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# DEFORESTATION FOR PASTURE ALTERS NITROGEN AND PHOSPHORUS IN SMALL AMAZONIAN STREAMS

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*Abstract.* The clearing of moist, lowland tropical forest for cattle pasture represents a widespread land use change that has consequences for soil biogeochemical cycles, as well as the links between soil processes and the concentrations of dissolved and particulate materials in rivers and streams. We examined how conversion of tropical forest to actively grazed cattle pasture in the Brazilian Amazon influenced the concentrations of different forms of nitrogen (N) and phosphorus (P) in soil solution and stream water. We compared two pairs of watersheds containing second-order streams that drained land in either forest or pasture at Fazenda Nova Vida, a cattle ranch in central Rondônia. Measurements were made during the dry season (low flows) and the wet season (high flows). Forest soil solution had higher $NO_3^-$ concentrations than pasture, but similar concentrations of $NH_4^+$ and $PO_4^{3-}$. Higher solution $NO_3^-$ led to higher ratios of dissolved inorganic N:P in forest soils. Pasture streams had higher concentrations of total suspended solids, particulate organic carbon (POC), and particulate organic N (PON) during the dry season, but not during the wet season. Pasture streams also had lower concentrations of $NO_3^-$ than forest streams. This was consistent with previous studies that found lower extractable $NO_3^-$ concentrations and lower rates of net N mineralization and net nitrification in the soils of the pasture watersheds compared with forest watersheds. Dissolved organic N (DON) dominated stream water dissolved-N concentrations in forest (53–76%) and pasture (67–84%). Higher dissolved inorganic N (DIN) concentrations in forest streams coupled with a trend toward higher DON and PON concentrations in pastures led to small differences in total N (TN) concentrations between land uses. Lower ratios of inorganic and total dissolved N:P in pasture streams suggested a switch from P limitation in forest streams to N limitation in pasture streams. Periphyton bioassays in forest and pasture streams confirmed that N limited algal growth in pasture streams where light was available. These results suggest that links among deforestation, soil biogeochemistry, and the stoichiometry of N and P reaching streams in small watersheds have the potential to influence the structure of these aquatic ecosystems.

*Key words: agriculture; Amazon; biogeochemistry; Brazil; deforestation; nitrogen; nutrient limitation; phosphorus; Rondônia; streams, tropical.*

## INTRODUCTION

Human-induced changes in land use, such as the clearing of forest, can substantially alter the chemical environment of small streams and the amount, chemical form, and timing of materials delivered to streams from adjacent terrestrial ecosystems. These changes may in turn influence the function of streams as habitat for a variety of aquatic organisms. The alterations to stream characteristics and nutrient regimes that follow land use change are also likely to have important influences on primary production and inputs of organic material that control stream trophic dynamics.

Forest clearing for agriculture has a number of direct influences on stream function. The removal of forest vegetation can change stream structure, the amount of sunlight reaching the stream surface, and stream water

temperature (Hill and Harvey 1990, Sweeney 1992). Deforestation can change soil biogeochemical processes and increase the amounts of particulate and dissolved material exported in stream water (Likens et al. 1970, Williams et al. 1997). The percentage of agricultural land in watersheds is also correlated with concentrations of dissolved nutrients in stream water (Dillon and Kirchner 1975, Smart et al. 1985, Jordan et al. 1997). Shifts in the relative abundance of these nutrients reaching aquatic ecosystems from land can alter the timing and magnitude of algal production (Fisher et al. 1992, Justic et al. 1995).

In the middle of the 20th century, tropical regions replaced the temperate zone as the region of the earth experiencing the greatest rate of forest conversion to new agricultural lands (Houghton 1994). The Amazon contains $\sim 5 \times 10^6$ km$^2$ of closed canopy moist forest (Skole and Tucker 1993) and $\sim 10^7$ km of river and stream channels (Junk and Furch 1985). Deforestation in the Brazilian portion of the Amazon from 1978 through the late 1998 ranged from $\sim 11\,000$ to $\sim 29\,000$

km²/yr (Instituto Nacional de Pesquisas Espaciais 1999), with cattle pasture comprising the largest single use of deforested lands (Fearnside 1987, Serrão 1992). Alterations to biogeochemical cycles in Amazonian watersheds as a result of this activity may have greater effects on freshwaters compared with temperate systems because of the high mobility of N following disturbance and the greater frequency of N limitation in the tropics (Downing et al. 1999). Despite the very large area over which forest clearing is now taking place in the Amazon, we know relatively little about the consequences of this change for biogeochemistry of the small streams that make up the majority of the total length of stream channels in the world's largest river basin.

In this study, we compare the concentrations of dissolved inorganic and organic forms of N and P in two pairs of second-order streams that drain either forest or pasture. We examine how stream particulate and solute concentrations are related to changes in soil biogeochemistry and soil solution that follow deforestation for pasture. With a series of algal bioassay experiments, we also discuss our tests of how changes in the relative abundance of N and P in stream water control production of stream periphyton.

## METHODS AND SITE DESCRIPTION

### Study area

We studied two pairs of small watersheds (~10 km²) at Fazenda Nova Vida, a large cattle ranch 50 km from the city of Ariquemes (10°30′ S, 62°30′ W) in central Rondônia (Plate 1). Terrain was gently rolling, with low-gradient, second-order, clear-water streams draining the basins. These streams generally remained flowing through all but the severest dry periods. One drainage basin in each pair was cleared for pasture in 1989; the other basin in each pair remained predominantly forested. These basins lie at 200–500 m elevation in a region generally underlain by Precambrian granitic rock (Projeto RADAMBRASIL 1978). The climate of central Rondônia is humid tropical. Mean annual relative humidity is 89%, mean daily temperature is 25.6°C, and mean daily temperature for the warmest and coolest months varies <5°C (Bastos and Diniz 1982). Rainfall averages 2.2 m/yr with a distinct dry season during June–October and a rainy season stretching November–May (Fig. 1). Rainfall averages >300 mm/mo in the wettest four months (December–March) and <40 mm/mo during the driest three months (June–August) (Bastos and Diniz 1982; H. Schmitz, unpublished data).

Forest in the cleared basins was converted directly to pasture by cutting, burning, and planting pasture grasses in the same year. Brush was cut in March, large trees were felled in June or July, slash was burned in late August or September, and the pasture grass *Brachiara brizantha* [Hochst] Stapf was seeded during De-

cember or January. The pastures were burned again in September 1992 to kill the regrowth of weeds and stump sprouts and to reduce the volume of dead wood. Pastures were not cultivated, nor were they amended with fertilizer or lime. Pastures were actively grazed beginning approximately one year after forest clearing and stocked throughout this study at ~1–1.5 animals/ha. This is typical management of extensive pastures on large cattle ranches in the region.

Native vegetation in the forested basins is classified as moist open tropical forest and consists of perennially evergreen broadleaf trees with a high number of palms (Pires and Prance 1986). Selective logging in the forests removed ~3–4 trees/ha during 1987–1990. Forest streams were shaded by a tree canopy (Plate 2), and forest stream channels contained unvegetated sandy point bars. Pasture stream channels were bordered by uplands planted to *B. brizantha* and had only scattered trees in the riparian zone (Plate 2). Pasture stream channels typically contained wetland grasses (*Paspalum* spp.), which sometimes forms floating mats that covered most of the stream channel.

Soil characteristics and soil N and P stocks and dynamics have been previously examined in these basins (Neill et al. 1995, Moraes et al. 1996, Garcia-Montiel et al. 2000). These basins are equivalent to the pastures cleared in 1989 in chronosequences 1 and 2 in these studies. Soils are well-drained Kandiudults and Paleudults (red-yellow podzolic latosols in the Brazilian classification). These and generally similar soils cover ~22% of the Brazilian Amazon (Moraes et al. 1995). Forest clearing for pasture at Nova Vida increases bulk density, total carbon and nitrogen concentrations, pH, effective cation exchange capacity, exchangeable base cations, and base saturation; and it decreases exchangeable aluminum (Moraes et al. 1996). Conversion of forest to pasture in these watersheds lowers soil $NO_3^-$ concentrations and rates of soil net N mineralization and net nitrification (Neill et al. 1995) and this occurs across Rondônia on a variety of soil types (Neill et al. 1997). At Nova Vida, soil $NO_3^-$ concentrations and net mineralization and nitrification rates decline with increasing pasture age (Neill et al. 1995). Clearing increases soil available P (resin and bicarbonate extractable forms) for a period of ~10 yr, after which the dominant change to the distribution of P among different soil fractions is an increase in organic P in pastures compared with the original forest (Garcia-Montiel et al. 2000).

### Field and laboratory analyses

Soil solution was collected from tension lysimeters (Soil Moisture Equipment, Goleta, California, USA) placed in the upland (terra firme) of the forest and pasture watersheds of Pair 1. These sites represented the uplands in each basin and were adjacent to soil collections. Five lysimeters were installed at 30 cm and at 100 cm at each site in September 1996. Water was
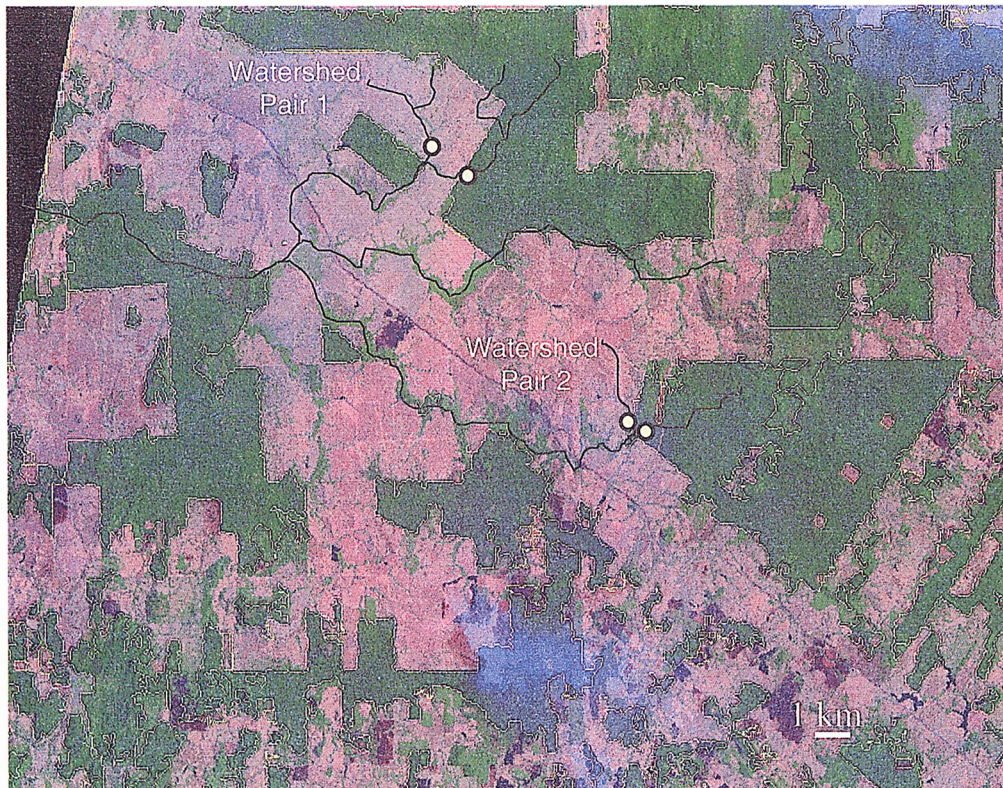
## Watershed Pair 1   Watershed Pair 2



PLATE 1 (top panel)   Landsat thematic mapper image of Nova Vida ranch in 1998 showing the paired watersheds and sampling locations. Forest is indicated by dark green areas, pasture by pink. Points sampled are indicated by the yellow dots. The image covers a 32 × 24 km area.

PLATE 2 (bottom four panels).   Photos of (top) forest and (bottom) pasture streams at Nova Vida. Flow in all cases represented nonstorm conditions during the wet season.
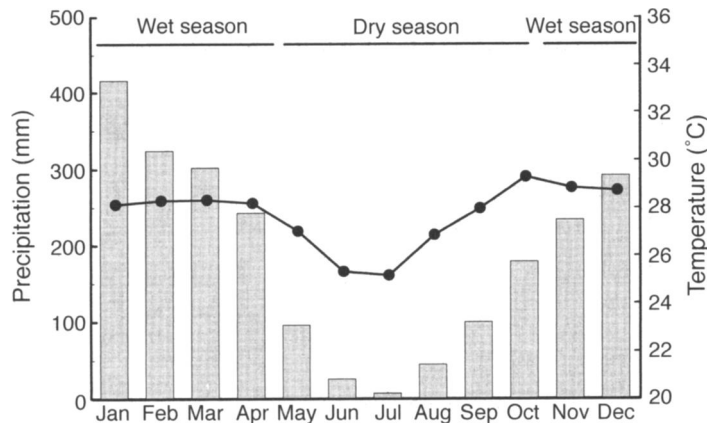
FIG. 1. Mean daily temperature (line) and mean monthly precipitation (bars) for 1984–1998, recorded at Fazenda Rancho Grande, ~20 km from Nova Vida (data provided by H. Schmitz).

collected from the lysimeters on four dates during the rainy seasons, twice in February 1997 and twice in March 1998. Samples were collected by placing a vacuum on the lysimeter and collecting water 24–48 h later. Collection was attempted in the dry seasons of 1997 and 1998, but lysimeters rarely contained enough water for analysis even after 5–7 d with a vacuum. Samples from the lysimeters were transferred to acid-washed polyethylene bottles, acidified to pH < 2 with HCl, and stored refrigerated.

We established permanent sampling points in the four streams for collection of water samples (Plate 1). We also measured instantaneous discharge and logged stream pH, specific conductance, temperature, and dissolved oxygen to characterize stream characteristics. We sampled within 1994–1998, during periods that spanned the wet and dry seasons (24 April–5 May and 8 September–23 October 1994, 5 February and 26 September 1996, 21 February–6 March 1997, 13 September–3 October 1997, 4–26 March 1997, 29 August–24 September 1998). Discharge was determined from cross-sectional area and flow rate several times during each sampling in 1997–1998 (Gore 1996). Flows were

measured at a minimum of 10 points across the stream channel with a hand-held FP-201 mechanical propeller type flow meter (Global Water Instrumentation, Gold River, California, USA). Water temperature was logged in each stream every two hours for one year with an Onset tid-bit temperature logger (Onset Computer, Pocasset, Massachusetts, USA). For several days during the wet and dry seasons during 1997 and 1998, pH, specific conductance, and dissolved oxygen were logged at each site with a YSI 600XL multi-parameter sonde (YSI, Yellow Springs, Ohio, USA). The sonde was moved among the four streams.

Stream discharges varied both seasonally and with individual rains (Table 1). We recorded zero discharge in the forest stream of watershed pair 2 on two occasions after extended rainless periods in the dry season. We recorded pH levels of 5.8–6.8 in all streams (Table 1). Specific conductance was 0.03–0.13 mS/cm in both of the forest and pasture streams during the wet season and was 0.05–0.11 mS/cm in the forest streams and 0.12–0.33 mS/cm in the pasture streams during the dry season (Table 1). Dissolved oxygen concentrations were higher in the forest streams (5.2–7.3 mg/L) com-

TABLE 1. Characteristics of forest and pasture streams at Nova Vida, measured during wet and dry seasons.

| Land use | Season | Base flows (L/s) | Storm flows (L/s) | pH | Specific conductance (mS/cm) | Dissolved oxygen (mg/L) | Mean daily temperature† (°C) |
|---|---|---|---|---|---|---|---|
| Watershed pair 1 | | | | | | | |
| forest | dry | 12–22 | 44–100 | 6.7–6.8 | 0.05–0.11 | 5.2–5.6 | 24.3 (0.09) |
| forest | wet | 713–740 | 1035–8030 | 6.3–6.3 | 0.03–0.03 | 5.8–6.2 | 25.6 (0.04) |
| pasture | dry | 14–23 | 24–40 | 6.7–6.7 | 0.26–0.33 | 0.1–0.2 | 24.6 (0.10) |
| pasture | wet | 157–193 | 297–1540 | 6.0–6.5 | 0.05–0.14 | 0.1–0.4 | 26.6 (0.06) |
| Watershed pair 2 | | | | | | | |
| forest | dry | 5–6 | 6–9 | 5.9–6.5 | 0.05–0.08 | 4.6–5.7 | 23.5 (0.11) |
| forest | wet | 36–90 | 151–1080 | 6.4–6.4 | 0.06–0.06 | 7.0–7.3 | 25.0 (0.04) |
| pasture | dry | 8–12 | 17–24 | 5 8–6.0 | 0.12–0.16 | 0.2–1.4 | 24.4 (0.10) |
| pasture | wet | 115–133 | 144–680 | 6.2 | 0.05–0.08 | 0.1–1.9 | 26.1 (0.05) |

*Note:* Shown are the ranges of values encountered during 1994–1998 except temperature, which is the mean of values collected every 2 h from August 1997 to August 1998.

† 1 SE appears in parentheses.

pared with pasture streams (0.1–1.9 mg/L) (Table 1). Mean daily temperatures differed by $\leq 1.1°C$ between forest and pasture streams in each watershed pair (Table 1).

The number of samples collected from each stream during each sampling period ranged from 1–13. In the field, duplicate stream water samples were filtered immediately through ashed and prerinsed Whatman GFF glass fiber filters (0.45-$\mu$ nominal pore size; Whatman, Clifton, New Jersey, USA) into acid washed polyethylene bottles and placed on ice. One 50-mL sample was acidified to pH < 2 with 1.0 mL of 6 m/L HCl solution and stored refrigerated. This sample was used for analysis of $NH_4^+$, $NO_3^-$, $PO_4^{3-}$, and total dissolved P. The unacidified sample was used to determine total dissolved N. Also in the field, ~500 mL of stream water was passed through an ashed 47-mm GFC filter for chlorophyll $a$ analysis. The filter was wrapped in foil, placed in a small Ziploc bag, put immediately on ice, and frozen the same day upon return to the field lab. One additional 1-L sample was collected and stored on ice for determination of total suspended solids (TSS) and filtration for particulate organic C (POC) and particulate organic N (PON) the same day in the field laboratory. Acidified samples for $NH_4^+$, $NO_3^-$, and $PO_4^{3-}$ were analyzed within one month; samples for total N and P were analyzed within 3–4 mo.

Ammonium ($NH_4^+$) in acidified water samples collected in 1994–1997 from lysimeters and streams was analyzed colorimetrically on an Alpkem RFA autoanalyzer (OI Analytical, College Station, Texas, USA) by the phenol–hypochlorite method (Alpkem Method No. A303-S020). Ammonium standards were prepared in a deionized water matrix to match the pH of the samples. Samples from 1998 were analyzed on the frozen, nonacidified samples using standards in deionized water. Laboratory tests on samples showed the two methods gave identical results. Nitrate was analyzed colorimetrically by cadmium reduction to $NO_2^-$ on an Alpkem RFA autoanalyzer (Alpkem Method No. A303-S171). Soluble reactive phosphate was measured colorimetrically on an Alpkem RFA autoanalyzer (Method No. A303-S200). Detection limits were <0.05 $\mu$mol/L for $NH_4^+$ and $NO_3^-$ and 0.01 $\mu$mol/L for $PO_4^{3-}$. Analyses were periodically checked against matrix blanks and quality control standards (SPEX Certiprep, Metuchen, New Jersey, USA). Reduction efficiency of the Cd column was checked by placing $NO_3^-$ and $NO_2^-$ standards of the same concentration at the beginning and end of each run. Sample storage time was less than two months.

Total dissolved N (TDN) was measured by alkaline digestion with persulfate. Digestion efficiencies were tested using reference standards of nitrophenol and a standard reference material (SPEX Certiprep). Digestions were run with persulfate and NaOH blanks. Total dissolved P (TDP) was measured by digestion with sulfuric acid and persulfate (Koroleff 1983). Digestions

were run with acid and persulfate blanks and efficiencies were checked by digestion of reference standards of ATP (SPEX Certiprep). Dissolved organic N was calculated as the difference between TDN and dissolved inorganic N. Dissolved organic P (DOP) was calculated as the difference between TDP and soluble reactive P. For both TSS and POC/PON, water was filtered through an ashed GFF filter (preweighed for TSS) until the filter clogged (typically 70–200 mL). Filters were allowed to air dry, then dried in an oven at 60°C. Particulate organic C and PON were determined by combustion of the filters in a Perkin Elmer 2400 elemental analyzer (Perkin Elmer, Wellesley, Massachusetts, USA).

Ceramic disk nutrient-diffusing bioassays to determine N or P limitation of stream periphyton (Gibeau and Miller 1989) were conducted during April 1994–September 1998, during both wet and dry seasons. Bioassay disks were made from 2.5 cm-diameter ceramic disks (LECO, Saint Joseph, Michigan, USA) fused to 40-mL plastic vials to which we added 2% agar containing four treatments: control (no addition), added phosphorus ($KH_2PO_4$ at 0.5 mol/L), added nitrogen ($NH_4Cl$ at 0.5 mol/L) and added nitrogen + phosphorus (ratio of 0.5 mol/L $NH_4Cl$ and 0.05 mol/L $KH_2PO_4$). Six disks of each treatment were placed in each stream for 8 d at ~20 cm water depth. Disks were collected and placed directly in the freezer. Chlorophyll $a$ on both the ceramic disks and the filters from the stream water collections was analyzed by extracting with 90% acetone for 24 h and reading on a fluorometer. Light levels (400–1100 nm) in the forest and pasture streams during the deployment of the bioassays during 1998 were measured using Onset Hobo LI loggers.

### Data analysis

Streams and lysimeters were sampled without true replication, because we collected only one sample from each stream each time it was visited. We treated samples collected from the same stream or lysimeter within wet or dry seasons as replicates. Differences between forest and pasture streams and between wet and dry seasons were tested using Bonferroni $t$ tests. Data on particulate and solute concentrations were tested for normality using the Univariate procedure of SAS (SAS Institute 1985) and transformed by $\ln(x + 1)$ to approximate a normal distribution. Chlorophyll concentrations from the bioassays were analyzed by analysis of variance after the same transformation. Watershed pair (1 or 2), land use (forest or pasture), and nutrient treatment (control, added P, added N, added N + P) were main effects in the model. Interactions of watershed pair by land use, watershed pair by nutrient treatment, land use by nutrient treatment and the three-way interaction among all main effects were also included.

### RESULTS

#### Soil solution

Soil solution $NH_4^+$ concentrations were similar in forest and pasture watersheds (Table 2). Solution $NO_3^-$

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TABLE 2. Concentrations of dissolved nitrogen and phosphorus in soil solution collected from lysimeters at 30 and 100 cm depth.

| Variable | Depth = 30 cm | | Depth = 100 cm | |
|---|---|---|---|---|
| | Forest | Pasture | Forest | Pasture |
| $NH_4^+$ ($\mu$mol/L) | 2.8 ± 1.6[a] (15) | 4.6 ± 2.5[a] (15) | 7.3 ± 2.4[a] (17) | 7.6 ± 5.1[a] (14) |
| $NO_3^-$ ($\mu$mol/L) | 111.2 ± 21.7[a] (15) | 3.3 ± 1.0[b] (15) | 144.3 ± 34.4[a] (17) | 2.6 ± 1.0[b] (14) |
| $PO_4^{3-}$ ($\mu$mol/L) | 0.64 ± 0.26[a] (15) | 0.87 ± 0.25[ab] (15) | 2.69 ± 0.81[b] (17) | 0.63 ± 0.23[a] (14) |
| DIN:DIP ratio | 475 ± 105[a] (15) | 10 ± 2[b] (15) | 157 ± 58[c] (17) | 26 ± 14[b] (14) |
| DON ($\mu$mol/L) | 68.2 ± 13.1[a] (7) | 33.4 ± 15.8[a] (6) | 72.3 ± 12.0[a] (4) | 32.4 ± 12.7[a] (5) |
| DOP ($\mu$mol/L) | 0.21 ± 0.04[a] (6) | 0.47 ± 0.10[ab] (3) | 1.25 ± 0.22[b] (5) | 0.42 ± 0.27[a] (4) |
| TDN:TDP ratio | 304 ± 61[a] (6) | 60 ± 5[b] (3) | 58 ± 34[b] (4) | 131 ± 64[ab] (4) |

*Notes:* For each entry, the mean value ± 1 SE appears on the first line, with sample size on the second line in parentheses. Main entries in the same row followed by the same superscript letter are not significantly different ($P > 0.05$).

concentrations, in contrast, were greater in forest than in pasture, and mean $NO_3^-$ concentrations in forest were 20–40 times greater than $NH_4^+$ concentrations at the same locations. Soil solution $NH_4^+$ and $NO_3^-$ concentrations did not differ between 30 and 100 cm depths. Phosphate was similar in forest and pasture at 30 cm, but higher in forest at 100 cm. High soil solution $NO_3^-$ concentrations in forest led to higher ratios of dissolved inorganic N to dissolved inorganic P (DIN:DIP) compared with pasture. Dissolved organic N (DON) did not differ between forest and pasture or between depths. Dissolved organic N concentrations in the forest at 30 and 100 cm made up 41–42% of total dissolved N (TDN). In the pasture, DON dominated and made up 88% of TDN, because $NO_3^-$ concentrations were low. Soil solution dissolved organic P (DOP) concentrations were low; they did not differ between forest and pasture at 30 cm, but were higher in forest at 100 cm. Concentrations of DOP were greater at 100 cm than at 30 cm in forest.

### Stream water suspended and dissolved material

Pasture streams had higher total suspended sediments concentrations than forest streams during the dry season, but not during the wet season (Table 3). Concentrations of water column chlorophyll *a* did not differ between land uses or season. Particulate organic C (POC) and particulate organic P (PON) concentrations were higher in pasture streams during the dry season, but not different between forest and pasture streams during the wet season.

Stream water $NH_4^+$ did not differ between forest and pasture streams during either the wet or the dry seasons (Table 3). In contrast, $NO_3^-$ concentrations were greater in forest streams than in pasture streams in watershed pair 1 during the dry season, but not during the wet

season, and $NO_3^-$ concentrations were greater in the forest stream of watershed pair 2 during both seasons. Dry season concentrations of $NH_4^+$ and $NO_3^-$ were greater than wet season concentrations in both pairs of streams. Nitrate dominated inorganic N in the forest streams, but $NH_4^+$ dominated in the pasture streams. Stream water $PO_4^{3-}$ concentrations were greater in the pasture stream of watershed pair 1 during the dry season, but not the wet season, and $PO_4^{3-}$ concentrations did not differ between forest and pasture streams in watershed pair 2 during either season. Wet and dry season $PO_4^{3-}$ concentrations differed little in the forest streams of both watershed pairs, but dry season $PO_4^{3-}$ concentrations were greater in the pasture streams. The pattern of dissolved inorganic N:P ratios in forest and pasture streams was similar to the pattern for $NO_3^-$ concentrations, with higher N:P ratios in the forest streams of both watershed pairs. In watershed pair 1, stream water N:P ratios were higher in the dry season than in the wet season; in watershed pair 2, N:P ratios did not differ seasonally. Dissolved inorganic N:P ratios were always at or above the Redfield ratio of 16:1 in forest streams and below 16:1 in pasture streams.

Concentrations of DON were similar in forest and pasture streams (Table 3). Higher mean DON concentrations in pasture streams combined with higher DIN concentrations in forest streams led to forest and pasture stream TDN concentrations that were much less different than the inorganic N concentrations. In forest streams, DON made up 53–54% of TDN during the dry season and 56–76% of TDN during the wet season. In pasture streams, DON made up 67% of TDN in the dry season and 83–84% of TDN in the wet season. Dissolved organic P concentrations were generally low (<1 $\mu$mol/L). Dissolved organic P was higher in the pasture stream of watershed pair 1 during the dry sea-

TABLE 3. Concentrations of suspended and dissolved materials in forest and pasture streams at Nova Vida during the dry and wet seasons.

| | Watershed pair 1 | | | | Watershed pair 2 | | | |
| | Dry season | | Wet season | | Dry season | | Wet season | |
| Variable | Forest | Pasture | Forest | Pasture | Forest | Pasture | Forest | Pasture |
|---|---|---|---|---|---|---|---|---|
| TSS (mg/L) | 6 9 ± 1 0a (15) | 48 0 ± 7 3b (18) | 7 6 ± 1 5a (23) | 13 0 ± 2 6a (26) | 5 4 ± 1 0a (12) | 39 8 ± 7 3b (14) | 16 4 ± 1 5a (16) | 9 4 ± 2 6a (16) |
| Chl $a$ (µg/L) | 0 8 ± 0 1abc (14) | 1 3 ± 0 2ab (17) | 0 6 ± 0 1bc (25) | 0 9 ± 0 1abc (29) | 0 8 ± 0 2ac (13) | 1 4 ± 0 4a (15) | 0 4 ± 0 1c (16) | 0 5 ± 0 1c (17) |
| POC (mg/L) | 1 2 ± 0 3ac (12) | 5 7 ± 0 6b (15) | 1 0 ± 0 1ac (25) | 2 6 ± 0 5a (24) | 0 8 ± 0 1c (9) | 4 6 ± 0 3b (11) | 1 8 ± 0 6ac (14) | 2 0 ± 0 4ac (15) |
| PON (mg/L) | 0 09 ± 0 02a (12) | 0 31 ± 0 03b (15) | 0 07 ± 0 01a (21) | 0 15 ± 0 02ac (24) | 0 08 ± 0 01a (9) | 0 24 ± 0 02bc (11) | 0 14 ± 0 06ac (14) | 0 12 ± 0 02ac (15) |
| $NH_4^+$ (µmol/L) | 4 5 ± 0 6ab (15) | 11 1 ± 2 6a (17) | 1 5 ± 0 1c (24) | 1 4 ± 0 3c (28) | 4 2 ± 0 7ab (14) | 9 1 ± 3 2a (14) | 2 1 ± 0 2bc (16) | 1 7 ± 0 3c (17) |
| $NO_3^-$ (µmol/L) | 10 9 ± 1 1a (15) | 0 8 ± 0 3c (18) | 1 9 ± 0 3b (24) | 1 4 ± 0 3bc (27) | 9 0 ± 0 6a (15) | 1 4 ± 0 3bc (15) | 6 9 ± 0 5a (16) | 0 8 ± 0 2bc (17) |
| $PO_4^{3-}$ (µmol/L) | 0 22 ± 0 05a (15) | 2 17 ± 0 32b (17) | 0 17 ± 0 02a (24) | 0 63 ± 0 13acd (27) | 0 82 ± 0 26cd (15) | 1 13 ± 0 17c (13) | 0 46 ± 0 08ad (16) | 0 37 ± 0 05ad (17) |
| DIN DIP ratio† | 102 ± 15a (14) [52] | 9 ± 7c (17) [6] | 24 ± 6b (24) [23] | 6 ± 1c (26) [6] | 24 ± 3b (15) [8] | 9 ± 2c (12) [8] | 25 ± 3b (16) [27] | 8 ± 2c (17) [7] |
| DON (µmol/L) | 18 3 ± 3 7ab (12) | 35 6 ± 6 9a (14) | 11 4 ± 0 8b (23) | 16 3 ± 1 9ab (23) | 1 6 ± 1 9ab (12) | 29 8 ± 6 8ab (11) | 12 5 ± 1 2ab (13) | 13 0 ± 1 7ab (13) |
| DOP (µmol/L) | 0 44 ± 0 07a (12) | 1 11 ± 0 37b (14) | 0 38 ± 0 05a (21) | 0 31 ± 0 04a (21) | 0 39 ± 0 11a (11) | 0 49 ± 0 08ab (9) | 0.30 ± 0 06a (13) | 0 32 ± 0 08ab (13) |
| TDN TDP ratio | 53 ± 5a (12) | 17 ± 3c (14) | 33 ± 4ab (21) | 24 ± 2bc (21) | 31 ± 2ab (11) | 26 ± 7bc (9) | 35 ± 4ab (13) | 29 ± 8bc (13) |

*Notes:* For each entry, the mean value ± 1 SE appears on the first line, with sample size on the second line in parentheses. Main entries in the same row followed by the same superscript letter are not significantly different ($P > 0.05$).

† The number in brackets is the value measured during the period when bioassays were deployed.

son, but there was no clear pattern of differences between forest and pasture streams (Table 3). Dissolved organic P made up 30–60% of TDP, but there were no clear trends with season or land use. The stream water ratios of TDN:TDP were higher in the forest stream of watershed pair 1 during the dry season, but TDN:TDP



FIG. 2. The contribution of $NH_4^+$, $NO_3^-$, dissolved organic N (DON), and particulate organic N (PON) to total N concentration in forest and pasture streams. Error bars represent 95% CI for mean total N.

ratios did not differ in the wet season or in watershed pair 1 nor in either season in watershed pair 2. These ratios were much less different than the DIN:DIP ratios, where higher values in forest streams resulted from elevated $NO_3^-$ concentrations. Averaged over wet and dry seasons, total N concentrations were greater in the pasture stream of watershed pair 1, but similar in the forest and pasture streams of watershed pair 2 (Fig. 2).
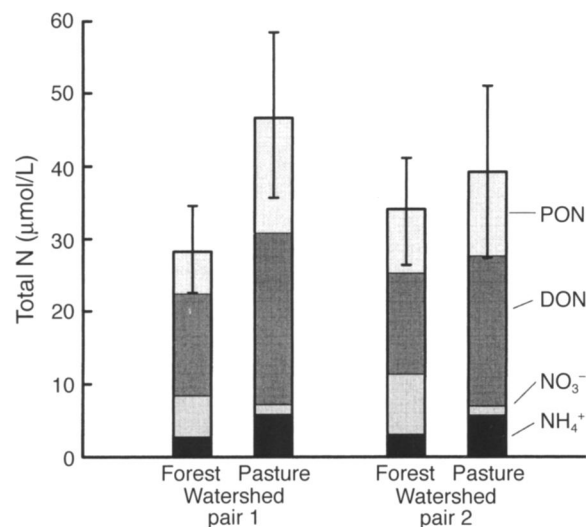
### N vs. P limitation of stream periphyton

Nitrogen and N + P increased algal growth in nutrient diffusing bioassays in pasture streams (Fig. 3). Algal growth did not respond to added N or P in the forest streams. Mean daily light levels were greater in the open pasture streams (44–81 lm/m² in forest vs. 1667–3406 lm/m² in pasture). The mean DIN:DIP ratios in forest and pasture streams during the deployment of the bioassays were similar to the ratios measured during the entire stream water sampling period (Table 3) and showed the same pattern of ratios above the 16:1 in forest and below 16:1 in pasture. These results indicated that algal growth was limited by light under the closed canopy of the forest and by N in the open canopy of the pasture. Algal growth was greater in the pasture of watershed pair 1, and the effect of watershed pair was significant ($F_{3,505} = 5.39$, $P < 0.0001$). Interactions of watershed pair × land use ($F_{1,505} = 11.52$, $P = 0.001$) and land use × nutrient treatment ($F_{3,505} = 4.73$, $P = 0.003$) were also significant.
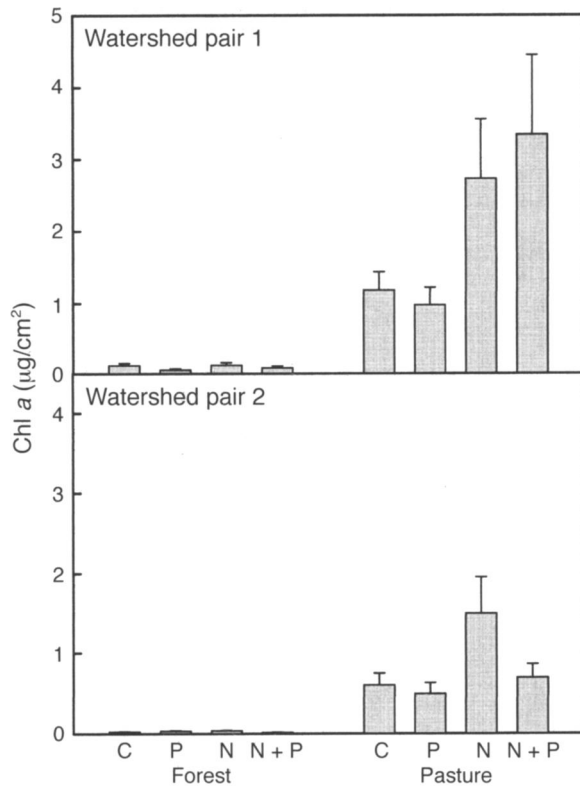
FIG. 3. Results of diffusing disk periphyton bioassays in forest and pasture streams. Nutrient addition treatments are: C (control, no addition), N (nitrogen), P (phosphorus), and N + P (nitrogen plus phosphorus). Chlorophyll a (Chl a) was measured as µg Chl a/cm² of ceramic disk surface. Significant effects were watershed pair (df = 1, 505; $F$ = 27.64; $P$ < 0 0001), land use (df = 1, 505; $F$ = 186.27; $P$ < 0.0001), nutrient treatment (df = 3, 505; $F$ = 5.39; $P$ = 0.001), watershed pair × land use (df = 1, 505; $F$ = 11.52; $P$ = 0.001), and land use × nutrient treatment (df = 3, 505; $F$ = 4.73; $P$ = 0.003).

## DISCUSSION

### Soil solution and stream water N and P

Soil solution and stream water concentrations suggest that high $NO_3^-$ production in forest soils leads to high $NO_3^-$ in forest soil solution and stream water, whereas lower $NO_3^-$ production in pasture soils results in lower $NO_3^-$ in pasture soil solution and stream water. The differences between forest and pasture were most pronounced during dry periods when dilution is less and when soil–water contact is greatest. The high soil solution $NO_3^-$ concentrations in forest were consistent with higher soil extractable $NO_3^-$ concentrations and higher rates of net N mineralization and net nitrification in tropical forest soils (Neill et al. 1995, Verchot et al. 1999). In pastures, lower soil extractable and solution $NO_3^-$ concentrations appeared to be most closely related to a decline in net N mineralization and net nitrification rates in pasture soils (Neill et al. 1995). High $NO_3^-$ concentrations are characteristic of soil water ter-

ra firme soils of intact moist tropical forests. The concentrations we measured were higher than the 20–50 µmol/L measured in Puerto Rico (McDowell et al. 1992) and Amazonia (McClain et al. 1994, Brandes et al. 1996), but the pattern of much higher concentrations of $NO_3^-$ relative to $NH_4^+$ was similar.

Our forest stream $NO_3^-$ concentrations were similar to those reported for forested catchments in the central Amazon (Lesack 1993, Williams and Melack 1997) and other lowland tropical catchments (Stoorvogel et al. 1997), but lower than for tropical montaine watersheds (McDowell and Asbury 1994). Forest stream $NO_3^-$ concentrations were approximately an order of magnitude lower than reported for temperate deciduous forest (Likens et al. 1977, Swank and Crossley 1988), but higher than reported for old growth temperate forests (Sollins et al. 1980, Hedin et al. 1995). Mean pasture stream $NO_3^-$ concentration (1.4 µmol/L) was lower than a catchment partially deforested for slash-and-burn agriculture (Williams et al. 1997). Ammonium concentrations from the forest and pasture streams were higher than reported for other forested tropical catchments (Lesack 1993, McDowell and Asbury 1994, Williams and Melack 1997).

Low soil solution $PO_4^{3-}$ concentrations in soil solution and the absence of any differences between forest and pasture soils indicated that $PO_4^{3-}$ leaching was minimal. This occurred despite elevated available P in surface soils (resin and bicarbonate extractable) at Nova Vida for a period of ~10 yr (Garcia-Montiel et al. 2000). This is consistent with the capacity of these highly weathered soils to fix available P in the form of Fe and Al sesquioxides (Uehara and Gillman 1981). The higher $PO_4^{3-}$ concentrations in pasture streams during the dry season probably resulted from increased dissolution of iron phosphates in pasture streams associated with anoxic conditions (S. Thomas, unpublished data), rather than P delivery in incoming shallow groundwater. Although $PO_4^{3-}$ leaching can occur in some agricultural settings under very high P loading (Vighi et al. 1991), this was unlikely in these pastures, because biomass burning represented the sole source of P input (Garcia-Montiel et al. 2000). While rock phosphate is used increasingly for reformation of Amazonian pastures in some areas (Nepstad et al. 1991), its use is still uncommon in Rondônia and it was not used in these watersheds.

Lower $NO_3^-$ concentrations in streams draining pastures differs from the common pattern in the temperate zone where streams draining crop and pasture lands typically have higher $NO_3^-$ concentrations than streams draining forested regions (Omernik 1977, Smart et al. 1985, Jordan et al. 1997). Nitrate runoff from watersheds in pasture is generally lower than from cropland, but still higher than from watersheds dominated by forest (Correll et al. 1992, Jordan et al. 1997). Several factors may contribute to differences in $NO_3^-$ runoff between temperate and tropical regions. Because crop-

land often receives much higher N inputs and contributes greater $NO_3^-$ to streams than pastures (Jordan et al. 1997), even small amounts of cropland can influence watershed $NO_3^-$ concentrations. But cropland currently makes up <3% of agricultural land in Rondônia (Instituto Brasileiro de Geografia e Estatística 1996) and none in our watersheds. At larger scales, the conclusion that native tropical forest is less retentive of inorganic N than temperate forest is supported by a pattern of greater inorganic N export in forested tropical rivers compared with temperate rivers of comparable runoff and land use (Howarth et al. 1996, Lewis et al. 1999).

In the forest, high concentrations of $NO_3^-$ and low concentrations of $PO_4^{3-}$ in soil solution support the interpretation that vegetation growing on the highly weathered soils of the Amazon is P- or Ca-limited but not N-limited, and that these ecosystems may be susceptible to gaseous N losses or N movement through soil solution to streams (Vitousek and Sanford 1986, Verchot et al. 1999). This differs substantially from the pattern in most temperate forest soils where plant growth is almost exclusively limited by N and where solution $NO_3^-$ concentrations, in the absence of relatively severe disturbance, are low (Sollins and Mc-Corison 1981, Hedin et al. 1995). While temperate forests differ widely in the importance of nitrification and the extent to which inorganic N cycles primarily through $NH_4^+$ or $NO_3^-$, high nitrification and high soil solution $NO_3^-$ concentrations appeared to be the common pattern in these Rondônia tropical forests. In this respect, they more closely resemble patterns in temperate forests that have been "saturated" with chronic anthropogenic inorganic N inputs, where nitrification, $NO_3^-$ pools and soil solution losses occur (Aber et al. 1989).

Dissolved organic N is increasingly recognized as an important component of the total N that moves through soil and into soil solution (Hedin et al. 1995). Dissolved organic N made up 41–42% of total dissolved N in soil solution in the forest. This percentage was lower than reported for a number of relatively undisturbed temperate forests where DON makes up the majority of dissolved N in soil solution. For example, the DON made up 60–98% of the total dissolved N (TDN) found in lysimeters in a variety of temperate forests (Sollins and McCorison 1981, Qualls et al. 1991, Hedin et al. 1995). The few comparable data on DON and DIN in soil solution from Puerto Rican tropical forests suggest that DON may make up 15–45% of total dissolved N at the break between terra firme upland forest and riparian zones (McDowell et al. 1992). The somewhat lower amount of DON relative to TDN in tropical compared with temperate forests may reflect higher nitrification rates and relatively more abundant $NO_3^-$ in soil solution. In pastures, the result that soil solution DON concentrations were lower, but comprised a higher proportion of TDN (88%), was also

consistent with decreased net N mineralization rates and lower solution $NO_3^-$ concentrations.

Organic N was the dominant form of dissolved N, making up 54–65% of TDN in forest streams and 77–79% of TDN in pasture streams. This is also less than DON in some small forest streams, like the Chilean temperate old growth forest streams studied by Hedin et al. (1995). Our results suggest that the role of DON becomes more important after forest clearing, but there was no indication that a modest increase of DON concentration in pasture streams was linked to greater DON concentration in pasture soil solution. Therefore, higher pasture stream water DON concentration is likely related to autochthonous production by aquatic grasses on pasture stream banks and in the channel. Particulate organic N was also an important component of total stream water N in forest (20–25%) and pasture (32–33%) streams. Higher dissolved inorganic N concentrations in forest streams coupled with higher DON and PON concentrations led to a relatively small increase in total N in the pasture stream of watershed pair 1 and to no difference between forest and pasture streams in watershed pair 2 (Fig. 3). Total N (TN) in pasture streams also contained a higher proportion of PON. In these respects, they differed from typical temperate streams draining watersheds with high percentages of crop or pasture land, which show higher TN, and a high percentage of TN as $NO_3^-$ compared with streams draining forested watersheds (Smart et al. 1985, Jordan et al. 1997). These differences are also likely related to the high density of aquatic plants in the Rondônia pasture streams.

Our established pastures with active grazing represent the dominant use of cleared land in Rondônia. Remote sensing inventories for the region (L. Guild, *personal communication*) indicate managed pastures comprise ~90% of total pastures, and the area of abandoned pastures is small. Because cattle were grazed in the two pasture watersheds during this study, we cannot separate the effects of cattle grazing from the effects of pasture land cover alone. Cattle could potentially directly alter the concentrations of particulate and dissolved materials in stream water in a number of ways, including by trampling, contributing nutrients directly to stream water, or altering channel banks or riparian vegetation. We examined stream water concentrations in established pastures (5–9 yr old during this study), not immediately after forest clearing. There is evidence from other tropical locations that both soil N availability and stream water $NO_3^-$ concentrations are higher for a period of several months to more than one year immediately following forest cutting and burning (Uhl and Jordan 1984, Matson et al. 1987, Malmer and Grip 1994, Williams et al. 1997).

*Stream water temperature and oxygen*

The differences in temperature between forest and pasture streams were small and probably play a rela-

tively minor role in stream ecological functioning. The conversion of forest to pasture was, however, associated with large decreases in stream water dissolved oxygen concentrations, from near saturation in forests to <20% of saturation in pastures. In forests, stream dissolved oxygen values were typical of tropical headwater streams with fast flows and high turbulent mixing; in pastures, stream dissolved oxygen values were in the range typically associated with heterotrophy resulting from high organic matter inputs (Welcomme 1985). Our observations suggest that changes in dissolved oxygen following deforestation may be caused by large increases in organic matter inputs and perhaps by a change in the form of organic matter from leaves of trees in forest to leaves of aquatic grasses in pasture. The structure of pasture streams resembled that of floodplain lakes, where prolonged periods of low dissolved oxygen concentrations are widespread and associated with dense mats of aquatic vegetation (Melack and Fisher 1983). Our observations suggest that this contrasting structure in forest and pasture streams is widespread in Rondônia. These changes could have consequences for aquatic organisms, especially fishes, whose movements are frequently related to water oxygen content (Welcomme 1985, Lowe-McConnell 1987).

### Role of the riparian zone and in-stream processes

Riparian forest can be effective at removing N moving from uplands to stream channels because of denitrification associated with anoxic conditions in riparian zones (Peterjohn and Correll 1984, Groffman et al. 1996). There is some evidence that the riparian zones of small tropical forest streams are sites of active denitrification and are effective at removing $NO_3^-$ produced in adjacent uplands (McDowell et al. 1992, McClain et al. 1994). These processes have not been examined in pasture riparian zones. In our watersheds, it was unlikely that the pattern of lower $NO_3^-$ concentrations in pasture streams was caused solely by interception of soil solution N in stream riparian zones, because we found the highest $NO_3^-$ levels in the forest streams where riparian vegetation was intact. In pastures, soil solution $NO_3^-$ concentrations at the riparian slope break, where soils remain well oxygenated, averaged <3 μmol/L, compared with 100–300 μmol/L in forest (C. Neill, unpublished data). This indicates that the amount of $NO_3^-$ potentially moving from uplands to riparian zones was less in pasture watersheds. It is possible that $NO_3^-$ concentrations in pasture streams could have been further decreased by uptake by rooted aquatic plants or by denitrification enhanced by low stream water oxygen concentrations, but these processes should accentuate a pattern of already low $NO_3^-$ reaching pasture streams. Brandes et al. (1996) argued on the basis of $^{15}N$ isotopic evidence that the riparian zone of small forest streams removed most of the $NO_3^-$ moving from the uplands to the stream, and

that remineralization of organic N and nitrification within the stream channel was the main source of stream water $NO_3^-$. We cannot rule out within-stream $NO_3^-$ production as a source for forest and pasture stream $NO_3^-$, but higher stream $NO_3^-$ concentrations in forest could still be explained if only a small percentage of the $NO_3^-$ in soil water moved through the riparian zone.

### N:P ratios and limitation of primary production

In the forest stream, DIN:DIP ratios exceeded the ratio of 16:1 required for balanced algal growth (Redfield et al. 1963). In the pasture stream, ratios <16:1 indicated a likely shift of the nutrient that limits algal production from P to N after clearing. In watershed pair 1, lower $NO_3^-$ concentration in the pasture stream was the dominant influence on DIN:DIP ratios, but a small increase in $PO_4^{3-}$ concentration also played a role. In watershed pair 2, the shift in DIN:DIP ratios was solely the result of lower $NO_3^-$ concentrations in the pasture stream. The bioassays confirmed the pattern indicated by the DIN:DIP ratios suggesting that deforestation leads to N limitation of periphyton in pasture streams. In contrast, light strongly limited periphyton growth in the forest streams. This was similar to other shaded streams, where light is the primary abiotic constraint on periphyton growth and where nutrient additions do not typically stimulate algal growth unless light also increases (Pringle et al. 1986, Lowe et al. 1986).

### Consequences of deforestation for small streams

Lower stream water $NO_3^-$ concentrations, increased PON concentrations, and a switch in the factors that limit stream periphyton production from light in the forest to N in pastures are the changes most likely to follow deforestation for pasture in small watersheds in Rondônia. Patterns of N cycling and N availability in soils, most notably higher $NO_3^-$ in forests, are consistent with higher forest stream water N concentrations. These effects may be potentially important for two reasons. First, land use changes in small watersheds influence nutrient concentrations, which could potentially alter food web structure through nutrient control of periphyton production. Conditions in small pasture streams (high light coupled with low $NO_3^-$) are different from those found in forest streams that are large enough to allow light to reach the water surface because of the altered N cycling in pasture watersheds. There is evidence in other rivers that ratios of N:P can have important consequences for the productivity of receiving waters (Fisher et al. 1992, Justic et al. 1995). Second, in medium-sized rivers of the Amazon, many important fish species rely on algal-based food webs, especially during their juvenile phase (Forsberg et al. 1993). Whether our findings can be translated to larger rivers and the consequence of any changes will depend on the degree of connection between larger rivers and

land uses in their watersheds and on the extent to which in-stream processing influences nutrient transport. These effects are now relatively unknown. Currently, ~13% of the forest of the Amazon Basin has been cleared (Instituto Nacional de Pesquisas Espaciais 1999), and the chemistry of the main-stem Amazon River remains relatively unaltered by land use compared with many of the world's other large rivers (Cole et al. 1993). But this is likely to change as the area occupied by pasture also grows. The changing nutrient inputs to rivers caused by land use change deserves increased attention for their effects on both aquatic biogeochemistry and aquatic ecosystem functioning.

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