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ECOSYSTEMS

Ecosystem Nutrient Use Efficiency, Productivity, and Nutrient Accrual in Model Tropical Communities

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ABSTRACT

Ecosystem nutrient use efficiency–the ratio of net primary productivity to soil nutrient supply–is an integrative measure of ecosystem functioning. High productivity and nutrient retention in natural systems are frequently attributed to high species diversity, even though some single-species systems can be highly productive and effective at resource capture. We investigated the effects of both individual species and life-form diversity on ecosystem nutrient use efficiency using model tropical ecosystems comprised of monocultures of three tree species and polycultures in which each of the tree species was coplanted with species of two additional life forms. Tree species significantly influenced nutrient use efficiency by whole ecosystems in monocultures; however, in polycultures, the additional life forms interacted with the influence exerted by the dominant tree. Furthermore, the presence of the additional life forms significantly increased nutrient uptake and uptake efficiency, but in only two of the three systems and 2 of the 4 years of the study period. These results indicate that the effect of life-form diversity on ecosystem functioning is not constant and that there may be temporal shifts in the influence exerted by different components of the community. Furthermore, although species (and life forms) exerted considerable influence on ecosystem nutrient use efficiency, this efficiency was most closely related to soil nutrient availability. These findings demonstrate that ecosystem nutrient use efficiency is an outcome not only of the characteristics of the species or life forms that comprise the system but also of factors that affect soil nutrient supply. The results argue against the simple upward scaling of nutrient use efficiency from leaves and plants to ecosystems.

Key words: *Cedrela odorata; Cordia alliodora*; diversity; *Euterpe oleracea; Heliconia imbricata; Hyeronima alchorneoides*; monocultures; nitrogen; nutrient use efficiency; nutrient retention; phosphorus; polycultures; productivity; scaling; tropical ecosystems.

INTRODUCTION

Ecosystem nutrient use efficiency is a measure of ecological functioning that integrates productivity and nutrient retention. Our research addresses the following questions: Does ecosystem-level nutrient use efficiency increase with the richness of species or life forms in a community? And what are the relative roles of species' traits and the nutrient-supplying capacity of the soil in determining nutrient use efficiency? Both of these questions have important implications for our understanding of the relationships between biodiversity and ecosystem functioning—specifically, those processes concerned with productivity and nutrient retention.

In humid climates, for example, where rainfall exceeds evapotranspiration, hydrologic losses of nutrients (via leaching and runoff) can be huge if nutrients accumulate in the soil solution and are not sequestered in plant tissues. Thus, plant growth

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and the nutrient uptake that accompanies it are vital mechanisms for retaining nutrients. The high productivity and nutrient retention observed in diverse natural and agricultural ecosystems are often attributed to their high species diversity. In experimental systems, it has been shown that the addition of species can lead to added productivity (Willey 1985; Naeem and others 1994; Hooper 1998; Hector and others 1999) and that greater diversity can lead to greater nutrient retention (Ewel and others 1991; Tilman and others 1996; Hooper 1998; Hooper and Vitousek 1998). Nevertheless, conflicting evidence indicates that some single-species (see, for example, Ewel 1999) or single–functional group (see, for example, Hooper 1998) systems can be as productive as diverse systems and equally effective at resource capture as more complex systems (Berish and Ewel 1988; Hooper and Vitousek 1998).

Nutrient use efficiency is studied by ecologists at three scales, most commonly those of leaf and whole plant. At the leaf level, nutrient use efficiency is the ratio of photosynthetic rate to concentration of nutrient (most often nitrogen) in the leaf lamina (see, for example, Field and Mooney 1986); at the plant level, it is the ratio of growth to nutrient uptake (see, for example, Hirose 1975). In this paper, we are concerned with the less commonly assessed nutrient use efficiency (NUE) at the ecosystem scale, defined as the ratio of net primary productivity (NPP) to the rate of soil nutrient supply:

$$\text{Ecosystem NUE} = \frac{\text{NPP}}{\text{Soil Nutrient Supply}} \quad (1)$$

This expression can be expanded as follows (see Bridgham and others 1995):

$$\text{Ecosystem NUE} = \frac{\text{NPP}}{\text{Nutrient Uptake}} \times \frac{\text{Nutrient Uptake}}{\text{Soil Nutrient Supply}} \quad (2)$$

Ecosystem nutrient use efficiency therefore depends on two component indexes: (a) plant-level nutrient use efficiency (that is, the NPP of the individuals that make up the system per unit of nutrient taken up by them), and (b) uptake efficiency (that is, total uptake by the individuals that make up the system per unit of nutrient supplied by the soil) (Shaver and Melillo 1984).

The first of these indexes, plant-level nutrient use efficiency, depends on productivity per unit of nutrient in the plant and mean residence time of nutrients in the plant (Berendse and Aerts 1987). Mean residence time of nutrients in plant tissues, in turn, depends on tissue turnover and nutrient resorption prior to tissue abscission. There are two ways that nutrient use efficiency of the individuals composing the system can influence nutrient use efficiency of the whole ecosystem. The first is through its influence on competitive interactions among species. Plants with high nutrient use efficiency should be able to tolerate lower nutrient availabilities; thus, they should be effective competitors in diverse communities where nutrients are in short supply (Tilman and others 1997). A system made up of such individuals should therefore have a higher productivity per unit of nutrient supplied by the soil than one made up of individuals with low nutrient use efficiencies. The second way that plant nutrient use efficiency can influence ecosystem nutrient use efficiency is through its influence on litter nutrient return (Hobbie 1992). High plant nutrient use efficiency—whether achieved by having long-lived leaves, low tissue nutrient concentrations, or high nutrient resorption prior to abscission—can result in a low rate of nutrient return to the soil. The return of nutrient-poor litter to the soil leads to reduced nutrient availability at the ecosystem level due to the slower breakdown of low-quality litter (Melillo and others 1982) and therefore to greater immobilization and nutrient retention in soil in the long term (Tilman and others 1997).

The other component of ecosystem nutrient use efficiency, uptake efficiency, can influence ecosystem nutrient use efficiency through its effect on nutrient retention. The uptake and sequestration of nutrients in biomass is an important means of preventing nutrient losses from an ecosystem via leaching from the soil (Nye and Greenland 1960; Vitousek and Reiners 1975). The larger the proportion of the soil's nutrient supply that is taken up by plants and sequestered in biomass, the smaller the proportion that remains to be potentially lost from the soil by leaching (Shaver and Melillo 1984). Effective uptake can be achieved through the following four mechanisms, which can operate independently or in concert: (a) temporal partitioning such that one species takes up nutrients at a time when others do not (for example, the early phenology of spring ephemerals in the understory of temperate deciduous forests [Muller 1978]), (b) spatial partitioning such that one species takes up nutrients from portions of the habitat that are inaccessible to other species (for example, the access to water, and presumably nutrients, from different soil depths by roots of evergreen and deciduous species [Jackson and others 1995]), (c) uptake of nutrients

in different proportions (for example, as demonstrated theoretically by Tilman [1988]), or (d) uptake of different forms of the same nutrient (for example, the use of inorganic soil nitrogen and diatomic nitrogen fixed by associated bacteria in mixtures of nonlegumes and legumes, respectively, as demonstrated by Martin and Snaydon [1982]).

It follows, therefore, as suggested by Tilman and others (1997) in the context of diversity and ecosystem productivity and by Hooper (1998) in the context of diversity and nutrient retention, that ecosystem nutrient use efficiency depends on the identity of the species making up the system, and not on a greater diversity of species per se. A combination of species with a high plant-level nutrient use efficiency should lead to high relative productivity per unit of nutrient available. Furthermore, a combination of species that is able to partition the available resource supply should lead to high total uptake per unit of nutrient available.

We investigated ecosystem nutrient use efficiency for both nitrogen (N) and phosphorus (P) in fast-growing tropical ecosystems as they aged from 2 to 6 years. The experimental design permitted us to compare nutrient use efficiency in single-species ecosystems and systems composed of three life forms, thus contributing to our understanding of the relationships between biodiversity and ecosystem functioning. The design also enabled us to compare nutrient use efficiency among ecosystems (both single-species and three-species) dominated by different species of the same life form (dicotyledonous trees), thereby helping to determine the degree to which an ecosystem property such as nutrient use efficiency is species-driven and the degree to which generalization at the level of life forms may be possible.

Methods

Study Site

This research was conducted at La Selva Biological Station in Costa Rica, where the mean annual temperature is 25.8°C and average yearly rainfall is approximately 4 m. There is a dry season from February to April, but even during those months mean monthly rainfall is seldom less than 0.1 m (Sanford and others 1994; Matlock and Hartshorn 1999).

The study was conducted in experimental plantations located on a level alluvial terrace 41 m above sea level. The soil profile shows several distinct depositional sequences (Haggar and Ewel 1994), though the site was not inundated by the two highest floods in recent history (1970 and 1996). The soil at the site is a eutric Hapludand—an andesitic soil of humid climates, with minimum horizon development and high base saturation (Weitz and others 1997). In the surface horizon, the soil is a sandy loam (0–15 cm depth), giving way to sandy loam–silty loam (down to about 90 cm) (Haggar and Ewel 1994). The soil is well drained, with low bulk density (0.67 g/cm^3) and high organic matter content (5.9%) (Haggar and Ewel 1995) and has high base saturation dominated by calcium (15.9 $Cmol_c/kg$) (Hiremath 1999). Values of extractable N at the site (13.7 μg/g potassium chloride extractable N, soil depth 0–10 cm) (Haggar and Ewel 1995) are high compared with values reported from a range of other tropical sites (4.1–12.6 μg/g, soil depth 0–15 cm) (Vitousek and Matson 1988). The site is also relatively rich in extractable P (14.4 μg/g acid ammonium fluoride extractable P, soil depth 0–10 cm) (Hiremath 1999) compared with values reported from elsewhere in the tropics (0.6 μg/g, soil depth 0–18 cm, and 1.7 μg/g, soil depth 0–26 cm, from Costa Rica) (Sollins and others 1994) (4.5 μg/g, soil depth 0–7 cm, and 10.8 μg/g, soil depth 0–15 cm, from Nigeria) (Greenland 1981).

Species

Three fast-growing tree species were used in this study—*Cedrela odorata* L. (Meliaceae), *Cordia alliodora* (R. & P.) Cham. (Boraginaceae), and *Hyeronima alchorneoides* Allemão (Euphorbiaceae). All three species are native to Costa Rica and occur in the forest at La Selva or in secondary vegetation in the region. The three tree species were chosen for their very different phenologies and architectures; thus, they represent an array of resource capture and resource use characteristics. *Cedrela* has monopodial growth, with orthotropic branches that form an open crown. It has large, pinnately compound leaves up to 1 m long, with 10–20 pairs of leaflets, each about 40 cm^2. At La Selva, *Cedrela* tends to be deciduous during the dry season (February–April). *Cordia*, like *Cedrela*, has monopodial growth, but with plagiotropic branches that are produced in whorls, creating an open, tiered crown. It has small (approximately 30 cm^2), simple leaves. Once it reaches reproductive maturity, *Cordia* loses its leaves during the wet season (around July at La Selva); as a juvenile, it maintains its foliage yearround, although it is partially deciduous during the dry season. *Hyeronima* has sympodial growth with orthotropic branches that form a dense crown. An evergreen, *Hyeronima* has very large, simple leaves as a juvenile (area, approximately 300 cm^2), but it

produces progressively smaller leaves as it ages, such that old individuals have leaves that are only about 60 cm^2.

The structural differences among the three species extend below ground as well. *Hyeronima* has a dense, compact root system; *Cordia*, in contrast, has a laterally extensive root system; and *Cedrela* is intermediate between the other two species (Haggar and Ewel 1995). The species' differences in root morphology are likely to affect their relative uptake of different soil nutrients: *Hyeronima*, with roots that explore the soil intensively may be more effective at uptake of PO_4^{3-}, an immobile soil nutrient; *Cordia*, on the other hand, with roots that explore the soil extensively, is likely to have higher uptake of NO_3^-, a mobile ion (Haggar and Ewel 1994). Foliar nutrient concentrations for the three species measured at the start of the study support this hypothesis (*Hyeronima*, 2.76% N, 0.35% P; *Cedrela*, 2.90% N, 0.22% P; *Cordia*, 3.39% N, 0.27% P).

The other two species used in this study are representatives of other important life forms in forests of the region—large, perennial monocots, one with an apical meristem (thus indeterminate height growth) and the other with a basal meristem. One of these is a palm, *Euterpe oleracea* Mart (Arecaceae), which occurs widely over northern South America, especially on fertile floodplains of the lower Amazon. It is a tall (larger than 20 m), multistemmed palm with pinnate fronds that rapidly colonizes disturbed, swampy areas (Henderson 1995). The second monocot, *Heliconia imbricata* (Kuntze) Baker (Heliconiaceae; hereafter, heliconia), is a large (up to 5 m tall), perennial, bananalike herb with leaf blades that are up to 2 m long. It colonizes gaps, forming clumps of monocarpic ramets, and is commonly found in young secondary vegetation (Stiles 1979).

Experimental Design

When it was annexed to La Selva Biological Station in the mid-1980s, the site was a recently abandoned cacao plantation. In early 1991, the vegetation on the site was felled and the overstory trees were harvested for timber; the slash was then burned. The experimental plantations were established immediately thereafter.

In early 1991, plantations (40 × 60 m) of *Cedrela, Cordia*, and *Hyeronima* were established in a randomized block design with three replicates of each species. Trees were planted so that each individual was 2 m from its six nearest neighbors, resulting in a density of 2887 trees per hectare, which is several times greater than is normal for these species in forestry plantations. The reason for the high planting density was to ensure that resource acquisition and productivity were maximized early in stand development. Each of the nine plantations was divided into halves. One half was left as a monoculture of trees; the other was underplanted with palms and heliconias in an additive design to create polycultures. In the polycultures, palms were planted in alternate rows, in alternate spaces between trees—that is, at one-fourth the tree density—and heliconias were planted in rows that were not planted with palms, in every available space between trees—that is, at half the tree density. Mid-1993, which was immediately after canopy closure occurred in all stands (Haggar and Ewel 1995), was chosen as the starting point for this study.

Net Primary Productivity

Net primary productivity (NPP) was estimated as the algebraic sum of biomass increments and litterfall. An estimate of fine-root production and mortality (from mid-1996 to mid-1997) enabled us to assess the contribution of fine-root (that is, roots less than 5 mm in diameter) mortality to NPP.

Biomass of trees (stems, branches, petioles or rachises, leaves, and coarse roots), palms (stems, fronds, and coarse roots), and heliconias (petioles, leaf blades, and coarse roots) was determined using allometric equations of the form $W = a X^b$, where W is biomass of the component being assessed and X is a compound measure of plant size (Satoo and Madgwick 1982). Starting in 1991, 24 individuals of each tree species and 18 individuals of each monocot species were harvested annually from zones specifically designated for destructive sampling in the study plots, and the entire root system of harvested individuals was excavated, taking care to include all roots greater than 5 mm in diameter. (The number of harvested trees was reduced to 18 in 1993 and six in 1996; the number of harvested monocots was reduced to nine in 1996.)

Harvested plants were separated into their biomass components, fresh mass of each component was determined in the field, and a subsample of each component was dried to constant mass at 70°C and weighed to obtain the wet-to-dry mass conversion factor. Inventories of plant size (height and diameter for trees; height, diameter, and number of fronds for palms; and height and number of ramets for heliconias) in June–July of each year provided input to the allometric equations. Tree biomass was best predicted by either $W = HD^2$ or HD (H = height, and D = diameter); palm biomass was best predicted by $W = HD$ or HDF (where F is the number of fronds); and heliconia biomass was best predicted by $W = HR$ (where R is the number of

ramets). Equations were modified annually as larger individuals were added to the data set with each new biomass harvest. The r^2 values obtained ranged from 0.29 to 0.95 (leaves), 0.67 to 0.92 (roots), and 0.82 to 0.97 (stems). Litter was collected biweekly from three 1.73 × 0.50 m traps in each plot, combined, separated by species, then dried at 70°C and weighed.

Change in the biomass of fine roots (that is, roots less than 5 mm in diameter) was determined by annual coring. Eight cores, each 5 cm in diameter and 110 cm deep, were sampled in each plot. Cores were combined by 10-cm depth intervals, and the composite samples were washed in a root elutriator. Roots that had been cleansed of soil were then separated by species and by diameter (less than 2 mm, 2–5 mm) before being dried to constant mass at 70°C and weighed.

An estimate of fine-root production for the period June 1996–June 1997 was obtained using the compartment–flow model of Santantonio and Grace (1987), in which the compartments consist of standing biomass of live and dead fine roots and the flows consist of production, mortality, and decay. Fine-root mortality, and thereby production, was estimated using difference equations that describe the change in standing biomass of live and dead fine roots as follows:

$$\Delta\text{Live Fine Roots} = \text{Production}-\text{Mortality} \quad (3)$$

$$\Delta\text{Dead Fine Roots} = \text{Mortality}-\text{Decay} \quad (4)$$

where the change in standing biomass of live and dead roots was measured by sequential sampling of live and dead roots. Roots were sampled monthly for the first 4 months and then once every 4 months for the remainder of the year. Eight cores, each 5 cm in diameter and 30 cm deep, were sampled in every plot. Cores were combined and the samples were washed in a root elutriator. The washed roots were then separated into live and dead roots (based on appearance), dried, and weighed.

The rate of fine-root decay was calculated from sequential sampling of roots in trenched plots (see, for example, Silver and Vogt 1993). Two or three rectangular plots, each 1.73 × 0.50 m, were established in all monoculture or polyculture plots, respectively. Plots were trenched to a depth of 50 cm and the trenches were back-filled. The trenches were recut monthly with a machete to sever any laterally ingrowing fine roots; the trenched plots were weeded at the same time. Fine roots were sampled with a 5-cm–diameter corer, four cores per plot, to a depth of 30 cm. The cores were then combined, washed, dried, and weighed. Roots were sampled at the time the trenched plots were established, and subsequent samples were taken after 2, 6, 10, 18, 34, and 55 weeks (*Hyeronima*), 2, 6, 10, 18, 31, and 55 weeks (*Cedrela*), and 2, 6, 10, 18, 28, and 55 weeks (*Cordia*). There was some ingrowth of roots in several of the experimental plots, presumably from below the depth to which plots were trenched (for example, *Hyeronima* monocultures at week 55, *Cordia* monocultures at week 28, *Cordia* polycultures at week 55). In the case of *Cedrela* monocultures, ingrowth occurred within the first 6 weeks, so decay constants estimated for *Cedrela* roots in polycultures were used in calculations pertaining to *Cedrela* monocultures. Decay constants (k in d^{-1}) were calculated using an exponential decay model, $B/B_o = e^{-kt}$, where B/B_o is the fraction of root mass remaining at time t (in days). Fine-root production was calculated for each interval over which changes in live and dead fine roots were measured (that is, monthly from June 1996 to October 1996 and every 4 months from October 1996 to June 1997). An estimate of annual fine-root production was then obtained by summing production over all measurement intervals.

Nutrient Uptake

Total nutrient uptake was calculated by summing net nutrient uptake (based on annual estimates of above- and belowground biomass), nutrients returned to the soil surface as litter (biweekly collections), nutrients lost to the canopy via stemflow and throughfall (measured during 1996), and nutrients lost via root mortality (measurements in 1996–97 of fine-root production and mortality). Net uptake of N and P was calculated by summing the products of nutrient concentrations in leaves, stems, branches, and petioles or rachises, and in fine and coarse roots, times the change in biomass of each fraction.

Nutrient concentrations were determined on tissue subsamples of individuals harvested annually to provide data for the allometric equations. The dried litter from biweekly collections was combined bimonthly to yield six composite litter samples over the year. Tissue and litter samples were dried at 70°C, ground to pass a 2-mm sieve and analyzed for total N and P (Luh Huang and Schulte 1985; LECO. 1995).

Foliar leaching losses were calculated by multiplying net concentrations of nitrate-N (NO_3^-), ammonium-N (NH_4^+), and phosphate-P (PO_4^{3-}) in samples of stemflow and throughfall water by estimates of total annual volumes of stemflow and throughfall. Net concentrations of NO_3^-, NH_4^+, and

PO_4^{3-} were obtained by subtracting concentrations in rainwater from concentrations in stemflow and throughfall water. Collection of stemflow and throughfall is described in Hiremath (1999).

Samples for stemflow and throughfall chemistry were obtained for 12 (stemflow) and eight (throughfall) rain events ranging from 0.5 to 33.1 mm. Samples for rainwater chemistry were collected for the same events in a 20-cm–diameter funnel placed in an adjacent clearing. Samples were filtered through a 0.45-μ glass fiber filter Type A/E; Gelman Sciences (Pall Corporation, East Hills, NY) fumigated with a drop of chloroform, and frozen until analysis. Samples were analyzed for PO_4^{3-N} following a modified antimony/molybdate protocol (Murphy and Riley 1962) on a spectrophotometer. Nitrate and NH_4^+ were analyzed on an Alpkem Autoanalyzer (OI Analytical, College Station, TX) using standard colorimetry (Alpkem 1986).

Soil Nutrient Supply

Soil N supply was assessed every 4 months by measuring net N mineralization and nitrification by in situ incubations of isolated soil cores (Anderson and Ingram 1989). Two pairs of cores, each 10 cm in diameter and 20 cm deep, were sampled in every plot. The two preincubation cores per plot were combined and 15 g of soil from the resulting composite sample were extracted with 100 ml of 2M KCl by shaking for 1 h. The extract was then filtered; the filtrate was analyzed for NH_4-N and NO_3-N using automated colorimetry (Technicon 1973). The other two cores in every plot were incubated in situ for 21 days, after which they were removed and processed in a manner identical to the initial, preincubation cores. Rates of net N nitrification ($NO_3\text{-}N_{final}–NO_3\text{-}N_{initial}$) and mineralization ($[NO_3\text{-}N_{final} + NH_4\text{-}N_{final}]–[NO_3\text{-}N_{initial} + NH_4\text{-}N_{initial}$]) were calculated as described in Haggar and Ewel (1994). It was not possible to calculate N mineralization rates for three of the 12 sampling dates due to missing extractable NH_4-N data. Therefore, nitrification rate, rather than mineralization rate, was used as the index of soil N supply, which was a reasonable approximation given the strong correlation between the two variables (especially for *Cedrela* and *Cordia*, though less so for *Hyeronima*). Net nitrification corresponding to each NPP measurement was estimated by averaging the three assessments of nitrification made during the year.

Extractable P obtained using an EDTA-modified bicarbonate extraction (modified Olsen extraction) (Hunter 1974) was used as a measure of soil P supply. Soil was sampled annually by coring to a depth of 70 cm. Three cores were taken per plot and cores were combined by depth (0–10, 10–25, and 25–70 cm). Soil was air-dried and ground to pass a 2-mm sieve; 2.5 g of soil were extracted with 25 ml of the extraction solution by shaking for 10 min, and the extract was analyzed for P colorimetrically (Murphy and Riley 1962). Extractable P was subsequently summed over the entire soil volume sampled using soil bulk densities measured by Weitz and others (1997).

Statistical Analysis

Interspecific; that is, among the dominant tree species, *Hyeronima, Cedrela*, and *Cordia*) and between-treatment (monoculture or polyculture) differences in means of NPP, nutrient uptake, soil nutrient supply, and nutrient uptake and use efficiency were analyzed using analysis of variance (ANOVA) (PROC Mixed; SAS Institute 2000). Species, treatment, and their interactions were treated as fixed effects; time was treated as a fixed, repeated measure; and block and its interactions with species and time were treated as random effects. Compound symmetry covariance structure was used, which assumes that variance is constant over time (SAS Institute 2000). Model residuals were examined to ensure that the assumption of equal variances was not violated. In cases where variance increased as a function of the mean, the data were log-transformed.

Results

Net Primary Productivity

Over the 4 years of the study, NPP ranged from about 2.7 to 10.8 g m^{-2} d^{-1} (equivalent to 10–39 Mg ha^{-1} y^{-1}) (Figure 1). Productivity was consistently high (more than 20 Mg ha^{-1} y^{-1}) in the *Hyeronima*-dominated systems, both the monocultures and the polycultures. In the first 3 years, there was no discernable difference between *Hyeronima* monocultures and polycultures due to the negligible growth of the palms and heliconia, but the two began to diverge in the 4th year (1996–97), a trend that has continued since then. In the *Cedrela*- and *Cordia*-dominated systems, NPP varied practically threefold over the duration of the study. Productivity of the *Cedrela*-and *Cordia*-dominated polycultures was extremely high in the 1st and 4th years (more than 25 Mg ha^{-1} y^{-1}) and was significantly higher than that of the monocultures ($P < 0.0001$ in both systems). For the 2 intervening years, on the other hand, neither the *Cedrela*- nor the *Cordia*-dominated systems showed any between-treatment differences in NPP. The striking difference between

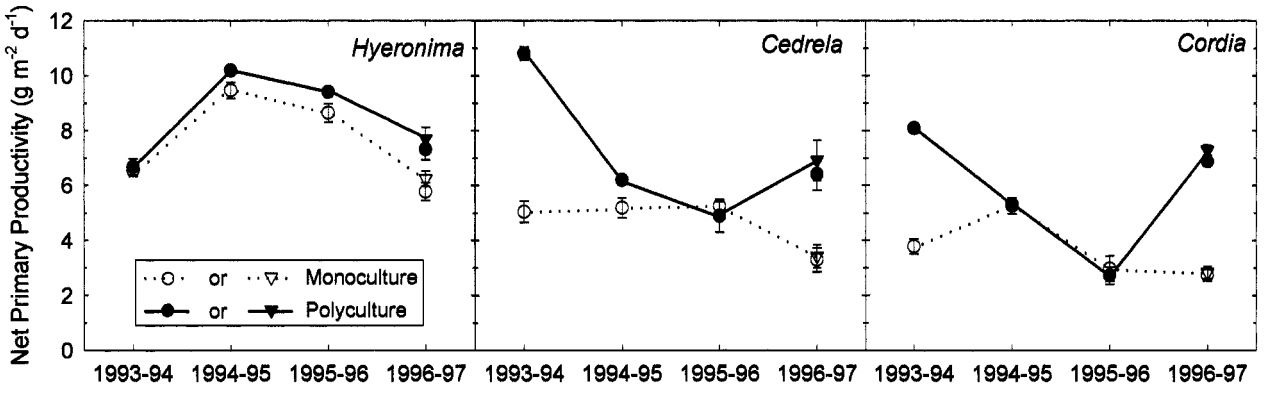

Figure 1. Net primary productivity of monocultures and polycultures dominated by *Hyeronima alchorneoides, Cedrela odorata,* and *Cordia alliodora*. Circles represent values determined from sequential biomass increments plus litterfall; triangles include mortality of fine roots. Values are means (standard error) of three blocks.

monocultures and the polycultures in the 1st year was due almost entirely to the heliconia; the difference between monocultures and polycultures in the 4th year was due largely to the palms.

Mortality of fine roots was estimated to be 0.10–0.80 g m^{-2} d^{-1} (about 0.4–3 Mg ha^{-1} y^{-1}) in 1996–97. This accounted for 2%–10% of NPP, indicating the degree to which values of NPP during other years, which were based on changes in standing stocks of roots, may have been underestimated (Figure 1).

Soil Nutrient Supply

Net N mineralization and nitrification averaged about 0.22 μg g^{-1} d^{-1} (approximately 112 kg ha^{-1} y^{-1}) over the 4 years of the study (Figure 2, upper panels). The rate at which N became available in the soil declined over time ($P = 0.063$ for N mineralization, $P = 0.009$ for nitrification), but there were no significant differences among species ($P = 0.115$ for N mineralization, $P = 0.801$ for nitrification) or between monocultures and polycultures ($P = 0.514$ for N mineralization, $P = 0.922$ for nitrification). Nitrification accounted for most of the N mineralization in these systems, and annual N supply was estimated by averaging the three measurements of nitrification made during each year.

Values of Olsen-extractable P ranged from about 2.5 to 8.0 g/m^2 (Figure 2, lower panels). More P was available in the soil of polycultures than in monocultures ($P = 0.007$) on all but one occasion, but differences among species were not significant ($P = 0.257$). Measured P was significantly higher ($P = 0.001$) for all species and treatments in 1996 than earlier in the study.

Nutrient Uptake

Nitrogen uptake varied about fivefold over the 4 years, and it differed significantly among dominant tree species ($P = 0.006$) (Figure 3, upper panels). *Hyeronima*-dominated systems showed an increase in N uptake in the first 3 years, followed by a decrease in the 4th year; the additional life forms did not contribute to additional N uptake ($P = 0.999$). Unlike the *Hyeronima*-dominated systems, in the *Cedrela*- and *Cordia*-dominated monocultures N uptake remained relatively constant over the 4 years. Furthermore, the additional life forms made a marked contribution to N uptake in the *Cedrela*- ($P < .0001$) and *Cordia*-dominated systems ($P = 0.002$), particularly in the 1st year (when heliconias grew vigorously) and the 4th year (when the palms grew vigorously).

The presence of palms and heliconias led to greater P uptake in both *Cedrela* and *Cordia* stands ($P < .0001$ in both systems) (Figure 3, lower panels). The effect of dominant tree species was not significant ($P = 0.112$), however.

Uptake Efficiency

Although dominant tree species did not have a significant effect on N ($P = 0.181$) uptake efficiency (that is, the ratio of nutrient uptake to soil nutrient supply), they did significantly affect uptake efficiency of P ($P = 0.015$) (Figure 4). Nitrogen uptake efficiency differed only between *Cedrela*-dominated monocultures and polycultures (where it was higher) ($P = 0.003$), while P uptake efficiency was higher in polycultures dominated by both *Cedrela* and *Cordia* ($P < .0001$).

Although we underestimated uptake efficiencies

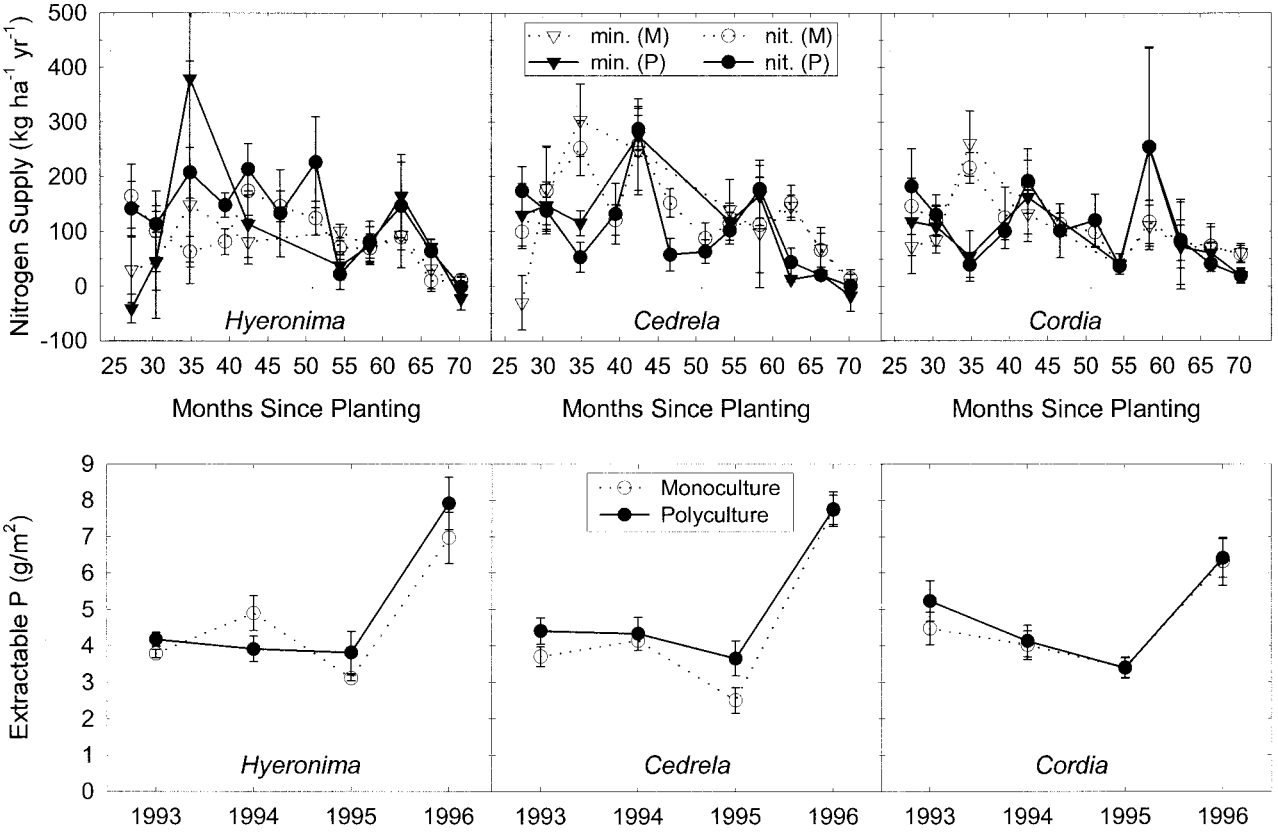

Figure 2. Supplies of nitrogen (upper panels) and phosphorus (lower panels) in monocultures and polycultures dominated by *Hyeronima alchorneoides, Cedrela odorata*, and *Cordia alliodora*. Each N value combined soil from two pre- and two postincubation soil cores in each of three blocks; each P value is a composite sample of three cores in each of three blocks. min. = mineralization; nit. = nitrification; M = monoculture; P = polyculture.

by not accounting for losses via washout from the crowns and fine root turnover in all years, these pathways accounted for very small amounts of total uptake. Nitrogen lost via foliar leaching (measured in 1995–96), for example, was a negligible fraction of total uptake (less than or equal to 0.4% in all systems except the *Cordia* polyculture where it amounted to 1%). The fraction of P lost via this pathway was greater (less than or equal to 4.3% except in the *Hyeronima* monocultures, where it accounted for *Cordia* and 8.3%). Fine-root turnover accounted for a somewhat larger fraction of total uptake, especially for N, and therefore had a greater impact on uptake efficiency.

Nutrient Use Efficiency

Ecosystem N use efficiency varied between three- and nine-fold over the 4 years for *Hyeronima*- and *Cedrela*-dominated systems, respectively (Figure 5, upper panel). There were significant effects of dominant species ($P = 0.025$), treatment ($P = 0.001$), and time ($P = 0.086$). *Hyeronima*-dominated monocultures had significantly higher N use efficiency than monocultures of *Cedrela* and *Cordia*. Although there was no difference in N use efficiency between *Hyeronima*-dominated monocultures and polycultures ($P = 0.436$), the additional life forms did significantly increase N use efficiency in the *Cedrela*- ($P = 0.001$) and *Cordia*-dominated ($P = 0.019$) systems.

Ecosystem P use efficiency, like that of N, was influenced by dominant species ($P = 0.004$), treatment ($P = 0.0003$), and time ($P = 0.0002$) (Figure 5, lower panels). As was the case with N, *Hyeronima*-dominated monocultures had significantly higher P use efficiency than monocultures of *Cedrela* and *Cordia* in most years. The heliconia and palms significantly affected P use efficiency by *Cedrela*- ($P = 0.003$) and *Cordia*-dominated ($P = 0.008$) systems, but the addition of those life forms had no effect on P use efficiency of the *Hyeronima*-dominated systems ($P = 0.961$).

Measurements of fine-root turnover in 1996–97 enabled us to calculate ecosystem nutrient use effi-

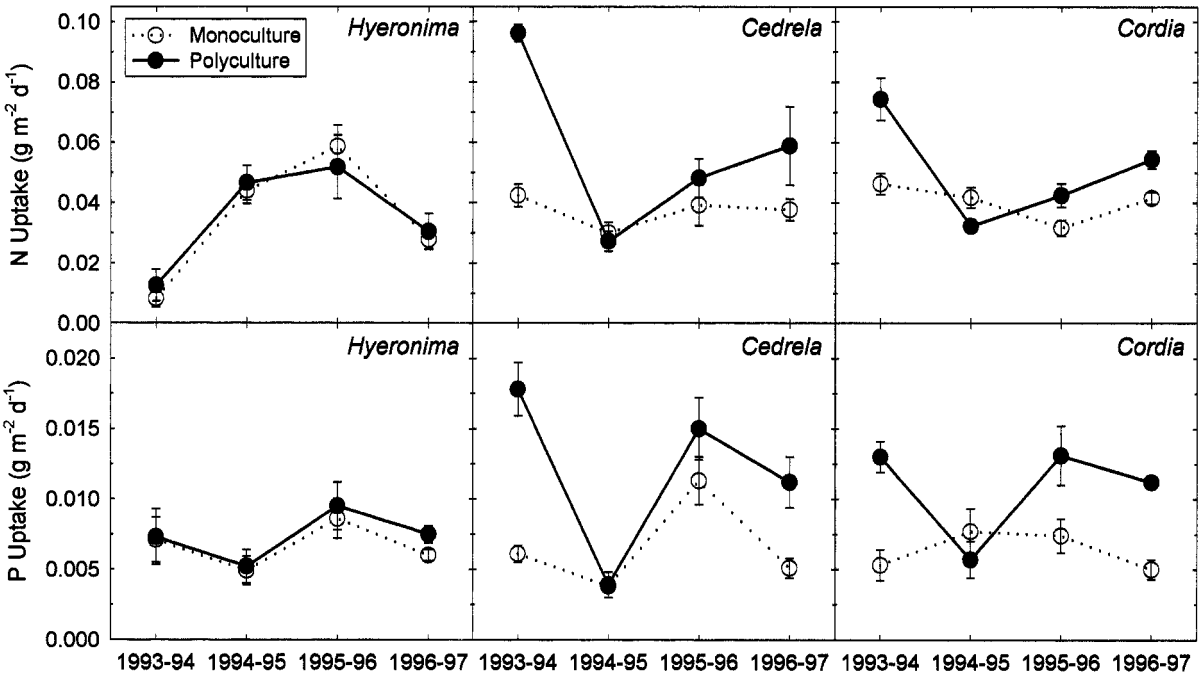

Figure 3. Uptake of N (upper panels) and P (lower panels) in systems dominated by *Hyeronima alchorneoides, Cedrela odorata*, and *Cordia alliodora* over the course of the study. Values are means (standard error) of three blocks.

ciency for that interval as the ratio of total NPP to soil nutrient supply. The result of failing to account for fine-root mortality in all years (see open bars, 1996–97, Figure 5) could have led to underestimates of ecosystem nutrient use efficiency of about 8%.

Discussion

Ecosystem N use efficiency measured in this study (that is, values of 100–1000) extends the upper range reported in other studies (70–240, calculated as the ratio of aboveground NPP to mineralization rate) (Lennon and others 1985; Bridgham and others 1995). Analogous estimates of ecosystem P use efficiency were not available for comparison with our measurements.

The dominant tree species, as well as the additional life forms, significantly influenced ecosystem N and P use efficiency, but these effects were not consistent over the 4 years of this study. Furthermore, the 4-year temporal patterns of ecosystem N use efficiency were very different from those of P use efficiency. These observations signal a need for information on the relative roles of species' traits, life-form richness, and the nutrient supplying capacity of the soil in determining ecosystem nutrient use efficiency.

Effects of Tree Species

The plants that make up an ecosystem can potentially increase ecosystem nutrient-use efficiency in one of two ways, either singly, or in combination (see Eq. [2]): (a) by having a high nutrient use efficiency (that is, high biomass production per unit nutrient uptake) and (b) by having a high uptake efficiency (that is, high nutrient uptake per unit of nutrient supplied by the soil).

The relative magnitudes of plant-level N and P use efficiency for the three tree species were *Hyeronima* > *Cedrela* > *Cordia* (Hiremath and others 2001), and these differences in plant-level NUE are reflected in the productivity patterns of the three monocultures. The relative differences in plant-level nutrient use efficiency of the dominant tree species also translate into the patterns of tree productivity observed in polycultures, supporting the idea (Tilman and others 1997) that higher plant-level nutrient use efficiency signals a greater tolerance of reduced nutrient availability, as would be expected in the densely packed polycultures. Productivity of the overstory of *Cordia* trees in polyculture dropped below that of trees in monoculture early in the course of the study (1993–94) (Haggar and Ewel 1997), signaling the early onset of belowground competition from the coplanted monocots,

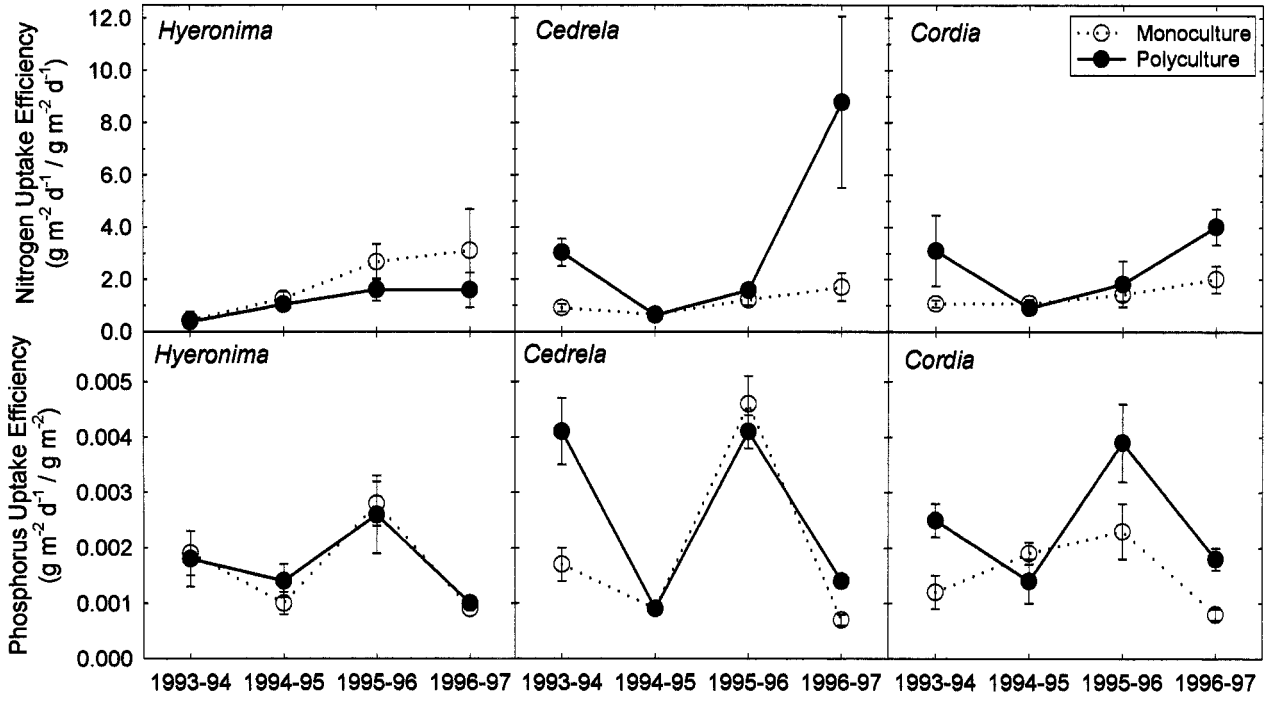

Figure 4. Nitrogen (upper panels) and phosphorus (lower panels) uptake efficiencies in monocultures and polycultures dominated by *Hyeronima alchorneoides, Cedrela odorata,* and *Cordia alliodora*. Points shown for 1995–96 include nutrient washout from the canopy; points shown for 1996–97 include nutrients in fine-root turnover. Values are means (standard errors) of three blocks.

and by 1994–95 was significantly lower. The same pattern was observed a year later in the *Cedrela*-dominated systems.

Given the links between plant- and ecosystem-level nutrient use efficiencies, we expected the *Hyeronima*-dominated systems to have the highest nutrient use efficiency, followed by the *Cedrela*- and then the *Cordia*-dominated systems. This expectation was borne out in the monocultures, but the pattern did not hold for the polycultures, where the presence of the additional life forms caused NUE of the *Cedrela*- and *Cordia*-dominated systems to surpass the *Hyeronima*-dominated system in some years (see Figure 5). Thus, high nutrient use efficiency of a stand dominant is not necessarily a good predictor of efficiency of the whole community: It is the mix of species and life forms that determines efficiency at the ecosystem level.

Implications of Life-form Diversity for Ecosystem Functioning

Anticipating complementary differences in modes of accessing soil nutrient supplies by different life forms, we predicted that the polycultures would have greater nutrient uptake and uptake efficiency than monocultures. The additional lifeforms did contribute to additional nutrient uptake in *Cedrela*- and *Cordia*-dominated polycultures, although this was not reflected in a commensurate decline in the extractable soil nutrient pool, as would be expected (see Tilman and others 1996). Instead, there was a decline in extractable NO_3^- and NH_4^+ (measured in the top 20 cm) over time, across all systems, and not in *Cedrela*- and *Cordia*-dominated polycultures alone. These findings suggest that the additional life forms may be accessing nutrients from greater soil depths than the trees—which is certainly a possibility for the palms, with their deeply penetrating cablelike roots that extend to a soil depth of 3 m or more.

The greater nutrient uptake and uptake efficiency due to the additional life forms in the *Cedrela*- and *Cordia*-dominated systems was manifest in 2 of the 4 years (see Figure 4)—one (1993–94) when the herbaceous heliconia flourished and a second (1996–97) when the palm grew vigorously (see Figures 1, 3, and 4). During the intervening 2 years, the impact of these additional life forms on uptake efficiency was small, and monocultures and polycultures had similar uptake efficiencies. We conclude that the impact of life-form diversity on nutrient use efficiency is not a static phenomenon;

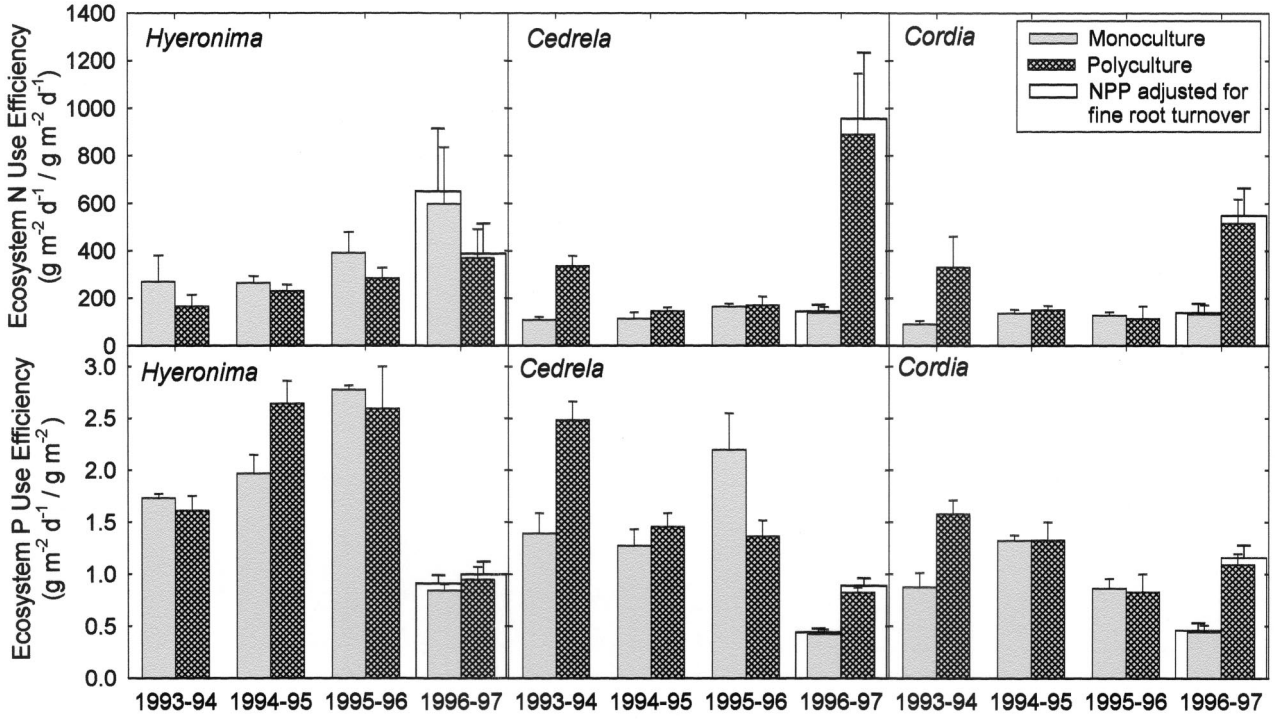

Figure 5. Ecosystem nutrient use efficiency estimated as the ratio of net primary productivity to rate of nitrification (upper panels) or to soil phosphorus (lower panels) in monocultures and polycultures dominated by *Hyeronima alchorneoides*, *Cedrela odorata*, and *Cordia alliodora*. Values are means (standard errors) of three blocks.

instead, it varies with the growth (thus nutrient uptake) of the community's components, rising when growth is vigorous and declining when growth slows.

Unlike nutrient uptake and uptake efficiency, nutrient accrual in biomass—which is critical to ecosystem nutrient retention—remained consistently high in these systems in all 4 years. This high nutrient accrual in biomass in polycultures of *Cedrela* and *Cordia* occurred despite a decline in standing biomass of the herbaceous heliconia following the postflowering dieback of many monocarpic ramets (1994–95 and 1995–96). During this period, there was compensatory uptake and sequestration of nutrients by the initially slower growing palms, as these systems developed from relatively simple two-tiered structures composed of tree overstories and heliconia understories, to more complex three-tiered structures composed of tree, palm, and heliconia strata.

The temporal relaying of nutrient uptake and sequestration observed in these systems is a potentially important mechanism for ecosystem nutrient retention as seral species replace one another. Furthermore, these systems highlight the temporal shifts in ecosystem functioning that can be attributed to different life forms, and may be of particular relevance in communities composed of long-lived, large-statured individuals.

Role of Soil Nutrient-Supplying Power

Over the 4 years of this study, there was an apparent decline in soil N availability and an increase in soil P across all systems (see Figure 2). These temporal changes in soil N and P availability cannot be explained by changes in soil organic matter—the principal reservoir of labile N and P in surface soil. Soil organic matter in the top 10 cm of soil remained relatively constant at around 3% in all systems (range, 2.2%–5% in the surface 10 cm of soil) throughout the study. The decline in the N-supplying capacity of the soil was associated with a decline in extractable N (that is, the initial values from mineralization determinations) across all systems (from 10.6 to 2.4 μg N/g soil over the 4-year period, averaged across all species and treatments). This most likely reflects an increasingly tighter cycling of N. The increase in P availability, on the other hand, may have resulted from P being retrieved from greater soil depths and deposited on the soil surface as litter. In these systems, almost 7 kg/ha of P are deposited on the soil in litter annually.

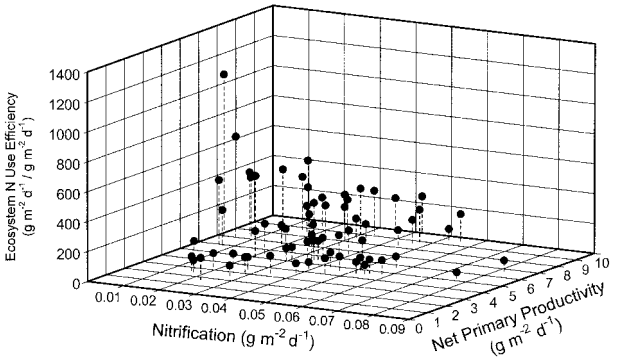

Figure 6. Ecosystem nitrogen use efficiency as a function of net primary productivity (its numerator) and soil N supply (its denominator). Data include monocultures and polycultures dominated by all three tree species over the 4-year duration of the study.

Both N and P use efficiency reflected patterns of NPP (see Figure 1 and compare Figure 5), the plant-related term in the nutrient use efficiency equation, though only weakly. There was a stronger link between patterns of nutrient uptake efficiency (a term that includes soil nutrient supply in the denominator) and N and P use efficiency (see Figure 4 and compare Figure 5). Therefore, to examine the relative importance of plant-level and soil-related influences on ecosystem NUE, we plotted nutrient use efficiency as a function of the factors used to define it in Eq. (1): NPP, an outcome of plant-level processes, and soil N supply, a result of factors affecting rates of litter decomposition and mineralization (see Figure 6). As expected, ecosystem N use efficiency showed a strong negative correlation with soil N supply (which is the denominator in the calculation of ecosystem nutrient use efficiency). What is more surprising, however, is that ecosystem N use efficiency responded only weakly to increases in NPP (the numerator in the calculation of ecosystem nutrient use efficiency). This indicates that even though species exerted a significant effect on nutrient use efficiency at the ecosystem level, this efficiency is also subject to substantial control by factors that influence soil nutrient supply.

Implications for Scaling

Moving from scales of leaves to plants to ecosystems involves an increasing number of nested terms in the equations used to calculate nutrient use efficiency (A. J. Hiremath *unpublished*). Because each increment of scale augments the error of estimates, uncertainty increases with upward scale. Despite the errors associated with upward scaling, the idea of being able to measure leaf- or plant-level traits and extrapolate to functioning at the landscape level is admittedly attractive, and some success has been achieved with respect to water, energy, and carbon fluxes between terrestrial ecosystems and the atmosphere (see, for example, Ehleringer and Field 1993; Sellers and others 1997). Nevertheless, for nutrient use efficiency, such upward scaling is tenuous at best due to the influence of a factor external to the plants—nutrient availability in the soil. Likewise, it is tempting to interpret vegetation and extrapolate to ecosystem functioning from patterns of soil fertility (as done successfully by Chadwick and others 1999), but this too is fraught with risk because of the important role exerted by plant species.

Although nutrient uptake efficiency and use efficiency reveal a great deal about the performance of leaves and plants, they are risk-laden estimators of ecosystem processes. The functioning of terrestrial ecosystems with respect to their capacities to take up nutrients from the soil and use those nutrients to facilitate growth clearly requires high-quality information on both the nutrient-supplying power of the soil and the capacity of the plants to use those nutrients effectively. Extrapolation from the smaller-scale processes integrated by leaf- and plant-level nutrient use efficiency can lead to erroneous estimates of functioning at the ecosystem level.

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