

ENHANCING NUTRIENT RETENTION IN TROPICAL TREE PLANTATIONS: NO SHORT CUTS

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Abstract. In the humid tropics large quantities of nutrients can be rapidly leached when the soil is unprotected by actively growing vegetation. We established experimental plantations of three indigenous tree species on a fertile Andisol in Costa Rica and managed them under 1- or 4-year cutting cycles with uncut stands as controls. Our goals were to test whether nutrient leaching was greatest under a regime of frequent disturbances that returned modest amounts of biomass to the soil surface (cutting and replanting on a 1-yr cycle) or less frequent disturbances that returned significantly greater amounts of plant tissues to the soil (cutting and replanting on a 4-yr cycle), and to compare those cutting cycles with nutrient leaching from uncut stands. Leaching of NO_3^- (over 9 yr), Ca^{2+} , Mg^{2+} , and K^+ (over 4 yr) from upper soil horizons was monitored. Water balance was determined by linking Penman-Monteith evaporation with changes in soil water storage modeled from soil physical parameters. Drainage water for solute measurement was sampled from porous ceramic cups at 1.1 m depth in the soil.

Disturbance frequency proved to be an important determinant of NO_3^- leaching. Average long-term NO_3^- leaching losses from stands on a 1-yr cutting cycle were extraordinarily large: $442 \text{ mmol}_c \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ($62 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ of N), compared to $187 \text{ mmol}_c \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ under a 4-yr cutting cycle and $71 \text{ mmol}_c \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ from uncut stands. Elevated NO_3^- leaching was primarily due to increased concentration in the soil solution (rather than increased water drainage), because cutting usually resulted in a reduction of $<10\%$ in evapotranspiration. Resilience of stands decreased with continued disturbance; under a 4-yr cutting cycle, stands tended to take longer to return to the low levels of NO_3^- leaching characteristic of undisturbed stands with each episode of cutting and replanting, while NO_3^- losses from annually cut stands became increasingly variable over time. Due to high concentrations of soil Ca at the site, the stands proved resistant to treatment-induced losses of base cations: no increases in Ca^{2+} or Mg^{2+} leaching accompanied elevated NO_3^- leaching, although K^+ leaching did increase under the 1-yr cutting cycle. Because of the potential for massive, sustained NO_3^- losses, development of land use systems for these soils should focus on minimizing frequency of disturbance.

Key words: hydrology; leaf area; nitrate and base-cation leaching; root length density; short-rotation forestry; tropical tree plantation.

INTRODUCTION

Actively growing vegetation diminishes nutrient leaching by taking nutrients out of the soil solution, decreasing drainage via transpiration, and adding organic matter to the soil in the form of dead leaves, branches, and roots (Vitousek and Melillo 1979). When vegetation enters dormancy, when forests are cleared, or when agricultural crops and trees are harvested, these processes are altered: Uptake and transpiration temporarily cease, and a pulse of organic matter is

added to the soil. An excess, even short-term, of rainfall over the sum of evaporation and runoff then leads to nutrient leaching. This typically occurs in the temperate-zone spring, at the onset of the rainy season in the seasonally dry tropics, or almost any time in the wet tropics. The high temperatures and readily available moisture that characterize humid tropical lowlands facilitate rapid decomposition and nutrient release, thereby exacerbating these losses.

Leaching can be acute in tropical shifting agriculture, where nutrient losses are one of several factors that lead practitioners to anticipate yield declines and shift to new sites (Nye and Greenland 1960, Sanchez et al. 1982, Trenbath 1984, Dagar et al. 1995, Juo et al. 1995). Site impoverishment through post-harvest nutrient leaching is not restricted to short-lived agricultural crops, however. It is a potential issue in plantation forestry, which today often involves rotation intervals

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of only a few years, especially in the humid tropics (Fownes and Harrington 1990, Brown et al. 1997, Nambiar and Brown 1997).

As rotation lengths shorten, nutrient leaching should increase because root systems are poorly developed and any nutrients released into the soil solution are vulnerable to loss. Under long-rotation cropping, post-harvest nutrient losses in drainage water are considered to have negligible effect on stand nutrient budgets (Mann et al. 1988), in part because the period of rapid loss is brief in comparison to the duration of the cutting cycle (McColl and Powers 1984, Raison and Crane 1986). But the higher losses anticipated as rotations shorten may be counterbalanced by the larger amounts of organic matter added to the soil when older vegetation is felled. More biomass added to the soil at the time when resource-capturing structures are poorly developed puts greater amounts of nutrients at risk of loss through leaching.

Thus, the relationship between rotation length and nutrient loss rates through leaching is uncertain, involving factors that exacerbate leaching losses both as a function of the time needed to develop leaching-reducing structures and processes on the one hand, and the amount of nutrient-rich biomass added to the soil at the end of a rotation on the other. Our study was designed to explore these trade-offs. Measurements of leaching losses of macronutrients (nitrate, calcium, magnesium, and potassium) were made in experimental plantations of three tropical tree species that were cut and replanted at intervals of one year or four years, or left to grow undisturbed.

METHODS

Soil, site preparation, species

The study took place in the Atlantic lowlands (elevation 40 m) of Costa Rica at La Selva Biological Station. Mean annual temperature is 25.8°C, and mean annual rainfall is 3962 mm; there is a dry season from February to April, although mean rainfall exceeds 100 mm in all months (Matlock and Hartshorn 1999). For annual summaries of data, we used a water year whose beginning coincided with the onset of the wet season; water year 1992, for example, begins on 1 May 1992 and extends to 30 April 1993. The experimental site is a flat, recently formed alluvial terrace: Rapid drainage in combination with flat topography and absence of micro-relief ensured that overland flow is virtually absent even during intense rainfall.

The soil belongs to the order Andisol (Eutric Haludand; Weitz et al. 1997), which comprises volcanic ash soils characterized by variable charge, high cation exchange capacity, and amorphous allophane clays that bind organic matter strongly. Soil at our site has typical Andic properties. The upper mineral (A) horizon, which extends to ~0.2 m, is a highly aggregated clay loam with many fine pores. The lower mineral (B) ho-

rizon, extending to ~0.6 m, is a sandy loam, also with many fine pores. There is a probable buried A horizon at ~0.7 m, followed by a C₁ horizon of coarse sand with few fine pores (A. F. Bouwman, *personal communication*). Cation availability is high in the A horizon (cation exchange capacity > 400 mmol_c/kg, base saturation > 50%) and the B horizon (cation exchange capacity > 300 mmol_c/kg, base saturation > 30%; Hagggar and Ewel 1994). The soil's pH in water ranges from 5.2 to 7.2; pH in KCl ranges from 4.6 to 5.6; organic carbon content ranges from ~3 to 4% in surface horizons and declines markedly with depth; and total N content is ~0.3–0.4%. Mineralization and nitrification rates are ~0.22 μg·g⁻¹·d⁻¹, or >100 kg·ha⁻¹·yr⁻¹ (Hiremath and Ewel 2001). Despite the propensity of volcanic-derived soils to bind P, N may be more limiting than P at our site: Foliar N:P tends to be less than the threshold value of 14 (Hiremath and Ewel 2001; see Koerselman and Meuleman 1996), and soil P is high relative to most tropical soils (>20 μg/g sodium-bicarbonate extracted P; Hagggar and Ewel 1994).

The experiment was carried out with three tree species that are indigenous to Mesoamerica; none of the species are known to have N-fixing symbionts. *Hyeronima alchorneoides* Allemao (Euphorbiaceae) is an evergreen canopy emergent that can reach 50 m in height (Clark and Clark 2001). It has simple, alternate leaves that are large when trees are young, but become smaller as the tree ages. *Cedrela odorata* L. (Meliaceae) is a deciduous canopy tree with pinnately compound leaves that are shed during the dry season. It produces wood that is prized both for furniture and paneling. *Cordia alliodora* (R. & P.) Cham. (Boraginaceae) is a deciduous canopy tree that sheds its leaves at the onset of the wet season as an adult. The species is used in agroforestry (Greaves and McCarter 1990) and produces wood that is used for furniture and paneling as well as general construction (Opler and Janzen 1983). Seed sources, nursery treatments, and out-planting are detailed in Hagggar and Ewel (1995, 1997).

In early 1991, the vegetation on the 8-ha site (an abandoned cocoa plantation) was felled, and the slash was burned. Immediately following manual clearing of charred logs, three 60 × 40 m stands of each species were established in each of three blocks. Trees were planted in rows that were offset to provide a 2.0-m spacing between trees and an initial stand density of 2887 trees/ha. Each 60 × 40 m stand was divided into three plots: a 10 × 40 m plot for the 1-yr cutting cycle, a 20 × 40 m plot for the 4-yr cycle, and a 30 × 40 m plot for uncut stands. A self-seeded groundcover of invasive herbs was weeded every 2–6 wk.

One-year cutting-cycle stands were cut and replanted annually from 1992 to 2000, and the 4-yr cutting-cycle stands were cut and replanted in 1995 and 1999. Trees in the 1-yr and 4-yr cutting-cycle stands had reached average heights of 1.6 m and 10.6 m, respectively, at the time of cutting; uncut trees had reached an average

height of 17.9 m by 1999. Operations were done from May to August, coinciding with the onset of the wet season. All biomass was left in place after cutting to eliminate export of nutrients in aboveground biomass as a cause of differential leaching rates among treatments.

Fine root sampling

Fine root density (<2 mm diameter) of trees was measured annually to assess the potential for nutrient uptake; methods and results from 1992 through 1994 are presented in Haggard and Ewel (1995, 1997). In 1995 and subsequent years, soil cores were taken from eight randomly selected locations per plot in uncut stands. Sampling was done in 0.1 m increments to a depth of 1.1 m, and in 1995, 1996, 1999, and 2000 sampling was done to a depth of 2 m to check for deeper roots. Roots were separated from soil using a hydro-pneumatic elutriator (Gillison's Variety Fabrication, Benzonia, Michigan, USA), dead roots were discarded, and live-root length was measured using the line-intersect method (Tennant 1975).

Water balance: precipitation, evapotranspiration, and soil moisture

The rate of water drainage at 1.1 m below the soil surface was estimated from a water balance. Precipitation was measured directly, evapotranspiration was estimated with a Penman-Monteith approach (Bigelow 2001), and changes in soil water storage in the upper 1.1 m of soil were estimated with a model based on soil physical properties. Meteorological data for calculating evapotranspiration (ET) were obtained from the weather station of the Organization for Tropical Studies, ~1 km from the study site (Sanford et al. 1994, Matlock and Hartshorn 1999). Instrumentation consisted of a tipping-bucket rain gauge (model 6011-B, Qualimetrics, Sacramento, California, USA), a platinum resistance thermometer and capacitive polymer chip for humidity housed in a radiation shield (HMP35C, Campbell Scientific, Logan, Utah, USA), and a pyranometer (LI-200 SZ, LI-COR, Lincoln, Nebraska, USA) for measuring solar radiation (S_t). Data were logged at 5-s intervals and recorded as hourly sums or means.

The Penman-Monteith equation requires inputs of net radiation (R_n), and three equations were tested for converting S_t to R_n : (1) a linear equation $R_n = a + bS_t$, where a and b are dimensionless constants, (2) different linear equations for wet and dry days, and (3) a mechanistic equation, $R_n = (1 - \rho)S_t + L_n$, where ρ is reflectivity of short-wave radiation, and L_n is net long-wave radiation. L_n was estimated as $c + \sigma T^4(d - 1)$, where σ is the Stefan-Boltzman constant, and c and d are universal fitting constants (Monteith and Unsworth 1990). Data for model evaluation were 2647 observations of mean hourly R_n (Bigelow 2001) and S_t measured during 1995. The fit of data to model was eval-

uated using the sums of squares principle (Hilborn and Mangel 1997), which adjusts the error sums of squares for the number of parameters in a model. The system of different linear equations on wet and dry days resulted in the lowest adjusted sum of squares; regression equations were $R_n = 0.667S_t$ ($r^2 = 0.602$) and $R_n = 0.706S_t$ ($r^2 = 0.817$) for dry and wet days, respectively (intercepts were omitted because they were nonsignificant).

As is typical for long-term meteorological records there were a number of days of missing data. When available, data from nearby (<1 km) weather stations were substituted for missing data (Bigelow 2001; H. Loescher, unpublished data). When substitute precipitation data recorded at hourly intervals were not available, gaps (104 d) were filled with daily totals by assuming that rain fell from 07:00 to 11:00 hours. Missing total solar radiation (S_t) data (170 d) were filled using linear equations that gave S_t as a function of photosynthetically active radiation. Equation parameters were obtained by linear regressions done on the 10 d of data prior to each gap. The r^2 for every set of parameters was ≥ 0.985 . A continuous, 439-d gap of relative humidity (h) data was filled by substituting saturated vapor pressure at nighttime temperatures, $e_s(T_{\min})$, for actual vapor pressure, e , in the expression $h = e/e_s(T)$. A test of this formula showed that estimated h was within 11% of measured h for 90% of observations in a year-long record. Other missing h and T data (26 d) were filled by substituting average values for day and hour from the rest of the data record.

The Penman-Monteith equation was linked with a canopy drainage routine for intercepted rain, and these equations required a number of parameters. Derivation of parameters for canopy conductance (g_c), aerodynamic conductance (g_a), canopy cover, and canopy water storage capacity are given in Bigelow (2001). Estimates of leaf area index (LAI) were obtained annually through harvest and allometry (Haggard and Ewel 1995, 1997). The pattern of seasonal fluctuations of leaf area in the deciduous species, *Cordia* and *Cedrela*, was estimated from visual observations and optical plant-canopy analyses (LAI-2000, LI-COR) performed monthly in all plots from mid-1999 through 2002.

Soil moisture was estimated using the model SWAP93, which incorporates Richards' equation for unsaturated flow through a soil profile (van den Broek et al. 1994). The profile was treated as having uniform properties in four horizons: 0–0.1, 0.1–0.3, 0.3–0.5, and 0.5–1.1 m. Parameters describing soil physical properties (saturated soil moisture θ_s , residual soil moisture θ_r , and fitting parameters n and α ; van Genuchten 1980) were derived by A. Weitz (unpublished data) for soil at a secondary forest site ~100 m from our study plots on the same alluvial terrace.

Time-domain reflectometry measurements of soil moisture (Trase II, Soil Moisture Equipment Corporation, Santa Barbara, California, USA) were used to

evaluate the water balance. Pairs of stainless-steel rods, each of which sampled a cylindrical soil volume 1 m deep by 0.2 m across, were installed vertically in three random locations in each plot. The model of Roth et al. (1990) was used to convert apparent dielectric constants into volume soil moisture, incorporating parameters obtained for our site (porosity = $0.711 \text{ m}^3/\text{m}^3$ and soil geometry factor $\alpha = 0.47$; Weitz et al. 1997). Readings were taken in 1995, and the average time between readings was 1 wk. Comparisons of simulated to measured volume soil moisture were made with linear regressions (SAS 1990); adequacy of simulations was assessed with the adjusted r^2 statistic.

Soil water sampling and chemical analysis

Daily fluxes of nutrients in drainage water were estimated by multiplying nutrient concentrations by daily water drainage at 1.1 m soil depth. Solute concentrations were assumed to change linearly between sampling dates. Soil water was sampled with $48 \times 60 \text{ mm}$, high-flow, round-bottom ceramic cups (Soil Moisture Equipment Corporation, Santa Barbara, California, USA) glued to 1.3 m long PVC pipes sealed at the top with rubber stoppers. Stoppers were perforated by a semirigid 7.7 mm diameter polyethylene tube whose tip was inserted inside a soft neoprene tube, and the assemblage was sealed by clamping the soft tube. Tension was placed on the samplers after $\geq 20 \text{ mm}$ of rain had fallen within 3 d, then water was collected after an additional $\sim 24 \text{ h}$. A tension of -16 kPa was used because tensiometer measurements indicated that saturated soil at 1 m drained to approximately this tension within 24 h (J. P. Haggard and A. Nobre, *unpublished data*), and our intent was to extract freely draining water rather than water that was tightly held by the soil. To collect water from a sampler, a hand-pump was applied to a flexible tube that was passed through the stopper assemblage to the bottom of the sampler. To inhibit nitrogen transformations, 0.05 mL of chloroform was added to samples, and then they were refrigerated. Soil water was first collected in June 1992, 11 mo after establishment of the plantations, and continued to be collected every $\sim 3 \text{ mo}$ for the first 2 yr, and then with varying frequency thereafter.

There were three soil water samplers in each of the nine stands (3 species \times 3 blocks) under a 1-yr cutting cycle. Until mid-1995, there were two samplers in each of the uncut and 4-yr cutting-cycle stands; prior to cutting the latter for the first time, additional samplers were installed to bring the number of samplers in each plot to three. Soil water from samplers within a plot was combined prior to analysis.

Analysis of solutions for NO_3^- was done on-site with an automated system (Technicon II, Scientific Instruments, Tarrytown, New York, USA); detection limit was estimated as $0.003 \text{ mmol}_c/\text{L}$. Analyses for Ca^{2+} , Mg^{2+} , and K^+ were done using inductively coupled plasma spectroscopy (ICP). Only four years of cation

data are presented in this paper because of concerns about accuracy of cation analyses collected from 1992–1994, and discontinuation of routine cation analyses after mid-1999. Additional analyses were made on samples collected in December 1999 to obtain a complete charge balance. Assays were done of CO_3^{2-} and HCO_3^- by titration; Al^{3+} by ICP; PO_4^{2-} by ion chromatography; Cl^- , SO_4^{2-} , and NH_4^+ by automated colorimetry, and Na^+ by flame atomic absorption spectroscopy.

Statistical analysis

The experiment was treated as a split-plot design in which block was a random effect, species was a fixed whole-plot effect, cutting cycle was a fixed sub-plot effect, and year was a fixed sub-sub-plot effect or repeated measure (Haggard and Ewel 1997). Analysis of variance was done using the GLM procedure in SYSTAT 9.0 (1998), and then error mean squares were transferred to a spreadsheet to complete the appropriate F tests. Following common practice for this design, we did not test for three-way interactions among block, species, and cutting cycle, nor for two-way interactions among block and cutting cycle (Montgomery 1984). Dependent variables were annual leaching losses of NO_3^- , Ca^{2+} , Mg^{2+} , and K^+ . Nitrate values reported as $0 \text{ mmol}_c/\text{L}$ were treated as being equal to the lower detection limit ($0.003 \text{ mmol}_c/\text{L}$) for statistical analyses (Newman et al. 1989). Model adequacy was tested by examining plots of residual against predicted values. There was little overlap of residuals of annual NO_3^- losses among cutting-cycle treatments, so annual NO_3^- losses were log-transformed prior to analysis.

Multiple comparisons were used to pose directed questions about NO_3^- leaching. Because some involved multiple contrasts (e.g., comparing leaching from one species against two other species) Scheffé's method was selected. Although this test is conservative and may predispose towards Type II errors, we allowed a relatively high probability of making a Type I error ($\alpha = 0.1$), which increased the likelihood of finding significant differences. All comparisons were made with a given water year, so the following parameter values were used for Scheffé's test: $N = 27$ (3 species \times 3 cutting cycles \times 3 blocks) for number of data points; $k = 9$ (3 species \times 3 cutting cycles) for number of treatment groups, and $s^2 = 0.298$ (sub-sub-plot error from the analysis of variance) for the variance component.

Questions addressed with multiple contrasts were as follows: First, was short-term NO_3^- leaching after cutting greater in 4-yr-old than in 1-yr-old stands? More N was sequestered in the biomass of the 4-yr-old stands, so we expected higher short-term (though not long-term) NO_3^- leaching rates there. Nitrate leaching was compared in years in which stands on 4-yr (and 1-yr) cycles were cut, i.e., water years 1995 and 1999, with the three species treated as a single group. Second, how

soon after cutting did stands again become retentive of NO_3^- ? Annual NO_3^- leaching from stands on a 4-yr-cutting cycle was compared to leaching from uncut stands in the years after the former had been cut, i.e., water years 1996–1998 and 2000. Species were examined individually because there were clear differences in rates of recovery of nutrient retention. Finally, did established stands of the three species differ in their propensity to retain NO_3^- ? Annual leaching from uncut stands of *Cedrela*, which appeared to develop increasing NO_3^- leaching losses over the course of the experiment, was compared with leaching from the two other species in the water years 1997–2000.

Factor analysis of solute concentrations from the December 1999 collection was done to identify relationships among ions and to assist in evaluating the dependence of cation leaching on NO_3^- concentrations. In factor analysis, the covariances among a set of variables (in our case, solute concentrations) are converted into a set of principal components. Typically, the two components that account for most variance are plotted against one another, and the position of the resulting vectors (one vector for each variable) can be viewed as a summary of the regression relationships among variables.

RESULTS

Root length and leaf area

Fine root length density (L_v) in the upper 0.1 m of soil averaged 0.22, 0.06, and 0.13 cm/cm^3 in established stands of *Hyeronima*, *Cedrela*, and *Cordia*, respectively (Fig. 1). Year-to-year variation in L_v was minor. All species had fine root development at soil depths below 1.1 m; in 1995 and 1996, an average of 27% of fine root length from 0–2 m soil depth occurred from 1.1–2.0 m. By 2000 and 2001, though, the proportion of fine roots concentrated in the 1.1–2.0 m depth in uncut stands was <4%. The presence of fine roots below 1.1 m indicates that nutrient uptake occurred below the level at which soil water was collected. In stands of 1-yr-old trees, in contrast, there were few roots at 1.1 m depth (Haggard and Ewel 1995), so there would have been little uptake below this level. Thus, water sampled at 1.1 m beneath the surface of 4-yr cutting cycle and uncut stands overestimates leaching from those stands, biasing the nutrient-retention interpretations toward the 1-yr cutting-cycle stands.

Hyeronima LAI in uncut stands eventually stabilized at $\sim 8 \text{ m}^2/\text{m}^2$, far higher than in uncut stands of the other two species, which were closer to $3 \text{ m}^2/\text{m}^2$ (Fig. 2, lower panel). Accordingly, uncut stands differed in the age at which they reached maximum LAI: *Cordia* at 2 yr, *Cedrela* at 3 yr, and *Hyeronima* at 6 yr. Stands on a 4-yr cutting cycle therefore spent a significant proportion of each cycle at less than maximum potential LAI, and stands on a 1-yr cutting cycle had only

achieved a small proportion of potential LAI by the time of each cutting.

Water balance

The long-term meteorological record showed annual variation best when data were summarized at weekly intervals (Fig. 3). The lowest weekly values of R_n , minimum daily temperature, and maximum daily vapor pressure deficit occurred in late December/early January. Simulated soil moisture closely matched measurements by time-domain reflectometry (Fig. 4). Adjusted r^2 varied from 0.522 to 0.702, and soil moisture in *Hyeronima* and *Cordia* stands was simulated better than in *Cedrela* stands (Table 1). Because the annual soil moisture cycle was well reproduced by the simulations, we were confident that our simulated soil moisture was satisfactory. Annual wetting and drying cycles were synchronized with the major dry season, as could be readily detected in most years (Fig. 5).

Simulated ET was constrained by the capacity of the soil to supply water, ceasing when soil moisture dropped to the level specified by the residual water content parameter (0.300–0.335 m^3/m^3). The effect was hardly noticeable in short cutting-cycle stands, where average annual ET as a fraction of potential ET was 0.98. The effect was greater in uncut stands because of their higher transpiration. Median ET as a fraction of potential ET was 0.97 in uncut stands, but in dry years, such as 1995–1996 (Table 2), the fraction dropped as low as 0.86. Soil moisture limitation may not have occurred in the field, though, because large, deep-rooted trees would have had access to water stored in lower soil horizons (Fig. 1).

Variation in drainage due to treatments and species was minor, in part because of the ability of the groundcover to compensate for differences in canopy-tree leaf area (Bigelow 2001). Mean annual drainage as a proportion of precipitation was 72%, with a range of 55–77% (Table 2). Most drainage occurred during the May–December wet season, and in years when the dry season was pronounced almost no drainage occurred in the dry season (Fig. 5). No clear El Niño–Southern Oscillation signal was observed, which is consistent with observations on the principal river of the watershed, the Sarapiquí (George et al. 1998).

Leaching losses

Nitrate concentrations were elevated ($\sim 0.4 \text{ mmol}_c/\text{L}$) in all treatments when first measured (Fig. 6) due to residual effects of site preparation and stand planting 11 mo earlier. Cutting and replanting on a 1-yr cycle maintained most mean NO_3^- concentrations between 0.05 and 0.6 mmol_c/L . In contrast, in stands that were uncut or on a 4-yr cutting cycle, NO_3^- concentrations had dropped to $< 0.01 \text{ mmol}_c/\text{L}$ by late 1992, 18 mo after planting. Cutting of 4-yr-old trees in 1995 and 1999 produced sharp peaks in NO_3^- concentrations, while NO_3^- concentrations in uncut stands remained

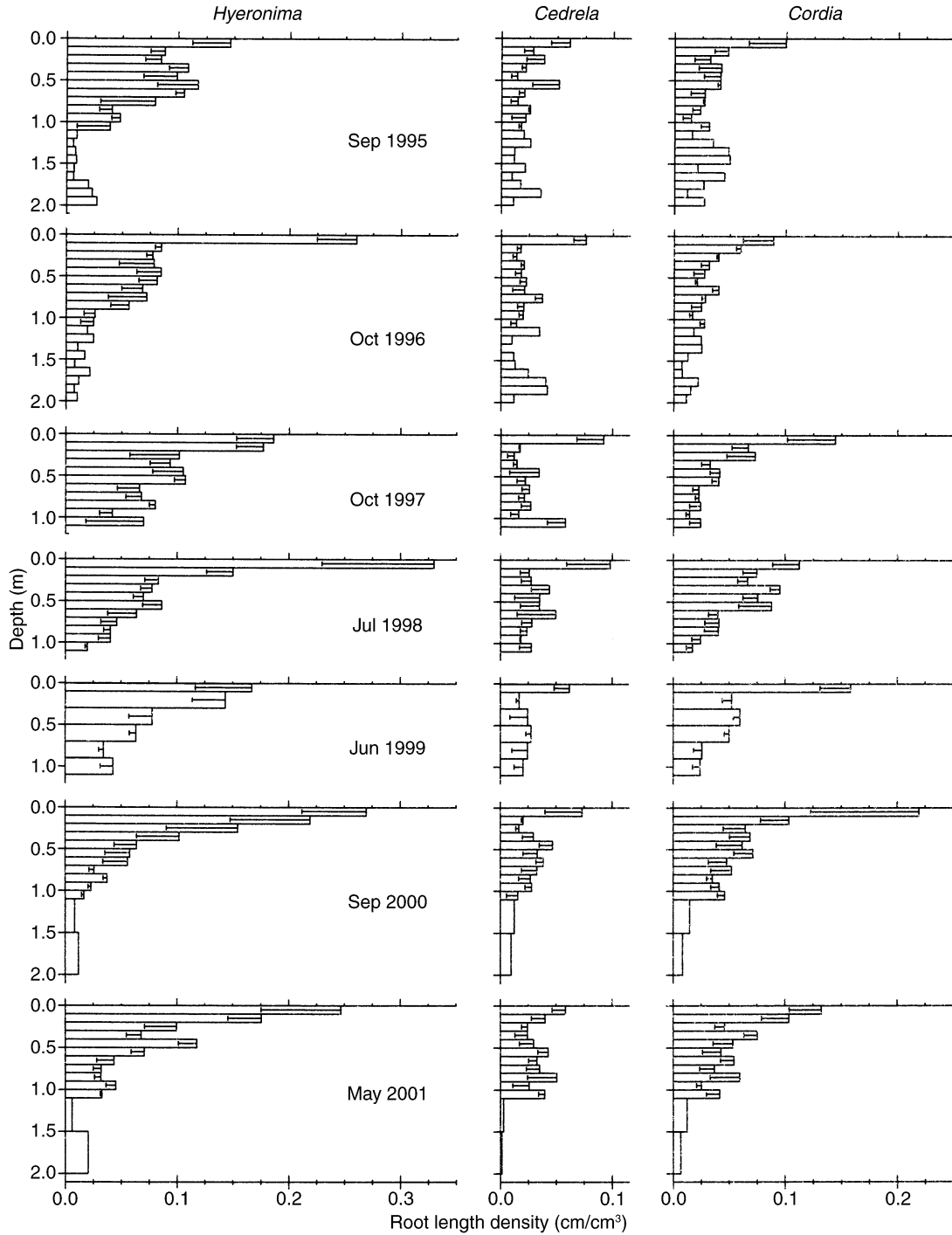


FIG. 1. Length density of fine roots (<2 mm diameter) of three tropical trees at La Selva Biological Station, Costa Rica. All values are from uncut treatments. Each datum was derived from a composite of eight cores. Means with standard errors are from three blocks; measurements below 1.1 m are from one block only.

low, with the exception of a trend for somewhat higher NO_3^- concentrations in *Cedrelela* stands.

Largely as a result of the responsiveness of NO_3^- concentrations, cutting-cycle treatment had highly significant effects on annual NO_3^- leaching losses

(ANOVA, $P < 0.001$; Table 3). Annual NO_3^- leaching from stands on a 1-yr cutting cycle (means of the three species) was $442 \text{ mmol}_c/\text{m}^2$, compared to $187 \text{ mmol}_c/\text{m}^2$ from stands on the 4-yr cycle and $71 \text{ mmol}_c/\text{m}^2$ from uncut stands. Variation due to species and block

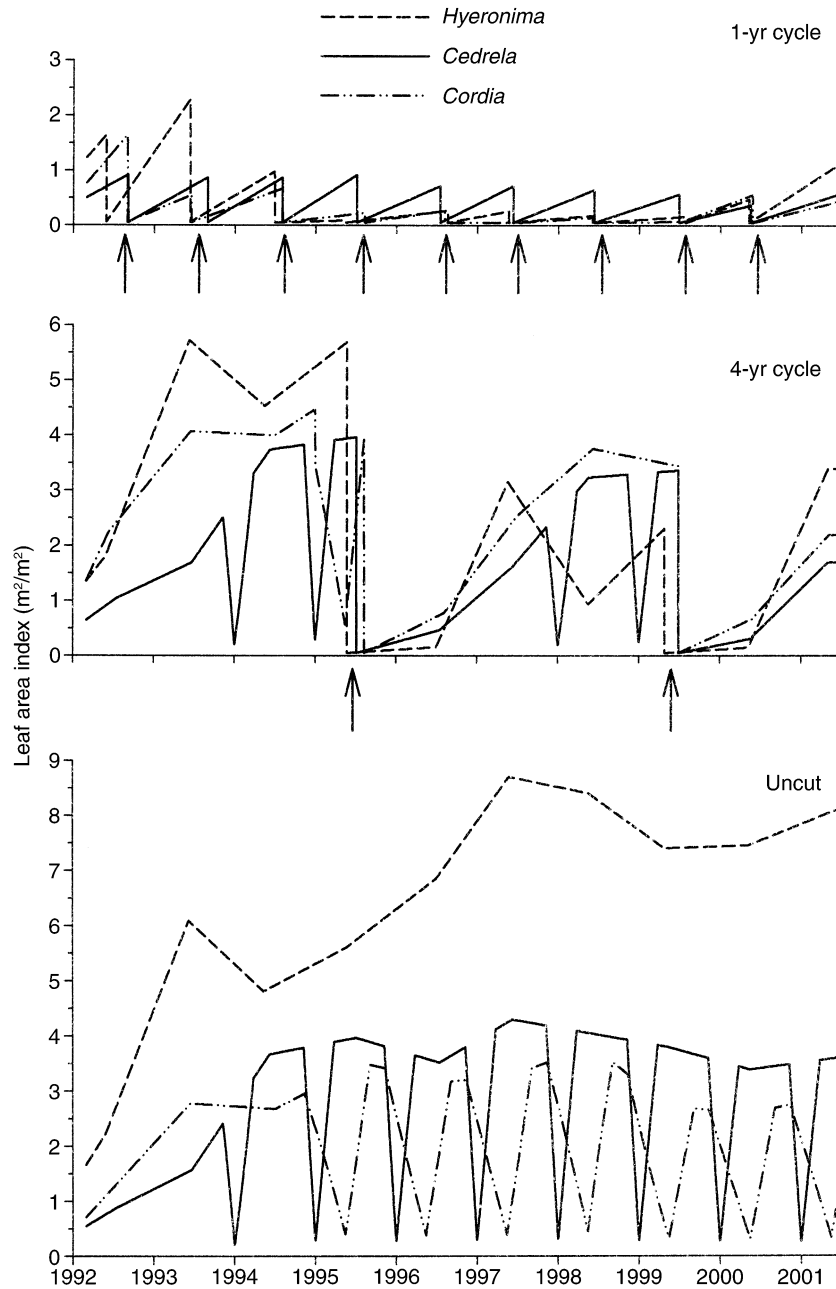


FIG. 2. Leaf area (one-sided) development of the three study species under three cutting cycles. Arrows indicate cutting and replanting of stands on 1-yr and 4-yr cutting cycles.

was less pronounced ($P < 0.05$ and $P < 0.01$, respectively).

Annual NO_3^- leaching losses viewed over time (Fig. 7) show that NO_3^- retention in the 4-yr cutting-cycle stands was again comparable to that in uncut stands by the second year after cutting (i.e., water year 1993), but that NO_3^- losses from 1-yr cutting-cycle stands remained high. Annual leaching losses from the former stands were $<71 \text{ mmol}_c/\text{m}^2$ (10 kg/ha of N) in water years 1993 and 1994. Losses remained low for uncut

stands, but increased to $323\text{--}360 \text{ mmol}_c/\text{m}^2$ in 4-yr cutting-cycle stands when they were cut and replanted in water year 1995. Nitrate leaching in this year was significantly greater by an average of 43% in stands on 4-yr compared to 1-yr cutting cycles.

Nitrate losses from stands on a 4-yr cutting cycle varied according to species and year after these stands were first cut in 1995, which accounts for the statistical interaction among year, cutting cycle, and species (Table 3). *Cordia* stands were the most resilient after cut-

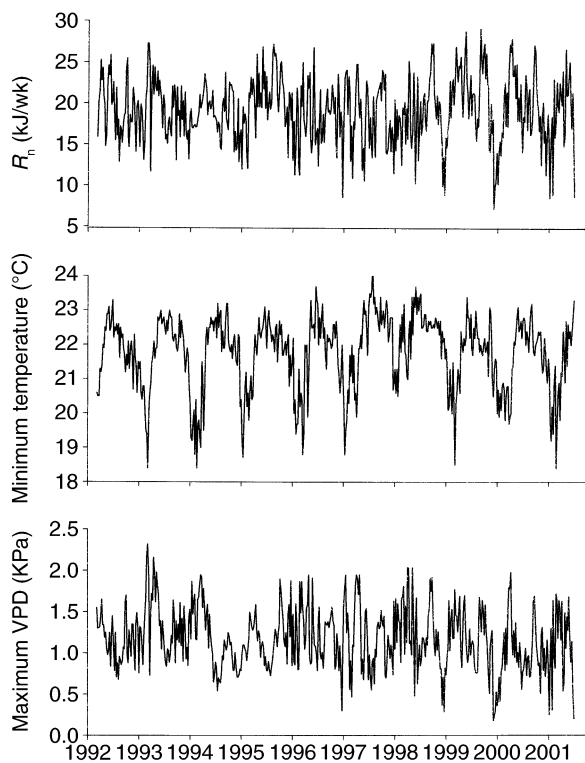


FIG. 3. Meteorological record from 1992–2001 at La Selva Biological Station, Costa Rica. Values are weekly sums (net radiation [R_n]) or weekly averages of maximum daily values (temperature and vapor pressure deficit [VPD]).

ting; NO_3^- leaching losses were indistinguishable from those in uncut stands (Scheffé's, $\alpha = 0.1$) one year after the 1995 cut, remaining so until the second cut of the 4-yr cutting-cycle stands in 1999. *Cordia* stands quickly resumed NO_3^- retentiveness after this second cut (i.e., in water year 2000) also. *Hyeronima* stands also quickly regained NO_3^- retentiveness after the 1995 cut (i.e., NO_3^- leaching did not differ from uncut stands in water years 1996–1997), but in 1998, NO_3^- leaching losses were significantly greater than in uncut stands and remained elevated after the second cut (Scheffé's, $\alpha = 0.1$).

Cedrela stands showed the most idiosyncratic NO_3^- leaching patterns. Despite the absence of disturbance in uncut stands, NO_3^- leaching in water years 1998 and 2000 was significantly greater than from uncut stands of *Hyeronima* and *Cordia* (Scheffé's test, $\alpha = 0.1$). In stands on the 4-yr cutting cycle, effective NO_3^- retention did not resume rapidly; NO_3^- leaching in 1996 was significantly greater than in the uncut stands. In water years 1997 and 1998, NO_3^- leaching losses did not differ between uncut and 4-yr cutting-cycle stands, but more as a result of elevated leaching losses in the uncut stands than resumption of effective retention in the cut stands. In water year 2000, after the second cut of the stands on a 4-yr cycle, NO_3^- leaching remained high ($>200 \text{ mmol}_e \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) in uncut and cut stands.

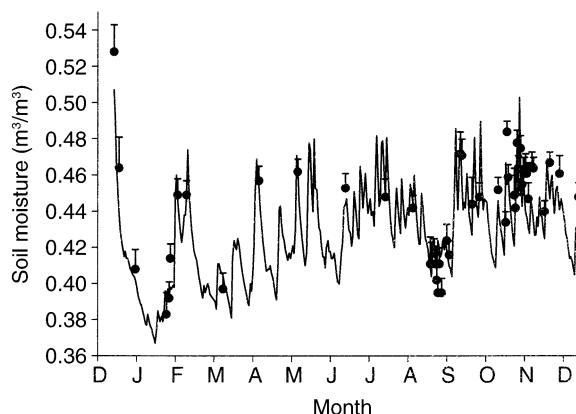


FIG. 4. Volume soil moisture during 1995 in upper 1 m of soil in *Hyeronima* stands under 1-yr cutting cycle. The line is soil moisture modeled from water balance, and circles are soil moisture measured by time domain reflectometry. Bars represent 1 SE ($n = 9$).

Cation concentrations (Table 4) were less variable than NO_3^- concentrations, and responses to experimental treatments were weaker. The main source of variation in cation losses was year (Table 3), probably because of interannual variation in drainage. For example, water year 1995 was much drier than subsequent years (Table 2), and cation losses also were low that year regardless of species or cutting cycle (Fig. 8). Potassium was the only ion for which there were significant increases in leaching losses resulting from cutting and replanting. Mean annual K^+ losses in stands on a 1-yr cutting cycle were $\sim 50 \text{ mmol}_e/\text{m}^2$ greater than in uncut stands, but the only increase in K^+ leaching in the 4-yr cutting-cycle stands occurred in *Cedrela* stands. Annual losses of Ca^{2+} and Mg^{2+} followed courses similar to each other, though the concentration of the former ion was over twice as great as the latter. There was a significant interaction between species and year (Table 3); Ca^{2+} and Mg^{2+} leaching were highest in *Cedrela* stands in the water year 1996, but by 1998 *Hyeronima* had highest Ca^{2+} leaching.

Ion interrelationships and soil solution charge balance

Cations followed a consistent pattern in their contribution to solution charge. Calcium made the largest contribution to positive solution charge, followed by Mg^{2+} , Na^+ , K^+ , and NH_4^+ (Fig. 9). Charge from Al^{3+} was orders of magnitude less than charge from other

TABLE 1. Coefficients of determination (r^2) for modeled soil moisture with respect to measured soil moisture in upper 1 m of soil.

Cycle	<i>Hyeronima</i>	<i>Cedrela</i>	<i>Cordia</i>
1-yr	0.687	0.552	0.652
4-yr	0.628	0.558	0.702
Uncut	0.614	0.581	0.522

TABLE 2. Precipitation (P), evapotranspiration (Et), and soil water drainage (D) from stands of three tropical tree species under three cutting cycles at La Selva Biological Station, Costa Rica (values are mm/yr).

Water year	<i>Hyeronima</i>						<i>Cedrela</i>		
	P	1-yr		4-yr		Uncut		1-yr	
		Et	D	Et	D	Et	D	Et	D
1992	3747	1069	2721	1190	2608	1212	2587	1026	2725
1993	3588	986	2621	1217	2392	1230	2379	974	2636
1994	4515	1063	3419	1334	3149	1341	3141	1030	3448
1995	3275	1156	2143	1187	2101	1507	1800	1129	2171
1996	4197	1039	3162	1030	3176	1385	2814	1023	3178
1997	4428	1008	3371	1006	3364	1324	3053	985	3392
1998	4548	1138	3395	1071	3466	1509	3009	1111	3423
1999	4532	1117	3423	1143	3398	1416	3138	1116	3425
2000	4032	1018	2999	1037	2979	1354	2655	1043	2974

Note: Annual hydrological measurements begin on 1 May and end on 29 April.

cations and is not shown. All cations except Al^{3+} were tightly clustered in the factor analysis, and were highly loaded onto factor 1 (Fig. 10).

In contrast to cations, anion concentrations were highly variable with respect to each other. Most negative charge in soil solution from stands on 1- and 4-yr cutting cycles came from NO_3^- , but in the uncut stands most negative charge came from HCO_3^- (Fig. 9). The sum of negative charge from HCO_3^- , SO_4^{2-} , Cl^- , and NO_3^- was consistently less than the sum of positive charge, indicating that unmeasured anions,

likely organic, contributed to negative solution charge. This anion gap has also been observed in temperate forest soils (Haines et al. 1982), where organic anions can contribute up to half of the negative charge in soil solution (Dijkstra et al. 2001). The HCO_3^- concentrations we observed are consistent with those in tropical soils, such as ours, with solution $\text{pH} > 6.0$ (Nye and Greenland 1960). Chloride and SO_4^{2-} contributed approximately equal amounts of negative charge, and charge from PO_4^{2-} is not shown in Fig. 9 because it would be less than the thickness of a line.

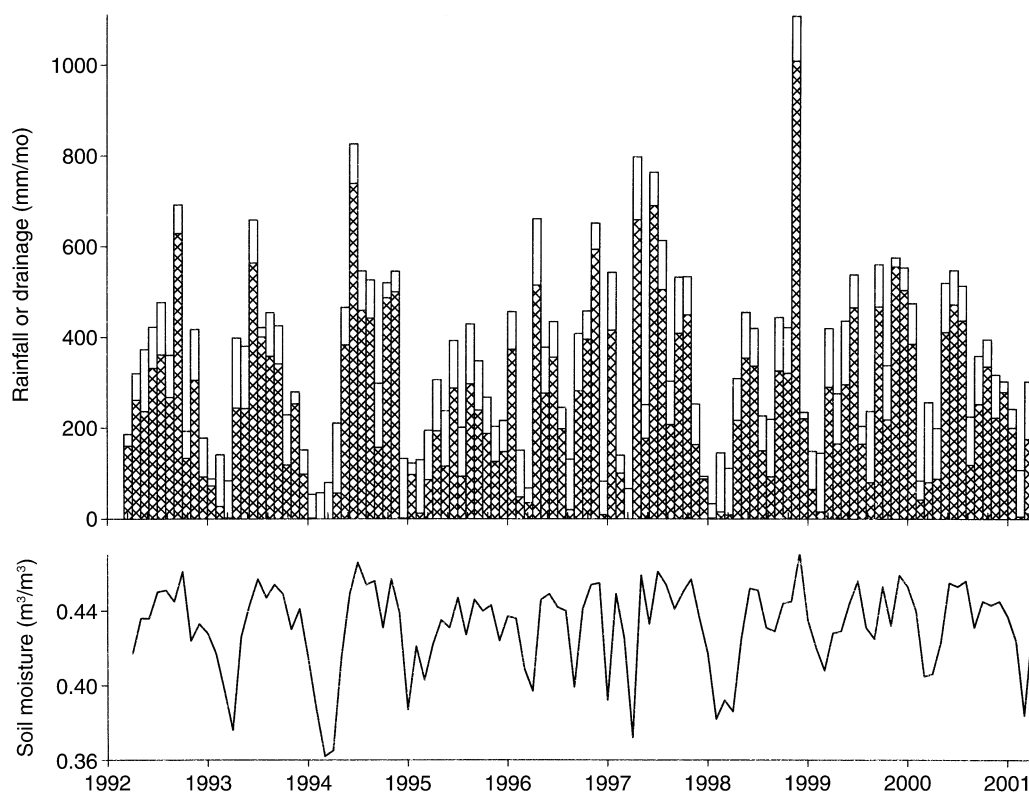


FIG. 5. Monthly precipitation, drainage, and mean soil moisture (upper 1 m) from 1992 to 2001 in *Hyeronima* stands at La Selva Biological Station, Costa Rica, under 1-yr cutting cycle. Drainage (hatched bars) is superimposed on precipitation (open bars).

TABLE 2. Extended.

<i>Cedrela</i>				<i>Cordia</i>					
4-yr		Uncut		1-yr		4-yr		Uncut	
Et	D	Et	D	Et	D	Et	D	Et	D
1062	2728	1055	2734	1087	2701	1203	2594	1123	2671
1011	2604	1005	2611	995	2615	1197	2413	1112	2497
1204	3276	1202	3278	1065	3414	1251	3218	1155	3317
1180	2111	1299	2008	1166	2134	1147	2153	1238	2060
1005	3198	1161	3038	1064	3139	1041	3166	1119	3083
995	3388	1119	3257	1022	3354	1102	3281	1072	3307
1197	3330	1261	3262	1160	3372	1318	3206	1182	3352
1140	3400	1184	3360	1133	3407	1140	3399	1117	3423
1012	3005	1090	2925	1064	2952	1033	2985	1054	2963

Factor analysis showed NO_3^- , SO_4^- , and PO_4^- in a cluster, indicating that they were positively correlated with each other. The cluster was orthogonal to HCO_3^- , suggesting that concentrations of HCO_3^- and the other anions varied largely independently. The two groups of anions straddled the cluster formed by the dominant cations, suggesting only weak relationships between concentrations of any given cation and anion.

DISCUSSION

Nitrate retention: loss of resilience with repeated cutting

Although elevated soil solution NO_3^- is a common response to forest cutting (Vitousek and Melillo 1979), leaching losses after cutting in our study were extraordinarily high. Stands under 1- and 4-yr cutting cycles lost an average 374 mmol_c/m^2 of NO_3^- (52.3 kg/ha of N) in the first year after cutting. Ecosystem N loss would have been even higher had these been production systems in which N is exported in biomass. In comparison, NO_3^- leaching of 128 $\text{mmol}_c/\text{m}^2\cdot\text{yr}^{-1}$ occurred after creation of a large gap in secondary tropical forest near our study site (Parker 1985), and a review of nutrient dynamics after clear-cutting in temperate forests showed a maximum NO_3^- loss of 78 $\text{mmol}_c/\text{m}^2\cdot\text{yr}^{-1}$, with most sites losing <25 $\text{mmol}_c/\text{m}^2\cdot\text{yr}^{-1}$ (Mann et al. 1988). Large, persistent NO_3^- losses in our stands are likely related to the unusual properties of Andic soils, which accumulate high amounts of N in stable complexes that form between organic matter and aluminum constituents (Shoji et al. 1993). Nitrogen in such complexes is considered recalcitrant; for example, an average of only 3.5% of the organic N in a range of Japanese Andisols was readily mineralized, in contrast to 8.2% in non-Andic soils (Shoji et al. 1993), but conceivably the disturbance of harvesting and replanting allows some of the recalcitrant N to become mineralized.

We expected that NO_3^- leaching losses in the year after cutting would be much greater in stands on a 4-yr compared to a 1-yr cutting cycle, because there was far more N accumulated in the tissues of 4-yr-old trees

(Bigelow 1998, Hiremath and Ewel 2001). This expectation was met in water year 1995 after the first cutting and replanting of stands on the 4-yr cutting cycle, yet the 43% increase in NO_3^- leaching relative to stands on a 1-yr cutting cycle was small given the much larger biomass of the 4-yr-old compared to 1-yr-old trees. Processes such as microbial immobilization or anion adsorption in subsoil (Sollins et al. 1988) may be playing a role in regulating NO_3^- retention. Cumulative NO_3^- losses, of course, were much greater in stands on a 1-yr cutting cycle because annual cutting and replanting kept the stands from building up the root density and growth demand necessary for effective NO_3^- retention.

Although loss rates from stands on a 1-yr cutting cycle did not diminish over the nine years reported herein, the large losses of NO_3^- (442 $\text{mmol}_c/\text{m}^2\cdot\text{yr}^{-1}$ or 60.5 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ of N) dictate that N availability must eventually wane. Indeed, NO_3^- retention in stands on both 1-yr and 4-yr cutting cycles became progressively less resilient to disturbance over time. Year-to-year and block-to-block variability increased noticeably in 1-yr cutting-cycle stands in the latter years of the experiment (Fig. 7), and in the 4-yr cutting cycle NO_3^- loss rates did not drop as low as in previous rotations once replanted stands were re-established. This loss of resilience of NO_3^- retention after repeated cutting and replanting cautions against simple prediction of N loss rates by multiplying NO_3^- loss measured during an early cutting cycle by the number of anticipated cycles.

Atmospheric inputs of N and subsoil retention of NO_3^- can mitigate NO_3^- leaching losses. A study of deposition using a sampler located <1 km from our study site showed atmospheric N inputs <36 mmol/yr (Eklund et al. 1997), a modest amount equivalent to roughly half the N leached as NO_3^- from our uncut stands. Therefore, atmospheric inputs cannot be considered a major factor offsetting the much larger NO_3^- losses from the stands on 1-yr and 4-yr cutting cycles. The role of anion retention in deep (>1 m) soil layers is less clear; NO_3^- retention in the subsoil has been

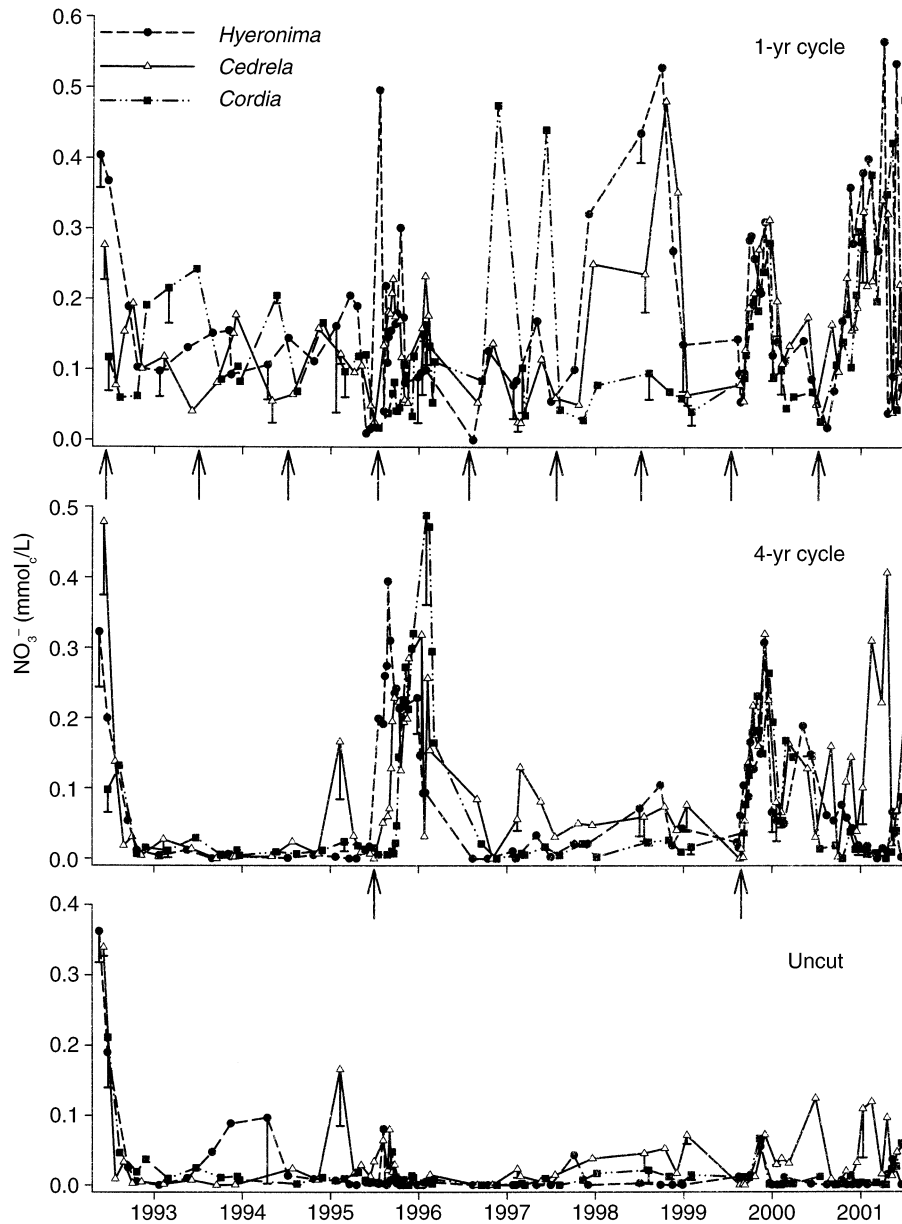


FIG. 6. Nitrate concentrations in soil water draining from tropical tree stands under three cutting cycles. Means and standard errors (shown only once per year for clarity) are presented from three blocks. Arrows indicate cutting and replanting of stands.

documented in other tropical sites (Matson et al. 1987, Cahn et al. 1993, Schroth et al. 1999), but has not been observed locally (Sollins et al. 1994). Given the rapidity with which drainage occurs at our site (Fig. 5), we believe it is unlikely that much subsoil retention has occurred, but cannot discount this possibility. In any event, under the 1-yr cutting cycle, roots do not grow deeper than 1 m in the soil (Haggard and Ewel 1994), and NO_3^- flushed past this point, whether retained in the subsoil or not, is inaccessible and should be considered a permanent loss of the site's nutrient capital.

Besides the overwhelming effects of cutting-cycle length on NO_3^- leaching, there were secondary effects of species. These effects showed up clearly in the uncut stands, where low soil water NO_3^- concentrations (~ 0.01 mmol/L) after establishment were comparable to those in established plantations and undisturbed forests in temperate and tropical regions (Sollins and McCorison 1981, Vitousek and Matson 1984, Van Miegroet et al. 1992, Brouwer 1996, MacDowell et al. 1996). Consistently higher NO_3^- concentrations in *Cedrela* stands beginning in 1997 (Fig. 6) resulted in significantly elevated NO_3^- leaching losses in 1998 and

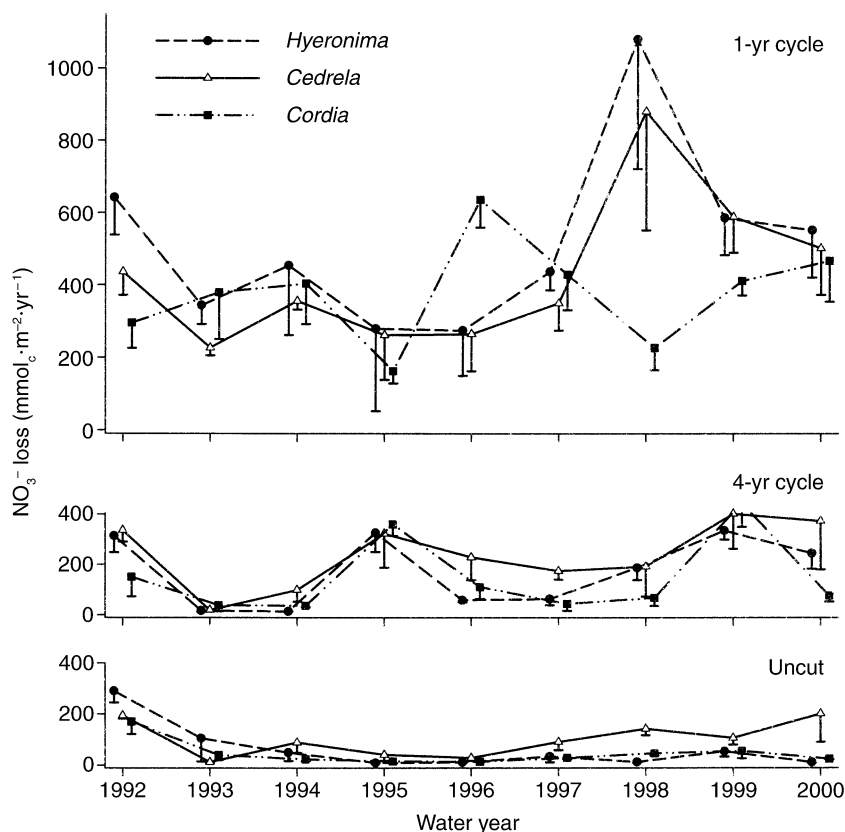


FIG. 7. Annual leaching (means and standard errors of three blocks) of NO_3^- from tropical tree plantations under three cutting cycles. Water year was measured from 1 May to 30 April.

2000, though earlier analyses did not detect differences in leaching among established stands of the three species (Bigelow 1998). It is unusual to find differences in NO_3^- leaching among established stands of plants of the same life-form, none of them with known nitrogen-fixing symbionts. Leaching from *Cedrela* stands is related to seasonal leafing phenology: Elevated NO_3^- in drainage water occurs most commonly in the early months of the year when trees have shed their leaves (Fig. 6).

Controls on cation losses

Concentrations of K^+ and Mg^{2+} in soil solution were comparable to those from other tropical sites (Russell and Ewel 1985, Brouwer 1996, Poels 1987), but Ca^{2+} concentrations were extraordinarily high: Mean Ca^{2+} concentration was $0.55 \text{ mmol}_c/\text{L}$, in comparison to a maximum of $0.15 \text{ mmol}_c/\text{L}$ reported in the other studies. The combined concentration of all cations was $\sim 1 \text{ mmol}_c/\text{L}$ (Fig. 9), more than twice the highest value from 20 temperate forests (Van Miegroet et al. 1992) and three times higher than the maximum value reported on more acid soils at La Selva Biological Station (Johnson et al. 1977). Despite such high solute loads in draining water, cation loss rates were less than maximum rates from undisturbed tropical forests. A review

of hydrologic cation outputs of seven undisturbed tropical forests showed annual Ca^{2+} losses of 49, 101, 124, 430, 813, 2908, and $3247 \text{ mmol}_c/\text{m}^2$; Mg^{2+} losses of 41, 85, 140, 355, 362, 420, and $642 \text{ mmol}_c/\text{m}^2$; and K^+ losses of 9, 24, 31, 38, 55, 125, and $194 \text{ mmol}_c/\text{m}^2$ (Bruijnzeel 1990). In our study, leaching loss rates averaged across all species, treatments, and years were $1580 \text{ mmol}_c \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ of Ca^{2+} , $592 \text{ mmol}_c \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ of Mg^{2+} , and $179 \text{ mmol}_c \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ of K^+ . High Ca^{2+} leaching rates are clearly related to the high values of exchangeable Ca^{2+} at our study site (Hagggar and Ewel 1994), but the origin of the Ca remains unknown because there is no obvious source of unweathered, Ca-rich rock at the site.

Hydrology exerted more control than any other factor on cation leaching rates, as shown by the effect of year on cation leaching ($P < 0.001$; Table 3). Still, the effects of experimental treatments on drainage rates were not large enough to affect leaching of Ca^{2+} and Mg^{2+} . These weak effects were unexpected given that drainage can increase dramatically after conversion of lowland tropical rainforest to other uses (Parker 1985, Abdul Rahim 1988, Malmer 1996). For example, drainage at 1-m depth increased by 49% in first year after conversion of lowland Amazonian rainforest to plantation forest (Klinge et al. 2001). In our experiment,

TABLE 3. Analyses of variance (split-plot/repeated-measures design) on annual leaching losses of nitrate (nine years; log-transformed) and base cations (four years) in drainage water at La Selva Biological Station, Costa Rica.

Source	NO ₃ ⁻				Ca ²⁺			
	df	MS	ES	<i>F</i>	df†	MS	ES	<i>F</i>
Block	2, 4	7.182	0.394	18.2**	2, 4	117 978	794 170	1.28
Species	2, 4	5.741	0.394	14.5*	2, 4	574 219	794 170	0.72
Species × block	4, 12	0.394	0.631	0.65	4, 12	794 170	155 754	5.09*
Cycle	2, 12	102.5	0.631	162***	2, 12	66 047	155 754	0.42
Species × cycle	4, 12	1.796	0.631	2.84	4, 12	131 378	155 754	0.84
Sub-plot error	12	0.631			12	155 754		
Year	8, 32	7.292	0.442	16.4**	3, 12	2 186 804	55 311	39.5**
Year × block	16, 32	0.365	0.442	0.82	6, 12	97 316	55 311	1.75
Year × species	16, 32	0.983	0.442	2.22*	6, 12	319 491	55 311	5.77**
Year × species × block	32, 96	0.442	0.298	1.48	12, 36	55 311	23 288	2.37*
Year × cycle	16, 96	3.937	0.298	13.2**	6, 36	125 900	23 288	5.40*
Year × species × cycle	32, 96	0.748	0.298	2.51*	12, 36	46 069	23 288	1.97
Sub-sub-plot error	96	0.298				23 288		

Note: MS is between-treatment mean square, ES is error mean square, and *F* is the quotient of MS and ES; df are numerator and denominator degrees of freedom, respectively. Boldfaced *F* values are significant at the 0.05 level, and asterisks denote level of significance: * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001.

† These degrees of freedom refer to Ca, Mg, and K.

drainage from frequently cut stands was usually <10%, and at most 20%, greater than drainage from uncut stands. There are several explanations for the modest impact of our experimental treatments on drainage.

First, even by tropical standards, the ~4 m of rain that falls annually at La Selva is large relative to potential evapotranspiration, so fluctuations in ET have limited effect on water budgets. Second, favorable soil physical

TABLE 4. Mean (±1 SE) annual concentrations (mmol_c/L) of base cations in drainage water.

Cation and cycle	Species	1995–1996	1996–1997	1997–1998	1998–1999
Ca²⁺					
1-yr	<i>H. a.</i>	0.512 ± 0.070	0.574 ± 0.090	0.516 ± 0.047	0.607 ± 0.097
	<i>C. o.</i>	0.660 ± 0.060	0.683 ± 0.008	0.423 ± 0.063	0.478 ± 0.055
	<i>C. a.</i>	0.514 ± 0.045	0.546 ± 0.073	0.435 ± 0.017	0.359 ± 0.021
4-yr	<i>H. a.</i>	0.581 ± 0.116	0.467 ± 0.031	0.488 ± 0.094	0.594 ± 0.082
	<i>C. o.</i>	0.668 ± 0.133	0.666 ± 0.086	0.573 ± 0.090	0.529 ± 0.074
	<i>C. a.</i>	0.588 ± 0.060	0.492 ± 0.099	0.466 ± 0.078	0.528 ± 0.057
Uncut	<i>H. a.</i>	0.585 ± 0.121	0.675 ± 0.097	0.526 ± 0.084	0.749 ± 0.119
	<i>C. o.</i>	0.559 ± 0.033	0.570 ± 0.039	0.503 ± 0.032	0.480 ± 0.040
	<i>C. a.</i>	0.453 ± 0.037	0.495 ± 0.036	0.413 ± 0.070	0.561 ± 0.011
K⁺					
1-yr	<i>H. a.</i>	0.075 ± 0.018	0.076 ± 0.016	0.060 ± 0.006	0.060 ± 0.013
	<i>C. o.</i>	0.084 ± 0.005	0.083 ± 0.006	0.054 ± 0.013	0.066 ± 0.003
	<i>C. a.</i>	0.080 ± 0.023	0.075 ± 0.021	0.062 ± 0.021	0.071 ± 0.013
4-yr	<i>H. a.</i>	0.046 ± 0.017	0.044 ± 0.009	0.032 ± 0.006	0.037 ± 0.008
	<i>C. o.</i>	0.085 ± 0.018	0.085 ± 0.014	0.072 ± 0.014	0.073 ± 0.013
	<i>C. a.</i>	0.063 ± 0.021	0.052 ± 0.015	0.046 ± 0.010	0.057 ± 0.018
Uncut	<i>H. a.</i>	0.043 ± 0.017	0.056 ± 0.017	0.027 ± 0.005	0.055 ± 0.019
	<i>C. o.</i>	0.067 ± 0.010	0.061 ± 0.011	0.052 ± 0.013	0.061 ± 0.008
	<i>C. a.</i>	0.052 ± 0.009	0.054 ± 0.005	0.036 ± 0.006	0.078 ± 0.027
Mg²⁺					
1-yr	<i>H. a.</i>	0.198 ± 0.020	0.195 ± 0.018	0.203 ± 0.008	0.218 ± 0.023
	<i>C. o.</i>	0.248 ± 0.012	0.249 ± 0.022	0.144 ± 0.018	0.185 ± 0.011
	<i>C. a.</i>	0.187 ± 0.018	0.180 ± 0.017	0.145 ± 0.012	0.124 ± 0.005
4-yr	<i>H. a.</i>	0.233 ± 0.042	0.181 ± 0.015	0.189 ± 0.032	0.248 ± 0.041
	<i>C. o.</i>	0.290 ± 0.099	0.262 ± 0.063	0.233 ± 0.072	0.222 ± 0.056
	<i>C. a.</i>	0.244 ± 0.055	0.188 ± 0.052	0.177 ± 0.048	0.221 ± 0.063
Uncut	<i>H. a.</i>	0.205 ± 0.044	0.229 ± 0.041	0.176 ± 0.031	0.275 ± 0.053
	<i>C. o.</i>	0.221 ± 0.031	0.216 ± 0.032	0.179 ± 0.043	0.189 ± 0.030
	<i>C. a.</i>	0.173 ± 0.009	0.182 ± 0.013	0.138 ± 0.028	0.226 ± 0.008

Notes: The period 1995–1999 encompasses the second cycle of stands on a 4-yr cutting cycle. Abbreviations are: *H. a.*, *Hyeronima alchorneoides*; *C. o.*, *Cedrela odorata*; and *C. a.*, *Cordia alliodora*.

TABLE 3. Extended.

K ⁺			Mg ²⁺			
MS	ES	F	MS	ES	F	F
44 083	24 883	1.77	147 861	224 209		0.65
28 412	24 883	1.14	111 962	224 209		0.49
24 883	7504	3.31*	224 209	94 329		2.37
33 234	7504	4.42*	98 595	94 329		1.04
8140	7504	1.08	19 729	94 329		0.20
7504			94 329			
29 250	885	33.0**	284 457	9326		30.5**
1173	885	1.32	16 670	9326		1.78
2725	885	3.07*	49 314	9326		5.28**
885	1639	0.54	9329	5257		1.77
2712	1639	1.65	24 146	5257		4.59**
590	1639	0.36	8933	5257		1.69
1639			5257			

characteristics mean that water is usually available in the upper soil layers and can be accessed even by shallowly rooted vegetation, tending to even out transpiration between tall and short vegetation. Additionally, underestimation of transpiration in uncut stands in drier years due to a modeling constraint on extraction of water from deep in the soil profile would have slightly limited our ability to detect true differences in drainage among treatments. The cumulative effect of these fac-

tors was to limit the measurable impacts of our experimental treatments on drainage and associated nutrient leaching.

Hydrological effects aside, the modest impact of our experimental manipulations of vegetation on cation leaching was surprising on two counts. First, NO₃⁻ production is an important cause of cation leaching in a range of systems (Nye and Greenland 1960, Raney 1960, Likens et al. 1969), because hydrogen ions pro-

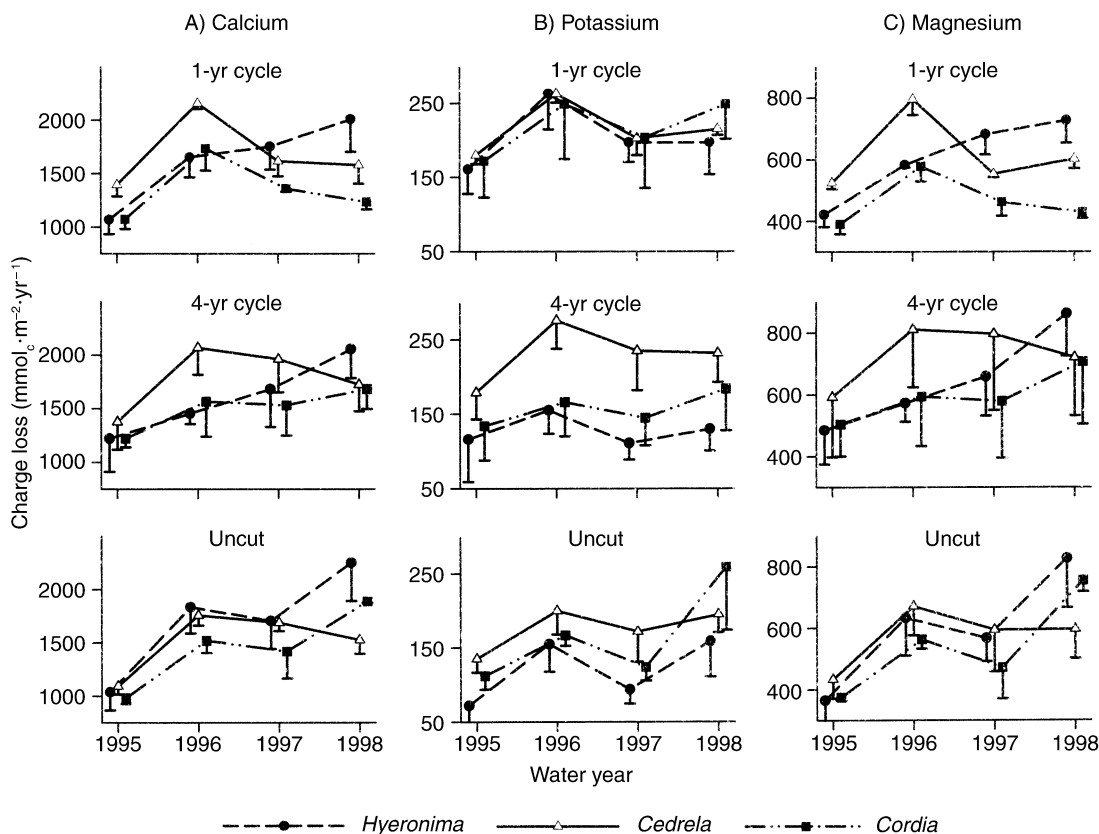


FIG. 8. Annual leaching of Ca²⁺, K⁺, and Mg²⁺ (means and standard errors of three blocks) from tropical tree plantations under three cutting cycles. Water year was measured from 1 May to 30 April.

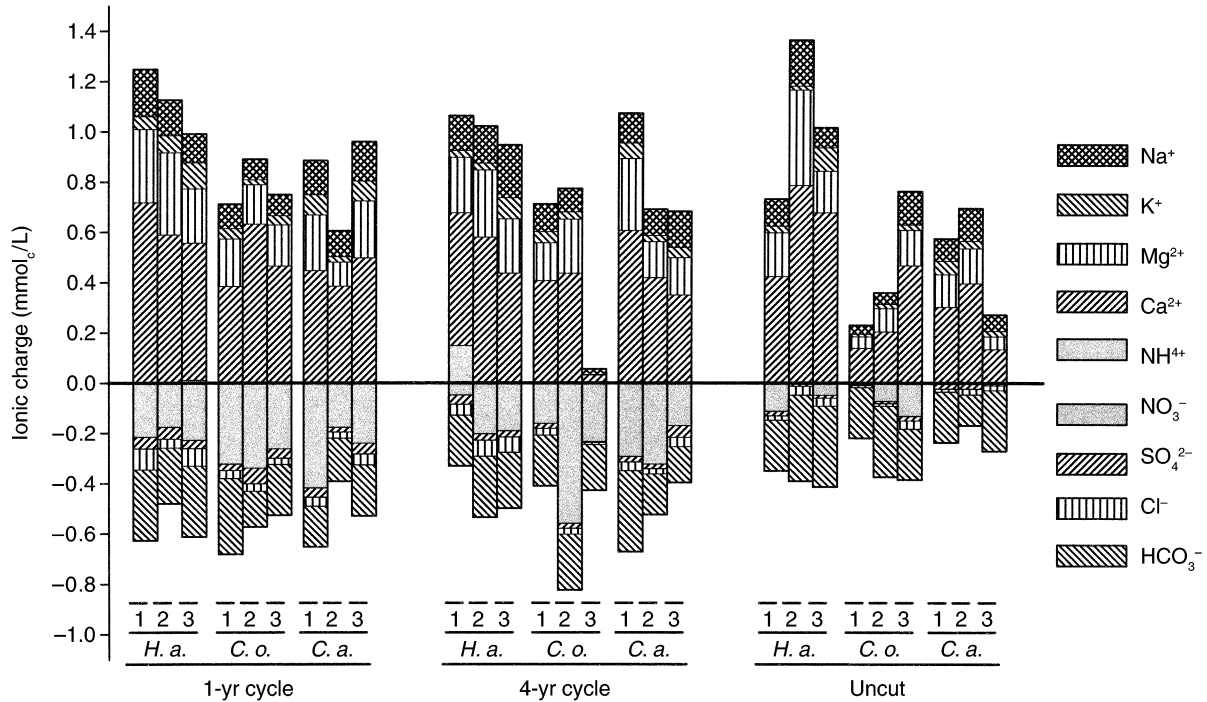


FIG. 9. Charge balance of ionic species in drainage water collected December 1999. Tree species are indicated by first initials: *H. a.*, *Hyeronima alchorneoides*; *C. o.*, *Cedrela odorata*; *C. a.*, *Cordia alliodora*. Groups of three adjacent bars represent three blocks. Phosphate and Al^{3+} are not represented because bar thickness would be less than the thickness of a line.

duced during nitrification can exchange with base cations on soil colloid complexes, bringing the cations into solution where they are vulnerable to leaching. Our cutting treatments had a strong effect on NO_3^- leaching, yet there was no concomitant increase in leaching of base cations other than K^+ . Second, nutrient

uptake affects leaching because a molecule once taken up from soil solution and stored in biomass is more resistant to being leached. In highly weathered, acid soils of the southeastern United States, differential uptake and sequestration of base cations among vegetation types can be a major determinant of Ca leaching (Johnson and Todd 1990). There were large differences in cation sequestration among our experiment treatments, given that after each cut in stands on 1- and 4-yr cutting cycles sequestration in living biomass of all nutrients was reduced to nil. Several factors must be invoked to account for the negligible impact of our cutting-cycle treatments on Ca^{2+} and Mg^{2+} leaching.

High solution strength moderated increases in negative charge from excess NO_3^- production due to cutting. For example, a 20-fold increase in NO_3^- , from 0.01 to 0.2 $mmol_c/L$, would only engender a 20% increase in solution cation charge, e.g., from ~ 1 to 1.2 $mmol_c/L$. Further, such increases in solution cation charge tended to be distributed evenly among cations (indicated by clustering of cation concentrations in Fig. 10), diminishing the impact on leaching of any individual cation. Concentrations of K^+ , the only cation with increased leaching under the cutting treatments, were poorly correlated with NO_3^- concentrations (Fig. 10), implicating a mechanism other than NO_3^- production for elevated leaching. Lack of uptake effects on cation leaching also is likely related to high cation exchange capacity (300–400 $mmol_c/kg$) and high base

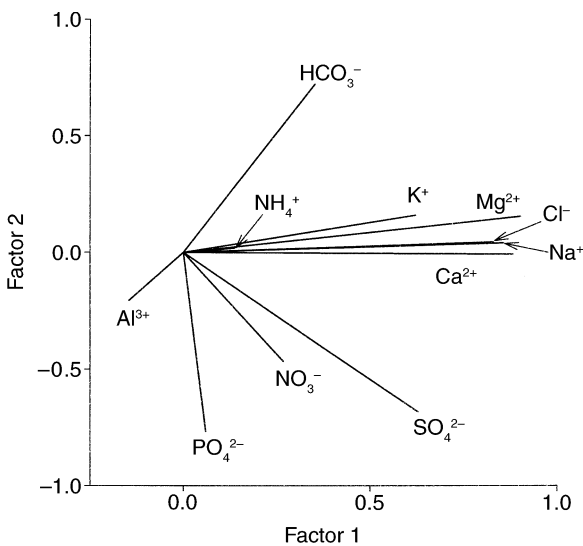


FIG. 10. Factor analysis of ionic species in drainage water collected in December 1999. Factors 1 and 2 explain 37% and 17% of total variance, respectively.

saturation (30–50%) in our soils. In such fertile soils, a cation taken up from soil solution can be immediately replaced by one from the exchange complex, countering any potential effect on leaching (Nye and Greenland 1960). In contrast, on the acid Ultisols of the southeastern USA where Ca uptake had a strong effect on leaching, cation exchange capacity in the A horizons was 41 mmol_c/kg and base saturation was 39% (Johnson et al. 1985). Finally, net rates of accumulation at our site were small compared to leaching; after eight years of growth there was an average Ca²⁺ content of 1800 mmol_c/m² in biomass of uncut stands, little more than the 1580 mmol_c/m² of Ca²⁺ that was leached in an average year (Fig. 8). In every case, the reason for lack of cutting-cycle effects on Ca²⁺ and Mg²⁺ can be traced to the tremendous native fertility of the study site soil.

A further concern in soils with pH-dependent, variable charge such as ours is that nitrification will decrease soil pH (Van Miegroet and Cole 1984), resulting in loss of negative charge density on soil colloid complexes and subsequent wholesale flushing of cations into soil solution (Sollins et al. 1988, 1994). Again, the well-buffered nature of the soil solution made it resistant to changes in pH from experimental treatments, and there was no evidence of rapid leaching of cations such as would be expected with progressive loss of cation exchange capacity.

Short-cycle cropping and sustainability

A central concern with short-cycle cropping systems is that stands spend a large portion of each cycle becoming established, allowing leaching of nutrients prior to full-site occupancy (McColl and Powers 1984, Raison and Crane 1986, Heilman 1992). In the present study, NO₃⁻ leaching patterns suggest that biotic control over nutrient losses had become largely re-established within 1.5 years of cutting and replanting stands, which is consistent with trends in re-establishment of root length and leaf area. Root length density (L_v) in established stands was lower than in many other systems; mean L_v in the upper 1.0 m of soil was 0.09, 0.03, and 0.05 cm/cm³ respectively for *Hyeronima*, *Cedrela*, and *Cordia*. In comparison, tree plantations can have L_v of 0.1–1.0 cm/cm³ (Van Rees and Comerford 1986, Hughes and Gandar 1993, Jama et al. 1998) or ≥ 1 cm/cm³ (Roberts 1976, Heilman et al. 1994) in the upper 1.0 m, although fruit orchards on fertile soils can have $L_v < 0.1$ cm/cm³ (Hughes et al. 1995).

In areas of the wet tropics such as our study site, where heavy storms can occur daily, it is likely that an L_v of 0.1 cm/cm³ in the upper 0.1 m of soil (where nitrification is most rapid) is necessary for effective NO₃⁻ retention. We obtain this result from depletion zone theory (Nye and Tinker 1977). In a stand with L_v of 0.1 cm/cm³, the mean distance to the midpoint between neighboring roots is 1.8 cm ($= (\pi L_v)^{-0.5}$), and

in one day a molecule of NO₃⁻ can diffuse up to 1.9 cm ($= 2 \times (10^{-5} \text{ cm}^2 \cdot \text{s}^{-1} \times 1 \text{ day})^{0.5}$) or far enough to meet the depletion zones formed by neighboring roots. Stands of *Cordia* had almost reached an L_v of 0.1 cm/cm³ in the upper 0.1 m within 12 mo of planting, *Cedrela* stands approached an L_v of 0.1 cm/cm³ within 24 mo of planting, and although *Hyeronima* had $L_v \geq 0.4$ cm/cm³ within 6 mo of planting, its roots initially were highly clumped around individual plants (Haggard and Ewel 1995). Despite this variation among species in the time to reach adequate L_v for NO₃⁻ retention, the values are reasonably close to the 1.5-year point at which nutrient retention resumed.

An infrastructure of roots must be accompanied by demand in the form of growing plants for effective extraction of NO₃⁻ from the soil, and LAI is an indicator of the strength of such demand. Because LAI did not peak until ~ 2.5 yr after cutting and planting (Fig. 2), it is likely that full demand strength did not develop until about this time; thus, the stands' demand for NO₃⁻ lagged behind the ability of root systems to take it up. Nevertheless, the re-establishment of stand-level control over leaching of NO₃⁻ by 1.5 yr indicated that demand was sufficient to halt most NO₃⁻ leaching by this time. Thus, stands on a 4-yr cutting cycle spend one-third to one-half of the cycle in the vulnerable pre-establishment phase. Stands on a 1-yr cutting cycle, of course, were continually maintained in the pre-establishment phase resulting in massive long-term NO₃⁻ leaching losses.

Are remedies available to counter the loss of soil nutrients under short-cycle cropping? In the context of industrial short-rotation forestry, it has been suggested that the cost of replacement of nutrients removed in harvested parts would be negligible (Wise and Pitman 1981, Mackensen and Fölster 2000). This perspective avoids the question of hydrological losses of nutrients, for which few data are available, and the present study suggests that such losses may be larger than anticipated. In any event, there are often impediments to fertilization of tree crops, especially for small-holders, so that self-sustaining systems are preferable (Nambiar and Brown 1997). Further, it may not be feasible to restore native soil fertility by application of inorganic fertilizer (Hiremath and Ewel 1998): An experiment is underway at our study site to test this proposition.

The seasonal pattern of rainfall and drainage in the Atlantic lowlands of Central America suggests that harvesting and planting activities might be timed for the drier season, thereby confining soil disturbance to periods when drainage rates are low (Fig. 5). Yet the onset of the wet season is the traditional time for planting of perennial crops and for good reason. Even the comparatively mild dry season at our study site is enough to desiccate young plants, and the pulse of nitrification that occurs with the onset of the wet season (Greenland 1958, Hiremath and Ewel 2001) is probably important for establishment of young plants. Consequently, there

is limited ability to moderate leaching losses by changing planting to a different season.

CONCLUSION

Andisols constitute <1% of soils in the developing world, but have an importance that belies their small area because they are among the most productive and densely populated soil types, in some regions supporting densities >400 people/km² (van Wambeke 1992, Shoji et al. 1993). Our study, in tropical tree plantations on an Andisol in Costa Rica, showed that disturbance frequency was more important than massiveness of the stand structure disrupted by cutting in determining average long-term rates of NO₃⁻ leaching. Under the most frequent disturbance regime, huge leaching losses of NO₃⁻ were sustained over almost a decade, though there was progressive loss of resilience in NO₃⁻ retention with repeated disturbance. Effects of tree species on leaching, although less drastic than disturbance frequency, were large enough to warrant consideration from the standpoint of plantation management. In contrast to many other systems, leaching of base cations (other than K⁺) due to elevated NO₃⁻ leaching did not prove to be a concern. Given the impact of disturbance frequency on nutrient leaching, development of cropping systems that minimize disturbance frequency, possibly through incorporation of perennial plants, should be a priority for these soils.

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