Biogeochemistry **13**: 87–115, 1991

Nitrogen limitation on land and in the sea: How can it occur?

PETER M. VITOUSEK[1] & ROBERT W. HOWARTH[2]
[1] *Department of biological Sciences, Stanford University, Stanford, CA 94305, USA*
[2] *Section of Ecology and Systematics, Cornell University, Ithaca, NY 14853, USA*

Received 1 October 1990; accepted 18 February 1991

Key words: biogeochemistry, energetic constraints, nitrogen fixation, phosphorus, succession, trace elements

Abstract. The widespread occurrence of nitrogen limitation to net primary production in terrestrial and marine ecosystems is something of a puzzle; it would seem that nitrogen fixers should have a substantial competitive advantage wherever nitrogen is limiting, and that their activity in turn should reverse limitation. Nevertheless, there is substantial evidence that nitrogen limits net primary production much of the time in most terrestrial biomes and many marine ecosystems.

We examine both how the biogeochemistry of the nitrogen cycle could cause limitation to develop, and how nitrogen limitation could persist as a consequence of processes that prevent or reduce nitrogen fixation. Biogeochemical mechansism that favor nitrogen limitation include:
— the substantial mobility of nitrogen across ecosystem boundaries, which favors nitogen limitation in the "source" ecosystem — especially where denitrification is important in sediments and soils, or in terrestrial ecosystems where fire is frequent;
— differences in the biochemistry of nitrogen as opposed to phosphorus (with detrital N mostly carbon-bonded and detrital P mostly ester-bonded), which favor the development of nitrogen limitation where decomposition is slow, and allow the development of a positive feedback from nitrogen limitation to producers, to reduced decomposition of their detritus, and on to reduced nitrogen availability; and
— other more specialized, but perhaps no less important, processes.
A number of mechanisms could keep nitrogen fixation from reversing nitrogen limitation. These include:
— energetic constraints on the colonization or activity of nitrogen fixers;
— limitation of nitrogen fixers or fixation by another nutrient (phosphorus, molybdenum, or iron) — which would then represent the ultimate factor limiting net primary production;
— other physical and ecological mechanisms.
The possible importance of these and other processes is discussed for a wide range of terrestrial, freshwater, and marine ecosystems.

Introduction

Nitrogen limitation to primary production is believed to be widespread. A requirement for nitrogen fertilizer is pervasive in intensive agricultural sites, and nitrogen is considered by many to be the element most likely to limit production in many natural terrestrial and marine ecosystems as well.

The physiology of nitrogen limitation is relatively well understood. Producers require larger quantities of nitrogen than of other nutrients, and nitrogen is more costly (energetically) to obtain and use (Gutschick 1981). A large fraction of the nitrogen in primary producers functions directly in capturing energy in photosynthesis (Evans & Seemann 1989), and there is a strong correlation between the amount of nitrogen in terrestrial plants and their photosynthetic capacity (Field & Mooney 1986).

Despite this widespread belief in the prevalence of nitrogen limitation and understanding of its physiological basis, it is not obvious why nitrogen should ever limit primary production on the ecosystem level, at least for long. The atmosphere contains an extraordinarily abundant and well-distributed pool of N_2, and there are many symbiotic and non-symbiotic organisms with the capacity to fix this nitrogen into more widely available forms. It would seem that where primary production is limited by nitrogen, nitrogen fixing organisms and symbioses should have an enormous competitive advantage — and that their activity should in turn add fixed nitrogen to and ultimately alleviate nitrogen limitation in the system as a whole. This logical argument against nitrogen limitation is in fact part of the basis for Redfield's (1958) classic analysis of marine biogeochemistry (see also Smith 1984). More recently, it also has been invoked in terrestrial (cf Walker & Syers 1976) and freshwater (cf Schindler 1977) ecosystems.

Whether nitrogen is actually limiting to primary production, and if so where, for how long, and why, is fundamental to our understanding of numerous facets of physiological, population, community, and ecosystem ecology. It also matters for understanding global phenomena and for predicting the effects of global change. For example, models developed by both Pastor & Post (1988) and Schimel et al. (1990) predict that greenhouse-induced increased temperatures would cause increased decomposition, increased nitrogen mineralization, and *hence* increased primary production in northern latitudes — thereby offsetting some of the increased carbon release from northern soils that could otherwise provide a positive feedback to global warming. Peterson & Melillo (1985) and Aber et al. (1989) suggest that enhanced nitrogen deposition resulting from nitrogen fixation during fossil fuel combustion can lead to significant carbon storage in recipient ecosystems — a phenomenon that could explain part of the north temperate terrestrial CO_2 sink suggested by Tans et al. (1990). On the other hand, Broecker (1982) concludes that changes in phosphorus supply from continents and shelf areas are sufficient to drive long-term changes in net carbon storage in pelagic marine ecosystems — despite evidence that nitrogen limits short-term carbon fixation in many of those areas.

In this paper, we briefly review evidence for nitrogen limitation in a range of terrestrial and aquatic ecosystems. We then examine a number of mechanisms that could explain the persistence of apparent or real nitrogen limitation in the face of the rather persuasive logic that it should be ephemeral or rare.

Definitions

In this paper, we define nutrient limitation to a particular process as being demonstrable when a substantial addition of a particular nutrient increases the rate or changes the endpoint of that process. Howarth (1988) identified three processes as being potentially nutrient limited:

- the growth of populations currently present,
- net primary production (NPP, defined as gross production or photosynthesis minus respiration of the producers), and
- net ecosystem production (NEP, defined as NPP minus heterotrophic respiration).

We emphasize nutrient limitation to NPP here, but all three processes are of interest, and all three interact at a variety of temporal scales. For example, net primary production is critical for determining the energetic base of an ecosystem and its rate of carbon and element cycling, but the response of NPP to a change in nutrient supply can be constrained by the responsiveness of the species present. Net ecosystem production is most important in determining the net effect of ecosystems upon downstream ecosystems and the atmosphere, but most changes in NEP resulting from alterations in nutrient supply are driven (initially) by changes in NPP.

It is very difficult or impossible to determine the *degree* of nutrient limitation of either NPP or NEP for a number of reasons, most importantly that the species present in a low nutrient site may respond a little to additions of a nutrient, but other species that require high levels of nutrients might have responded still more had they been present (Bradshaw et al. 1960, 1964; Chapin et al. 1986; Howarth 1988; Grubb 1989). We will therefore discuss only the presence or absence of limitation by particular nutrients.

The time scale over which we examine nutrient limitation is important. A month-long nutrient enrichment experiment may be appropriate for lake phytoplankton, where the community composition can change completely on this time scale, but may simply represent short-term noise in a forest. Even within a type of ecosystem, multiple time scales are important. For example, Walker & Syers (1976) argued quite convincingly that phosphorus should ultimately limit primary production in terrestrial ecosystems — but "ultimately" may mean after millions of years of soil development. We are concerned with why it may take millions of years for phosphorus limitation to be expressed — and with why nitrogen often appears to limit production in soils that are "only" tens to hundreds of thousands of years old. In this paper, we will emphasize nutrient limitation that can be demonstrated on time scales ranging from a few days to a few years.

Our best information on nutrient limitation comes from nutrient addition experiments; an increase in NPP and/or NEP in a well-controlled, well-replicated nutrient addition experiment establishes, indeed defines, the existence of nutrient limitation. Often, however, such experiments are nearly or wholly lacking in important types of ecosystems, and we must make inferences based upon indirect evidence such as element ratios in primary producers or their detritus, or the ratios of elements cycling through the biota or present in the external milieu. Such element ratios are useful within a given type of ecosystem, in that they reflect the relative abundance or scarcity of a particular element rather closely (Redfield 1958; Reiners 1986). However, they are not very useful in comparisons across types of ecosystems, because (for example) differences in the utilization of carbon for structure (wood) or nitrogen for defensive compounds (alkaloids) in forest versus grassland or macrophytes versus phytoplankton can alter the meaning of element ratios substantially (Atkinson & Smith 1983; Vitousek et al. 1988). In any case, the use of element ratios or tissue concentrations to infer nutrient limitation is inherently less satisfying than experimental studies of nutrient additions.

Evidence for nutrient limitation

Terrestrial ecosystems

Nitrogen is often considered to be the element most often limiting to net primary production in terrestrial ecosystems (cf Gutschik 1981, 1987; Lee et al. 1983; Binkley 1986; Kimmins 1987; Tilman 1988). The evidence for that assertion is fairly good in the temperate and boreal zones; fertilization with nitrogen alone often leads to increased productivity in temperate forests (Mitchell & Chandler 1939; Miller 1981), boreal forests (Agren 1983; van Cleve & Zasada 1976; van Cleve et al. 1983; Bonan

1990), temperate grasslands (Valiela 1983; Hunt et al. 1988; Huenneke et al. 1990), and arctic and alpine tundra (Bliss 1963; Shaver & Chapin 1980). Limitation by phosphorus and other elements also occurs, sometimes jointly with nitrogen limitation and sometimes on relatively unusual soils (ie deep glacial outwash, organic soils). In water-limited systems such as short-grass steppe and desert, water often represents the primary limit to production, but nitrogen is often the nutrient that becomes limiting when water supply is enhanced (Dodd & Lauenroth 1979; van Breman & de Wit 1983; Fisher et al. 1988).

Indirect evidence based on element ratios also supports the generalization that nitrogen is often in short supply in the temperate and boreal zones. On average, temperate and boreal forests have high carbon:nitrogen ratios and relatively low nitrogen:phosphorus ratios in the organic material that they contain or circulate (Vitousek 1982; Melillo & Gosz 1983) — except where they are dominated by symbiotic nitrogen fixers, or where they receive very large inputs of anthropogenically fixed nitrogen from the atmosphere. Moreover, there is an overall positive correlation between ecosystem nitrogen inputs and NPP (Kelly & Levin 1986) and an overall inverse correlation between NPP and carbon:nitrogen ratios (Pastor et al. 1984; Zak et al. 1989). Where the appropriate experiments and measurements have been made, fertilization with nitrogen often both increases NPP and decreases carbon:nitrogen ratios substantially (Miller et al. 1976).

Production in many tropical savannahs and grasslands is demonstrably nitrogen-limited (van Breman & de Wit 1983; Högberg 1989), but there is relatively little direct evidence bearing on nutrient limitation in natural tropical forests. Cuevas & Medina (1988) did demostrate that tree roots in a lowland tropical forest on an oxisol proliferated vigorously in response to spot additions of calcium or phosphorus (but not nitrogen), suggesting deficiencies of those elements, while roots in a forest on a spodosol responded to added nitrogen. Indirect evidence from element ratios suggests that nitrogen generally is *not* limiting in lowland tropical forests — carbon:nitrogen ratios are low, and nitrogen:phosphorus (or calcium, magnesium, or potassium) ratios are very high by global standards in forests on the oxisols and ultisols that make up the majority of tropical forest soils (Vitousek 1984; Vitousek & Sanford 1986; Jordan 1985). Nitrogen-fixing legumes are often important components of the plant community in such sites. In contrast, tropical montane forests and forests developed on sandy soils (spodosols and psamments) generally have higher carbon:nitrogen ratios and could be limited by nitrogen (Cuevas & Medina 1986, 1988; Vitousek & Sanford 1986; Vitousek et al. 1988). Two fertilization studies in the montane tropics have identified nitrogen (or nitrogen and phosphorus) as limiting to primary production (Vitousek et al. 1987; Tanner et al. 1989).

Finally, long-term production in modern intensive agricultural systems generally is limited by nitrogen — whether or not the natural systems from which they were derived are nitrogen limited. Phosphorus, potassium, and often other elements are also applied extensively, but most often their effects on crop yield are interactive with those of nitrogen.

Freshwater ecosystems

NPP in most lakes in the temperate zone is clearly limited by phosphorus, at least on the time scale of whole growing seasons or years (Edmondson 1970; Schindler 1977; Schindler et al. 1978; Vollenweider 1976). Short-term nutrient enrichment experiments in closed containers have sometimes suggested that carbon rather than phosphorus is limiting; however, this is an artifact of separating waters from sources of resupply of carbon dioxide from the atmosphere and sediments (Schindler 1981). Whole-lake nutrient enrichment experiments have demonstrated that phosphorus limits NPP even in waters having a very low carbon dioxide content (Schindler 1977; Schindler et al. 1978).

In contrast to limitation of NPP, the growth of a particular algal population is often limited by nutrients other than phosphorus. For instance, the growth of diatom populations in many freshwater lakes is commonly limited by silicon (Tilman et al. 1982, 1986; Schelske et al. 1986). However, at low silicon levels, diatoms are replaced by other algal species having low silicon requirements without any demonstrable effect on NPP.

The growth of many phytoplankton species also can be limited by nitrogen when the availability of nitrogen is low compared to that of phosphorus. As with silicon, however, this typically has little influence on NPP in temperate-zone lakes. The low availability of nitrogen favors dominance by nitrogen-fixing cyanobacteria (Schindler 1977; Flett et al. 1980; Tilman et al. 1982; Smith 1983) which replace the species whose growth was nitrogen limited.

NPP in some tropical lakes could be limited by nitrogen rather than by phosphorus (Melack et al. 1982; Hecky & Kilham 1988). There is some evidence that certain oligotrophic temperate-zone lakes can also be nitrogen limited (Goldman 1988), and some saline lakes also appear to be limited by nitrogen or elements other than phosphorus (Campbell & Prepas 1986).

Howarth (1988) recently reviewed the evidence for nutrient limitation of NPP in pelagic marine ecosystems. Many workers have long considered NPP in estuaries and marine ecosystems to be nitrogen limited. Evidence supporting this comes principally from short-term bioassays (Ryther & Dunstan 1971; Vince & Valiela 1974; Smayda 1974; Norin 1977, Graneli 1978, 1981, 1984; Carpenter & Capone 1983; D'Elia et al. 1986) and from the relatively low concentrations of dissolved inorganic nitrogen compared to dissolved phosphorus in many marine ecosystems (Thomas 1966; Ryther & Dunstan 1971; Boynton et al. 1982; Nixon & Pilson 1983; Graneli 1984; Valiela 1984; D'Elia et al. 1986; Smith et al. 1986). Both lines of evidence can be criticised (McCarthy & Goldman 1979; Smith 1984; Hecky & Kilham 1988; Howarth 1988), but taken cumulatively, the data to tend to suggest that NPP in many temperate-zone coastal marine ecosystems is indeed nitrogen limited (Howarth 1988).

In contrast, Redfield (1958) argued that production in the world's oceans should be limited by phosphorus, since nitrogen fixation could make up any nitrogen deficits. Broecker (1982) and Smith (1984) have argued similarly that NEP should be phosphorus limited. However, cynobacteria (mostly *Trichodesmium*) are sparse and rates of nitrogen fixation are very low over most of the ocean (Carpenter 1983; McCarthy & Carpenter 1983; Howarth et al. 1988 a, b). Nonetheless, the sinks for nitrogen in open ocean waters are small, and the low rates of nitrogen fixation may be sufficient to alleviate nitrogen deficiencies. In the oligotrophic, subtropical Pacific, the low levels of nitrogen and phosphorus are present nearly in the relative abundances required by phytoplankton, although nitrogen appears to be slightly less abundant (Jackson & Williams 1985; Smith et al. 1986). Other elements may also control primary production in some open ocean waters; in many oceanic waters (Southern Ocean, subarctic Pacific, and equatorial Pacific), both phosphorus and nitrogen are relatively abundant (Martin et al. 1989). Martin and colleagues (Martin & Fitzwater 1988; Martin et al. 1989; Martin et al. 1990) have proposed that iron may limit net primary production in these waters (but see Banse 1990; Dugdale & Wilkerson 1990; Peng & Broecker 1991).

Net ecosystem production in many tropical lagoons and embayments appears to be phosphorus limited (Smith 1984), as does photosynthesis and growth of tropical seagrasses and macroalgae in many (Short et al. 1985, 1990; Littler et al. 1988; Powell et al. 1989) but not all (La Pointe et al. 1987; McGlathery et al. in press) locations. NPP appears to be limited by phosphorus in some temperate zone estuaries during at least some seasons (Myers & Iverson 1981; D'Elia et al. 1986).

Why nitrogen limitation?

The brief survey of nutrient limitation above makes it clear that nitrogen is at least the proximate limiting nutrient to net primary production in many of Earth's ecosytems for much of the time. Ultimately, this nitrogen limitation can persist only if biological nitrogen fixation does not respond to nitrogen deficiency with an increase sufficient to reverse that deficiency in nitrogen-limited sites. However, a variety of differences in the biogeochemical cycle of nitrogen as compared to other elements (particularly phosphorus) could initiate or accentuate nitrogen limitation in many ecosystems. We will review these differences briefly by contrasting the biogeochemical cycles of nitrogen and phosphorus, the two leading candidates for the title of "most limiting nutrient" globally. We will then examine a number of reasons why the activity of biological nitrogen fixers could fail to increase substantially in nitrogen limited ecosystems despite the strong competitive advantage they should enjoy.

Biogeochemical mechansism affecting nitrogen limitation

First, in terrestrial ecosystems nitrogen and phosphorus differ in their ultimate source, with nitrogen derived primarily from the atmosphere and phosphorus from rock weathering. Accordingly, nitrogen is nearly absent from new soils and would be expected to be limiting to both NPP and NEP there — as indeed it generally is (cf. Stevens & Walker 1970; Marrs et al. 1983; Vitousek et al. 1987). In contrast, the amount and availability of phosphorus declines during long-term soil development, eventually reaching a "terminal steady state" of profound phosphorus limitation (Walker & Syers 1976; Cole & Heil 1981). This difference may help to explain why tropical forests on very old, deeply leached soils appear to be strongly phosphorus (or calcium or potassium) limited (Vitousek & Sanford 1986; Cuevas & Medina 1988), while glaciation is frequent enough in temperate and boreal ecosystems to avoid this "terminal steady state". It does not explain why NPP and perhaps NEP in many temperate and boreal areas is nitrogen limited; 12,000 to 20,000 years of post-glacial time should be sufficient to accumulate enough nitrogen from precipitation and nitrogen fixation to alleviate the nitrogen limitation that occurs in new soils (Vitousek & Reiners 1975; Peterjohn & Schlesinger 1990).

Second, nitrogen and phosphorus differ in their mobility through soils, with nitrogen being much more readily lost to terrestrial ecosystems through leaching to aquatic systems or volatilization and denitrification to the atmosphere. Consequently, nitrogen loading from natural terrestrial ecosystems to aquatic systems often is proportionally greater than phosphorus loading (Kelly & Levin 1986), a difference that could contribute to phosphorus limitation in lakes.

Could the greater mobility of nitrogen cause a tendency towards nitrogen limitation in terrestrial ecosystems? Nitrogen losses clearly are sufficient to cause nitrogen limitation in some disturbed terrestrial ecosystems. Nitrogen retention within ecosystems is dominated by biological processes (plant uptake and microbial immobilization) (Vitousek & Matson 1985). When these are disrupted by intense or prolonged disturbance such as cultivation, the initial response is nitrogen mobilization leading to a large increase in nitrogen availability that can support a burst of "pioneer" agriculture. With continued cultivation, however, a large proportion of total soil nitrogen eventually is lost to harvest, erosion, leaching to streamwater and groundwater, and volatilization and denitrification. The residual nitrogen is in organic forms that are highly recalcitrant to decomposition. In contrast, phosphorus is retained within terrestrial ecosystems by both biological and geochemical mechanisms (notably adsorption and precipitation with iron, aluminum, manganese, and calcium) (Wood et al. 1984); hence phosphorus losses primarily occur through harvest and erosion even under prolonged cultivation. The net result is that losses of soil nitrogen average 25—50% of the original total after 40 or more years of intensive cropping in temperate grassland (Haas et al. 1957; Cole et al. 1989), while phosphorus losses average 5—15% (Haas et al. 1961; Tiessen et al. 1983). Moreover, the relatively labile forms of organic nitrogen are depleted disproportionately in comparison with phosphorus (Parton et al. 1988). This difference in mobility probably explains why productivity in most long-term, intensive agricultural ecosystems becomes dependent on large and repeated additions of nitrogen fertilizer or on frequent rotations of legumes.

Natural disturbance is pervasive in terrestrial ecosystems (Pickett & White 1985) — could it cause elevated nitrogen losses that lead ultimately to nitrogen limitation? There is evidence that nitrogen mobilization and losses are increased by a variety of natural disturbances, including insect defoliation (Swank et al. 1981) and forest dieback (Matson & Boone 1984), but the magnitude of nitrogen losses following most natural disturbances examined thus far is rather small. However, fire is one form of both natural and human-caused disturbance that unquestionably causes disproportionately high losses of nitrogen. Fire volatilizes nitrogen as it releases most other nutrients into available forms (Raison 1979; Lobert et al. 1990; Crutzen & Andreae 1990). Frequent fire can therefore be expected to lead to nitrogen limitation (Vitousek et al. 1982). At the same time, fire also reduces competition for light and releases phosphorus into readily available forms; it could therefore enhance nitrogen fixation

(Reiners 1981). There is substantial evidence for elevated nitrogen fixation following fire (Eisele et al. 1989), but high frequencies of fire (often as a consequence of human activity) clearly cause nitrogen losses in excess of any replacement by nitrogen fixation (Ojima 1987). Moreover, although fire volatilizes substantial quantities of nitrogen, it also increases the short-term availability of residual soil nitrogen. Consequently, a short-lived flush of available nitrogen can partially repress nitrogen fixation during the brief period in which light and phosphorus are elevated after fire (Hobbs & Schimel 1984). Overall, fire is probably a significant cause of nitrogen limitation in terrestrial systems in which it is frequent.

Are nitrogen losses from undisturbed terrestrial ecosystems sufficient to lead to nitrogen limitation? At first glance, it would appear not; hydrologic nitrogen balances (N in bulk precipitation versus N loss by leaching) generally yield nitrogen inputs well in excess of outputs (cf Likens et al 1977). The major exceptions are observed where nitrogen availability within intact systems is high, as in old, non-aggrading forests on fertile soils and in the lowland tropics (Vitousek & Reiners 1975; Coats et al. 1976; Lewis 1988). Where nitrification is substantial, denitrification to N_2 could be responsible for more nitrogen loss, but such fluxes are notably difficult to estimate on an areal basis. Losses of the more easily measured gas N_2O (a product of nitrification and denitrification) are much greater from lowland tropical forest ecosystems than elsewhere (Keller et al. 1986; Matson & Vitousek 1987). Together, these observations are consistent with the occurrence of substantial nitrogen losses only where nitrogen is not limiting.

On the other hand, nitrogen losses from terrestrial ecosystems must be more or less equal to inputs on long time scales; for example, Peterjohn & Schlesinger (1990) estimated that more than 70% of total nitrogen inputs to a desert eosystem over the past 10,000 years had been lost, and similar calculations can be made for any terrestrial ecosystem. Whether these losses occur episodically following disturbance or more-or-less continuously by denitrification is uncertain, but in either case the greater mobility of nitrogen than phosphorus tends to drive terrestrial ecosystems towards nitrogen limitation.

Third, differences in the cycling of nitrogen and phosphorus through sediments can favor the development of either nitrogen or phosphorus limitation in aquatic ecosystems, and similar processes can be important in soils. In many temperate-zone estuaries and coastal marine ecosystems, phosphorus mineralized during decomposition is readily released from the sediments (Rowe et al. 1975; Boynton et al. 1980), while denitrification in sediments is a major process removing available nitrogen from both freshwater lakes and coastal marine ecosystems (Knowles 1982; Seitzinger et al. 1984; Seitzinger 1988). Consequently, nutrient fluxes from sediments are relatively depleted in nitrogen compared to phosphorus (Nixon et al. 1980), and nitrogen limitation should be favored. Smith et al. (1989) proposed that sediment denitrification operates as part of an organic carbon-controlled regulatory cycle that maintains proximate nitrogen limitation to NPP (although not to NEP) in coastal waters. One facet of this cycle is that any accumulation or addition of dissolved inorganic nitrogen can cause the fixation of more organic carbon, which in turn can cause the reduction of any accumulated nitrate when it decomposes.

Phosphorus release from sediments is not always high; fluxes of nutrients from lake sediments can be either enriched or depleted in nitrogen compared to phosphorus as a consequence of phosphorus adsorption in sediments (Kamp-Nielsen 1974; Khalid et al. 1977; Schindler et al. 1977). Recently, Caraco et al. (1989, 1990) suggested that phosphorus fluxes from sediments are regulated in part by sulfate concentrations; when sulfate levels are low, phosphorus tends to adsorb to the sediment, whereas high sulfate levels favor release of phosphorus to the water column.

In tropical marine calcareous sediments, phosphorus can be tightly adsorbed (Morse et al. 1985), often contributing to phosphorus limitation in these ecosystems (Short et al. 1985, 1990). However, concentrations of dissolved phosphorus are high in some calcareous sediments (Hines & Lyons 1982; McGlathery et al. in press), perhaps because high organic matter concentrations compete with phosphorus for adsorption sites (Krom & Berner 1980). Nitrogen limitation can occur under these conditions (McGlathery et al. in press).

Phosphorus adsorption could also affect the degree of phosphorus versus nitrogen limitation in some terrestrial ecosystems. Phosphate adsorption is particularly marked in the variable-charge iron and aluminum sesquioxide clay-dominated soils of tropical regions (Uehara & Gillman 1981); such clays are amphoteric, with net positive charge under acidic conditions, and they bind phosphate nearly irreversibly (Sollins et al. 1988; Sollins 1989). Many tropical agricultural systems require fertilization with very large quantities of phosphorus to overcome this phosphorus fixing capacity (Uehara & Gillman 1981). Accordingly, the observed pattern of very high C:P and N:P ratios in the vegetation of many tropical forests (putative phosphorus limitation) could be due in part to phosphorus adsorption. Adsorption of nitrate-nitrogen also occurs on such soils (Kinjo & Pratt 1971; Matson et al. 1987), but it is neither as complete nor as irreversible as phosphorus adsorption.

Fourth, biochemical differences between nitrogen and phosphorus could be significant on the ecosystem level. Most importantly, organic nitrogen is directly carbon-bonded (C-N) and often in structural or complexed forms, while organic phosphorus is usually ester-bonded (C-O-P) and often soluble. Plant roots, mycorrhizae, algae, bacteria, and fungi all can produce extracellular phosphatases that cleave the ester phosphate bond (McGill & Cole 1981; Hunt et al. 1983, Howarth 1988); all therefore can invest nitrogen in obtaining phosphorus, and thereby synchronize the release of phosphorus from organic forms with their own phosphorus requirements. In contrasts, multiple enzyme systems must be involved in the breakdown of structural or phenolic nitrogen-containing organic compounds before any nitrogen can be released into available forms. Synchronizing plant requirements with nutrient supply is therefore much more difficult for nitrogen than for phosphorus, and extracellular enzyme systems may be less rewarding (in part because they require investing limited nitrogen on the chance of obtaining more nitrogen, all in competition with microorganisms [D. Valentine, pers. comm.]). This distinction is appealing, although the experimental evidence supporting it is weak. If it is correct, slow rates of decomposition should impede nitrogen cycling more than phosphorus cycling (Jackson & Williams 1985; Smith et al. 1986; Vitousek & Walker 1987). In terrestrial systems, climatic control makes decomposition much more rapid in lowland tropical than temperate or boreal regions (Meentemeyer 1978), and this difference in biochemistry therefore represents another mechanism that could cause a tendency towards nitrogen limitation in temperate and boreal ecosystems where organic matter is accumulating, and limitation by other nutrients in lowland tropical regions.

In terrestrial ecosystems, this difference between the nitrogen and phosphorus cycles also means that nitrogen limitation can set in motion a positive feedback that maintains or accentuates nitrogen limitation — whatever its initial cause (Vitousek et al. 1982; Pastor & Post 1986). Nitrogen-deficient plants produce tissue and litter that has higher carbon:nitrogen ratios and relatively higher contents of lignin and other recalcitrant compounds than plants with sufficient nitrogen (Vitousek 1982; Pastor et al. 1984). Their tissue therefore decomposes relatively slowly, and the microorganisms decomposing it immobilize large quantities of nitrogen for long periods of time (Melillo et al. 1982). This immobilization in turn reduces nitrogen availability to plants, and the cycle continues towards greater nitrogen limitation as long as organic nitrogen continues to accumulate. Some of these mechanisms apply equally well to phosphorus (i.e. phosphorus limitation leads to high carbon:phosphorus ratios in litter), but to the extent that organic phosphorus can be mineralized on demand (McGill & Cole 1981), the complete feedback cycle will not operate.

Finally, a number of additional mechanisms that favor nitrogen over phosphorus limitation have been suggested. Grazing by some species of zooplankton apparently can regenerate phosphorus more effectively than nitrogen because relatively more phosphorus is excreted in soluble forms and relatively more nitrogen is retained in fecal pellets (Knauer et al. 1979; Lehman 1984). In terrestrial ecosystems, reabsorption of phosphorus from senescing foliage may be more effective on average than is reabsorption of nitrogen (Walbridge in press), and there is some evidence that the fraction of foliar phosphorus reabsorbed is more dependent on phosphorus nutrition than is the case for nitrogen (Birk & Vitousek 1984, in Binkley 1986). The generality and overall significance of these mechanisms is uncertain.

Nitrogen fixation and nitrogen limitation

Despite the number of mechanisms that can lead to nitrogen limitation of net primary production, the logic that such limitation (for whatever reason it occurs) should give nitrogen-fixing organisms or symbioses an overwhelming competitive advantage over non-fixers seemingly remains unassailable. The activity of nitrogen fixers could in turn bring the amount and availability of nitrogen into a rough equilibrium with the availability of other resources, compensating for whatever mechanisms are driving the ecosystem toward nitrogen limitation. This is in fact the common response in temperate zone lakes (Schindler 1977; Flett et al. 1980). Why doesn't it occur and alleviate nitrogen limitation of net primary production in all ecosystems?

We believe that three mechanisms or classes of mechanisms can prevent nitrogen fixation from responding to and reversing nitrogen limitation. These include:

1. Nitrogen fixation rates are low because of energetic constraints on the activity of nitrogen-fixing organisms.
2. Rates of nitrogen fixation are themselves limited by some other nutrient; that is, ecosystem-level nitrogen limitation can be viewed as limitation by some other element in disguise.
3. Nitrogen-fixing organisms cannot become established or are unable to fix nitrogen at significant rates due to other ecological or physical constraints.

There is of course no reason to anticipate that only one of these mechanisms limits nitrogen fixation in all sites where nitrogen limitation of net primary production occurs. Rather there is good reason to believe they can interact.

The energetic cost of nitrogen fixation

Nitrogen could limit primary production because the energetic cost of fixing dinitrogen can be high relative to that of taking up ammonium or nitrate. Gutschick (1981) calculated that it costs a symbiotic nitrogen fixer 8—12 g of glucose to acquire 1 g of nitrogen via fixation — not including the construction or maintenance costs of any specialized structures. The operational cost of nitrate reduction is equally high, although it does not require the construction or maintenance of large specialized structures such as root nodules or heterocysts. Moreover, the costs of nitrate reduction may be more apparent than real if reduction can be coupled to photosynthetic electron transport. Finally, ammonium acquisition is energetically inexpensive — discounting any increased investment in roots or symbionts that might be required to overcome the low mobility of ammonium in most soils.

Gutschick (1981, 1987) suggested that in terrestrial ecosystems, symbiotic nitrogen fixers are often present in early successional sites but are absent from climax sites — even though nitrogen remains limiting (indeed, may become limiting) to net primary production in the older sites. He suggested that nitrogen limitation could persist in late-successional or climax ecosystems because as energy becomes limiting in a closed-canopy plant community, nitrogen fixers could lose some of the competitive advantage that they would otherwise enjoy under low-nitrogen conditions. Their relative advantage should decline to zero at the point where the cost to non-fixers of acquiring nitrogen from the soil (investment in roots, uptake and nitrate reduction) balances the cost to fixers of fixing dinitrogen. The productivity of non-fixers will be limited by nitrogen at that point, and any addition of nitrogen should therefore increase NPP on the ecosystem level at least temporarily.

This mechanism could be reinforced by the difficulty that nitrogen fixers experience in colonizing and growing up through the understory of closed-canopy community (Bormann & Gordon 1984). When light levels in the understory are low, it may be impossible for energy-limited understory plants to pay the construction, maintenace, and operational costs inherent to nitrogen fixation — even if nitrogen strongly limits NPP in the system as a whole (Tilman 1986). Nitrogen limitation would then persist even though fixers would offset or reverse nitrogen limitation if they could colonize and reach the canopy. Only in disturbed and early successional sites, or in sites where leaf area remains low through succession due to limitation by some other resource, are nitrogen fixers able to colonize. That successional pattern of colonization is often observed in the temperate zone (Boring et al. 1988), although not in the many tropical forests in which legumes are important components of the community at all stages of succession. Where nitrogen fixing symbioses to persist in late-successional temperate sites, it is generally in water-limited open-canopied sites or as epiphytes (cf Denison 1979).

An entirely different mechanism can reduce nitrogen fixation in many early secondary successional sites. The activity of symbiotic nitrogen fixers is repressed by high levels of available nitrogen, and disturbance generally causes a substantial but short-lived flush of available nitrogen (Bormann & Likens 1979; Vitousek & Matson 1985; Vitousek et al. 1989). Consequently, nitrogen fixation can be suppressed because nitrogen does not limit net primary production at the only time in secondary succession when colonization by nitrogen fixers would be energetically feasible.

Nitrogen fixation by the widespread nonsymbiotic heterotrophic bacteria in terrestrial ecosystems may be constrained by a different kind of energy limitation. The activity of soil microorganisms generally is believed to be limited by the supply of labile organic carbon rather than by nitrogen or other nutrients (Alexander 1977; Flanagan & Van Cleve 1983; Hunt et al. 1988). Heterotrophs that spend scarce energy on nitrogen fixation therefore should be at a competitive disadvantage relative to other heterotrophs, even in systems where net primary prouction is nitrogen limited — and even though nitrogen fixation might ultimately increase the supply of labile organic carbon in those systems. The decomposition of wood, which has very low nitrogen concentrations, may be an exception; heterotrophic nitrogen fixation often is observed in decaying wood (Cornaby & Waide 1973; Roskoski 1980).

Light availability may also play a major role in regulating nitrogen fixation in aquatic ecosystems (Levine & Lewis 1987: Smith, in press). Nitrogen fixation by benthic cyanobacterial mats (and by cyanobacterial symbionts on benthic macrophytes) is prevalent in both freshwater and marine ecosystems when high levels of light strike the bottom (reviewed in Howarth et al. 1988a). This generally occurs in very shallow systems or in highly oligotrophic ecosystems where planktonic biomass is low. Such nitrogen fixation is one reason to expect phosphorus limitation in some oligotrophic, tropical lagoons (Smith 1984; Smith & Atkinson 1984; Howarth 1988). In deeper systems or in more productive temperate-zone estuaries, insufficient light strikes the bottom to support significant nitrogen-fixation by benthic cyanbacteria. Nitrogen fixation in hyper-eutrophic lakes may also be light limited due to extreme self-shading by phytoplankton (Smith, in press). We suspect that the high turbidity and deep mixed layers found in many temperate zone estuaries could also limit the activity of planktonic N-fixing cyanobacteria (see below).

Nitrogen fixation by heterotrophic bacteria occurs commonly in both marine and freshwater sediments. This fixation too appears to be energy limited, and rates of nitrogen fixation increase as the organic carbon concentration of the sediment increases (Howarth et al. 1988a). However, rates of denitrification can also be carbon controlled (Smith et al. 1989), and denitrification exceeds nitrogen fixation by heterotrophic bacteria in any sediment where both processes have been measured (Seitzinger 1988). The result is generally a net loss of available nitrogen from the ecosystem.

Nitrogen limitation is limitation by another nutrient in disguise

In its simplest form, this suggestion holds that phosphorus or another nutrient sets the limit for both net primary production and net ecosystem prouction in an ecosystem, and that nitrogen fixation then brings the availability of nitrogen near, but not to, this limit. Nitrogen fixation diminishes short of the limit set by phosphorus availability because both terrestrial and aquatic nitrogen fixers systematically have a greater demand for phosphorus than do non-fixers (Doremus 1982; Dixon & Wheeler 1983; McCarthy & Carpenter 1983; Högberg 1989), so that nitrogen fixers cannot compete effectively for very low levels of phosphorus. Consequently, nitrogen fixation decreases substantially at a phosphorus level where most primary producers can still obtain phosphorus — and at equilibrium, nitrogen fixers are limited by phosphorus while most primary producers are nitrogen limited. Fertilization with nitrogen would then be expected to cause a rapid but short-lived increase in NPP and perhaps NEP. However, addition of phosphorus would not increase NPP immediately, but it would increase nitrogen fixation, and hence eventually lead to greater overall biomass, NPP, and NEP (Redfield 1958; Schindler 1977; Smith 1984). A short-term experiment of the sort commonly used by marine scientists would always suggest nitrogen limitation, however — even at the new equilibrium following phosphorus fertilization, most of the primary producers would in fact experience a proximate nitrogen limitation. Nevertheless, the ultimate limitation to ecosystem-level primary production would be set by phosphorus. The equilibrium of N:P ratios observed in oligotrophic pelagic ecosystems suggests that this mechanism may be important — although on a fairly long time scale (Smith 1984; Howarth 1988), in contrast to the rapid responses observed in temperate lakes.

We are aware of only one experiment that tested this hypothesis directly in a coastal marine ecosystem on an appropriate time scale. In the summer of 1988, mesocosm tanks at the Marine Ecosystem Research Laboratory (MERL) facility in Narragansett, Rhode Island, were fertilized with phosphate alone, nitrogen alone, phosphate + nitrogen, or left unfertilized. The amount of phosphate added was equivalent (per volume of surface water) to that used in the Lake-227 experiment at the Experimental Lakes Area (Schindler et al. 1978, Flett et al. 1980), except that a one-time addition was used in the MERL experiment. The rate of nitrogen addition was ten times higher than this (per mole). The addition of nitrogen strongly stimulated gross primary production and NEP throughout the growing season; in marked contrast to the Lake-227 experiment, phosphorus additions to the MERL mesocosms had no effect on production, and most of the phosphorus stayed in solution (Frithsen et al. 1988, and unpublished data). Also in contrast to the Lake-227 experiment (Flett et al. 1980), N-fixing species of planktonic cyanobacteria did not respond to the phosphate addition in the MERL mesocosms and were virtually absent from all of the mesocosms (Frithesen, Oviatt, Cole & Howarth, unpublished data). Although measurable nitrogen fixation occurred in the plankton of the phosphate-addition mesocosms (presumably by heterotrophic bacteria), rates were not significantly greater than in the control mesocosms.

Phosphorus is not the only element that can regulate rates of nitrogen fixation; a strong case can be made that molybdenum, iron, sulfur, or other elements could limit nitrogen fixation and hence overall primary production. Molybdenum is particularly intriguing because it is essential for most nitrogen fixers, but not required for organisms growing on ammonium as their sole nitrogen source. Indeed, Howarth & Cole (1985) suggested that the apparent difference in nutrient limitation between freshwater and marine ecosystems (with most freshwater system clearly phosphorus limited and many coastal marine systems apparently nitrogen limited) may be caused by differences in molybdenum availability. While molybdenum concentrations are higher in marine than in most freshwater ecosystems, the high sulfate concentrations in marine environments could interfere with molybdate uptake and thereby limit nitrogen fixation (Howarth and Cole 1985; Howarth et al. 1988b). The extremely low particulate molybdenum concentrations in seawater further suggest a low biotic availability of this element (Howarth et al. 1988b).

Short-term experiments that manipulate either molybdenum or sulfate concentrations in saline waters have given variable results, sometimes but not always stimulating rates of nitrogen fixation (Howarth & Cole 1985; Paerl et al. 1987; Wurtsbaugh 1988). Longer term experiments are required to test the molybdenum-control hypothesis. However, a study of

13 saline lakes in Alberta supports the suggestion that molybdenum availability can partially regulate nitrogen fixation. Marino et al. (1990) found that molybdenum availability (as determined by the sulfate: molybdenum ratio) was the best predictor of the relative abundance of species of nitrogen-fixing cyanobacteria in the plankton of these lakes. Interestingly, phosphorus concentrations were negatively correlated with the abundances of nitrogen-fixing cyanobacteria in these saline lakes (Marino et al. 1990).

An argument can also be made for iron regulation of rates of nitrogen fixation by plankton in marine ecosystems (Rueter 1982; Howarth et al. 1988b), where iron concentrations are typically very low (Martin et al. 1989). While iron is required by all organisms, nitrogen-fixing organisms and symbioses require more than non-fixers. Thus, nitrogen fixation in marine environments could be iron limited while net primary production by the phytoplankton community as a whole remained proximately nitrogen limited. Iron was probably not a factor in the saline lakes studied by Marino et al. (1990) since it was relatively abundant in all of them.

In natural terrestrial ecosystems, there is substantial evidence that nitrogen fixation is dependent on phosphorus availability (Dixon & Wheeler 1983; Silvester 1983; Högberg 1989). Nitrogen fixation generally is most important in early stages of soil development, where the nitrogen:phosphorus ratio in soil is low due to the absence of nitrogen from most parent material (Stevens & Walker 1970; Walker & Syers 1976; Gorham et al. 1979). Additionally, some experimental studies have yielded a significant effect of nitrogen:phosphorus ratios on nitrogen fixation (Eisele et al. 1989). However, many terrestrial systems that are strongly nitrogen limited and have adequate phosphorus nonetheless do not support nitrogen fixation. There is some evidence that molybdenum and other micronutrient additions can regulate nitrogen fixation in pasture ecosystems (Gadgil et al. 1981; Dixon & Wheeler 1983), and suggestions that molybdenum additions stimulate rates of nitrogen fixation in some forest soils (Silvester 1989). The low pH of many forest soils may cause strong adsorption of molybdenum, thereby keeping its availability low (Bhella & Dawson 1972; Jarrell and Dawson 1978; Crews et al. 1989).

Ecological and physical constraints on nitrogen fixation

In addition to the energetic constraints and biogeochemical controls on nitrogen fixation, a variety of ecological and other physical constraints may play a role in regulating rates. Paerl and his colleagues (Paerl 1985; Paerl et al. 1987; Paerl & Carlton 1988) have discussed the potential influence of turbulence on planktonic nitrogen fixation. Turbulence can not only physically break up colonies of cyanobacteria (Carpenter & Price 1976), it can lower the likelihood of anoxic microzones in colonies. Such microzones can favor nitrogen fixation by protecting the oxygen-sensitive enzyme nitrogenase (Paerl 1985; Paerl & Carlton 1988). Anoxic microzones may also increase the availability of molybdenum by favoring the extracellular reduction of molybdate to reduced molybdenum compounds; this would overcome the negative effect of sulfate on molybdenum assimilation (Howarth et al. 1988b). The higher turbulence thought to occur in marine ecosystems than in many freshwater lakes may therefore adversely affect nitrogen-fixing cyanobacteria in the plankton (Paerl & Prufert 1987). The lower concentration of dissolved organic matter in seawater may also affect nitrogen-fixing cyanobacteria adversely, either by lowering the likelihood of anoxic microzones (Paerl et al. 1987) or by decreasing the availability of iron and molybdenum through reduced complexation (Howarth et al. 1988b).

Ecological constraints on nitrogen fixation have received less attention but may be important in some circumstance. A recent experiment at Cornell University's Experimental Ponds Facility demonstrated that grazing by cladoceran zooplankton could prevent cyanobacterial blooms in the plankton (Howarth et al. 1990, and unpublished data). In ponds having similar nitrogen and phosphorus concentrations and fertilization regimes, but where copepods rather than cladocerans were the dominant zooplankton, large blooms of nitrogen-fixing cyanobacteria dominated the phytoplankton community. Could heavier grazing pressures in marine ecosystems contribute to the relative lack of nitrogen-fixing cyanobacteria there? And what ecological constraints to nitrogen fixation (ie grazing on protein-rich tissues) exist in terrestrial ecosystems?

Conclusions

We have reviewed a wide range of mechanisms that could cause nitrogen limitation in natural terrestrial and marine ecosystems. All of these are logically consistent, but rarely is there sufficient evidence to allow tests of the relative or absolute importance of any of these mechanisms in any site or class of sites. We speculate that the pattern of nitrogen limitation on land (widespread except in lowland tropical forests and perhaps very old temperate soils) probably reflects energetic constraints on the colonization of nitrogen fixers in communities with closed canopies, the influence of fire and other disturbances that mobilize nitrogen more rapidly than other elements, and positive feedbacks between low nitrogen availability, low litter quality, and low rates of decomposition. Rapid rates of decomposition in lowland tropical forests and the prevalence of canopy legumes reduce the likelihood of nitrogen limitation there, and the widespread occurence of very old soils in the tropics (due in part to the absence of glaciation) increases the probability of limitation by phosphorus or other rock-derived nutrients. In temperate-zone freshwater systems, it is not clear that there is any persistent nitrogen limitation to explain; enhanced nitrogen fixation offsets any temporary nitrogen deficiency. However, nitrogen fixation clearly is not responsive to nitrogen deficiency in most planktonic coastal marine systems on the same time-scale as in lakes; there must be some factor that slows nitrogen fixation in marine relative to freshwater systems, and micronutrient limitations combined with energy limitations remain a viable explanation. For all of these ecosystems, many of the possible reasons for nitrogen limitation could be supported or ruled out with appropriate experiments.

Acknowledgements

We thank T. Crews, C. B. Field, V. Gutschick, A. H. Linkins, W. H. Schlesinger, and especially S. V. Smith for helpful comments on earlier versions of this manuscript, and C. Nakashima for preparing several drafts. PMV was supported by NSF Grant BSR-89-18382 and NASA Grant NAGW-1068; RWH was supported by NSF Grant BSR-8905364.

References

Aber JD, Nadelhoffer JK, Steudler PA & Melillo JM (1989) Nitrogen saturation in northern forest ecosystems — hypotheses and implications. BioScience 39: 378—386

Agren GI (1983) Nitrogen productivity of some conifers. Can J Forest Res 13: 494—500

Alexander M (1977) An Introduction to Soil Microbiology. John Wiley and Sons, New York

Atkinson MJ & Smith SV (1983) C:N:P ratios of benthic marine plants. Limnol. Oceanogr. 26: 1074—1083

Banse K (1990) Does iron really limit phytoplankton production in the offshore subarctic Pacific? Limnol. Oceanogr. 35: 772—775

Bhella HS & Dawson MD (1972) The use of anion exchange resin for determining available soil molybdenum. Soil Sci. Soc. Amer. Proc. 36: 177—178

Binkley D (1986) Forest Nutrition Management: John Wiley and Sons, New York. 299 pp

Birk EM & Vitousek PM (1984) Patterns of N retranslocation in loblolly pine: response to N availability. Ecol. Soc. Amer. Bull. 65: 100

Bliss LC (1963) Alpine plant communities of the Presidential Range, New Hampshire. Ecology 44: 678—697

Bonan GB (1990) Carbon and nitrogen cycling in North American boreal forests. II. Biogeographic patterns. Can. J. Forest Res. 20: 1077—1088

Boring LR, Swank WT, Waide JB & Henderson GS (1988) Sources, fates, and impacts of nitrogen inputs to terrestrial ecosystems: review and synthesis. Biogeochemistry 6: 119—159

Bormann BT & Gordon JC (1984) Stand density effects in yound red alder planations: productivity, photosynthate partitioning, and nitrogen fixation. Ecology 65: 394—402

Bormann FH & Likens GE (1979) Pattern and Process in a Forested Ecosystem. Springer-Verlag, NY. 253 pp

Boynton WR, Kemp WM & Keefe CW (1982) A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. In: Kennedy VS (Ed) Estuarine Comparisons (pp 69—91). Academic Press, New York

Bradshaw AD, Chadwick MJ, Jowett D, Lodge RW & Snaydon RW (1960) Experimental investigations into the mineral nutrition of several grass species. III. Phosphate level. J. Ecology 48: 631—637

Bradshaw AD, Chadwick MJ, Jowett D & Snaydon RW (1964) Experimental investigations into the mineral nutrition of several grass species. IV. Nitrogen level. J. Ecology 52: 665—676

Broecker WS (1982) Glacial to interglacial changes in ocean chemistry. Prog. Oceanogr. 2: 151—197

Campbell CE & Prepas EE (1986) Evaluation of factors related to the unusually low chlorophyll levels in prairie saline lakes. Can. J. Fish. Aquat. Sci. 43: 846—854

Caraco N, Cole JJ & Likens GE (1989) Evidence for sulfate-controlled phosphorus release from sediments of aquatic systems. Nature 341: 316—318

Caraco N, Cole JJ & Likens GE (1990) A comparison of phosphorus immobilization in sediments of freshwater and coastal marine systems. Biogeochemistry 9: 277—290

Carpenter EJ (1983) Nitrogen fixation by marine *Oscillatoria* (*Trichodesmium*) in the World's oceans. In: Carpenter EJ & Capone DG (Eds) Nitrogen in the Marine Environment (pp 65—103). Academic Press, New York

Carpenter EJ & Capone DG (Ed) (1983) Nitrogen in the Marine Environment. Academic Press, New York. 900 pp

Carpenter EJ & Price CC (1976) Marine *Oscillatoria* (*Trichodesmium*): Explanation for aerobic nitrogen fixation without heterocysts. Science 191: 1278—1280

Chapin FS III, Vitousek PM & Van Cleve K (1986) The nature of nutrient limitation in plant communities. Am. Nat. 127: 48—58

Coats RN, Leonard RL & Goldman CR (1976) Nitrogen uptake and release in a forested watershed, Lake Tahoe Basin, California. Ecology 57: 995—1004

Cole CV & Heil RD (1981) Phosphorus effects on terrestrial nitrogen cycling. Ecol. Bull. (Stockholm) 33: 363—374

Cole CV, Stewart JWB, Ojima DS, Parton WJ & Schimel DS (1989) Modelling land use effects of soil organic matter dynamics in the North American Great Plains. In: Clarholm M & Bergström L (Eds) Ecology of Arable Land: Perspectives and Challenges (pp 89—98). Kluwer Academic, Dordrecht

Cornaby BW & Waide JB (1973) Nitrogen fixation in decaying chestnut logs. Plant Soil 39: 445—448

Crews T, Marino R & Howarth RW (1989) Constraints on the availability of molybdenum to plants and nitrogen fixers at Hubbard Brook, New Hampshire. Suppl. Bull. Ecol. Soc. Am. 70: 89

Crutzen PJ & Andreae MO Biomass burning in the tropics: impact on atmospheric chemistry and biogeochemical cycles. Science 250: 1669—1678

Cuevas E & Medina E (1986) Nutrient dynamics within Amazonian forests. I. Nutrient flux in fine litter fall and the efficiency of nutrient utilization. Oecologia 68: 466—472

Cuevas E & Medina E (1988) Nutrient dynamics within Amazonian forests. II. Fine root growth, nutrient availability, and leaf litter decomposition. Oecologia 76: 222—235

D'Elia CF, Sanders JG & Boynton WR (1986) Nutrient enrichment studies in a coastal plain estuary: Phytoplankton growth in large-scale, continuous cultures. Can. J. Fish. Aquat. Sci. 43: 397—406

Denison WC (1979) *Lobaria oregana*, a nitrogen fixing lichen in old growth Douglas-fir forests. In: Gordon JC, Wheeler CT & Perry DA (Eds) Symbiotic Nitrogen Fixation in the Management of Temperate Forests (pp 266—275). Oregon State University, Corvallis

Dixon ROD & Wheeler CT (1983) Biochemical, physiological, and environmental aspects of symbiotic nitrogen fixation. In: Gordon, JC & Wheeler CT (Eds) Biological Nitrogen Fixation in Forest Ecosystems: Foundations and Applications (pp 108—171). Nijhoff/Junk Publishers, The Hague

Dodd JL & Lauenroth WK (1979) Analysis of the response of a grassland ecosystem to stress. In: French NR (Ed) Perspectives in Grassland Ecology (pp 43—58). Springer-Verlag, New York

Doremus C (1982) Geochemical control of dinitrogen fixation in the open ocean. Biol. Oceanogr. 1: 429—436

Dugdale RC & Wilkerson FP (1990) Iron addition experiments in the Antarctic: a reanalysis. Global Biogeochemical Cycles 4: 13—19

Edmondson WT (1970) Phosphorus, nitrogen, and algae in Lake Washington after diversion of sewage. Science 169: 690—691

Eisele KA, Schimel DS, Kapustka LA & Parton WJ (1989) Fire-stimulated N_2 fixation as a result of altered N:P ratios. Oecologia 79: 471—464

Evans JR & Seemann JR (1989) The allocation of protein nitrogen in the photosynthetic apparatus: costs, consequences, and control. In: Briggs W (Ed) Photosynthesis (pp 183—205). Alan R. Liss, New York

Field CB & Mooney HA (1986) The nitrogen/photosynthesis relationship in wild plants. In: Givnish TJ (Ed) On the Economy of Plant Form and Function (pp 25—55). Cambridge University Press, Cambridge, England

Fisher FM, Zak JC, Cunningham GL & Whitford WG (1988) Water and nitrogen effects on growth and allocation patterns of creosote bush in the northern Chihuahuan Desert. J. Range. Manag. 41: 387—395

Flanagan PW & Van Cleve K (1983) Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. Can. J. Forest Res. 13: 795—817

Flett RJ, Schindler DW, Hamilton RD & Campbell NER (1980) Nitrogen fixation in Canadian Precambrian Shield lakes. Can. J. Fish. Aquat. Sci. 37: 494—505

Frithsen JB, Oviatt CA, Pilson MEQ, Howarth RW & Cole JJ (1988) A comparison of nitrogen vs. phosphorus limitation of production in coastal marine ecosystems. EOS 69(44): 1100

Gadgil RL, Knight PJ, Sandberg AM & Allen PJ (1981) Molybdenum, sulphur, and boron deficiency in lupin *(Lupinus arboreus* Sims) at Pouto Forest. N.Z. J. For. Sci. 11: 114—127

Goldman CR (1988) Primary productivity, nutrients, and transparency during the early onset of eutrophication in ultra-oligotrophic Lake Tahoe. California-Nevada. Limnol. Oceanogr. 33: 1321—1333

Gorham E, Vitousek PM & Reiners WA (1979) The regulation of chemical budgets over the course of terrestrial ecosystem succession. Ann. Rev. Ecol. Syst. 10: 53—88

Graneli E (1978) Algal assay of limiting nutrients for phytoplankton production in the Oresund. Vatten 2: 117—128

Graneli E (1981) Bioassay experiments in the Falsterbo channel — nutrients added daily. Kieler Meeresforch., Sonderh. 5: 82—90

Graneli E (1984) Algal growth potential and limiting nutrients for phytoplankton production in Oresund water of Baltic and Kattegat origin. Limnologica (Berlin) 15: 563—569

Grubb PJ (1989) The role of mineral nutrients in the tropics: a plant ecologist's view. In: Proctor, J (Ed) Mineral Nutrients in Tropical Forest and Savanna Ecosystems (pp 417—439). Blackwell Scientific, Oxford

Gutschick VP (1981) Evolved strategies in nitrogen acquisition by plants. Am. Nat. 118: 607—637

Gutschick VP (1987) A Functional Biology of Crop Plants. Timber Press, Portland. 230 pp

Haas HJ, Evans CE & Shih SH (1957) Nitrogen and carbon changes in Great Plains soils as influenced by cropping and soil treatments. USDA Tech. Bull. 1164. 111pp

Haas, HJ, Gounes DL & Reichmann GA (1961) Phosphorus changes in Great Plains soils as influenced by cropping and manure applications. Soil. Sci. Soc. Amer. Proc. 25: 214—218

Hecky RE & Kilham P (1988) Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effects of enrichment. Limonol. Oceanogr. 33: 796—822

Hines ME & Lyons WB (1982) Biogeochemistry of nearshore Bermuda sediments. I. Sulfate reduction rates and nutrient regeneration. Mar. Ecol. Progr. Ser. 8: 87—94

Hobbs NT & Schimel DS (1984) The effects of fire on nitrogen mineralization and fixation in mountain grassland and shrub communities. J. Range Manage. 37: 402—405

Högberg P (1989) Root symbioses of trees in savannas. In: Proctor J (Ed) Mineral Nutrients in Tropical Forest and Savanna Ecosystems (pp 121—136). Blackwell Scientific, Oxford

Howarth RW (1988) Nutrient limitation of net primary production in marine ecosystems. Ann. Rev. Ecol. Syst. 19: 89—110

Howarth RW & Cole JJ (1985) Molybdenum availability, nitrogen limitation, and phytoplankton growth in natural waters. Science 229: 653—655

Howarth RW, Hairston NG Jr, Gerardi J & Schaffner WR (1990) Interactions between plankton community composition and N cycling in experimental ponds. ASLO meeting, June 10—15, 1990

Howarth RW, Marino R, Lane J & Cole JJ (1988a) Nitrogen fixation in freshwater, estuarine, and marine ecosystems. 1. Rates and importance. Limnol. Oceanogr. 33: 669—687

Howarth, RW, Marino R & Cole JJ (1988b) Nitrogen fixation in freshwater, estuarine, and marine ecosystems. 2. Biogeochemical controls. Limnol. Oceanogr. 33: 688—701

Huenneke LF, Hamburg SP, Koide R, Mooney HA & Vitousek PM (1990) Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecology 71: 478—491

Hunt HW, Stewart JWB & Cole CV (1983) A conceptual model for interactions of carbon, nitrogen, phosphorus, and sulfur in grasslands. In: Bolin B & Cook RB (Eds) The Major Biogeochemical Cycles and Their Interactions (pp 303—326). John Wiley and Sons, New York

Hunt HW, Ingham ER, Coleman DC, Elliott ET & Reid CPP (1988) Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. Ecology 69: 1009—1016

Jackson GA & Williams PM (1985) Importance of dissolved organic nitrogen and phosphorus to biological nutrient cycling. Deep-Sea Res. 32: 223—235

Jarrell WM & Dawson MD (1978) Sorption and availability of molybdenum in soils of Western Oregon. Soil. Sci. Soc. Amer. J. 42: 412—415

Jordan CF (1985) Nutrient Cycling in Tropical Forest Ecosystems: Principles and Their

Application in Conservation and Management. John Wiley and Sons, Chichester, England. 179 pp

Kamp-Nielsen L (1974) Mud-water exchange of phosphate and other ions in undisturbed sediment cores and factors affecting the exchange rate. Arch. Hydrobiol. 73: 218—237

Keller M, Kaplan WA & Wofsy SC (1986) Emissions of N_2O, CH_4, and CO_2 from tropical soils. J. Geophys. Res. 91: 11,791—11,801

Kelly JR & Levin SA (1986) A comparison of aquatic and terrestrial nutrient cycling and production processes in natural ecosystems, with reference to ecological concepts of relevance to some waste disposal issues. In: Kullenberg G (Ed) The Role of Oceans as a Waste Disposal Option (pp 165—203). Reidel

Khalid RA, Patrick WH & DeLaune RD (1977) Phosphorus sorption characteristics of flooded soils. Soil. Sci. Soc. Am. J. 41: 305

Kimmins JP (1987) Forest Ecology. Macmillian Publishing, New York. 531 pp

Kinjo T & Pratt PF (1971) Nitrate adsorption. II. In competition with chloride, sulfate, and phosphate. Soil. Sci. Soc. Amer. Proc. 35: 725—728

Knauer GA, Martin JH & Burland KW (1979) Fluxes of particulate carbon, nitrogen, and phosphorus in the upper water column of the northeast Pacific. Deep-Sea Res. 26A: 97—108

Knowles R (1982) Denitrification. Microbiol. Rev. 46: 43—70

Krom MD & Berner RA (1980) Adsorption of phosphate in anoxic marine sediments. Limnol. Oceanogr. 25: 797—806

Lapointe BE, Littler MM & Littler DS (1987) A comparison of nutrient-limited productivity in macroalgae from a Caribbean barrier reef and from a mangrove ecosystem. Aquat. Bot. 28: 243—255

Lee JA, Harmer R & Ignaciuk R (1983) Nitrogen as a limiting factor in plant communities. In: Lee JA, McNeill S Rorison IH (Eds) Nitrogen as an Ecological Factor (pp 95—112). Blackwell Scientific, Oxford

Lehman JT (1984) Grazing, nutrient release, and their impacts on the structure of zooplankton communities. In: Meyers DG & Strickland JR (Eds) Trophic Interactions Within Aquatic Ecosystems. Westview Press, Boulder, Colorado

Levine SN & Lewis WM (1987) A numerical model of nitrogen fixation and its application to Lake Valencia, Venezuela. Freshwater Biology 17: 265—274

Lewis WM (1986) Losses of nitrogen and phosphorus from a nutrient-poor moist tropical forest. Ecology 67: 1275—1282

Likens GE, Bormann FH, Pierce RS, Eaton JS & Johnson NM (1977) Biogeochemistry of a forested ecosystem. Springer-Verlag, New York. 146 pp

Littler MM, Littler DS & Lapointe BE (1988) A comparison of nutrient- and light-limited photosynthesis in psammophytic versus epilithic forms of *Halimeda* (Caulerpales, Halimedacae) from the Bahamas. Coral Reefs 6: 219—225

Lobert JM, Scharffe DH, Hao WM & Crutzen PJ (1990) Importance of biomass burning in the atmosphere budget of nitrogen-containing trace gases. Nature 346: 552—554

Marino R, Howarth RW, Shamess J & Prepas E (1990) Molybdenum and sulfate as controls on the abundance of nitrogen-fixing cyanobacteria in a saline lakes in Alberta. Limnol. Oceanogr. 35: 245—259

Marrs RH, Roberts RD, Skeffington RA & Bradshaw AD (1983) Nitrogen and the development of ecosystems. In: Lee JA, McNeill S & Revison IH (Eds) Nitrogen as an Ecological Factor (pp 113—136). Blackwell Scientific, Oxford

Martin JH & Fitzwater SE (1988) Iron deficiency limits phytoplankton growth in the northeast Pacific subarctic. Nature 331: 341—343

Martin JH, Gordon RM, Fitzwater S & Broenkow WW (1989) VERTEX: Phytoplankton/iron studies in the Gulf of Alaska. Deep-Sea Res. 36: 649—680

Martin, JH, Fitzwater SE & Gordon RN (1990) Iron deficiency limits phytoplankton growth in Antarctic waters. Global Biogeochem. Cycles 4: 5—12

Matson PA & Boone RD (1984) Natural disturbance and nitrogen mineralization: waveform dieback of mountain hemlock in the Oregon Cascades. Ecology 65: 1511—1516

Matson PA & Vitousek PM (1987) Cross-system comparison of soil nitrogen transformations and nitrous oxide fluxes in tropical forests. Global Biogeochem. Cycles 1: 163—170

Matson PA, Vitousek PM, Ewel JJ, Mazzarino MJ & Roberton GP (1987) Nitrogen transformation following tropical forest felling and burning on a volcanic soil. Ecology 68: 491—502

McCarthy JJ & Carpenter EJ (1983) Nitrogen cycling in near-surface waters of the open ocean. In: Carpenter EM & Capone DG (Eds) Nitrogen in the Marine Environment (pp 487—512). Academic Press, New York

McCarthy JJ & Goldman JC (1979) Nitrogenous nutrition of marine phytoplankton in nutrient-depleted waters. Science 203: 670—672

McGill WB & Cole CV (1981) Comparative aspects of cycling of organic C, N, S, and P through soil organic matter. Geoderma 26: 267—286

McGlathery KJ, Howarth RW & Marino R (1991) Nutrient limitation of the macroalga, *Penicillus capitatus*, associated with subtropical seagrass meadows in Bermuda. Estuaries, in press

Melack JM, Kilham P & Fisher TR (1982) Responses of phytoplankton to experimental fertilization with ammonium and phosphate in an African soda lake. Oecologia 52: 321—326

Melillo JM, Aber JD & Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63: 621—626

Melillo JM & Gosz JR (1983) Interactions of the biogeochemical cycles in forest ecosystems. In: Bolin B & Cook RB (Eds) The Major Biogeochemical Cycles and Their Interactions (pp 177—221). John Wiley and Sons, Chichester, England

Miller HG (1981) Forest fertilization: some guiding concepts. Forestry 54: 157—167

Miller HG, Cooper JM & Miller JD (1976) Effects of nitrogen supply on nutrients in litterfall and crown leaching in a stand of Corsican pines. J. Appl. Ecol. 13: 233—248

Mitchell HL & Chandler RF Jr (1939) The nutrition and growth of certain deciduous trees of northeastern United States. Black Rock For. Bull. 11: 1—94

Morse JW, Zullig JJ, Bernstein LD, Millero FJ, Milne P, Mucci A & Choppin GR (1985) Chemistry of calcium carbonate-rich shallow water sediments in the Bahamas. Am. J. Sci. 285: 147—185

Myers VB & Iverson RI (1981) Phosphorus and nitrogen limited phytoplankton productivity in northeastern Gulf of Mexico coastal lagoons. In: Neilson BJ & Cronin LE (Eds) Estuaries and Nutrients (pp 569—581). Humana

Nixon SW & Pilson MEQ (1983) Nitrogen in estuarine and coastal marine ecosystems. In: Carpenter EM & Capone DG (Eds) Nitrogen in the Marine Environment (pp 565—648). Academic Press, New York

Nixon SW, Kelly JR, Furnas BN, Oviatt CA & Hale SS (1980) Phosphorus regeneration and the metabolism of coastal marine bottom communities. In: Tenore DR & Coull BC (Eds) Marine Benthic Dynamics (pp 219—242). Univ South Carolina

Norin LL (1977) ^{14}C-bioassays with the natural phytoplankton in the Stockholm archipelago. Ambio. Spec. Report 5: 15—21

Ojima DS (1987) The short-term and long-term effect of burning on tallgrass prairie ecosystem properties and dynamics. PhD Diss., Colorado State University

Paerl HW (1985) Microzone formation: Its role in the enhancement of aquatic N_2 fixation. Limnol. & Oceanogr. 30: 1246—1252

Paerl HW & Prufert LE (1987) Oxygen-poor microzones as potential sites of microbial N_2 fixation in nitrogen-depleted aerobic marine waters. Appl. Env. Micro. 53: 1078—1087

Paerl HW, Crocker KM & Prufert LE (1987) Limitation of N_2 fixation in coastal marine waters: Relative importance of molybdenum, iron, phosphorus, and organic matter availability. Limnol. Oceanogr. 32: 525—536

Paerl HW & Carlton RC (1988) Control of nitrogen fixation by oxygen depletion in surface-associated microzones. Nature 332: 260—262

Parton WF, Cole CV, Stewart JWB, Ojima DS & Schimel DS (1988) Dynamics of C, N, P, and S in soils: a model. Biogeochemistry 5: 109—131

Pastor J & Post WM (1986) Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. Biogeochemistry 2: 3—27

Pastor J & Post WM (1988) Response of northern forests to CO_2-induced climate change. Nature 334: 55—58

Pastor JJ, Aber JD, McClaugherty CA & Melillo JM (1984) Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. Ecology 65: 256—268

Peng T-H & Broecker WS (1991) Dynamical limitations on the Antarctic iron fertilization strategy. Nature 349: 227—229

Peterjohn WT & Schlesinger WH (1990) Nitrogen loss from deserts in the southwestern United States. Biogeochemistry 10: 67—79

Peterson BJ & Melillo JM (1985) The potential storage of carbon caused by eutrophication of the biosphere. Tellus 37B: 117—127

Pickett STA & White PS (Eds) (1985) The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando. 472 pp

Powell GVN, Kenworthy WJ & Fourqurean JF (1989) Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. Bull. Mar. 44: 324—340

Raison RJ (1979) Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. Plant Soil 51: 73—108

Redfield AC (1958) The biological control of chemical factors in the environment. Am. Scientist 46: 206—226

Reiners WS (1981) Nitrogen cycling in relation to ecosystem succession: a review. Ecol. Bull. (Stockholm) 33: 507—528

Reiners WS (1986) Complementary models for ecosystems. Am Nat 127: 59—73

Roskoski JP (1980) Nitrogen fixation in hardwood forests of the northeastern United States. Plant Soil 54: 33—44

Rowe GT, Clifford CH, Smith KL & Hampton PL (1975) Benthic nutrient regeneration and its coupling to primary productivity in coastal waters. Nature 225: 215—217

Rueter JG (1982) Theoretical Fe Limitations of microbial N_2 fixation in the oceans. EOS 63: 945

Ryther JH & Dunstan WN (1971) Nitrogen, phosphorus, and eutrophication in the coastal marine environment. Science 171: 1008—1013

Schelske CL, Fahnenstiel GL & Haiback M (1986) Phosphorus enrichment, silica utilization, and biogeochemical silica depletion in the Great Lakes. Can. J. Fish. Aquat. Sci. 43: 407—415

Schimel DS, Parton WJ, Cole CV, Ojima DS & Kittel TGF (1990) Grassland biogeochemistry: Links to atmospheric processes. Climatic Change 17: 13—25

Schindler DW (1977) Evolution of phosphorus limitation in lakes. Science 195: 260—262

Schindler DW (1981) Interrelationships between the cycles of elements in freshwater ecosystems. In: Likens GE (Ed) Some Perspectives of the Major Biogeochemical Cycles (pp 113—123). John Wiley and Sons, Chichester, U.K.

Schindler DW, Fee EJ & Ruszczynski T (1978) Phosphorus input and its consequences for phytoplankton standing crop and production in the Experimental Lakes Area and similar lakes. J. Fish. Res. Bd. Can. 35: 190—196

Schindler DW, Hesslein R & Kipphut G (1977) Interactions between sediments and overlying waters in an experimentally eutrophied Pre-Cambrian shield lake. In: Golterman HL (Ed) Interactions Between Sediments and Fresh Water (pp 235—245). Junk, The Hague

Seitzinger SP (1988) Denitrification in freshwater and coastal marine ecosystems: Ecological and geochemical significance. Limnol. Oceanogr. 33: 702—724

Seitzinger SP, Nixon SW & Pilson MEQ (1984) Denitrification and nitrous oxide production in a coastal marine ecosystem. Limnol. Oceanogr. 29: 79—83

Shaver GR & Chapin FS III (1980) Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. Ecology 61: 662—675

Short FT, Davis MW, Gibson RA & Zimmerman CF (1985) Evidence for phosphorus limitation in carbonate sediments of the seagrass *Syringodium filiforme*. Est. Coast. Shelf. Sci. 20: 419—430

Short FT, Dennison WC & Cappone DG (1990) Phosphorus-limited growth of the tropical seagrass *Syringodium filiforme* in carbonate sediments. Mar. Ecol. Prog. Ser. 62: 169—174

Silvester WB (1983) Analysis of nitrogen fixation. In: Gordon JC & Wheeler CT (Eds) Biological Nitrogen Fixation in Forest Ecosystems: Foundations and Applications (pp 173—212). Nijhoff/Junk Publishers, The Hague

Silvester WB (1989) Molybdenum limitation of asymbiotic nitrogen fixation in forests of Pacific Northwest America. Soil Biol. Biochem. 21: 283—289

Smith SV (1984) Phosphorus versus nitrogen limitation in the marine environment. Limnol. Oceanogr. 29: 1149—1160

Smith SV & Atkinson MJ (1984) Phosphorus limitation of net production in a confined aquatic ecosystem. Nature 307: 626—627

Smith SV, Hollibaugh JT, Dollar SJ & Vink S (1989) Tomales Bay, California: A case for carbon-controlled nitrogen cycling. Limnol. Oceanogr. 34: 37—52

Smith SV, Kimmer WJ & Walsh TW (1986) Vertical flux and biogeochemical turnover regulate nutrient limitation of net organic production in the North Pacific Gyre. Limnol. Oceanogr. 31: 161—166

Smith VH (1983) Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science 221: 669—671

Smith VH (1991) Nitrogen, phosphorus, and nitrogen fixation in lacustrine and estuarine ecosystems. Limnol. Oceanogr., in press

Sollins P (1989) Factors affecting nutrient cycling in tropical soils. In: Proctor J (Ed) Mineral Nutrients in Tropical Forest and Savanna Ecosystems (pp 85—95) Blackwell Scientific, Oxford

Sollins P, Robertson GP & Uehara G (1988) Nutrient mobility in variable- and permanent-charge soils. Biogeochemistry 6: 181—199

Stevens PR & Walker TW (1970) The chronosequence concept and soil formation. Quart. Rev. Biol. 45: 333—350

Swank WT, Waide JB, Crossley DA & Todd RL (1981) Insect defoliation enhances nitrate export from forested ecosystems. Oecologia 51: 297—299

Tanner EVJ, Kapos V, Freskos S, Healey JR & Theobald AN (1989) Nitrogen and phosphorus fertilization of Jamaican montane forest trees. J. Trop. Ecol. 6: 231—238

Tans PO, Fung IY & Takahashi T (1990) Observational constraints on the global atmospheric CO_2 budget. Science 247: 1431—1439

Thomas WH (1966) Surface nitrogenous nutrients and phytoplankton in the northeastern tropical Pacific Ocean. Limnol. Oceanogr. 11: 393—400

Tiessen H, Stewart JWB & Moir JO (1983) Changes in organic and inorganic phosphate in particle size fractions of two soils during 60 to 90 years cultivation. J. Soil. Science 34: 815—823

Tilman D (1986) Nitrogen-limited growth in plants from different successional stages. Ecology 67: 555—563

Tilman D (1988) Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton. 360 pp

Tilman D, Kilham SS & Kilham P (1982) Phytoplankton community ecology: The role of limiting nutrients. Ann. Rev. Ecol. Syst. 13: 349—372

Tilman D, Kiesling R, Sterner R, Kilham SS & Johnson FA (1986) Green, blue-green, and diatom algae: Taxonomic differences in competitive ability for phosphorus, silicon, and nitrogen. Arch. Hydrobiol. 106: 473—485

Uehara G & Gillman G (1981) The mineralogy, chemistry, and physics of tropical soils with variable charge clays. Westview Press, Boulder, Colorado

Valiela I (1983) Nitrogen in salt-marsh ecosystems. In: Carpenter EM & Capone DG (Eds) Nitrogen in the Marine Environment (pp 649—678). Academic Press, New York

Valiela I (1984) Marine Ecological Processes. New York: Springer-Verlag. 546 pp

van Breman H & de Wit CT (1983) Rangeland productivity and exploitation in the Sabel. Science 221: 1341—1347

Van Cleve K & Zasada J (1976) Response of 70-yr-old white spruce to thinning and fertilization in interior Alaska. Can. J. For. Res. 6: 145—152

Van Cleve K, Oliver L, Schlentner R, Viereck LA & Dyrness CT (1983) Productivity and nutrient cycling in taiga forest ecosystems. Can. J. For. Res. 13: 747—766

Vince S & Valiela I (1973) The effects of ammonium and phosphate enrichments on chlorophyll a, pigment ratio and species composition of phytoplankton of Vineyard Sound. Mar. Biol. 19: 69—73

Vitousek PM (1982) Nutrient cycling and nutrient use efficiency. Am. Nat. 119: 553—572

Vitousek PM (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65: 285—298

Vitousek PM & Matson PA (1985) Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. Ecology 66: 1360—1376

Vitousek PM & Reiners WA (1975) Ecosystem succession and nutrient retention: a hypothesis. BioScience 25: 376—381

Vitousek PM & Sanford RL Jr (1986) Nutrient cycling in moist tropical forest. Ann. Rev. Ecol. Syst. 17: 137—167

Vitousek PM & Walker LR (1987) Colonization, succession, and resource availability; ecosystem-level interactions. In: Gray A, Crawley M & Edwards PJ (Eds) Colonization, Succession and Stability (pp 207—223). Blackwell Scientific, Oxford

Vitousek PM, Gosz JR, Grier CC, Melillo JM & Reiners WA (1982) A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. Ecol. Monogr. 52: 155—177

Vitousek PM, Walker LR, Whiteaker LD, Mueller-Dombois D & Matson PA (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238: 802—804

Vitousek PM, Fahey T, Johnson DW & Swift MJ (1988) Element interactions in forest ecosystems: succession, allometry, and input-output budgets. Biogechemistry 5: 7—34

Vitousek PM, Matson PA & Van Cleve K (1989) Nitrogen availability and nitrification during succession: Primary, secondary, and old-field seres. Plant Soil 115: 229—239

Vollenwieder RA (1976) Advances in defining critical loading levels for phosphorus in lake eutrophication. Mem. 1st Ital. Idrobiol. Dott. Macro. de marchi 33: 53—83

Walbridge MR (1991) Phosphorus availability in acid organic soils of the lower North Carolina coastal plain: Estimation and control of P availability and plant response. Ecology, in press

Walker TW & Syers JK (1976) The fate of phosphorus during pedogenesis. Geoderma 15: 1—19

Wood T, Bormann FH & Voight GK (1984) Phosphorus cycling in a northern hardwood forest: Biological and chemical control. Science 223: 391—393

Wurtsbaugh WA (1988) Iron, molybdenum and phosphorus limitation of N_2 fixation maintains nitrogen deficiency of plankton in the Great Salt Lake drainage (Utah, USA). Verh. Internat. Verein. Limnol. 23: 121—130

Zak DR, Host GE & Pregitzer KS (1989) Regional variability in nitrogen mineralization, nitrification, and overstory biomass in northern lower Michigan. Can. J. Forest. Res. 19: 1521—1526