophication demonstrate (Schindler 1977). On land, the cycles of N and P are coupled through biological demand, but they differ so substantially in sources and dynamics that either element may be or may become in short supply compared to the other. As human activities continue to increase N inputs across more of Earth's surface, some areas will continue to be transformed by that added N. In others, limitation by P or other resources will develop, or become deeper and more widespread.

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