

SPECIES AND ROTATION FREQUENCY INFLUENCE SOIL NITROGEN IN SIMPLIFIED TROPICAL PLANT COMMUNITIES

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Abstract. Among the many factors that potentially influence the rate at which nitrogen (N) becomes available to plants in terrestrial ecosystems are the identity and diversity of species composition, frequency of disturbance or stand turnover, and time. Replicated suites of investigator-designed communities afforded an opportunity to examine the effects of those factors on net N mineralization over a 12-year period. The communities consisted of large-stature perennial plants, comprising three tree species (*Hyeronima alchorneoides*, *Cedrela odorata*, and *Cordia alliodora*), a palm (*Euterpe oleracea*), and a large, perennial herb (*Heliconia imbricata*). Trees were grown in monoculture and in combination with the other two life-forms; tree monocultures were subjected to rotations of one or four years, or like the three-life-form systems, left uncut. The work was conducted on fertile soil in the humid lowlands of Costa Rica, a site with few abiotic constraints to plant growth. Rates of net N mineralization and nitrification were high, typically in the range of 0.2–0.8 $\mu\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$, with net nitrification slightly higher than net mineralization, indicating preferential uptake of ammonium (NH_4^+) by plants and microbes. Net rates of N mineralization were about 30% lower in stands of one of the three tree species, *Hyeronima*, than in stands of the other two. Contrary to expectations, short-rotation management (one or four years) resulted in higher net rates of N mineralization than in uncut stands, whether the latter were composed of a single tree species or a combination of life-forms. Neither additional species richness nor replenishment of leached N augmented mineralization rates. The net rate at which N was supplied tended to be lowest in stands where demand for N was highest. Careful choice of species, coupled with low frequency of disturbance, can lead to maintenance of N within biomass and steady rates of within-system circulation, whereas pulses, whether caused by cutting and replanting or by the phenological traits of the species selected or combined, subject N supplies to leaching loss.

Key words: biodiversity; *Cedrela*; *Cordia*; *Costa Rica*; disturbance; *Euterpe*; *Heliconia*; *Hyeronima*; mineralization; nitrification; nitrogen; plant crop rotation.

INTRODUCTION

Nitrogen (N) is the inorganic nutrient required by plants in far greater quantities than any other, and it routinely limits biological processes. Interactions between plants and N availability are of particular interest because of reciprocal effects: N availability affects plant performance, and plants in turn affect N availability. Not surprisingly, plant species having different physical (e.g., fine-root density; Wedin and Tilman 1990) and chemical (e.g., carbon:lignin; Gower and Son 1992) traits affect soil N in different ways (Stone 1975, Smith et al. 1998). Furthermore, many ecological processes are influenced by community composition, a topic at the heart of current debate concerning biodiversity and ecosystem functioning (Hooper et al. 2005). There is no a priori reason to believe that N availability should not

be responsive to diversity, especially if species partition resources spatially or temporally.

Superimposed on those plant/community–soil interactions are temporal effects that manifest themselves at different scales: seasons, rate of stand turnover or disturbance, and successional trends. For example, increases of N availability often accompany the onset of rains in the seasonally dry tropics (Raghubanshi et al. 1990, Garcia-Méndez et al. 1991), a phenomenon likely due to lysis of microbes following soil rewetting (Kieft et al. 1987). Likewise, soil disturbance (logging, tree falls, slash and burn) commonly results in an increase in N mineralization (e.g., Vitousek et al. 1979, Vitousek and Andariese 1986, Vitousek and Denslow 1986, Matson et al. 1987). Following disturbance-induced pulses, young secondary successional ecosystems typically have relatively low rates of net N mineralization, gradually returning to the higher levels that characterize more mature ecosystems (e.g., Robertson 1984, Vitousek et al. 1989).

Long-term data from replicated, investigator-designed ecosystems in the humid tropical lowlands afforded an opportunity to examine several of these effects in a single

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study. The routine estimates of soil N availability were in situ net mineralization and nitrification. Although net mineralization is an imperfect measure of N availability because plants use organic N (Lipsom and Näsholm 2001) and compete with microbes for inorganic N (Kaye and Hart 1997), it remains a useful measure for comparing sites and treatments. This is particularly the case where N cycles predominantly through inorganic forms, especially nitrate (NO_3^-), such as lowland tropical forests (Schimel and Bennett 2004: Fig. 2D). Examples of the useful application of net N mineralization, in addition to those related to disturbance and succession cited above, include comparisons among ecosystems (e.g., Melillo 1981, Matson and Vitousek 1987, Marrs et al. 1988, Reich et al. 1997, Owen et al. 2003), across short (e.g., DiStefano and Gholz 1989, Idol et al. 2003) and long (Vitousek 2004) chronosequences, between treatments such as forest harvesting and site preparation (e.g., Burger and Pritchett 1984, Waide et al. 1988, Piatek and Allen 1999), and in response to changes in land use (e.g., Reiners et al. 1994, Neill et al. 1997, Scowcroft et al. 2004).

The tropical lowland site where the work reported here was conducted is one in which N is abundant and processes are both rapid and uninterrupted by cold or drought. This paper presents the results of 12 years of in situ net N mineralization measurements on replicated plots. During the course of the study, N was of particular interest with respect to nutrient-use efficiency (Ewel and Hiremath 1998, Hiremath 2000, Hiremath and Ewel 2001, Hiremath et al. 2002), leaching losses (Bigelow et al. 2004), productivity and resource partitioning (Haggard and Ewel 1997), and soil organic-matter dynamics (Russell et al. 2004). Although net N mineralization was the routine measure of N availability, it was supplemented with other measures to meet the needs of particular studies (e.g., Reich et al. 2003, Silver et al. 2005). The net N mineralization data also provided a context for the more detailed, process- and mechanism-oriented N-transformation work at the site of Carney et al. (2004), Carney and Matson (2005, *in press*), and Silver et al. (2005).

In addition to providing foundation data for the kinds of studies enumerated above, the 12-year data set made it possible to test a number of general predictions regarding net rate of N mineralization: (1) rates would increase with time in uncut plots (as is presumably typical in succession), (2) rates would be higher in three-life-form plots than in monocultures (due to higher combined productivity fueling mineralization), (3) rates would decline with time in plots cut and replanted repeatedly (due to reduction in substrate for mineralization and eventual N impoverishment), (4) rates in plots cut and replanted at intermediate time steps would be intermediate between those cut annually and those that were uncut, (5) rates would be higher in the soil beneath the species with the most N-rich foliage (whose N-rich litter drives mineralization), and (6) rates would be

rejuvenated in fast-rotation plots where leached N was replaced by fertilization (due to N uptake by the trees, whose litter would then refuel microbial transformation of organic matter). Although a number of those predictions are so well established as to be considered valid generalizations by many ecologists, the results described here revealed more exceptions than validations.

METHODS

Site description

The field research was conducted at La Selva Biological Station (10°26' N, 83°59' W), Costa Rica. Mean annual temperature is 28.5°C and mean annual precipitation is ~4000 mm. January through March are drier months, even though each of them receives >100 mm of rainfall (Sanford et al. 1994, Matlock and Hartshorn 1999).

In 1991, experimental plantations were established after felling and burning the second-growth vegetation on an abandoned cacao plantation. The site is a level alluvial terrace, 41 m above sea level. The soil, which shows evidence of several depositional sequences, is a eutric Hapludand (Weitz et al. 1997). Like many Andisols, its horizons show little development, and it is extremely fertile, especially considering the high rainfall of the area. Cation exchange capacity is high (>400 mmol_c/kg), as are base saturation (>50%, dominated by calcium) and concentrations of total N (~0.3–0.4%), total soil organic carbon (25–37 mg/g), KCl-extractable N (>13 µg/g), and extractable phosphorus (14.4–>20 µg/g) (Haggard and Ewel 1994, 1995, Hiremath and Ewel 2001, Russell et al. 2004).

The plantations were part of a long-term study to examine the effects of rotation frequency and life-form diversity on soil fertility (e.g., Bigelow et al. 2004, Russell et al. 2004), plant–pest interactions (e.g., Hummel 2000, Mata 2002), and productivity (e.g., Haggard and Ewel 1994, 1997, Hiremath and Ewel 2001). Effects of rotation frequency were assessed by comparing three kinds of monospecific tree plantations: (1) cut and replanted annually, (2) cut and replanted every four years, and (3) left uncut, while effects of life-form diversity were assessed by comparing the uncut monocultures with uncut plots containing a tree species plus two additional life-forms. Cut vegetation was not removed from plots, and the same species was replanted at the same density as the original immediately following cutting.

Three such experiments were run, each using a different tree species: *Hyeronima alchorneoides* Allemão (Euphorbiaceae), *Cedrela odorata* L. (Meliaceae), and *Cordia alliodora* (R. & P.) Cham. (Boraginaceae). These species were chosen because they represent a wide range of architecture, physiology, and phenology. *Hyeronima* is a long-lived emergent tree that produces a dense heartwood. It is evergreen and sustains a dense crown that is very effective at capturing light. *Cedrela* is dry-

TABLE 1. Stand structural characteristics for three dominant tree species.

Cut frequency	Life-forms	Height (m) [†]	Basal area (m ² /ha)	LAI
<i>Hyeronima</i>				
Annual	Tree	1.8 [7.8]	1.7	1.7
Every 4 years	Tree	11.1 [14.2]	15.3	4.0
Uncut	Tree	23.1 [29.1]	27.0	2.7
Uncut	Tree, palm, herb	23.3 [29.4], 6.0 [17.6], n.a.	26.3, 14.3, n.a.	6.1
<i>Cedrela</i>				
Annual	Tree	1.3 [4.9]	2.1	1.0
Every 4 years	Tree	8.9 [17.2]	12.8	1.7
Uncut	Tree	17.4 [29.2]	19.3	1.7
Uncut	Tree, palm, herb	19.8 [32.5], 8.5 [21.4], n.a.	7.0, 31.1, n.a.	5.3
<i>Cordia</i>				
Annual	Tree	1.3 [5.4]	1.0	0.9
Every 4 years	Tree	11.1 [19.2]	14.2	1.6
Uncut	Tree	20.4 [31.1]	23.0	1.9
Uncut	Tree, palm, herb	16.3 [28.2], 7.7 [24.9], n.a.	8.9, 31.5, n.a.	4.5

Notes: Values are means at ends of rotations (1- or 4-year) or study (12–13 years for uncut stands). Basal areas and leaf area indices (LAI) are means of three replications at each rotation.

[†] Heights are averages of all trees and palms across all replications. Data are means, with maximum height in brackets; n.a. = not applicable.

season deciduous and produces a medium-density, highly valued wood. Its pinnately compound leaves are ~0.5 m long, and its crown geometry is irregular due to repeated attacks by a mahogany shoot borer (*Hypsipyra*). *Cordia* is a fast-growing colonist of abandoned agricultural lands and an invader of pastures on fertile soils. In sharp contrast with *Hyeronima*, it has an open, tiered crown that permits substantial light to penetrate to the understory. The polycultures were planted additionally with two very different monocots: a large, perennial herb, *Heliconia imbricata* (Kuntze) Baker (Heliconiaceae), at half the density of the trees, and a multi-stemmed palm, *Euterpe oleracea* Mart (Arecaceae), at one fourth the density of the trees. *Heliconia* has long (>2 m), erect, banana-like leaves and achieves a height of 6 m. This colonist of openings and clearings produces multiple monocarpic ramets. *Euterpe*, which attains a height of 25 m, is prized for its fruits in the lower Amazon, where it is native. All species except *Euterpe* are native to the immediate surroundings.

In each plantation, including the three-life-form polycultures, the trees were planted at high density: 2887 trees/ha. Plantations older than three years were thinned lightly at irregular intervals to avoid stand stagnation without diminishing use of available resources. The design was a split plot, with each treatment (three rotation frequencies and two levels of life-form diversity) represented in three blocks of each of the three tree species. Subplots subjected to annual rotations were 10 × 40 m, those cut every 4 yr were 20 × 40 m, and those that were uncut were 30 × 40 m. Additional details on layout, seed sources, and species traits are in Haggard and Ewel (1994, 1995, 1997) and Hiremath and Ewel (2001). Typical stand structure values are given in Table 1.

After eight rotations (i.e., felling without biomass removal followed immediately by replanting with seedlings of the same species), data indicated that the plots

subjected to annual cutting had lost large amounts of N to leaching: ~40 kg/ha for each of eight years (Bigelow et al. 2004). At that point (in 1999), the annual-rotation plots were divided in half: one portion was fertilized with N and the other remained unfertilized. Fertilizer was applied every two weeks using a liquid formulation of urea plus NO₃⁻ (31% N, volume/volume) at a rate of 320 kg·ha⁻¹·yr⁻¹ (i.e., approximately the amount leached over the preceding eight years). The fertilizer was applied uniformly across the soil surface, not concentrated around individual plants, and an equal volume of water was sprayed concomitantly on control plots.

Nitrogen mineralization

Because of our interest in determining the temporal dynamics and relative magnitudes of potential N limitations in the plantations, we routinely measured rates of net N mineralization and nitrification from 1991 to 2003. Measurements were made every two months during the first two years and quarterly thereafter. At each date, N mineralization was measured in 36 plots (45 plots beginning with the N fertilization experiment in 1999): four (1991–September 1999) or five (September 1999 forward) treatments (1-yr rotation with and without added N, 4-yr rotation, uncut monoculture, and uncut polyculture) × three tree species (*Hyeronima*, *Cedrela*, *Cordia*) × three replications of each treatment.

Two randomly selected points were chosen in each plot, and two sharpened PVC pipes, 10 cm in diameter by 30 cm long, were driven into the ground to a depth of 20 cm adjacent to each point. One pipe was removed and its soil was extruded (for initial assessment of NO₃⁻ and ammonium, NH₄⁺); the other pipe was loosely covered with a plastic bag (to exclude rainfall) and left in situ for ~21 d. The 20-cm sampling depth and 21-d incubation period were chosen based on results of a 1991 pilot study at the site (Haggard and Ewel 1994); nitrification was

approximately linear over a 21-d incubation period and declined thereafter. The extruded soil from each initial core was taken to the laboratory for extraction of NO_3^- and NH_4^+ and determination of moisture content (by measuring mass loss upon oven drying to constant mass at 105°C). Extraction consisted of shaking 15 g of soil in 100 mL of 2 mol/L KCl for 1 h then filtering through number 42 Whatman filter paper. Two drops of chloroform (CHCl_3) were added to each extract prior to refrigeration. The covered cores were left in the field for ~21 d at which time they too were extruded and extracted like the initial cores. Following field measurements, the sample points were permanently marked to avoid inadvertent selection of the same point at future sampling dates.

Over the 12-year study, analyses of NO_3^- and NH_4^+ were done in five laboratories, all of which used standard procedures recommended by the manufacturers of the autoanalytic instruments employed (Technicon and Lachat). Cross-calibration among laboratories was not possible (because of sequential changes of equipment among them), but samples included commercially prepared NO_3^- standard solutions (Fisher Scientific). Those same laboratories and instruments were also used for analysis of N in plant tissues, and each set of plant samples included digests prepared from National Institute of Standards and Technology standards of peach leaves (SRM 1547) and pine needles (SRM 1575). Concurrence with standards was satisfactory in all cases except samples taken in late 2003 and early 2004; unsatisfactory results from the commercial laboratory that analyzed those samples led to truncation of the data set in June 2003 because of concern that longer-term storage and reanalysis of the mineralization extracts would yield invalid results.

Statistical analyses

Nitrate and NH_4^+ values obtained from the two sample points within each plot were averaged prior to statistical analysis. Net mineralization was calculated as the sum of NO_3^- plus NH_4^+ after incubation minus the sum of initial NO_3^- plus NH_4^+ , and nitrification was determined by subtracting initial NO_3^- from post-incubation NO_3^- . Mineralization and nitrification were converted to daily rates by dividing the amounts by the length of the incubation period, which was usually 21 days but ranged from 19 to 22 days.

Because of the size of the data set (>2800 values) and the time period covered (12 years), substantial care was exercised in screening the data. Basic statistical parameters and frequency histograms (SAS: UNIVARIATE procedure [SAS Institute 1999]) were examined by tree species and treatment. Extreme values on box-and-whisker plots were examined individually in the context of related pre- and post-incubation values from the same sampling point. The approach was conservative: all low values (i.e., below the detection limit of 0.1 $\mu\text{g/L}$) were retained without question, as I had no objective way to

distinguish valid data from laboratory error at the low end of the scale; only two of >2800 data points, each a mean of two measurements, were discarded as presumed outliers at the high end of the scale.

Frequency distributions of the NO_3^- and NH_4^+ data were skewed to the right, so the data were log-transformed prior to analysis. The data were analyzed (SAS: MIXED procedure [SAS Institute 1999]) as a split-plot experimental design with blocks as a random factor, tree species as the whole-plot factor, and treatment (rotation frequencies of 1 year, 4 year, or uncut, and life-form diversity of 1 or 3 types) as the subplot factor. Because of multiple measurements over time at each block-tree species-treatment combination, a repeated-measures analysis was performed fitting a fixed effect for each of the 39 measurement times and allowing for serial correlation in the covariance structure. The effect of N addition to the 1-year rotation treatment was analyzed similarly, with fertilizer addition (0, +) as the subplot factor, and $n = 11$ measurement times covering the period subsequent to the onset of fertilization.

RESULTS

Pre-incubation NO_3^- N concentrations were in the range of <0.1 $\mu\text{g/L}$ to 25 $\mu\text{g/L}$, and those of NH_4^+ N ranged from <0.1 to 16 $\mu\text{g/L}$. Nitrate dominated the background N pools in the soil, as there were far more low concentrations, and therefore much lower median values, of NH_4^+ N than of NO_3^- N (Fig. 1a and b). Rates of net N mineralization and nitrification were high and quite similar (Fig. 1c and d). Net nitrification, which tended to be slightly higher than mineralization, was typically in the range of 0.2–0.8 $\mu\text{g N}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$, with mean values >1.0 $\mu\text{g N}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ not uncommon (Fig. 1c). Net NO_3^- immobilization occurred in only 6.4% of the assays. The fact that net nitrification regularly exceeded net mineralization suggests that plants and microbes preferentially took up NH_4^+ . Also, because the low concentrations of NH_4^+ were associated with relatively large changes in the concentration of NO_3^- , it is apparent that there was substantial through flow of soil NH_4^+ , with the pool created by breakdown of organic matter quickly drawn down by the action of autotrophic bacteria, oxidizing it to NO_3^- . This was true across all treatments, all three tree species, and throughout the 12-year study.

Net N mineralization rates (Fig. 1d) are summarized (means of three blocks) as a function of time for each of the four main treatments, by species, in Fig. 2 (*Hyeronima alchorneoides*), Fig. 3 (*Cedrela odorata*), and Fig. 4 (*Cordia alliodora*). Time was a highly significant contributor to variance in all analyses, and this is apparent on Figs. 2–4 in two ways. First, N mineralization rates in most treatments tended to be higher during the early years of the study than in the last decade, when they declined to relatively lower rates. Second, although Figs. 2–4 show indications of time-

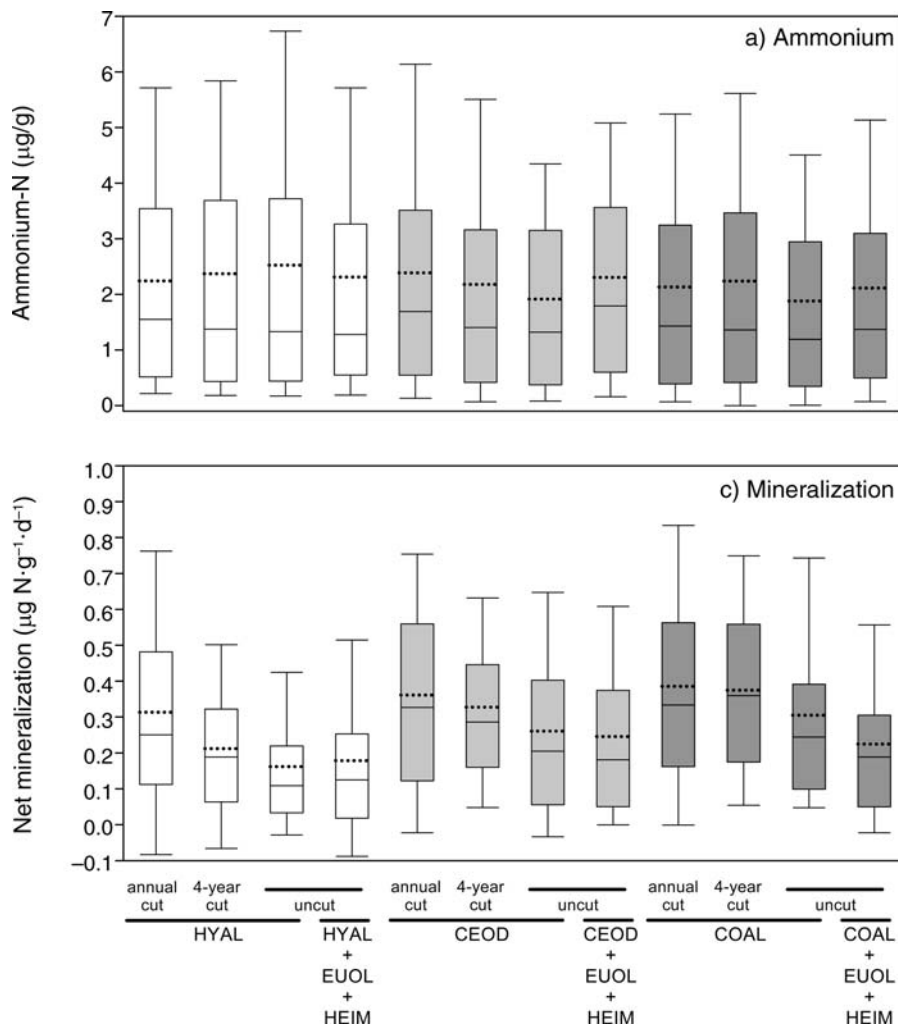


FIG. 1. Amounts and net rates of transformations of soil N in 12 experimental ecosystems. Plots show means (solid horizontal lines), medians (dotted horizontal lines), 25th and 75th percentiles (box ends), and 10th and 90th percentiles (whiskers) compiled from all values over a 12-year time course. Measurements were made every three months. Species, abbreviated in capital letters, are: HYAL, *Hyeronima alchorneoides*; CEOD, *Cedrela odorata*; COAL, *Cordia alliodora*; EUOL, *Euterpe oleracea*; and HEIM, *Heliconia imbricata*. Note scale differences between (a) ammonium and (b) nitrate panels.

dependent oscillations (see, for example, Fig. 2, lower panels), there was no significant effect due to season (in any treatment) or to time since cutting (in the case of the 1- and 4-yr cutting-cycle treatments). Among the covariance parameters, serial correlation between measurements did not differ significantly from zero. It is likely that those apparent oscillations reflect combined impacts of cutting cycles, soil moisture, and other time-dependent variables, but it is not possible to disarticulate the factors involved with this data set.

Tree species and cutting frequency each strongly affected rates of N mineralization (Table 2). Mineralization rates were almost 30% lower in plantations dominated by *Hyeronima* than in those dominated by *Cedrela* or *Cordia* (Table 2, Fig. 5). Stands cut annually or every four years had significantly higher rates of N

mineralization than those that were uncut (Table 2, Fig. 6). Rates of N mineralization did not differ significantly between uncut monocultures and stands composed of three life-forms (Table 2, Fig. 6). Somewhat surprisingly, four years of biweekly additions of N fertilizer to the annual-rotation plots, amounting to $320 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, had no significant affect on net mineralization rates, even after >3 years of applications ($F = 1.36$, $P > F = 0.89$).

DISCUSSION

The rates of N mineralization observed are high by global standards, though not as high as rates reported from nearby forests, also at La Selva, by Vitousek and Denslow (1986), who worked in intact forest on an Ultisol, in contrast to the recent alluvium where I

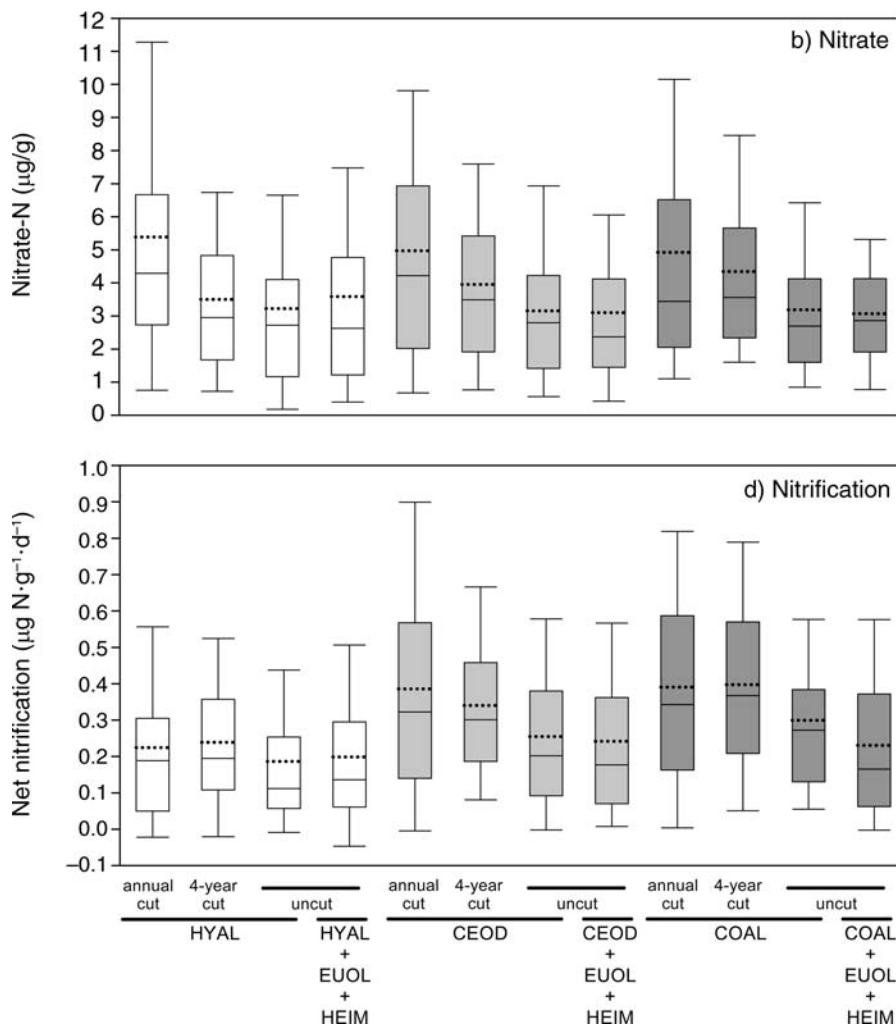


FIG. 1. Continued.

worked. Their values, based on sequential monthly incubations to a soil depth of 15 cm, ranged from 647 to 922 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, whereas my values, based on annualized mean daily rates to a depth of 20 cm, rarely exceeded 500 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. Marrs et al. (1988) sampled soil at an elevation of 100 m at La Selva and measured rates only slightly lower than those reported by Vitousek and Denslow (1986). Likewise, Reiners et al. (1994) measured N transformations in an Ultisol subjected to four land uses at and near La Selva, and found rates in mature forest that were higher than those reported here, but their rates from abandoned pasture are comparable to my findings. It is tempting to attribute differences to vegetation maturity and diversity, but methodology, sampling depth, land-use history, and soil type are all factors likely to have contributed. For example, potential N mineralization (based on ex situ incubations) at La Selva was higher in residual soils (derived from basaltic lava that weathered in situ) than in the recent alluvium similar to that of my study site (Matson

and Vitousek 1987, Vitousek and Matson 1988). Gross N-cycling rates were also higher in old growth forests (on both residual and alluvial soils) than in the plantations (Silver et al. 2005).

Rates of net nitrification were high in the plantations, typically in the range of 0.1 to 0.6 $\mu\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$. These fall toward the upper end of values compiled by others (e.g., Melillo 1981, Vitousek et al. 1989, Reiners et al. 1994, Neill et al. 1997, Reich et al. 1997). High rainfall, warm temperature, and fertile soil combine to provide an environment very amenable to supplying the large quantities of N required for rapid plant growth. Unlike nitrification, net rates of ammonification were extremely low and almost invariably negative, as would be expected from the rapid conversion NH_4^+ to NO_3^- , or from microbial immobilization, during incubation. Thus, although absolute concentrations of NH_4^+ present at any given time were extremely low, rates of NH_4^+ through flow must have been very high to provide the substrate for the high rates of nitrification observed.

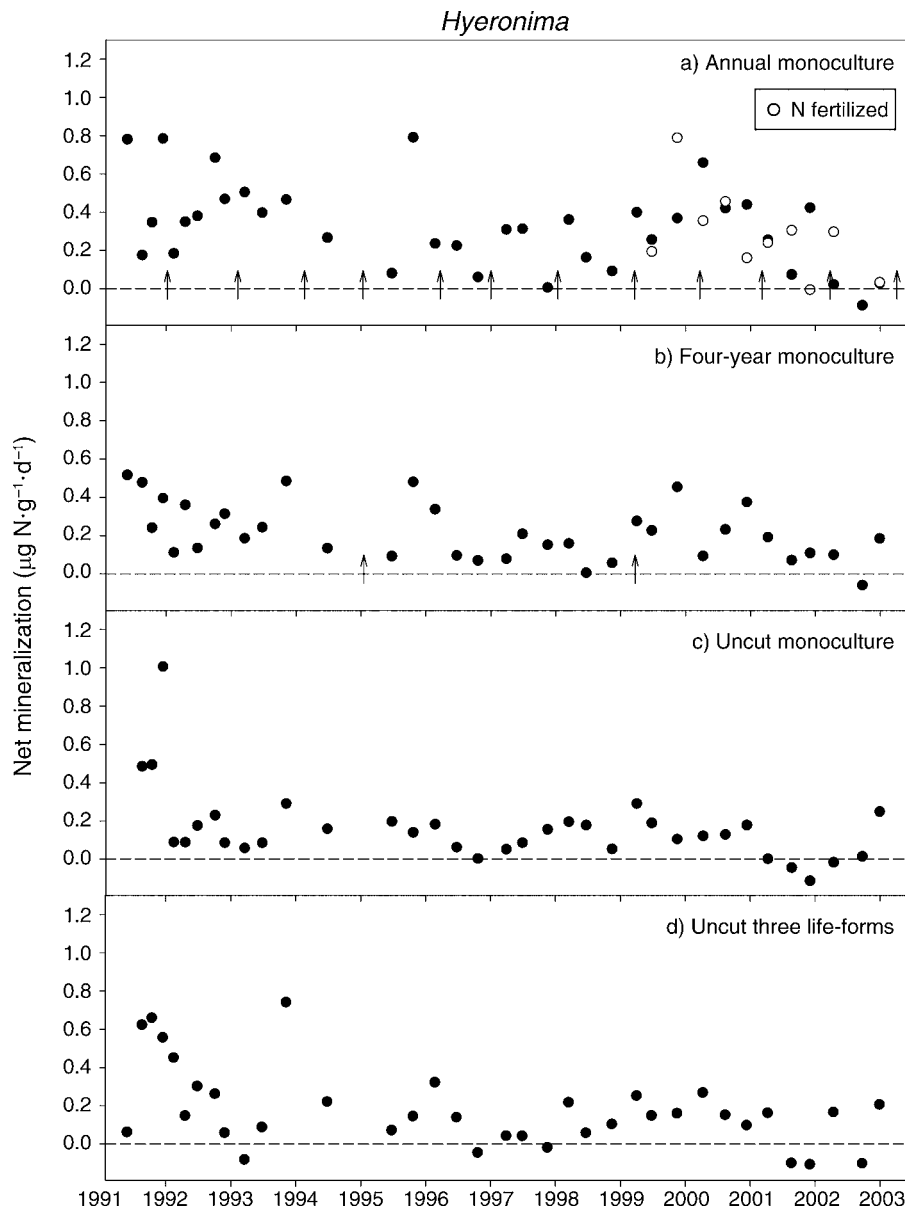


FIG. 2. Time course of net N mineralization in four treatments during 12 years in experimental ecosystems dominated by *Hyeronima alchorneoides*. Each point is the mean of three replications, with two samples per replication. Nitrogen fertilization (open circles, panel a, annual monoculture) began in September 1999. Arrows indicate dates of cutting and replanting.

This was confirmed by the high rates of gross mineralization in the *Cordia* plantations ($3.9 \mu\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) and correspondingly high gross rates of NH_4^+ consumption ($3.2 \mu\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) reported by Silver et al. (2005). The oxidation of that NH_4^+ was likely effected by *Nitrosopira multiformis* and *Nitrosomonas communis* (Carney et al. 2004).

Temporal changes

The 12-year time courses of net mineralization rates (Figs. 2–4) are marked by high values in the years immediately after the experiments were established. Site

preparation (early 1991) was followed by a period of elevated concentrations of NO_3^- and NH_4^+ , and high net rates of nitrification and mineralization. Matson et al. (1987) observed even higher levels of soil N activity in a tropical volcanic soil where the vegetation had been felled and burned, and others report increases in net mineralization following disturbance (e.g., Burger and Pritchett 1984, Vitousek and Matson 1985, Waide et al. 1988). The surprising thing about the post-disturbance pulse at the study site, however, was not the fact that it occurred, but the fact that it persisted as long as it did in uncut plantations—roughly three years. By then the canopy

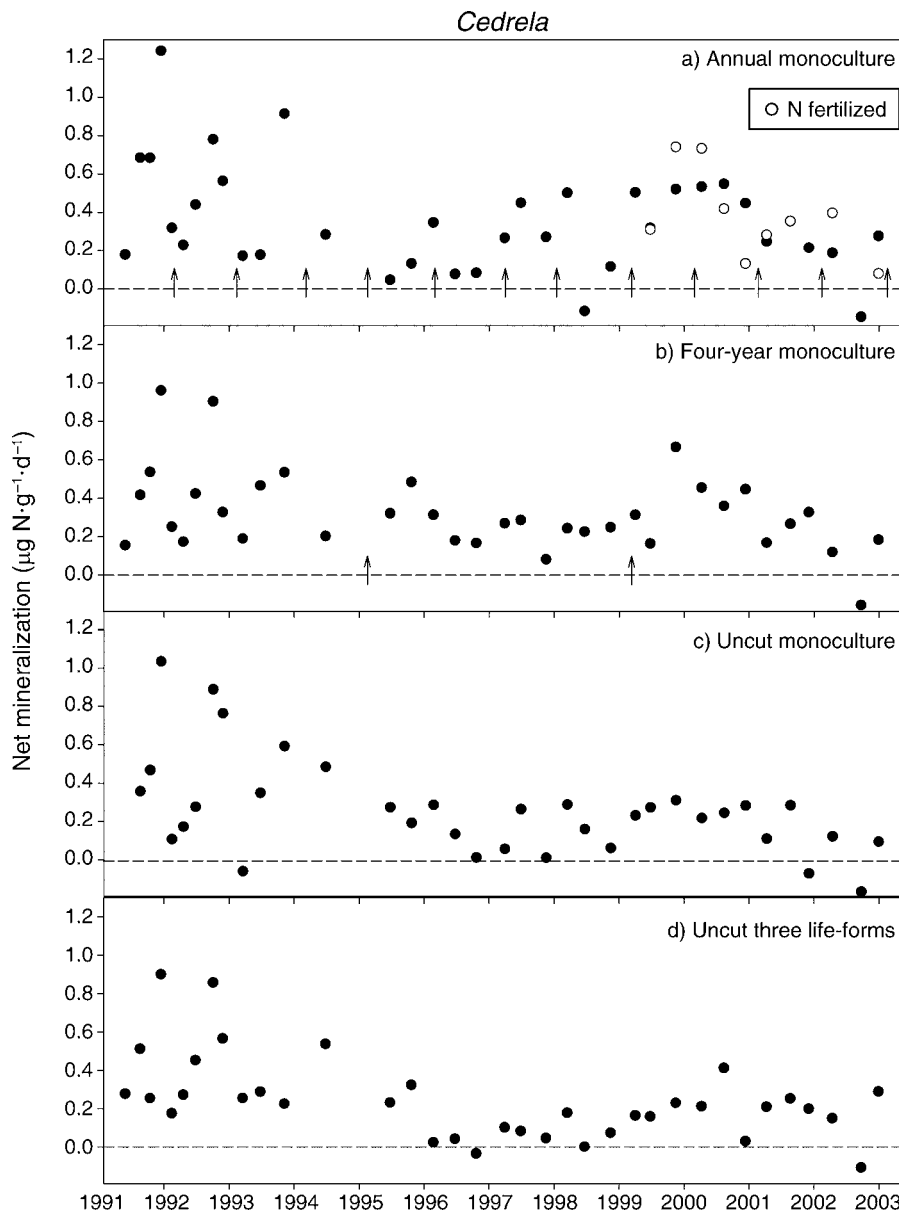


FIG. 3. Time course of net N mineralization in four treatments during 12 years in experimental ecosystems dominated by *Cedrela odorata*. The format is as in Fig. 2.

had been closed for a year or more, root systems had intersected, leaf area was high ($LAI > 2$) (Haggard and Ewel 1995), evapotranspiration was high (Bigelow 2001), and nutrient concentrations in leachate waters were low (Bigelow et al. 2004). Two possible mechanisms, each a result of the fire, that may have been responsible were the increase in fine, mineralizable substrate and the rise in soil pH that persisted for the first 2–4 years.

In a 12-year data set such as this, one might expect regular seasonal oscillations in N-transformation activity. In fact, some of the time courses (Figs. 2–4) give hints of regular pulses, especially on plots that were uncut (panels c and d). Part of the reason that those

pulses proved impossible to resolve statistically may be that, although La Selva experiences a drier season of about three months, even then the average monthly rainfall is >0.1 m; the sampling regimen was not specifically keyed to season, and year-to-year variation in rainfall further masked any differences that might have been due to soil moisture.

Species

Net N mineralization rates were about 30% lower in stands dominated by *Hyeronima* than in stands dominated by the other two species, *Cedrela* and *Cordia* (Fig. 5). This translates to a difference in net mineralization of

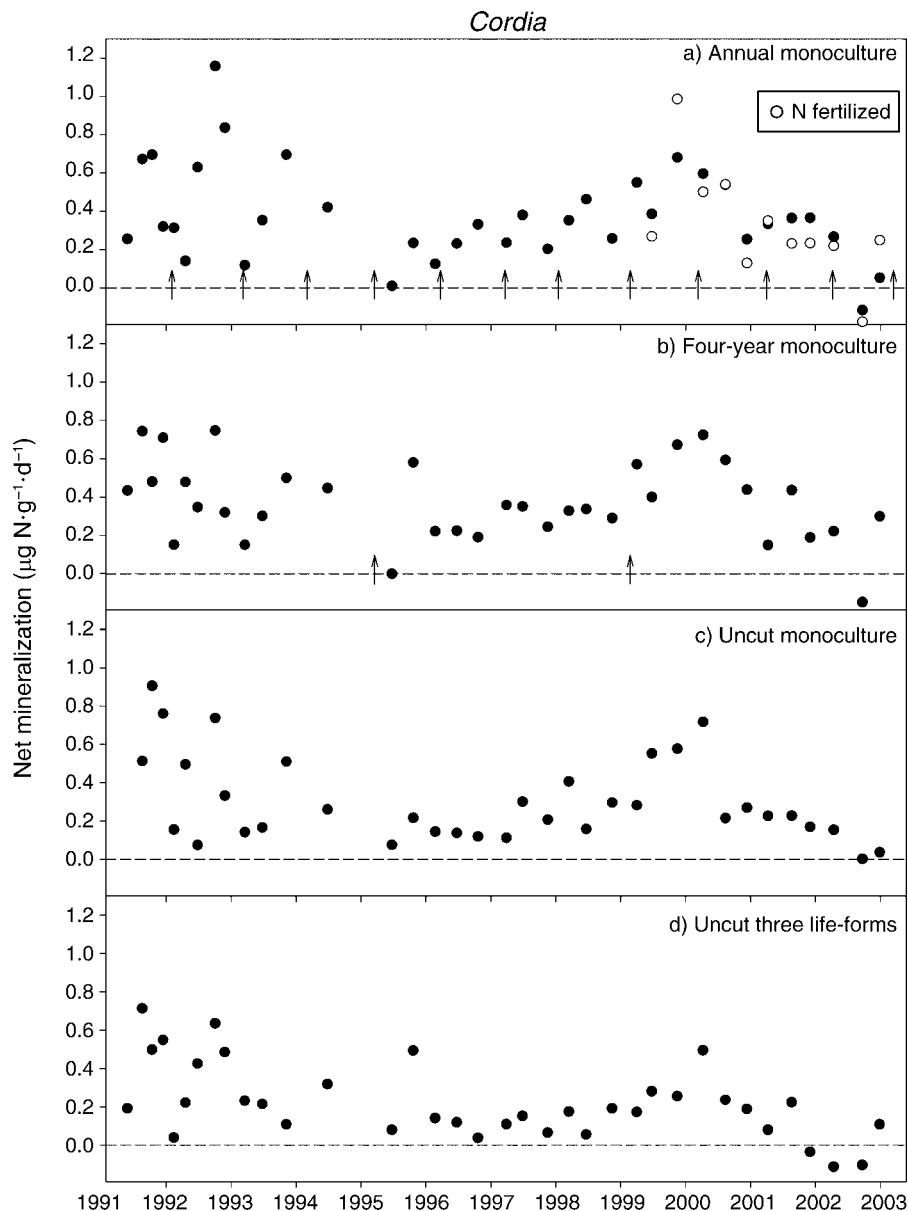


FIG. 4. Time course of net N mineralization in four treatments during 12 years in experimental ecosystems dominated by *Cordia alliodora*. The format is as in Fig. 2.

TABLE 2. Effects of dominant tree species, cutting and replanting frequency (annual, every four years, or uncut), life-form diversity (one or three types), and date of measurement (36 times over 12 years) on net N mineralization.

Source of variation	df	F	P
Tree species	2, 4	10.71	0.025
Treatment	3, 18	21.70	≤0.001
Tree species × treatment	6, 18	1.63	0.196
Measurement time	35, 1209	18.95	≤0.001

about $40 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. Curiously, this is approximately equal to the annual loss rate of N through leaching from the fast rotation (annual) plantations of *Cedrela* and *Cordia* (Bigelow et al. 2004). Thus, stands where N was mineralized fastest were the stands where N was lost the fastest, although it was probably a difference in demand rather than a difference in supply that drove the leaching.

Despite a good deal of work on the effects of species on soil N dynamics (e.g., Melillo et al. 1982, McLaugherty et al. 1985, Reich et al. 1997, Finzi et al. 1998, Chen and Stark 2000, Satti et al. 2003), the specific mechanisms that control transformation rates remain only partially explained (Lovett et al. 2004). Nevertheless, it is clear

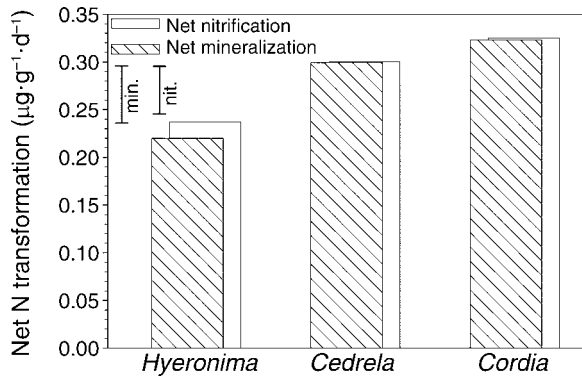


FIG. 5. Effect of dominant tree species on net N nitrification and mineralization. Vertical bars show least significant differences ($P < 0.05$) for nitrification (nit.) and mineralization (min.). Transformations were significantly lower in stands dominated by *Hyeronima alchorneoides* than in those dominated by *Cedrela odorata* and *Cordia alliodora*.

that a number of species traits contributed to the reduced rates of N mineralization in *Hyeronima* stands. Leaf-tissue N concentrations are high in all three species, but those of *Hyeronima* are lower than those of the other two: ~2.2% compared with 2.6 and 3.6% (mass basis) for *Cedrela* and *Cordia*, respectively. Its freshly abscised leaves have a higher C:N (~60) than do *Cedrela* (40) and *Cordia* (24), and this carries over to C:N ratios of the soil (~11, 9.2, and 9) and concentrations of light particulate organic matter (315, 180, and 150 g/m² under *Hyeronima*, *Cedrela*, and *Cordia*, respectively) (Russell et al. 2004). The foliar N:P of *Hyeronima*, ~11–12, is lower than that of the other two species: 14–15 in *Cedrela* and 17–18 in *Cordia*; by some guidelines (e.g., Koerselman and Meuleman 1996) *Hyeronima* is N limited, although its aboveground net primary productivity is about twice that of the others (Hiremath et al. 2002). It is the only

evergreen species among the three, its leaves are the largest, and its leaf litter forms a conspicuous layer on the forest floor. The density of fine roots in *Hyeronima* is higher than that of the other two species (Haggard and Ewel 1997), and its fine roots tend to be thicker (>1 mm). Together, these leaf and fine-root traits provide a relatively lower quality raw material for microbial transformations, resulting in lower rates of net mineralization.

The efficiency of N use at the whole-tree level is the ratio of NPP (net primary productivity) to N uptake. Values of this ratio (when the trees were 4–5 years old) were 150 in *Hyeronima*, 145 in *Cedrela*, and 95 in *Cordia* (Hiremath et al. 2002). The order of those efficiencies is the inverse of the rates of net N transformations in the soil (Fig. 6): *Cordia* > *Cedrela* > *Hyeronima*. *Cordia* had fast turnover of N and relatively low use efficiency; it returned a large proportion of its N to the soil, which presumably became a factor driving mineralization rates. *Hyeronima*, at the other end of the spectrum, coupled high productivity with relatively slower turnover, leading to higher use efficiency and proportionately less return of N to the soil where it would have become a substrate for mineralization. Thus, a high-demand species such as *Cordia* would not be expected to fare well on N-poor sites (and indeed it does not), even though it fosters higher N mineralization rates, whereas a more efficient user of N, such as *Hyeronima*, should be, and is, tolerant of relatively N-poor soils.

Life-form diversity

The findings of this study do not support the perspective that “more diversity is better,” at least from the perspective of net N mineralization. In fact, average net mineralization rates in the three-species plots were slightly lower, on average, than those in the uncut monocultures (though not significantly so; Fig. 6). Part

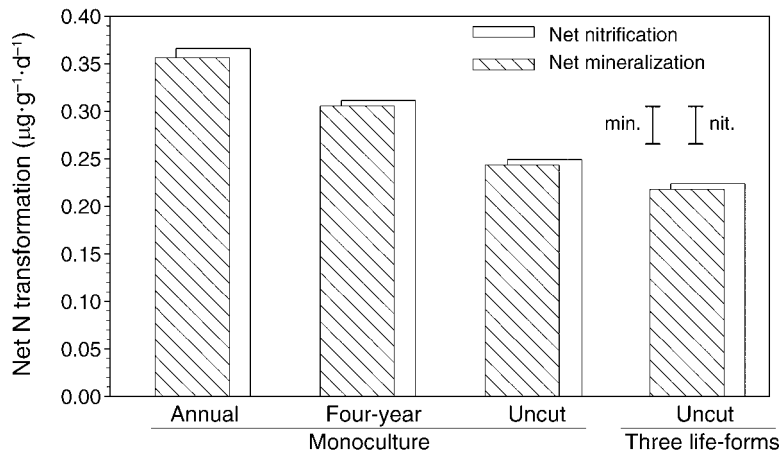


FIG. 6. Effects of rotation frequency and life-form diversity on net N nitrification and mineralization. Vertical bars show least significant differences ($P < 0.05$) for nitrification (nit.) and mineralization (min.). Transformations were significantly higher in fast-rotation stands (one year and four years) than in uncut stands. Increasing the number of life-forms from one (tree) to three (tree + palm + perennial herb) did not significantly affect N transformation rates.

of the reason for this counterintuitive finding may be the low quality of litter produced by the palm, *Euterpe*. Palms have high fiber content and, as a result, high C:N; furthermore, their abscised fronds do not lie tightly appressed to the soil. The result is exceptionally slow decomposition (Ewel 1976), probably accompanied by net immobilization of N. Furthermore, the net mineralization rates of the leaf litter produced by each of the three tree species was relatively high (Fig. 5), and that apparently counterbalanced the slower mineralization of palm fronds, leading to combined rates in polycultures that were very similar to those of the lowest average rates in uncut monocultures (of *Hyeronima*, Fig. 5).

That is not, however, to diminish the "insurance" value of multiple-species communities in N retention. Some evidence from the plots substantiates this. In three instances during the course of the research, uncut plots incurred major lightning strikes. One of those strikes occurred in an uncut monoculture of *Hyeronima*, where it killed or severely damaged 14 trees. The other two strikes hit polycultures where patches of dicotyledonous trees died, but the interplanted monocots did not; the *Heliconia* resprouted from the base, and a number of sprouts of each clump of *Euterpe* survived. Leaching losses of NO_3^- rose significantly in the *Hyeronima* monoculture (as detected by porous cup samplers in the killed-tree zone), but not in the polycultures, where the two monocots apparently compensated for the loss of the trees.

Once again, the biodiversity and ecosystem-functioning issue comes down to the attributes of the species involved. At least with respect to N cycling, rapid mineralization due to one species can apparently be offset by slow mineralization of a cohabitant. With respect to speed of N cycling, it is the choice of species, based on the attributes of the organic matter they produce, that is more important than a simple enumeration of species richness.

Rotation frequency

Frequency of disturbance proved to be a more important influence than life-form diversity on N transformations (Fig. 6). On plots where trees were cut and replanted annually (Figs. 2a, 3a, and 4a), elevated net mineralization was sustained throughout the study; on plots cut and replanted every four years, net mineralization rates tapered off with stand age then surged again for a year or two after cutting (Figs. 2b, 3b, and 4b); and on the uncut plots, both monocultures and polycultures (Figs. 2c–d, 3c–d, and 4c–d), the rates were relatively steady and low from about 1995 onward. Annual cutting and replanting, for example, put about 200 kg N/ha into circulation year after year. These high rates, coupled with young vegetation whose roots did not fully exploit the soil, resulted in very high rates of N leaching (Bigelow et al. 2004). In the uncut, three-life-form systems, in contrast, annual net N mineralization

rates were >40% lower, at about 115 kg/ha. Thus, in communities where N demand was presumably highest, the rate at which it was supplied was lowest.

What mechanisms might account for the burst of net mineralization following cutting and replanting? Of the two logical candidates—organic-matter inputs and soil disturbance—organic-matter inputs are the most likely driver of the process. Cutting delivered a vast amount of fresh organic matter, much of it (the foliage) high in N, to the soil surface. Typically this ranged from about 50 to >200 kg/ha of leaf biomass in the annual rotation stands and 1500–3000 kg/ha in the four-year rotations. Although this organic matter provided substrate for microbial activity for considerable time after its deposition, mineralization rates did decline after about two years in the four-year rotations, when the woody debris from large branches and tree trunks having high C:N would have become the main source of organic matter. Tree cutting itself did not lead to much soil disturbance, but replanting, which involved digging a small hole for each seedling, impacted 5–10% of the soil each time a site was replanted. Nevertheless, N mineralization was measured at randomly selected points in the interstices among trees, and it is unlikely that microbial activity would have been stimulated very far from the point of disturbance.

High rates of N transformation might resume as succession proceeds toward old-growth forest at La Selva (Vitousek and Denslow 1986, Matson and Vitousek 1987, Vitousek and Matson 1988, Reiners et al. 1994). Robertson (1984), for example, found that nitrification rates increased during the first eight years of succession then leveled off. Nevertheless, the dynamics I observed followed the opposite pattern, one in which high frequency of disturbance sustained high rates of mineralization, and rates declined with lack of disturbance and with time. The higher rates reported for intact forest at La Selva might eventually be attained if observed over a longer time period, but no increase was apparent during the 12 years covered by this data set. Vitousek et al. (1989) concluded that successional trends in N transformation can take many directions, and this may be one more example. A possible contributing factor is dominance of forests at La Selva by a N-fixing legume, *Pentaclethra maculosa* (Hartshorn and Hammel 1994) and the absence of N-fixing trees in the plantations.

Nitrogen replenishment

The fertilizer applied to the annual-rotation stands during the last four years of the study was intended to replenish N that had leached earlier. Thus, it was a formulation intended to feed plants directly, not to stimulate nitrification or mineralization (as done, for example, by Marrs et al. [1988] and Hall and Matson [2003]). Urea plus NO_3^- were a vulnerable pair in the warm, wet climate of La Selva, primarily because both

are highly mobile in soil solution. Furthermore, urea hydrolyzes to ammonium carbonate, and the resulting increase in pH leads to formation of ammonia, which volatilizes readily (Russell 1973).

In fact, fertilization did stimulate gross nitrification, but not gross mineralization (Silver et al. 2005), leading to the suggestion that fertilization may have primed the nitrifier community (Hall and Matson 2003). The effect of fertilization, however, did not carry over to net rates of N transformation, presumably because it was converted to nitrous oxide (N₂O), N₂, or NH₄⁺. In the case of these young plantations, where fertilizer was applied uniformly to the soil surface (in imitation of the way the original N had leached) and not concentrated around small trees where it might have been taken up by roots, the added N accelerated through flow, but this resulted in disproportionately more loss to the site than to enrichment.

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