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The Impact of Accelerating Land-Use Change on the N-Cycle of Tropical Aquatic Ecosystems: Current Conditions and Projected Changes

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The impact of accelerating land-use change on the N-Cycle of tropical aquatic ecosystems: Current conditions and projected changes

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Abstract. Published data and analyses from temperate and tropical aquatic systems are used to summarize knowledge about the potential impact of land-use alteration on the nitrogen biogeochemistry of tropical aquatic ecosystems, identify important patterns and recommend key needs for research. The tropical N-cycle is traced from pre-disturbance conditions through the phases of disturbance, highlighting major differences between tropical and temperate systems that might influence development strategies in the tropics. Analyses suggest that tropical freshwaters are more frequently N-limited than temperate zones, while tropical marine systems may show more frequent P limitation. These analyses indicate that disturbances to pristine tropical lands will lead to greatly increased primary production in freshwaters and large changes in tropical freshwater communities. Increased freshwater nutrient flux will also lead to an expansion of the high production, N- and light-limited zones around river deltas, a switch from P- to N-limitation in calcareous marine systems, with large changes in the community composition of fragile mangrove and reef systems. Key information gaps are highlighted, including data on mechanisms of nutrient transport and atmospheric deposition in the tropics, nutrient and material retention capacities of tropical impoundments, and N/P coupling and stoichiometric impacts of nutrient supplies on tropical aquatic communities. The current base of biogeochemical data suggests that alterations in the

N-cycle will have greater impacts on tropical aquatic ecosystems than those already observed in the temperate zone.

Introduction

Global nutrient cycles have been greatly altered by land-use changes over the last century. Studies in the temperate zone, for example, suggest that river export of nitrogen has increased by 3- to 20-fold in developed areas since industrialization (Howarth et al. 1996). Much of this increased load apparently results from human inputs of urban and agricultural waste (including sewage and fertilizers) and increased runoff due to cultivation and urbanization (Cole et al. 1993; Howarth 1998). In spite of the fact that we are only now beginning to understand the implications of these land-use changes for temperate freshwaters and seas, ecosystem alteration in the tropics is increasing even more rapidly than changes impacting temperate zones. The purpose of this analysis is to draw together information on temperate and tropical zone impacts on nutrient cycles to explore how differences among tropical and temperate zones may impact the trajectory of change in the coupling of land and water in the tropics.

Large-scale land-use changes are occurring in the tropical Americas, and these have important implications for the future of freshwater and marine ecosystems (Seeliger 1992; Yanez-Arancibia & Lara-Dominguez 1998). Global rates of tropical deforestation are estimated at about 20 million ha^{-1} yr^{-1}(Bruijnzeel 1996), and are rising especially rapidly in countries with high population and national debt (Rudel & Roper 1996). Tropical lands are most frequently converted to agricultural or degraded landscapes (Houghton 1994; Skole et al. 1994), which are often less efficient sinks for carbon and other elements (Asner et al. 1997; Houghton 1994), have dramatically altered regional hydrology (Bruijnzeel 1996), and are subject to large losses of nutrient elements such as nitrogen (N) or phosphorus (P) (Ojima et al. 1994). It is likely that tropical aquatic ecosystems will frequently experience increased silt, water, and nutrient loads as land-use perturbations proceed.

Reactions of tropical aquatic ecosystems to large-scale alterations in nutrient fluxes are less well documented than those demonstrated at higher latitudes. In temperate zones, changes in land-use have caused increases in nutrient loading (especially P) to lakes and rivers, resulting in wide-spread alterations of water quality (Cooke et al. 1993) and losses of resource-productive ecosystems (Ross 1997). Increased nutrient loads (especially N) carried by rivers (Cole et al. 1993) have also increased nutrient inputs to many of the world's great coastal zones (Meybeck 1982; Meybeck 1998;

Turner & Rabalais 1991), accelerated coastal hypoxia (Diaz & Rosenberg 1995; Justić et al. 1993), and impacted economically important estuarine and coastal fisheries (Diaz et al. 1992; Yanez-Arancibia 1998). Although freshwater and marine fisheries and aquaculture yields are important protein sources in developing coastal nations (Bailey et al. 1996; Yanez-Arancibia 1985), we know relatively little about the potential impact of land-use alteration on the large scale biogeochemistry of tropical aquatic ecosystems (Twilley & Day 1998).

The purposes of this article are to use information on tropical and temperate ecosystem alterations to summarize the current evidence concerning this issue, identify probable patterns of change, and recommend key directions for future research. We trace the tropical N-cycle from pre-disturbance conditions, through the likely phases of disturbance and highlight some of the implications of differences between tropical and temperate systems that might influence the trajectory of disturbance in the tropics. Because the outcome of perturbation of the N-cycle will be determined by its coupling or decoupling with changes in the P-cycle, we also explore the likely impacts of altered N:P ratios on aquatic ecosystems.

Pre-disturbance N-export: Influence of vegetation, precipitation, and latitude

The effects of altered N cycling in tropical ecosystems can be understood most easily in the context of N dynamics in undisturbed or minimally disturbed tropical ecosystems. The predisturbance N concentrations and runoff fluxes depend upon water runoff rates and vegetative cover which differ between tropical and temperate latitudes. Background N-export rates of watersheds where disturbance through atmospheric deposition and landscape change is minimal average about 5 kg ha^{-1} yr^{-1}, of which about 65% is in the particulate or dissolved organic form, while 35% is dissolved inorganic N (Lewis et al. this volume). Nitrogen export rates of undisturbed tropical watersheds are about five-fold greater than those seen in temperate regions, given similar rates of runoff (Figure 1). The principal exceptions to this trend are the Rio Negro, a black-water tropical river carrying an exceptionally low load of suspended particulate matter and a very low N-export rate, and the Mackenzie and Lena Rivers, which are large rivers carrying large sediment loads at high latitudes. Predisturbance, low-sediment river systems like the Rio Negro and most temperate pristine rivers follow one relationship between water runoff and N-export, while most tropical rivers and very large high-latitude rivers follow a different, much higher, relationship (Figure 1). This
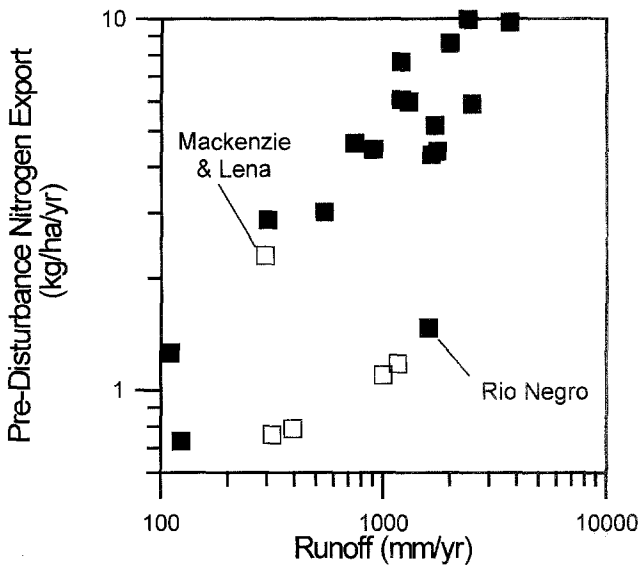
Figure 1. Relationship of pre-disturbance nitrogen export rate to the hydraulic runoff in tropical rivers (■ Lewis et al., this volume) and estimates of pristine nitrogen export in the temperate zone and arctic (□ Howarth et al. 1996). The Mackenzie and Lena Rivers are sediment laden arctic rivers, while the Rio Negro is a tropical river with very low suspended sediment load.

can be seen even more clearly in Figure 2, where predisturbance N export rates are plotted against the average latitude of the river.

Pristine tropical landscapes may have relatively high N loss rates which result from high rates of N fixation and the general lack of N limitation in tropical terrestrial ecosystems (Martinelli et al., this volume; Vitousek 1984; Vitousek & Howarth 1991). It is likely, therefore, that predisturbance tropical watersheds conserve less N and allow more to be fixed, so that N concentrations exported from disturbed tropical watersheds may be even greater than those seen in temperate systems. This conclusion is consistent with high concentrations of inorganic N in tropical rivers that are indicative of weak N retention by tropical moist forests (Lewis et al. 1995). These data suggest that anthropogenic impacts of perturbation to tropical N-cycles may be set against a backdrop of high N transport of tropical aquatic systems.

Projected changes in atmospheric N-loading of tropical waters

If tropical patterns of urbanization, industrialization, and agricultural development proceed as they have in temperate zones, development in the tropics will impact both the background atmospheric deposition rates of N and the
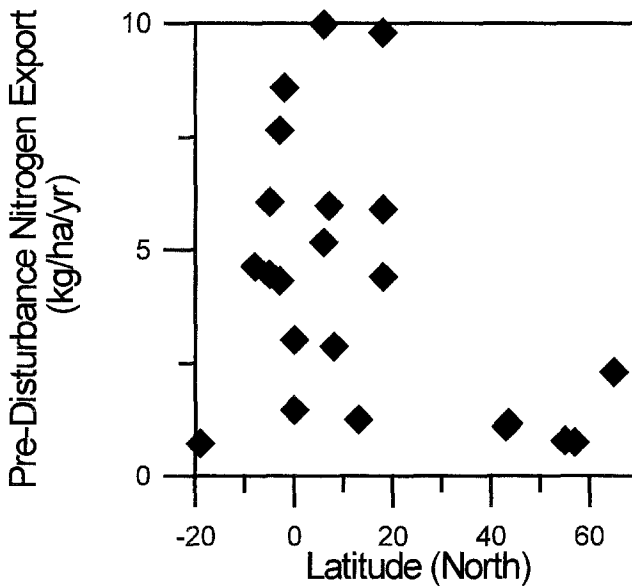
Figure 2. Geographical distribution of pre-disturbance nitrogen export rates. Data are from the sources cited in Figure 1.

rates of processing and export to aquatic systems. For example, fire mobilizes large amounts of N not only during the agricultural development phase but also after conversion of tropical landscapes (e.g., Lewis 1981). Pre-industrial and modern atmospheric inputs of nitrogen to a wide variety of catchments over a range of latitudes have been estimated elsewhere (Howarth et al. 1996) following the models of Prospero et al. (1996). Pre-industrial background deposition rates probably drove pre-industrial N-export by rivers, because measured nitrogen export rates in the temperate zone are generally about the same as the model estimated pre-industrial atmospheric N input (Figure 3). In the tropics, N export exceeds likely rates of deposition by a considerable amount because of N fixation by terrestrial vegetation. Atmospheric deposition rates are likely to increase in developing areas of tropical Asia and America as they have in industrialized parts of the temperate zone (Galloway 1989; Galloway et al. 1994).

Although industrialization has not yet occurred on as broad a scale in the tropics as it has in the temperate zone, probable changes in N-export of tropical ecosystems can be inferred from modeled values of pre- and post-industrial deposition rates across a range of latitudes (Figure 3). Pre-industrial N deposition in the tropics is calculated to be about twice that of temperate sites, probably because natural sources of volatilization of N to the atmosphere are greater in tropical N-rich ecosystems. Modern N-deposition in the
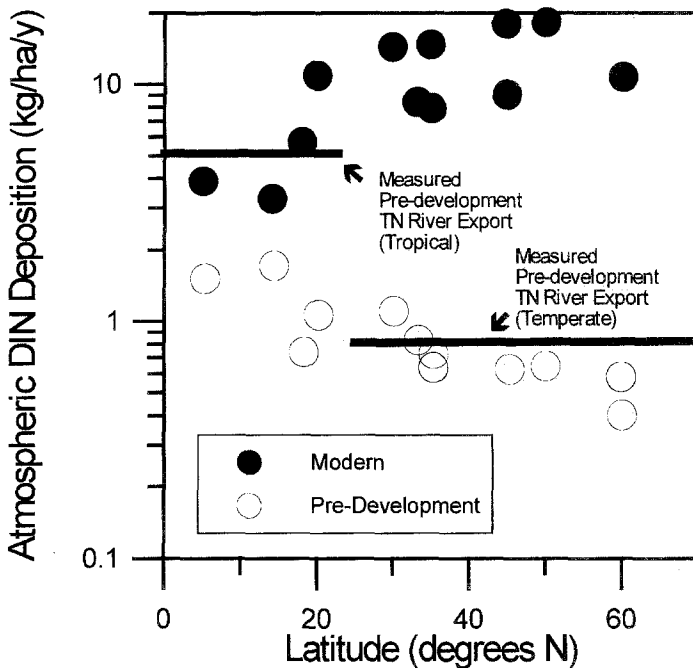
Figure 3. Relationship latitude and model-predicted pre-development and modern atmospheric NO_x-N and NH_y-N (summed) atmospheric deposition to latitude. Data on atmospheric deposition are from Prospero et al. (1996) for the large watersheds analyzed by Howarth et al. (1996). Pre-development, tropical total nitrogen export line is the average from Lewis et al. (this volume) and temperate pre-development total nitrogen export is the average from Howarth et al. (1996).

temperate zone, however, has probably increased more than 10-fold, while relatively undisturbed tropical systems have N-deposition rates very close to pre-industrial rates (*see also* Soto & Stockner 1996). If similar patterns of development and industrialization are followed in the tropics, it is likely that atmospheric N-deposition will increase more radically, such that tropical N-deposition may move to even higher levels than the rates currently found in industrialized temperate catchments. N export to tropical waters may be proportionately greater in the tropics than in the temperate zone because N is, in general, not as frequently limiting to the growth of tropical vegetation and thus not retained as effectively by vegetation in tropical terrestrial systems (Mattson et al., this volume; Vitousek & Howarth 1991).

The inference that N throughput will be greater in disturbed, industrialized tropical systems than in temperate zones assumes that the sources of present-day tropical atmospheric N deposition are not diminished by disturbance. If, for example, the source of atmospheric N deposition is currently rede-

position of forest-fixed N, and forest biomass is reduced substantially, then deforestation may result in decreased rates of N deposition, although contrary examples have been documented (Lewis 1981). If forests are converted to pasture, less N may be released to the atmosphere (Neill et al. 1995). Further, if terrestrial nitrogen fixation is fueling high background N export rates from tropical watersheds, increased atmospheric N deposition may reduce this fixation, and thus only a slight change in N release may be observed from these watersheds. In general, however, available data suggest that disturbed tropical landscapes will often have greatly increased rates of N deposition.

Changes in the partitioning of nitrogen in atmospheric deposition and riverine transport

The partitioning of nitrogen in atmospheric deposition and fluxes in rivers may also change with altered land-use. Models suggest that the American tropics currently receive about a 2:1 mix of NO_y and NH_x in atmospheric deposition (Prospero et al. 1996), a ratio which is very close to that probably received by tropical ecosystems (Figure 4) in the absence of industrialization. If mechanisms of release and deposition are altered in the tropics as they have been with temperate industrialization, the proportion of NO_y relative to NH_x deposition should increase so that NO_y might become the more dominant source of inorganic nitrogen in tropical precipitation (Figure 4). On the other hand, expanding agriculture might lead to greater NH_x deposition due to volatilization of anhydrous ammonia. An analysis of heavily developed temperate regions shows that NO_y deposition dominates in some systems, while NH_x dominates in others (Howarth et al. 1996; Howarth 1998). Presumably either of these forms could become dominant in the tropical regions as they become more developed, depending upon the balance between industrial/urban and agricultural development.

Tropical rivers and streams are often relatively rich in DON ($\approx 35\%$ of total N, Lewis et al., this volume; McDowell & Asbury 1994), as is true for undisturbed temperate systems (Hedin et al. 1995; Vitousek et al. 1997). In temperate regions, increased inputs of nitrogen from human activity result in a proportionally greater riverine export of nitrogen in the form of nitrate (Jaworski et al. 1997). This is true whether the major inputs of nitrogen are from agriculture or atmospheric deposition, and whether atmospheric deposition is dominated by NO_y or NH_x (Vitousek et al. 1997). An analysis of nitrate fluxes from the largest rivers in the world suggests that this is also true for disturbed tropical watersheds, as nitrate fluxes are correlated with watershed population densities in both temperate and tropical regions (Cole et al. 1993; Peierls et al. 1991).
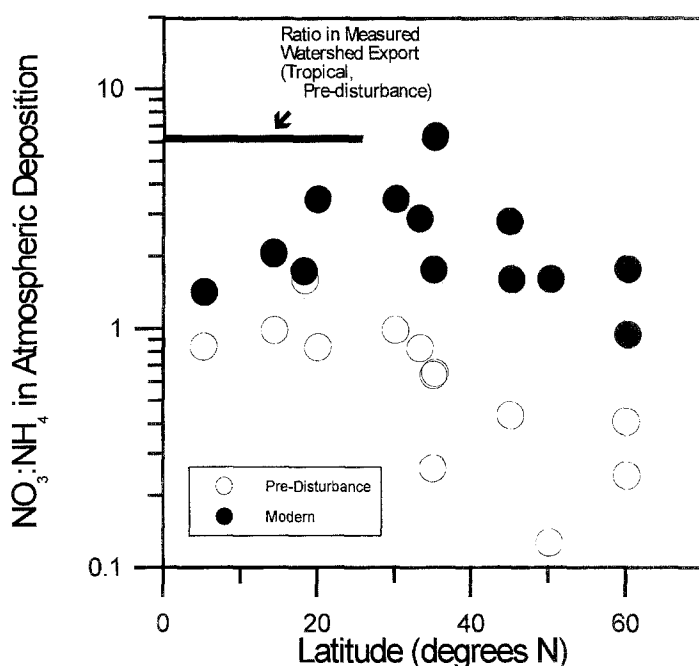
Figure 4. Latitudinal trend in the atmospheric NO_x-N:NH_y-N ratio from pre-disturbance and modern estimates. Calculations below the sources listed in Figure 3. The solid line indicates the average ratio NO_x-N:NH_y-N in water exported from pre-disturbance tropical watersheds (Lewis et al., this volume).

The trajectory of land development and its effects on nitrogen export to tropical waters

Development in tropical and temperate zones typically proceeds through several stages of development, land-use change, urbanization, and industrialization. Generally, grasslands (Garrity & Agustin 1995) then forests (Murdiyarso & Wasrin 1995) are converted to agricultural production, followed by movement of rural populations to urban areas (Hall & Hall 1993), then increased industrialization and land-use changes (e.g., water extraction, urban sprawl) necessitated by growing urban centers. This has already been established as a consistent pattern of land-use transformation in the tropics (Behrens et al. 1994; Brondizio et al. 1993; Eastwood & Pollard 1992; Sussman et al. 1994).

The development of tropical landscapes is likely to result in substantially higher N export as a result of increased atmospheric deposition and increased agriculture. Lessons learned in the temperate zone suggest that the phases of progressive intensification of human development gradually reduce ecosys-

tem complexity. Examples of this progression are found in the tropics, where vast areas of native forest are being cleared and replaced by managed systems ranging from pastures and agricultural fields to urban and industrial centers. Evidence that this trajectory is proceeding in the tropical Americas is that forest and woodland coverage has decreased by 4.1%, pasture and croplands have increased 3%, while 4.7% of the population has moved to urban centers over the last decade (World Resource Institute 1996). Our present knowledge of controls on N cycling in disturbed temperate systems and data collected in a variety of individual tropical watersheds allow some general predictions to be made on likely changes in N export from tropical landscapes subjected to progressive phases of development.

The progression of tropical development from pristine to highly altered (e.g. intensive agriculture, urban/industrial systems) is likely to result in a predictable sequence of changes to N exports. Normally this would be characterized by (1) an initial pulse in N exports via leaching and erosion upon cutting of mature forests and other vegetation, (2) a second pulse in N exports via leaching and erosion upon burning, (3) a continual increase in N exports as anthropogenic N inputs to the system override natural cycles, (4) a decrease in N fluxes as large-scale water management systems are built to hold water behind dams for irrigation or other uses, and (5) an eventual leveling off as anthropogenic inputs and outputs establish a new equilibrium. Although other trajectories of development might occur, this hypothesis and the progression of events it implies are illustrated in Figure 5 and are described and justified in detail below.

Phase 1 – *Deforestation* – Rapid forest losses are typical of all phases of disturbance in developing tropical nations (e.g., Salati et al. 1991). In warm, humid tropical climates, the labile components of cut forest slash quickly decompose and rains leach newly remineralized nitrogen into the soil column (Williams et al. 1997a, b). As the root systems of the previous forest begin to die and decompose, less leached nitrogen is absorbed, and nitrate levels in infiltrating waters remain elevated. When the water table rises, this pulse of nitrate moves laterally toward the streamside where the fate of nitrate is strongly influenced by the condition of streamside soils and vegetation. If the riparian zone remains forested and intact, the pulse of nitrate is diminished via denitrification in water-logged, organic rich, and anoxic streamside soils (McClain et al. 1994). Where the riparian zone has also been cut, the streamside buffering capacity is reduced, and higher levels of dissolved nitrogen will enter the stream via groundwater baseflow. Baseflow itself increases because of reduced plant uptake of infiltrating rainwater (Bruijnzeel 1990). After the pulse of nutrient is received by lentic freshwaters, denitrification is likely very rapid because anoxic lakes or lakes with anoxic hypolimnia are common
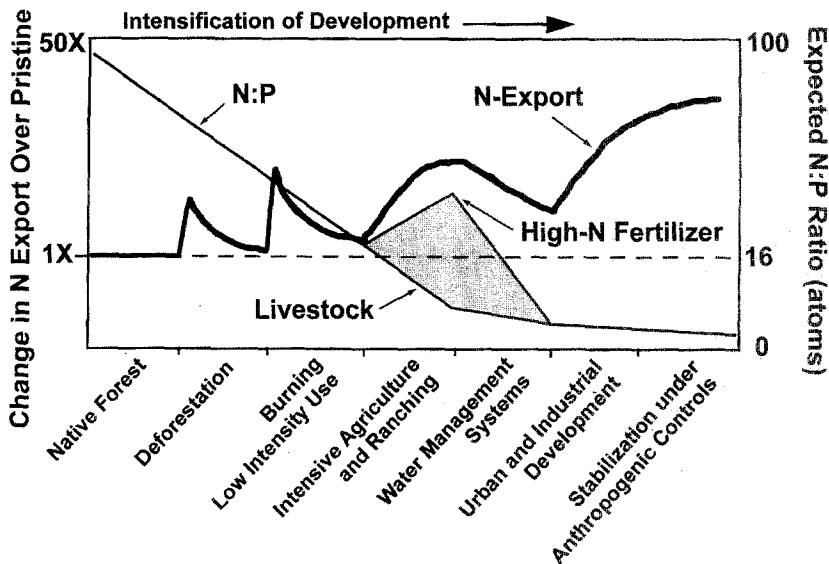
Figure 5. Expected trend in nitrogen loading and the N:P ratio of tropical aquatic systems as tropical development proceeds (see text).

in the tropics (e.g., Saijo et al. 1997; Salati et al. 1982; Tundisi 1981; c.f. Gonzalez et al. 1991) at least in areas where hydraulic budgets have not been greatly augmented (Furch & Junk 1993; c.f. Villar et al. 1996).

Erosion of particulate N also increases following deforestation, as destruction of soil structure leads to decreased infiltration capacities and greater overland flow (Bruijnzeel 1990). This condition can be exacerbated by higher rainfall amounts at the soil surface when canopy interception is reduced. Erosion and hydraulic loads to streams are also increased in response to the building of roads into deforested areas. The erosive inputs of particulate N to nearby streams are strongly dependent on the buffering capacity of the riparian zone. Labile forms of organic matter will eventually be exhausted, but erosive inputs may remain high. Increased hydraulic loads from cleared land can decrease denitrification because of augmented hydraulic flushing (Quirós 1990; Villar et al. 1996) while increased erosion can decrease transparency of tropical waters so much that nutrient retention is significantly reduced (Tundisi et al. 1981).

Phase 2 – *Burning and Low-Intensity Use* – After forest clearing, slash is often burned to clear debris, thus releasing organically-bound nutrient stocks to the soil. Burning transfers as much as 96% of organic N and >40% of the P to the atmosphere (Hölscher et al. 1997; Kauffman et al. 1995), but these nutrients will probably be redeposited within tropical ecosystems (Victoria et al. 1991). When slash is physically removed from the site, the losses of

all nutrients are significant (Fernandez et al. 1997). Burning slash leads to a second pulse of dissolved N in subsurface flow, atmospheric redeposition, and a reinvigoration of erosion (Juo & Manu 1996). Part of the increase in nitrate is to balance the additional positive charge brought by significant increases in the influx of base cations after burning. Again, the presence or absence of an intact riparian zone can strongly influence the degree to which a particular stream is impacted by burning of the upland forest surrounding it.

Lesack and Melack (1996) have suggested two different scenarios for the impact of development on precipitation chemistry and nutrient balances of tropical forests. In one, the conversion of forest to pasture or cropland could result in less material entrained into the atmosphere by convection, which would in turn reduce the flux of recycled nutrients to the remaining islands of forest. The reduced amount of rainfall predicted by Shukla et al. (1990) after deforestation of the Amazon would exacerbate this scenario. Alternatively, conversion of forest to pasture or cropland could result in an increase in dust in the atmosphere, with more material entrained into the atmosphere than from the former forest. Because repeated burning may be used to control secondary vegetation after conversion, emissions of some chemical species could be further enhanced relative to the uncut forest. Hence, the flux of recycled nutrients to remnants of forest might increase as the surrounding landscape is converted from forest to pasture or cropland.

Land subjected to slash and burn practices is usually developed as pastures or small-scale agricultural fields (Brondizio et al. 1994). Where these agricultural practices remain at low intensity (i.e. without application of fertilizers), the exports of dissolved nitrogen should again tend to decrease after the initial pulse, reflecting a gradual depletion in N stocks. The slash-and-burn cycle may be repeated multiple times over several years. Without fertilization of the infertile soils dominating the tropics, the nutrient status of tropical soils will diminish until agricultural land-use must be abandoned. In cases of intensive agriculture, fertilizer use on infertile tropical lands may eventually exceed rates of application in temperate systems to sustain economic levels of production. Therefore, depleted soils and associated loss of inorganic fertilizers may be more acute in tropical agriculture than temperate zones.

Phase 3 – *Intensive Agriculture and Ranching* – As land-use intensifies, anthropogenic sources and sinks of N should become the dominant N fluxes. Nitrogen fertilizers are often applied at rates greater than plants' requirements and there is nearly always a significant excess of nitrogen beyond that removed from agricultural fields as harvested crops (Hölscher et al. 1997; Keftasa 1994; Chowdhury & Rosario 1993). The rest of the nitrogen is stored in the soil, leached in surface runoff or in groundwater (Deare et al. 1995), or volatilized to the atmosphere. The amount of nitrogen leached from agri-

cultural fields is greater in tilled fields than in pastures (Neill et al. 1995) and is greater in sandy soils than in clayey soils. When expressed as a percentage of nitrogen added in fertilizer, the nitrogen leaching from agricultural soils in surface and groundwaters varies from 28% to 85% (Hölscher et al. 1997; Kühne 1993; Poss & Saragoni 1992). Even when agricultural soils are not fertilized, they leach more nitrogen than do forests, perhaps due to lowered evapotranspiration and greater water runoff (Uhl & Jordan 1984; Seyfried & Rao 1991; Sur et al. 1992; Vitousek & Melillo 1979). When runoff water from tropical agricultural systems runs through wetlands before reaching streams, a large proportion of the leached nitrogen can be denitrified (Arheimer & Wittgren 1994; Peterjohn & Correll 1984; Pinay & Decamps 1988; Vought et al. 1994). Very high rates of denitrification may occur in the hyporheic zones of tropical streams (Sjodin et al. 1997). In the absence of substantial wetland buffer strips or hyporheic denitrification, however, levels of nitrate in streams may rise to levels well above those required by freshwater biota, so aquatic communities may be greatly altered by intensive agriculture (Pedrozo & Bonetto 1989). Physical practices related to intensive land cultivation also increase erosion and, therefore, further augment exports of particulate N.

In addition to nitrogen leaching from agricultural fields, agriculture can contribute to nitrogen mobilization in the landscape through increased volatilization to the atmosphere and subsequent deposition, particularly of NH_x. Howarth (1998) has demonstrated that at the scale of large regions, NH_x deposition is strongly correlated with riverine export of nitrogen, and that NH_x deposition appears to be a strong surrogate measure of the leakiness of "surplus" nitrogen from agricultural systems.

Phase 4 – *Water Management Systems* – Reservoir development often accompanies the initiation of large-scale intensive agriculture (Matsumura-Tundisi et al. 1981). It is also associated with increasing urban populations, industrialization, and hydroelectric power needs in the tropics (Tundisi 1981, 1994). The impact of reservoir development should generally lead to a decrease of nutrient exports from catchments (Bonetto et al. 1994; Pedrozo et al. 1992; Tundisi & Matsumura-Tundisi 1981; Vorosmarty et al. 1997). Reservoirs increase water residence times, thus allowing greater biotic uptake by aquatic vegetation, and the establishment of anoxic bottom water conditions that promote denitrification, acting to reduce exports of N to downstream receiving waters. Nutrient retention may be extremely dynamic, however, since some tropical lakes apparently retain nutrients during periods of low water but release them during the rainy season (Furch & Junk 1993). Experience in temperate ecosystems (Fleisher & Stibe 1991) suggests that N retention in lakes and natural wetlands varies between about 10% and 90% (including biotic uptake, sedimentation, and denitrification), depending upon
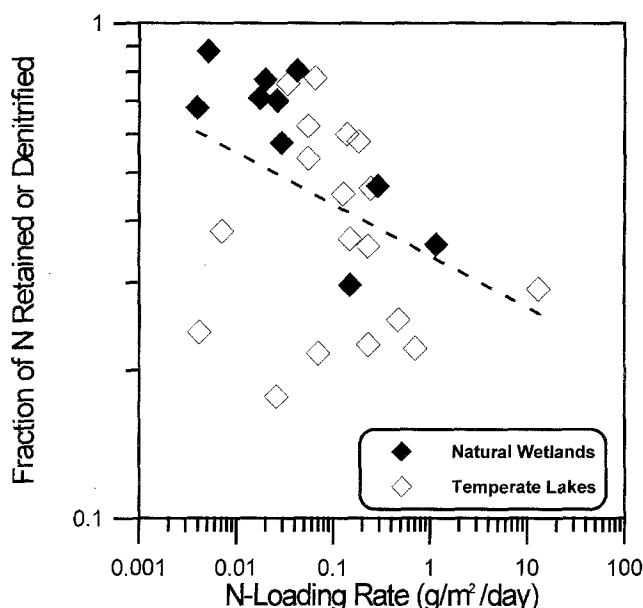
Figure 6. Relationship between nitrogen "retention" (including denitrification losses) and nitrogen loading rate in temperate zone lakes and ponds (Fleisher & Stibe 1991). The dashed line indicates the least squares regression relationship between the logarithms of the two variables ($n = 28$, $r = 0.39$, $p < 0.05$).

the hydraulic and biotic characteristics of the water body (Howarth 1998). Wetlands have very high rates of N retention (Figure 6), but N retention decreases as N-loading rises above about 0.1 g m^{-2}day^{-1} (Figure 6). Although the data plotted in Fig. 6 may be somewhat optimistic compared to riverine N retention (Day & Kemp 1985), temperate data suggest that impoundments and wetlands can retain large amounts of N, but that their N removal efficiency will decrease as N-loading rises. The impact of tropical impoundments on N loads may be less than impoundments in temperate systems, however, if N fixation rates in tropical waters are very high, or if high turbidity hampers biotic nutrient uptake (e.g., Arcifa et al. 1981b).

Phase 5 – *Major Urban and Industrial Development* – Within major urban and industrial areas, natural cycles of N are nearly completely overwhelmed by anthropogenic sources. High inputs of human waste and effluent from industrial activities enrich rivers with organic and inorganic nitrogen. Where light or turbulence do not renew oxygen, river waters may become hypoxic and the river biota may shift toward species tolerant of low oxygen conditions. Even the nutrient retention capacity of impoundments may be hampered because of very high rates of cultural eutrophication that accompanies urbanization in the tropics (Tundisi 1987; Arcifa et al. 1981a).

Without remedial measures, river exports of N will increase in proportion to anthropogenic inputs, unless denitrification is very rapid.

In large tropical river basins, several of these phases are likely to be active simultaneously in the landscape. Consequently, the downstream effects of each will be integrated into a single export to coastal waters. The magnitude of this integrated export will depend partially upon the proportion of the basin subject to each phase of development.

Impacts of tropical development on the relative availability of N and P

It is now well known that N, P, or other nutrients (Downing 1997) can limit primary production in freshwater and marine systems, and that the limiting nutrient is determined by the relative availability of ambient N, P and other essential nutrients. Therefore, understanding the expected changes in ecosystem function due to alteration of N cycling must include a consideration of accompanying alterations in other important nutrients, especially P. In fact, if the N:P ratios of receiving waters are high (i.e., higher than 16:1 in atomic units; Redfield 1934), the impacts of enhanced N-export may be low because P will be the principal element limiting freshwater production.

It is likely that N:P ratios in aquatic ecosystems will vary along a predictable trajectory across the phases of development presented above. Background N:P ratios tend to be very high in waters exported from undisturbed tropical terrains (Bruijnzeel 1991; Williams & Melack 1997), often higher than 100:1 (as atoms; Table 1). In minimally impacted tropical freshwaters, denitrification is quite rapid (Salati et al. 1982; Saijo et al. 1997) and warm, anoxic waters keep P mobile (Furch & Junk 1993), so N:P ratios are typically quite low (Bonetto et al. 1994; Pedrozo & Bonetto 1989; Pedrozo et al. 1992; Rai & Hill 1980). In some tropical regions, however, oxic conditions and waters rich in iron and dissolved organic matter may reduce P concentrations keeping N:P high (Gonzalez et al. 1991; Tundisi et al. 1991).

As forests are cleared, the N:P in exported waters will decrease. Storm related erosion, common in deforested areas, yields significantly lower N:P due primarily to increased transport of particulate matter containing relatively high concentrations of P. Burning volatilizes more of the N contained in biomass than the P (Hölscher et al. 1997; Kauffmann et al. 1995). The N:P ratio should therefore decline steadily throughout the burning phase of deforestation (Figure 5) unless most volatilized N is redeposited locally. Agricultural development can have different impacts on N:P ratios, because grain cultivation (e.g., maize) often uses large nitrogen amendments (e.g., anhydrous ammonia), which leads to high N:P ratios of runoff, while animal husbandry leads to lower N:P ratios (e.g., <20) characteristic of effluents

Table 1. Data represent the N:P ratios (molar) found in various known aquatic nutrient sources or in water fluxes leaving different land-uses.

Source	N:P (atomic)	Reference
Unfertilized fields	547	Loehr 1974
Soils, medium fertility	166	Vollenweider 1968
Forested areas	157	Loehr 1974
Rural lands	135	Loehr 1974
Soils, fertile	74	Vollenweider 1968
Tropical forests	52	Loehr 1974
Agricultural watersheds	44	Uttormark et al. 1974
Forest export	38	Beaulac & Reckhow 1982
Mixed agriculture	35	Beaulac & Reckhow 1983
Sewage effluent	22	Golterman 1975
Cattle manure seepage	20	Loehr 1974
Non-row crop export	18	Beaulac & Reckhow 1982
Fertilizer, average	17	Turner & Rabalais 1991
Redfield ratio	16	Redfield 1934; Harris 1986
Feedlot runoff	14	Loehr 1974
Pastureland runoff	13	Beaulac & Reckhow 1982
Urban stormwater	13	Loehr 1974
Sewage	12	Vollenweider 1968
Urban runoff	11	Beaulac & Reckhow 1982
Pastureland runoff	11	Loehr 1974
Urban runoff	10	Uttormark et al. 1974
Row crop export	9	Beaulac & Reckhow 1982
Sewage	6	Vallentyne 1974
Septic tank effluent	6	Brandes et al. 1974
Bird feces	2	Portnoy 1990

from manures (Table 1). The N:P ratio should further be reduced as nutrient-enriched waters pass through impoundments, especially if they are deep and have long water-residence times, because denitrification occurs at the sediment-water boundary in reservoirs and soluble P is released in anoxic sediments. Some upward pressure may be put on N:P, however, if land clearing leads to drastically altered hydrology that flushes normally anoxic waters where denitrification was naturally common. Urban and industrial sewage has a low N:P ratio (Downing & McCauley 1992), so long-term trends in heavily impacted tropical regions should stabilize at low N:P ratios typical

of urbanized conditions. Thus, not only should nutrient export change with land-use, but nutrient supply ratios are likely to decline as development of tropical watersheds proceeds.

Tropical freshwater responses to N- and P-loading

The relative importance of N or P as a limiting nutrient depends not only upon their ratio in the inputs, but on several internal processes (Howarth 1988). These internal processes include recycling within the water column, sedimentation, resuspension or release from the bottom, and nitrogen fixation. Hence, proper evaluation of freshwater responses to altered N-loading requires a comparative analysis of how these processes alter nutrient cycling and availability.

As indicated above, disturbance will likely lead to a decrease in ratios of available N and P, although assembling a data set that is geographically representative of loadings to tropical lakes and streams is problematic. Different N and P fractions (i.e. dissolved inorganic, total dissolved, dissolved organic, particulate, or total) have been measured in various systems, and it is unclear whether the measured fractions are available for biological uptake, or whether sampling or analytical problems have yielded a clear view of tropical nutrient fluxes. Phrasing the hypothesis as a comparison between tropical and temperate regions may also confound the analysis, because the variability arising from land-use patterns could override that arising from geographical differences. Hence, the data we have chosen to make such comparisons below are from the least disturbed catchments possible.

The N:P ratios of total N and P fluxes in rivers draining into the North Atlantic (Table 2) supports the hypothesis that tropical freshwaters should generally be more sensitive to N-loading than temperate ones because the N:P ratios in tropical water flowing from large tropical drainage basins are at, or below, the Redfield atomic ratio (ca. 16), while the ratios in water leaving large temperate American and European basins (even those in undeveloped areas) are generally above 16 (Søballe & Kimmel 1987). Another approach is to examine yields of N and P from different land-uses. Based on North American data, as the dominant land-use changes from forests or mixed agriculture to pastures, crops, and finally to urban uses, total N to total P export shifts from values above atomic N:P ratios of 16 to values near or below 16 (Table 1). Moreover, Billen et al. (1991) found that total dissolved nutrient concentrations increased and dissolved N:P ratios decreased in a set of temperate catchments with land-use ranging from forested to agricultural to urbanized. Further, Peierls et al. (1991) reported strong statistical evidence for increased nitrate concentrations in rivers worldwide as a function of

Table 2. Regional N to P atomic ratios (Howarth et al. 1996) expressed as ratios of total N fluxes to total P fluxes. Data are for river systems flowing into the North Atlantic Ocean.

River/ Region	N:P Ratio
North America	42
Central America, Caribbean and Orinoco basin	15.5
Amazon and Tocantins basin	4.4
Western Europe	22

population density, and Howarth (1998) found the same relationship for total N export from large temperate regions. Therefore, a tendency toward lower N to P ratios favoring N limitation could be attributed to increased agricultural development and urbanization independent of latitude.

Detailed analysis of the relative severity of N or P limitation in fresh-waters requires N and P data on a wide range of tropical waters, although complete data are rarely available. Although not necessarily reflecting total N:P, more frequently available nitrate to orthophosphate molar ratios vary widely within the tropics (Table 3) with values for African rivers and streams below the molar Redfield ratio (16) and most values for South America above 16. The N:P ratios of fluvial fluxes of total dissolved N and P for the South and Central American waters in Table 4 are at or above the Redfield ratios. Waters of the Paraguay River (Pedrozo & Bonetto 1989), the Paraná flood plain (Pedrozo et al. 1992), some Amazonian lakes (Forsburg 1984; Rai & Hill 1980) have low N:P, while other Amazon lakes (Forsburg 1984) and some lakes in Brazil (Tundisi et al. 1991) and Venezuela (Gonzalez et al. 1991) have high N:P. It appears that there may be regional differences in the prevalence of N limitation among the freshwater ecosystems of the tropics.

There are few measurements of atmospheric deposition in the tropics spanning at least one year and including inorganic and organic fractions of N and P (e.g. Bootsma et al. 1996; Lesack & Melack 1991; Lewis 1981); such data are sparse even for temperate regions. Hence, it is not possible to assemble a representative set of data on external loading via atmospheric deposition appropriate for testing hypotheses about the relative importance of N or P in tropical systems. The few data available show molar N to P ratios for dissolved inorganic N:P or total dissolved N and P that range from mid 20s to almost 200. Dry deposition of P is likely to lower these ratios, assuming that the particulate P is available for algal uptake.

The extent to which the N:P ratio in external inputs determines the nutrient status of freshwater ecosystems depends partially on the relative magnitude

Table 3. N to P ratios of rivers in various tropical regions expressed as molar NO_3 to PO_4 concentrations. Ratios of dissolved inorganic nutrients are used here because data in total river N and P budgets are frequently unavailable in the tropics.

River/ Region	Ratio
Africa	
Uganda (Viner 1975)	
Mt. Elgon rivers	4
Karamoja rivers	2
Central Uganda	3
Semliki tributaries and Ituri forest streams	5
Kigezi highlands rivers	5
Ruwenzori mountains	13
Kenya (Melack & McIntrye 1991)	
Aberdare and Bahati rivers	8
Cherangani Hills rivers	2
Zambezi (Hall et al. 1976)	1
South America (Lewis et al. 1995)	
Orinoco basin	
Orinoco (lower)	19
Apure	7
Caura	63
Caroni	87
Amazon basin	
Amazon (Obidos)	14
Solimoes (Ica)	16
Japura	24
Jurua	21
Negro	30
Madeira	10
Trombetas	62
Xingu	57
Tapajos	100

Table 4. N to P ratios expressed as fluxes of total dissolved N to total dissolved P or as fluxes of NO_3-N plus dissolved organic N to PO_4-P plus dissolved organic P. These nutrient ratios are used here because data on total river N and P budgets are frequently unavailable in the tropics.

River/ Region	Ratio (molar)	Reference
Paraguay	51	Hamilton et al. (1997)
Amazon basin		
Ica	20	JR Richey (unpubl.)
Jutai	20	JR Richey (unpubl.)
Jurua	15	JR Richey (unpubl.)
Japura	18	JR Richey (unpubl.)
Purus	18	JR Richey (unpubl.)
Negro	15	JR Richey (unpubl.)
Madeira	15	JR Richey (unpubl.)
Mota Brook	194	Lesack (1993)
Mota Brook	46	Williams & Melack (1997)
Orinoco (lower)	31	Lewis & Saunders (1989)
Apure	15	Saunders & Lewis (1988)
Costa Rica		
Northwestern streams	42	Newbold et al. (1995)

of external inputs, internal recycling and vertical mixing and losses, and their respective N:P ratios. Such information is available for only a few tropical lakes. Two contrasting examples (Lake Malawi and Lake Calado, Brazil) help demonstrate the balance between external and internal nutrient supply.

Lake Malawi, one of the African Great Lakes, has a hydraulic flushing time of 750 years and is permanently anoxic below about 200 m (Hecky et al. 1996). The annual fluvial and atmospheric inputs to the mixed layer have N to P molar ratios of 23 and 43, respectively. About 80% of the N input is supplied by nitrogen fixation. Vertical mixing provides about 88% of the P, but essentially no N to the mixed layer. Fluvial outflow is small and has an N:P ratio of 30; loss to burial in sediments is unmeasured; an N:P ratio for annual burial of about 30 is estimated for neighboring Lake Tanganyika. Although the N:P ratios in fluvial and atmospheric inputs would indicate a P-limited mixed layer, the dominance of vertical mixing as the route of supply of phosphorus (N:P $\approx$ 0), requires a large N supply by nitrogen fixation to avoid severe N limitation. The presence of a continuous oxic-anoxic interface in the water column acts as a sink for dissolved inorganic N because of denitrification, but has little influence on the upward flux of P (Hecky et al. 1996).

The common occurrence of anoxic hypolimnia in tropical lakes may be an important factor leading to low N to P ratios associated with vertical mixing, which is often a major source of nutrients to the euphotic zone, and which may stimulate N fixation or lead to N limitation.

Lake Calado, a shallow floodplain lake bordering the Solimões River in the central Amazon basin, ranges in area from about 2 to 8 km^2 as a function of annual variation in river stage (Lesack & Melack 1995). Estimates of inputs, recycling and exports of N and P for Lake Calado have been published (Doyle & Fisher 1994; Fisher et al. 1991; Melack & Fisher 1990). Inputs to Lake Calado from rain, upland runoff, groundwater seepage, adjacent lakes, and riverine inflows had an aggregate molar N:P ratio of 32. Internal recycling by bacteria and zooplankton within the water column and by regeneration from sediments had molar N:P ratios of 4 and 7, respectively. Because the magnitude of internal recycling exceeded external supply, the overall N:P ratio for supply was 5. Losses via burial as sediments and outflow to the river (but not including gaseous losses of N) had an N:P ratio of 20. Nitrogen fixation provided about 8% of the total annual N inputs. While these annual N:P supply ratios are indicative of N limitation, experimental enrichments, and physiological assays detected weekly and seasonal differences in nutrient limitation due in part to the variable incursion of river water (Setaro & Melack 1984). Hence, short-term variations in the relative magnitude of various routes of nutrient supply with different N:P ratios can change the importance of N or P as limiting nutrients. The Lake Malawi and Calado data suggest that increases in N loading of freshwaters will have a proportionately greater impact on tropical lakes than temperate ones.

Some information on the relative probabilities of N- or P-limitation in tropical freshwaters can be gained by examining average total N and P concentrations in tropical waters. Although such data are relatively rare, a joint PAHO/WHO program created to predict responses of unimpacted tropical lakes to cultural eutrophication assembled N and P data on 24 warm, tropical lakes in Argentina, Brazil, Colombia, Ecuador, Mexico, Puerto Rico, and Venezuela (Salas & Martino 1991). When these data are compared with similar data collected in temperate lakes (Downing & McCauley 1992), it appears that they follow quantitatively different trends (Figure 7). Tropical lakes in the Americas are generally very rich in nutrients and therefore have N:P ratios that cluster closer to N:P = 16, but are not dissimilar from rich temperate lakes. A greater proportion of tropical lakes (29%) than temperate (3%) have N:P < 16 (Downing & McCauley 1992). This suggests that denitrification in tropical ponds, lakes, and streams must be very rapid because water leaving tropical forests has high N:P ratios (Figure 7; Bruijnzeel 1991; Williams & Melack 1997).
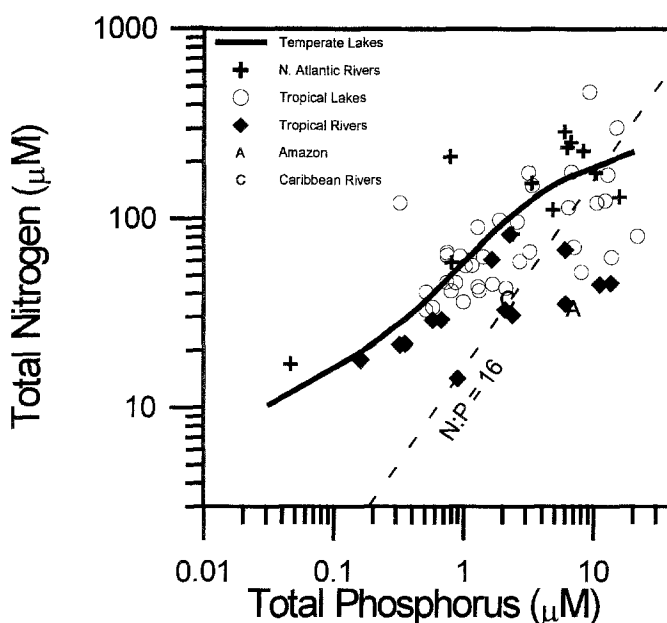
Figure 7. Relationship between the nitrogen and phosphorus concentration in temperate and tropical freshwater ecosystems. The solid line shows data on temperate lake nutrients shows the LOWESS fitted general trend derived from several hundred sets of measurements on average temperature lake nutrients (Downing & McCauley 1992). Tropical lake data are from Salas & Martino (1991). Concentrations of N and P in tributaries to the North Atlantic, including Caribbean rivers ("C") and the Amazon & Tocantins Basins ("A") are flow weighted averages from Howarth et al. (1996). Other tropical river data are principally pristine South American rivers and streams (Lesack 1993; Lewis et al. 1995) and data from the Gambia River in Africa (Lesack 1984).

Because low ambient N:P ratios are indicative of N limitation (Downing & McCauley 1992; Elser et al. 1990), it is likely that N is more frequently limiting to freshwater production in tropical lakes despite the high N:P in nutrient supplies from undisturbed forested catchments. Likewise, undisturbed tropical streams and rivers have lower concentrations of N for a given concentration of P than do tropical lakes or temperate lakes and rivers (Figure 7). This suggests that N is lost from aquatic systems more rapidly in the tropics than the temperate zone (e.g. through denitrification), and phosphorus erosion from tropical landscapes and phosphorus mobilization in aquatic environments are more rapid. Whatever the pathway, it is clear that nitrogen is frequently limiting to production in tropical freshwaters (Saijo et al. 1997; Furch & Junk 1993; Forsburg 1984; Henry et al. 1984).

In summary, it is difficult to predict with certainty how tropical freshwater systems will respond to altered nutrient supplies and ratios because of the

relative paucity of data. It is especially important to make measurements of organic N and P fractions in atmospheric deposition, and to conduct studies that include recycling, vertical mixing and losses as well as inputs. Based on the available data on N:P ratios in fluvial inputs and lakes, however, it seems likely that N will be more frequently limiting to production in tropical freshwater systems than in the temperate zone. The common occurrence of an oxic-anoxic interface in the water column of tropical lakes may increase the likelihood of low N:P ratios, stimulating nitrogen fixation or leading to intensified nitrogen limitation.

Ecological effects of N/P alterations on tropical aquatic communities

The evidence presented above suggests that the probable sequence of disturbance will lead to N and P enrichment and progressive declines in the N:P of nutrient supplies. The coupling of the major biogeochemical cycles is critically important for evaluating the ecological impact of changes in them (Elser in review; Howarth 1988; Howarth et al. 1996; Sterner et al. 1997; Wollast et al. 1993). Resource ratio competition theory (Tilman 1982) can help develop broad predictions about the impact of increased N loading and stoichiometric shifts in supply with tropical disturbance.

To illustrate stoichiometric changes in tropical aquatic ecosystems, "Zero net growth isoclines" (combinations of N and P supply rates where population growth rate exactly balances losses such that net growth is zero) for nine hypothetical algal species are shown in Figure 8. The competitive abilities of various algal taxa usually follow a normal distribution (Andersen 1997), and thus in most situations the greatest diversity of algal taxa will be supported at intermediate N:P supply ratios. The species at the upper left of the figure are good competitors for P, but relatively poor competitors for N. The species to the right are good competitors for N but poor competitors for P. The "ultimate" good competitor for N is an N-fixing species (e.g. species 8 and 9) that might be abundant under the relatively N-limited conditions in the tropics. If much N, but little P, is supplied, good P-competitors will dominate. If much P, but little N, is supplied, as will probably be the case under increased disturbance in the tropics, good N-competitors (e.g., species 7 and 8) will reduce N levels below those at which other taxa can survive.

Resource ratio theory predicts different community responses of temperate and tropical systems to increased loading. Temperate lakes are usually P-limited with naturally high N:P loading ratios (Region A, Figure 8), so increased N loading accompanied by a proportional increase in P inputs (arrow I, Figure 8) has had significant yet modest effects on community structure. In N-limited (low N:P) waters (scenario B, Figure 8) or those
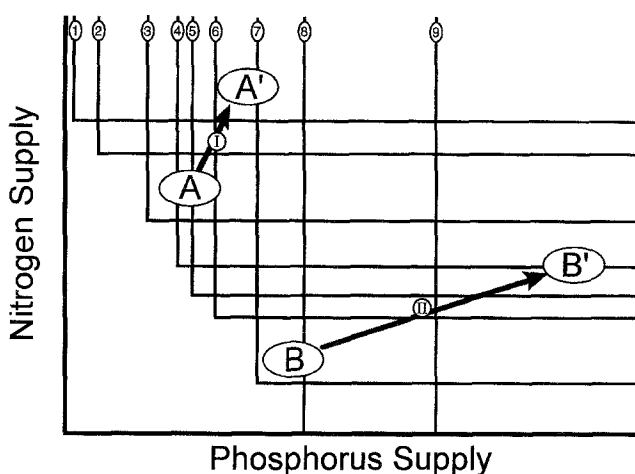
Figure 8. A generalized set of "zero net growth isoclines" ('ZNGI's) for 9 hypothetical algal species in which there is a trade-off in competitive abilities for N and P. For a given species, the ZNGI indicates the set of minimal supply rates for N and P at which net growth rate falls to zero for a given total loss rate. Species 1 and 2 are particularly good competitors for P but have elevated requirements for N supply. Conversely, species 8 and 9 represent N-fixing taxa with high minimal P requirements. The trajectories indicated by arrows I and II show scenarios of algal community response to perturbations of N supply under contrasting ecological conditions, representing changes observed in temperate freshwaters (I) and predicted for tropical freshwaters (II).

where N and P are nearly co-limiting, such as those that are common among oligotrophic lakes in the western U.S. (Horne & Galat 1985; Morris & Lewis 1988) and among many lakes in the tropics (Figure 7.; Lewis 1996; Setaro & Melack 1984; Wurtsbaugh et al. 1985), increased N loading that is coupled to increased P loading (N:P load decreasing; arrow II, Figure 8) would have relatively large effects on algal community structure, simplifying the community to those very few species adapted to extremely low N:P supply ratios. Given the predominantly low N:P of runoff under anthropogenic influence (Table 1), increasing disturbance in the tropics will lead to disproportionate enrichment of P relative to N, resulting in decreasing N:P ratios (Figure 5). Nitrogen limitation is therefore likely to become progressively more severe as disturbance and development proceed, leading to an even greater decrease in algal diversity than that seen in culturally eutrophied temperate freshwaters.

Discrepancies between the highly variable elemental composition of phytoplankton and the rigidly regulated composition of consumers (Andersen & Hessen 1991; Elser et al. 1996; Elser et al. 1998; Sterner et al. 1993; Sterner & Hessen 1994) will likely destabilize tropical freshwaters under increasing landscape disturbance. The growth and reproduction of consumers can be

limited by the nutrient content of its food (Sterner 1994), creating trophic bottlenecks (Elser et al. 1998; Sterner et al. 1997) that limit the rates and ratios at which consumers cycle nutrients (Elser et al. 1988; Olsen et al. 1986; Sterner 1990; Urabe 1995). Models (i.e., Andersen 1993, 1997) predict that if N loading is coupled to increased P loading as expected in tropical freshwaters, trophic destabilization will result from tropical eutrophication. Because major biomolecules (e.g. proteins vs. nucleic acids) differ little in nitrogen content (Elser et al. 1996) but greatly in phosphorus content, most consumer taxa should have similar nutritional requirements for N but broadly variable P requirements. Worsening food quality resulting from N limitation may eventually drive food C:N ratios to a critically high level where the majority of grazer taxa suffer nutritional imbalances. Under increasing algal N limitation such as that expected in the tropics, impacts on food webs may potentially disruptive to ecosystem function. Because tropical freshwater systems are currently frequently N-limited, it is likely that ecosystem-level impacts of land-use change will be more severe than those seen in the temperate zone.

Altered nutrient export to estuaries

Evidence has been presented above that tropical freshwaters supply more nutrient flux than undisturbed rivers of the temperate zone (Figures 1 and 7), that the nitrogen contained in this flux is roughly 35% dissolved inorganic N (Lewis et al., this volume), and that tropical headwater streams have lower N:P ratios than their counterparts in the temperate zone (Table 2, Figure 7). Future land-use change in the tropics will be likely to greatly alter N flux to tropical estuaries (Figure 3); this N-flux will be increasingly dominated by dissolved inorganic forms of N (Figure 4); and nutrients may be increasingly supplied at N:P below the Redfield ratio (Table 1, Figure 3). These observations combine to suggest that tropical estuaries of the future will experience nutrient supplies that are much higher than current concentrations, and that these supplies will have decreasing N:P ratios leading to eutrophication and stronger nitrogen limitation. Increased nutrient loading to estuaries will probably accentuate nitrogen limitation.

Shifts in N and P limitation in tropical coastal ecosystems

The often high levels of nutrient loading and the low N:P in inputs to tropical coastal systems from rivers suggest that marine waters near river outflows must frequently be N-limited. Suspended silt loads carried by tropical rivers, however, block light and probably also result in light-limited production of

benthic and planktonic systems. Nutrient inputs and factors limiting primary productivity in tropical coastal waters will therefore vary according to a continuum of geomorphological settings that differ in nutrient concentrations and light availability from deltaic, estuaries and lagoons, to reef and planktonic environments. The amounts of solar, chemical and mechanical energy together with regional geomorphology must establish the template from which site-specific patterns of primary productivity will develop. Together, these geophysical factors control the distribution of resources (such as light and nutrients) as well as establishing levels of stress (temperature and salinity) that largely determine the net productivity of aquatic ecosystems. These characteristics will strongly influence the responses of marine ecosystems to increased nutrient flux.

Most classification systems of marine ecology have accounted for the importance of the physical nature of coastal environments to the types of communities that develop (Hedgpeth 1957; Odum et al. 1972). Geomorphic and geophysical characteristics of coastal zones, along with regional climate, have been recognized as important constraints on the structure of tropical coastal ecosystems (Yanez-Arancibia 1987) including plant formations, such as mangroves (Blasco 1984; Thom 1982; Twilley 1995). In addition, the relative contributions of primary producers to total energy flow of coastal systems can be associated with regional patterns of geomorphology and hydrography, particularly river inflow (Mann 1975; Welsh et al. 1982). For example, the ratio of wetland area to the area of coastal waters has been suggested as important to the contribution of coastal wetlands to the secondary productivity of estuaries (Mann 1975; Rojas Galaviz et al. 1992; Welsh et al. 1982). Landform characteristics of a coastal region and environmental processes such as river discharge, tides, wind and waves control the types of primary producers, their relative spatial distribution and abundance, as well as rates of primary productivity. Classes of environmental settings based on energy spectrum and source of sediments have been used to generalize patterns of coastal geomorphology including reefs, lagoons, estuaries (drowned river valleys), and deltas (Figure 9). The response of coastal ecosystems to increases in N will likely be associated with these different patterns of geophysical forces and geomorphological processes.

The susceptibility of tropical coastal systems to eutrophication will vary with the geomorphological setting (Figure 9). Conceptual templates of coastal systems that integrate geomorphology and water residence time (geophysical processes) with biogeochemical processes allow understanding of the ways in which coastal ecosystems will respond to nutrient inputs. Variation of available light and nutrients are two key factors limiting primary productivity among the geomorphological types. Reefs are among the marine environ-
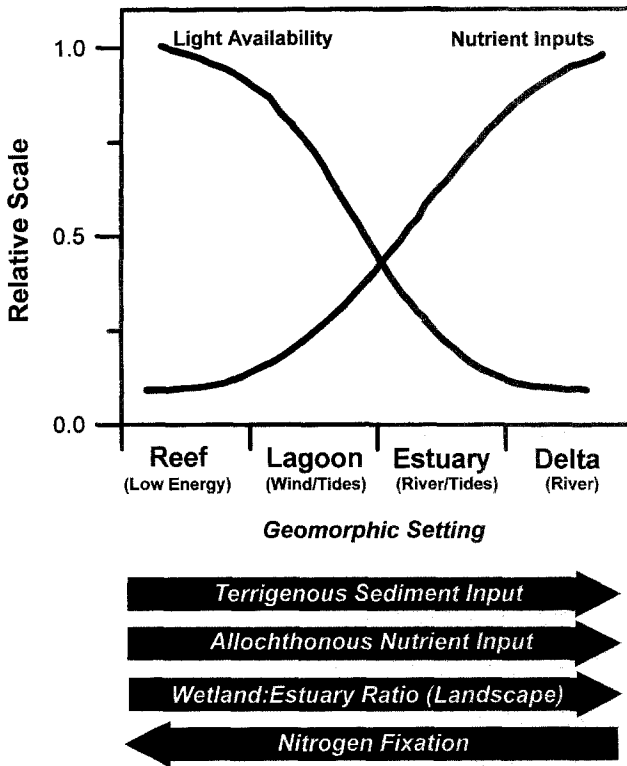
Figure 9. Conceptual framework of variations in the distribution of available light and nutrients inputs among different types of estuaries based on geomorphology from carbonate reefs to river-dominated deltas. Hypotheses concerning the relative amounts of sediment and nutrient inputs, including nitrogen fixation, and wetland:estuary ratio are indicated with increasing amounts of each occurring in the direction of the arrows.

ments most remote from terrestrial disturbance impacts on the global N-cycle. Reef environments have *in situ* production of sediments that are low in nutrients, have very clear waters and low wave energies that support productive seagrass and coral communities, yet phytoplankton production is low. On the other extreme, deltaic environments have very limited light, but are rich in nutrients, where high productivity is associated with intertidal communities that receive fertile sediments. There is a transition in the relative contribution of planktonic, benthic, and intertidal primary producers to net ecosystem productivity along this continuum of geomorphological settings related to the distribution of light and nutrient resources. The trajectory that each type of primary producer will follow as nutrient levels increase will determine the pattern of eutrophication in each coastal setting. In the case of reefs, benthic and planktonic producers will be sensitive to nutrient loading compared to

deltaic systems where the response to nutrient loading will be less dramatic and more spatially removed to high light environments downstream of river plumes (see below). The issue of nutrient limitation, then, is a key issue in geomorphological settings that are less light limited, compared to more fertile environments where light limitation may currently be more critical than nutrients. Therefore, whereas responses of deltaic systems to increased nutrient loading may be minor, the extent of the high production zone surrounding the river delta will be greatly expanded, altering large-scale patterns in natural marine production gradients.

The paradigm that N is the key limiting nutrient to coastal marine ecosystems has largely been restricted to temperate environments (Howarth 1988). Stoichiometric data on nutrient export from freshwater ecosystems (e.g. Tables 2 and 4; Figure 7) as well as direct experimental evidence (Teixeira & Tundisi 1981; Downing et al. 1999) suggest that N limitation may also be general in tropical coastal ecosystems. There is now increasing evidence, however, that P may be a key nutrient limiting the primary productivity of some tropical marine ecosystems, particularly in carbonate dominated sediment environments (Corredor et al., this volume; reef settings in Figure 9), or in the open tropical ocean (Downing 1997). As is the case in temperate coastal systems, it is important that the role of nutrient limitation be described relative to specific types of primary producers. In the tropics, it is clear that P rather than N can limit primary productivity of mangrove (Feller 1995) and seagrass (Short et al. 1985) communities. In addition, tropical planktonic and macroalgae communities can be limited by P availability in at least some oligotrophic reef environments (Fourqurean et al. 1993). The relative importance of P biogeochemistry to carbon dynamics and new production of tropical marine ecosystems has been proposed from stoichiometric studies of coastal systems in Hawaii (Smith 1984). These studies provide a systems-level understanding of how productivity will respond to eutrophication of shallow reef environments (D'Elia & Wiebe 1990). As in tropical freshwaters, the impact of N loading on marine environments strongly depends upon shifts in the stoichiometry of the nutrient supply.

There is little information to indicate how the diverse types of coastal environments in Figure 9 will respond to N enrichment. It is clear that tropical marine systems with calcareous sediments can be P-limited when nutrient fluxes are low. These systems are sensitive to eutrophication, which could cause a shift to N control of production if the P immobilization capacity of calcareous environments is compromised, or there is an eventual shift to light limitation. If N loading increases to P-limited systems without alterations in the P load, they will become more severely P-limited, and algal C:P will increase, eventually influencing seston quality. If changes in P rise more

rapidly than N loading, as expected (see above and Figure 5), it is likely that P limitation will be replaced by N limitation, even in calcareous tropical marine ecosystems. There is a critical need for information on the biogeochemistry of C, N, and P in coastal ecosystems of the tropics, particularly in reaction to shifts in N:P ratios as a result of internal nutrient regeneration processes (see similar needs in lakes, above). The conceptual framework proposed here suggests that these patterns of biogeochemistry and susceptibility to N loading will vary depending on the geophysical and geomorphological characteristics of the coastal landscape.

Evidence of the effects of anthropogenic nutrients on coastal tropical ecosystems

Tropical coastal planktonic communities are most frequently nitrogen or light limited, and the impact of natural river exported nutrients (low in N:P) will eventually extend far beyond the river mouth. The seasonal influence of tropical rivers such as the Orinoco and Amazon has been shown to extend throughout the Eastern Caribbean Basin (Yoshioka et al. 1985). Recent evidence suggests that tropical river-borne nutrients are carried great distances because they are complexed with dissolved organic matter, and these complexes only slowly degrade by UV and bacterial activity (Bonilla et al. 1993; Carlsson et al. 1993; Moran & Hodson 1994). Although there is some controversy concerning the relative roles of N and P in limiting marine plankton production (Downing 1997; Downing et al. 1999; Howarth 1988; Smith 1984; Vitousek & Howarth 1991), the predominance of nitrogen fixing cyanobacteria in nutrient depleted oceanic waters (Carpenter 1983; Margalef 1971) and the preferential uptake of nitrogen by phytoplankton when nutrient limitation is relieved through upwelling (Corredor 1979) suggest that N is the most frequently limiting nutrient in the Caribbean and tropical Atlantic planktonic systems. Further evidence of current N limitation in the tropics is supplied by the high rates of N limitation seen in coastal waters (Diaz et al. 1990), and the strong responses of cyanobacteria to inorganic N enrichment (Corredor et al. 1994).

Human activities in the tropics have already begun to cause large imbalances in the marine coastal nitrogen cycle. Anthropogenic nutrient inputs due to increased fertilizer use, land development, soil erosion and sewage discharges have brought about rapid changes in algal communities. Filamentous cyanobacteria and chlorophytes have begun to dominate the phytobenthos in many places. The filamentous cyanophyte *Microcoleus lyngbyaceus* has now formed monospecific mats over the shallow benthos around Puerto Rico, in response to anthropogenic eutrophication (Corredor et al. 1994; Diaz et

al. 1990). These mats have displaced the normal benthic community and depleted dissolved oxygen. Fleshy green algae can rapidly overgrow corals in response to anthropogenic nutrient inputs, as shown for Hawaiian reefs (Smith 1984). While excessive proliferation of these species has not been documented in marine waters of the American tropics, other algae (e.g. the calcareous green alga *Halimeda*) have shown rapid growth (Corredor, unpublished). Increased inputs of nutrients to tropical systems are already leading to large changes in these communities.

Although coastal denitrification significantly buffers the impact of increased nitrogen loading in the temperate zone (Seitzinger 1988), nitrification in tropical marine systems may be more severely constrained by relatively low oxygen concentrations of warm waters, especially those with active microbial floras typical of polluted coastal zones. Denitrification rates in mangrove ecosystems are controversial (Corredor & Morell 1994; Rivera-Monroy & Twilley 1996). Nitrogen delivered to the tropical marine ecosystem, therefore, will probably persist longer and thereby have a greater impact than in temperate marine ecosystems.

Overview of hypotheses and needs for future research

The preceding overview and comparisons suggest that differences in background nutrient environments between tropical and temperate systems will lead to greater impacts of human population growth and agricultural and industrial development on tropical aquatic ecosystems. Tropical freshwater systems are more frequently N-limited than temperate zones, while tropical marine systems may be more frequently P-limited than comparable areas in temperate zones. This means that disturbances to pristine tropical lands will likely lead to greatly increased primary production in freshwaters, an expansion of the high production, N- and light-limited zones around river deltas, and a switch from P- to N-limitation with large changes in the community composition of fragile mangrove and reef ecosystems.

This review was assembled using as much empirical data on tropical nutrient cycles as we could find, but many facets of this issue will only be resolved by filling in critical gaps in existing knowledge. Although it is clear from existing evidence that N loss rates are higher from undisturbed tropical ecosystems than their temperate counterparts, it is unclear why these N-export rates are so high or how these N-loss mechanisms will react to altered landuse. Under pristine conditions, even modeled atmospheric N-deposition is calculated to be higher in the tropics than temperate zones, but we currently have little solid data on how atmospheric N-deposition might react to disturbance or how expected increases in $NO_x:NH_y$ will impact denitrification or

river transport of atmospheric N. Research on the mechanisms of nutrient transport and atmospheric deposition in the tropics is vital to understanding the probable impacts of land-use disturbance.

We have used a conceptual model built from tropical and temperate geochemical experience to project a trajectory of change in aquatic N concentrations and N:P stoichiometry as land-use is altered in the tropics. Although we think it likely that tropical ecosystems will follow this trajectory, the N-flux and N:P database is quite thin and needs field testing. Critical questions concern shielding tropical aquatic systems from excess nutrient, sediment, and nutrient loads through the use of riparian buffers and other management practices throughout the phases of deforestation, burning and agricultural development. The proper management of reservoirs and water-management projects offer a potentially important means of controlling nutrient loads, thus research is needed to examine characteristics of the growing number of tropical impoundments that might lead to more effective nutrient retention and lowered downstream impacts on freshwater and marine ecosystems. Research is needed to evaluate ways to buffer the major changes in nitrogen export that can be expected from large-scale disturbance and development of tropical lands.

We strongly emphasize the need for research that recognizes the impact of altered nutrient stoichiometry on tropical aquatic ecosystem function. Although it appears that N limitation of freshwater systems is more prevalent in the tropics than temperate zones, research on the prevalence and mechanism of N limitation in tropical ecosystems is needed to understand how freshwater production and community structure will be altered by land-use changes. The database on N and P cycling in tropical freshwater lakes, ponds and rivers is particularly incomplete, and we need a fuller understanding of the mechanisms coupling or uncoupling the fluxes of N, P and other major nutrients from disturbed tropical ecosystems. Relationships between tropical aquatic community structure and nutrient stoichiometry must be worked out, especially to predict how noxious algal species are impacted by altered stoichiometry and nutrient supply. The potential destabilization of trophic interactions by altered nutrient ratios suggests that research is needed to determine the optimal N and P needs of key components of tropical aquatic food webs.

The tropics contain a large variety of marine ecosystems that vary in nutrient limitation from P-limited mangroves and reefs to N-limited coastal zones to deltaic receiving waters limited by light penetration through turbid waters. Prediction of the impact of altered nutrient flux requires a better understanding of how light, N and P limitation combine to determine rates of production and community structure in tropical marine littoral, benthic, and planktonic

ecosystems. Disruption of land-use patterns will clearly alter nutrient availability to the marine environment, but it is important to determine how light and nutrients might interact to alter large-scale patterns in marine production. Impacts of changing ratios of nutrient supply on calcareous tropical marine communities (e.g. reefs) are particularly poorly understood, thus prediction of tropical marine impacts requires knowledge of the mechanisms through which nutrient stoichiometry influences marine nutrient limitation.

Land-use changes have greatly altered temperate nutrient cycles, and similar land-use changes are occurring at a rapid rate in the tropics. The current base of biogeochemical data suggests that alterations in the N-cycle will have greater impacts on tropical ecosystems than those already seen in temperate zones. As tropical development proceeds, the research outlined above could go far toward protecting tropical aquatic ecosystems from the problems experienced in the temperate zone as a result of anthropogenic enhancement of nutrient flux.

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