
Nutrient Use Efficiency in Three Fast-Growing Tropical Trees

Ankila J. Hiremath, John J. Ewel, and Thomas G. Cole

ABSTRACT. We measured nutrient use efficiency (NPP/nutrient uptake) in three species of tropical trees, *Hyeronima alchorneoides*, *Cedrela odorata*, and *Cordia alliodora*. We tested the prediction that on fertile soils species with very different biomass and nutrient allocation and turnover would converge on a common value of nutrient use efficiency. Due to high soil fertility, nutrient use efficiencies of the species studied were low (95–150 and 433–962 for N and P use efficiency, respectively). Nutrient use efficiency was examined in terms of its components, nutrient productivity and the mean residence time of nutrients. Although the species converged on the same nitrogen (but not phosphorus) use efficiency, differences in nutrient productivity and nutrient residence time may confer varying abilities to deal with nitrogen limitation. A combination of high nutrient productivity and longer nutrient retention (e.g., *Hyeronima*) signals an ability to prosper on infertile sites, whereas high nutrient productivity in the absence of long nutrient retention (e.g., *Cedrela*) indicates a capacity for high productivity, but only on fertile soil. Nutrient use efficiency and its components help explain species' distributions in natural communities and can be important criteria in selecting perennial plants for human use. *For. Sci.* 48(4):662–672.

Key Words: Litterfall, nitrogen, nutrient uptake, phosphorus, productivity.

NUTRIENT USE EFFICIENCY, the ratio of biomass production to nutrient uptake (Hirose 1975), is an index that helps explain species' distributions across landscapes that vary in soil fertility (Rundel 1982, Vitousek 1982, Schlesinger et al. 1989). Comparisons of natural communities along gradients of soil fertility indicate that plants on less fertile soils use nutrients more efficiently than those on more fertile soils, as evidenced by less nutrient return to soil in litterfall (Vitousek 1982, 1984, Cuevas and Medina 1986, Silver 1994). In addition to its utility in explaining patterns and processes in natural ecosystems, nutrient use efficiency is also a useful tool when matching species to site in agriculture and forestry (Gabelman and Gerloff 1983, Dambroth and El Bassam 1990, Sauerbeck and Helal 1990).

Nutrient use efficiency can be assessed at several scales: leaf, plant, or ecosystem (Grubb 1989, Ewel and Hiremath 1998). At the whole-plant level, nutrient use efficiency as

defined above (i.e., the ratio of productivity to uptake) can be disaggregated to the product of nutrient productivity and the mean residence time of nutrients (Berendse and Aerts 1987). Nutrient productivity, defined as the ratio of plant biomass increment to total nutrients in the plant (Ågren 1983), depends on the efficiency with which foliar nutrients are used for photosynthesis (Garnier et al. 1995) and on biomass and nutrient allocation to photosynthetic tissue; it is an instantaneous measure of nutrient use efficiency. Mean residence time is a function of longevity, whether of a plant part or of the plant as a whole, and nutrient retention within plants, as measured by nutrient resorption prior to tissue abscission.

There may be evolutionary trade-offs between selection for traits that lead to higher nutrient productivity and those that lead to longer nutrient retention. Berendse and Aerts (1987) proposed that fertile conditions select for greater nutrient productivity at the expense of nutrient

Ankila J. Hiremath can be reached at the Ashoka Trust for Research in Ecology and the Environment, 659 5th A Main Road, Hebbal, Bangalore 560024, India—Phone: (+80) 353 0069; Fax: (+80) 353 0070; E-mail: <hiremath@atree.org>. John J. Ewel and Thomas Cole are with the USDA Forest Service, Institute of Pacific Islands Forestry, 1151 Punchbowl Street Suite 323, Honolulu HI 96813.

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retention, whereas infertile conditions select for longer nutrient retention at the expense of productivity. More recently, it has been demonstrated that mean residence time of nutrients may be an inherent species characteristic, whereas nutrient productivity is phenotypically responsive to changes in nutrient availability: as soil fertility increases, mean residence time of nutrients is conserved, whereas nutrient productivity decreases (Aerts and Caluwe 1994, Vázquez de Aldana and Berendse 1997, but see Aerts 1989). We predict, then, that on fertile soils, species having very different biomass and nutrient allocation and turnover would converge on a common value of nutrient use efficiency: there may be multiple combinations of productivity and nutrient uptake values that achieve the same efficiency of nutrient use.

We examined the plant-level nutrient use efficiency of three tree species growing on a site where growth is unconstrained seasonally, and soil fertility is uniform and high. By examining nutrient use efficiency and its biotic determinants—productivity, nutrient contents of tissues, and nutrient residence times—we were able to test the prediction that species having very different biomass allocation patterns and leaf characteristics, including leaf longevity (Haggar and Ewel 1995, Hiremath 2000), would have similar nutrient use efficiencies if grown on a site where growth was almost unconstrained by abiotic factors. Nutrient use efficiency was assessed for nitrogen (N) and phosphorus (P), the two nutrients that most commonly limit productivity in terrestrial systems. The tree species tested are all fast-growing species important to tropical forestry: *Hyeronima alchorneoides* Allemão (Euphorbiaceae), *Cedrela odorata* L. (Meliaceae), and *Cordia alliodora* (R. & P.) Cham. (Boraginaceae).

Methods

Study Site and Species

This research was conducted in experimental plantations at La Selva Biological Station in the Atlantic lowlands of Costa Rica. La Selva pertains to Holdridge's Tropical Wet Forest life zone (McDade and Hartshorn 1994). Mean annual temperature at La Selva is 25.8°C, and average yearly rainfall is approximately 4 m, with a dry season from February to April (Sanford et al. 1994).

The experimental plantations are on a level alluvial terrace, 41 m above sea level. The soil is a eutric Hapludand—an andesitic soil of humid climates, with minimum horizon development and high base saturation (Weitz et al. 1997). The soil is well drained, with low bulk density (0.67 g/cm³) and high organic matter content (5.9%) in the surface soil (0–10 cm). Soil at the site is relatively rich in extractable N (13.7 µg/g, soil depth 0–10 cm, potassium chloride extraction) and P (14.4 µg/g, soil depth 0–10 cm, acid ammonium fluoride extraction) compared with values reported from a range of other tropical sites (e.g., 4.1–12.6 µg/g N [Vitousek and Matson 1988] and 0.6–10.8 µg/g P [Moormann et al. 1981, Sollins et al. 1994]).

When it was annexed to La Selva in the mid-1980s, the site was a recently abandoned cacao plantation. In early 1991, the

vegetation was felled, the overstory trees were harvested, and the slash was burned; the experimental plantations were established immediately thereafter.

All three species used in this study are fast-growing tropical hardwoods native to Costa Rica. They occur in the forest at La Selva or in abandoned pastures and secondary vegetation in the neighboring region. *Cedrela odorata* (hereafter, *Cedrela*) is confamilial with the true mahoganies (*Swietenia* spp.) and, like mahogany, is highly prized for its timber. Its natural range extends from southern Mexico to Peru and Argentina, and to the West Indies to Trinidad and Tobago. It is widely planted in the neotropics and has been introduced to parts of Africa and southeast Asia (Glogiewicz 1998). To a lesser extent, it is also planted as an overstory tree with coffee (Glover and Beer 1986) and in managed fallows (Hammond 1995). *Cordia alliodora* (hereafter, *Cordia*), like *Cedrela*, is distributed widely in the neotropics and extends from central Mexico to northern Argentina and the islands of the Caribbean. Its timber is highly valued, and it has been planted extensively since the early 1900s, both in its native range and in Africa and the Pacific region (Greaves and McCarter 1990). *Hyeronima alchorneoides* (hereafter, *Hyeronima*) is a massive canopy emergent in the forests at La Selva and can attain a height of up to 50 m (Hartshorn and Hammel 1994). It has dense, durable wood. For a tree that has such dense wood, *Hyeronima* is remarkably fast-growing as a juvenile under high light conditions—growing as much as 3 m per year—although it may take several hundred years to reach its full size in the forest (Clark and Clark 1992). Of the three tree species, it has been the least studied, though it is becoming better known as a species with potential to be used in reforestation (Butterfield and Espinoza 1992).

The three species 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 that can be up to a meter long, with 10–20 pairs of leaflets, each about 40 cm². 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, simple leaves, each about 30 cm². 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 year round, although it is partially deciduous during the dry season. *Hyeronima* has sympodial growth with orthotropic branches that form a dense crown. *Hyeronima* is evergreen, with very large, simple leaves as a juvenile (area ~280 cm²); the tree produces progressively smaller leaves as it ages, such that emergent trees in the forest have leaves that are only about 60 cm². By age 2 yr in the experimental plantations, *Hyeronima* stands had developed a dense canopy, with a high leaf area index (LAI ~6) and very little light penetration to the understory, compared to the more open canopies of *Cordia* and *Cedrela* (Haggar and Ewel 1995).

In addition to differences in architecture, leaf morphology, and phenology, the species also differ greatly in foliar nutrient concentrations. Although N and P concentrations

in leaves of all three species are high (due, no doubt, to the fertile soils of the study site), they differ markedly among species, as was manifest at the outset of the experiment: at age 2 yr *Cordia* had higher foliar N concentrations (3.39 %) than the other two species (2.90 and 2.76 % for *Cedrela* and *Hyeronima*, respectively). In contrast, foliar P concentrations were higher in *Hyeronima* (0.35 %) than in *Cordia* (0.27 %) or *Cedrela* (0.22 %).

The differences among the three species in their architecture above ground are also reflected in their architecture below ground. *Hyeronima* has the densest, most compact root system. *Cordia*, in contrast, has a laterally extensive root system, and *Cedrela* is intermediate between the other two species. *Hyeronima* allocates the greatest amount of biomass to fine roots and has the highest fine root length density, although *Cordia* has the highest specific root length of the three species (Haggard 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 P, an immobile soil nutrient; *Cordia*, on the other hand, with roots that explore the soil extensively, is likely to have higher uptake of N, a mobile soil nutrient (Haggard and Ewel 1994). Foliar nutrient concentrations of the three species support this hypothesis.

In early 1991, plantations (40 × 30 m) of *Cedrela*, *Cordia*, and *Hyeronima* were established in a randomized block design with three replicates. In each plot, trees were planted in rows 1.73 m apart. Within rows, individuals were spaced at 2 m intervals; individuals in successive rows were offset by a meter. The resulting planting pattern has each tree at the center of a hexagon, 2 m from its six closest neighbors. The overall density was 2,887 trees per ha, 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. The plots were lightly thinned to prevent stand stagnation in August 1993, in March 1995, and again in early June 1996, so that at the start of this study the average density was about 1,600 (*Hyeronima*, *Cordia*) to 2,000 (*Cedrela*) trees per ha, and at the end of the study the average density was about 1,100 (*Cordia*) to 1,200 (*Hyeronima*, *Cedrela*) trees per ha.

Nutrient Use Efficiency

Nutrient use efficiency was estimated for June 1995–June 1996, when the trees were 4 to 5 yr old. Plant nutrient use efficiency is denoted as follows:

$$\text{Plant NUE} = \frac{\text{NPP}}{\text{Total Nutrient Uptake}}$$

where NPP is net primary productivity of an individual, and total nutrient uptake includes nutrients accrued in standing above and belowground biomass as well as nutrients taken up but subsequently lost in litter or by leaching from the crown.

In addition, to understand the mechanisms underlying nutrient use efficiency by the three species, nutrient use

efficiency was examined in terms of its components, nutrient productivity (i.e., productivity over nutrient standing stock) and mean residence time of nutrients (i.e., nutrient standing stocks over uptake) (Berendse and Aerts 1987). An assumption underlying this definition of nutrient use efficiency is that a steady state has been reached, such that biomass and nutrients accrued are equivalent to biomass and nutrients returned to the soil. Nutrient use efficiency then becomes the ratio of productivity to nutrients in litterfall (assuming other pathways of nutrient return to the soil are negligible). Although the study species (aged 4.5 yr at the midpoint of our study) obviously do not meet the steady state assumption in the case of wood, they do in the case of foliage. Stand-level leaf area of all three species reached plateaus following canopy closure (at 10, 14, and 16 months for *Cordia*, *Hyeronima*, and *Cedrela*, respectively; Haggard and Ewel 1995). Thus, we were able to estimate nutrient productivity as productivity per unit of foliar nutrient ("canopy nutrient use efficiency"; Harrington et al. 1995) and mean residence times of nutrients as mean residence times of nutrients in foliage.

Net Primary Productivity

Net primary productivity (NPP) was estimated as the algebraic sum of above- and belowground biomass increments and litterfall. Our calculations of NPP for 1995–1996 do not account for fine root mortality, which was measured in 1996–1997 and found to be 2 to 10% of NPP (Hiremath and Ewel 2001).

Biomass of trees (stems, branches, petioles or rachises, leaves, and coarse roots) was determined using allometric equations of the form $W = aX^b$, where W is biomass of the component being assessed and X is a compound measure of plant size (Satoo and Madgwick 1982, p. 15–31). Dry weights of entire components or subsamples thereof were determined after drying to constant weight at 70°C. From the start of the experiments trees (including roots > 5 mm in diameter) were harvested annually from areas in each plot specifically designated for destructive sampling and added to the allometric equations, such that by 1996 each equation comprised data from 108 individuals. Biomass was best predicted by either $W = HD^2$ or HD (H = height, and D = diameter). The r^2 values obtained ranged from 0.75 to 0.93 (leaves), 0.82 to 0.91 (roots), and 0.88 to 0.96 (stems). Inventories of tree size (height and diameter) in mid-1995 and mid-1996 provided input to the allometric equations.

Change in biomass of fine roots (i.e., roots ≤ 5 mm diameter) was determined by annual coring. Eight cores, each 5 cm in diameter and 110 cm deep, were taken in each plot. Cores were combined by 10 cm depth intervals, and the composite samples were washed in a root elutriator before being dried and weighed. Litter was collected biweekly from three 1.73 × 0.50 m traps in each plot and the samples were combined. Fine root biomass per tree, and litter produced per tree, were calculated by dividing total fine root biomass per unit area, and litter per unit area, respectively, by the number of individuals per unit area.

Nutrient Uptake

Nutrient uptake was estimated as the sum of net nutrient uptake and nutrients lost in litterfall and foliar leaching. Net uptake of N and P was calculated by summing the products of nutrient concentrations in leaves, stems, branches, petioles or rachises, and coarse and fine 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 from mid-1995 to mid-1996. 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 Corp. 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. (Stemflow collar construction and stemflow volume determination are detailed in Hiremath 1999. Throughfall volume determination is detailed in Casey 1996). Samples

for throughfall and stemflow chemistry were obtained for 8 and 12 rain events, respectively; the events ranged from 0.5 to 33.1 mm. Samples were filtered through a 0.45 μ glass fiber filter (Gelman Sciences Type A/E), fixed with a drop of chloroform, and frozen until analysis. Samples were analyzed for PO_4^{3-} on a spectrophotometer following a modified antimony/molybdate protocol (Murphy and Riley 1962). Nitrate and NH_4^+ were analyzed on an Alpkem Autoanalyzer using standard colorimetry (Alpkem 1986).

Differences in net primary productivity, nutrient uptake, nutrient productivity, mean residence time, and nutrient use efficiency were analyzed using a one-way analysis of variance with species as the main effect. Interspecific differences in mean productivity, uptake, and nutrient use efficiency were tested using orthogonal contrasts. Analyses were done with the GLM procedure in SAS (SAS Institute 2000).

Results

Productivity

Net primary productivity per individual ranged from about 6.6 kg/yr for *Cordia* to about 19.8 kg/yr for *Hyeronima* (Table 1). This is equivalent to NPP of 11 to 32 $\text{Mg ha}^{-1} \text{ yr}^{-1}$. Leaf turnover rates, calculated on the basis

Table 1. Mean biomass, litter production, NPP, and stand density of the three species. Changes in biomass plus litterfall do not sum to NPP because the biomass of trees thinned during the growth interval is not shown. Values are means (standard errors) of trees in three replicate blocks.

Variable	Year or interval	<i>Hyeronima</i>	<i>Cedrela</i>	<i>Cordia</i>
Leaves (kg/individual)	Mid-1995	2.45 (0.33)	0.99 (0.01)	1.39 (0.11)
	Mid-1996	4.62 (0.46)	1.63 (0.04)	1.97 (0.12)
Branches (kg/individual)	Mid-1995	6.11 (0.47)	3.48 (0.07)	2.93 (0.30)
	Mid-1996	8.79 (0.54)	7.50 (0.22)	3.91 (0.07)
Petioles or rachises (kg/individual)	Mid-1995	*	0.40 (0.01)	0.06 (0.01)
	Mid-1996	*	0.57 (0.01)	0.10 (0.01)
Trunks (kg/individual)	Mid-1995	21.0 (1.56)	9.59 (0.18)	11.51 (1.66)
	Mid-1996	35.87 (2.15)	19.12 (0.51)	18.38 (0.33)
Fine roots (≤ 5 mm diam.) (kg/individual)	Mid-1995	1.43 (0.17)	0.32 (0.04)	0.46 (0.03)
	Mid-1996	2.44 (0.29)	1.05 (0.34)	0.91 (0.10)
Coarse roots (> 5 mm diam.) (kg/individual)	Mid-1995	5.22 (0.27)	3.84 (0.08)	3.63 (0.43)
	Mid-1996	7.67 (0.34)	5.56 (0.13)	4.73 (0.12)
Leaf litter (kg/yr per individual)	1995–1996	4.50 (0.15)	2.94 (0.19)	2.82 (0.37)
Branch litter (kg/yr per individual)	1995–1996	0.41 (0.13)	0.12 (0.04)	0.31 (0.14)
Stand density (individuals/ha)	1995	1,608 (77)	2,035 (74)	1,670 (79)
Stand density (individuals/ha)	1996	1,256 (47)	1,232 (32)	1,129 (120)
NPP (kg/yr per individual)	1995–1996	19.75 (1.29)	9.48 (0.63)	6.59 (1.24)

* *Hyeronima* petioles were included with branches.

of standing leaf area and annual litterfall, were highest for *Cedrela* (2.3 yr⁻¹) followed by *Cordia* (1.9 yr⁻¹) and then *Hyeronima* (1.4 yr⁻¹). This correlates with leaf lifespans measured by direct tagging of leaves (about 50, 99, and 176 days for *Cedrela*, *Cordia*, and *Hyeronima*, respectively; Hiremath 2000), although estimates of lifespans based on leaf turnover rates (equivalent to about 159, 197 and 259 days for *Cedrela*, *Cordia*, and *Hyeronima*, respectively) were greater than measured leaf lifespans. It is likely that handling and tagging of leaves shortened their lifespans. Alternatively, it is possible that calculations based on leaf turnover rates (calculated as litter biomass × specific leaf area of litter divided by canopy leaf area) overestimated lifespans: Mass loss from litter collected biweekly may underestimate litter leaf area, leading to an underestimate of leaf turnover.

Nutrient Uptake

Tissue concentrations of N and P tended to be highest in *Cordia* and lowest in *Hyeronima* (Table 2). Similarly, concentrations of N and P in *Cordia* litter tended to be higher than those of the other two species, probably as a consequence of their higher foliar nutrient concentrations.

Concentrations of NH₄⁺ and PO₄³⁻ in stemflow and throughfall (about 0.11 to 0.40, and 0.04 to 0.95 mg/L of NH₄⁺ and PO₄³⁻, respectively) were elevated relative to concentrations in rainwater (about 0.10 and 0.02 mg/L of NH₄⁺ and PO₄³⁻, respectively), indicating leaching of these ions. Average NO₃⁻ concentrations in stemflow and throughfall (about 0.01 to 0.04 mg/L) on the other hand, were

lower than in rainwater (about 0.05 mg/L), indicating that NO₃⁻ is retained in the crown (Hiremath 1999).

Hyeronima had the greatest total N uptake of the three species (Figure 1a) and differed significantly from both *Cedrela* (*P* = 0.05) and *Cordia* (*P* = 0.02). A large fraction of total N taken up was lost in litterfall by all three species: *Hyeronima* shed about half its total N uptake, whereas *Cedrela* and *Cordia* lost more than two-thirds of the N they took up. Loss of N via leaching by stemflow and throughfall was a negligible proportion of total uptake (<0.5 %).

Total P uptake did not differ significantly among species (Figure 1b; *P* = 0.24). For *Cordia*, about a third of total P taken up was lost in litterfall; for *Cedrela* and *Hyeronima*, on the other hand, only about a fourth of total P taken up was lost in litterfall. Leaching of P from the crowns constituted a considerable fraction of total uptake, ranging from about 1.7 to 10.9 %.

Nutrient Use Efficiency

Despite an almost 40% difference in N use efficiency between *Hyeronima*, the species with the highest N use efficiency, and *Cordia*, the species with the lowest N use efficiency (Figure 2a), the three species did not differ significantly (*P* = 0.20). Phosphorus use efficiency, on the other hand, differed among the three species: phosphorus use efficiency by *Hyeronima* was greater than that of *Cordia* (*P* = 0.01), as well as *Cedrela* (*P* = 0.02) (Figure 2b).

Nutrient productivities of *Cedrela* and *Hyeronima* were higher than that of *Cordia* with respect to both N (*P* = 0.02) and P (*P* = 0.01; Table 3). Mean residence time of N in

Table 2. Tissue nitrogen and phosphorus concentrations. Values are percent mass, and are means (standard errors) of composite samples from three blocks.

Compartment	Nitrogen			Phosphorus		
	<i>Hyeronima</i>	<i>Cedrela</i>	<i>Cordia</i>	<i>Hyeronima</i>	<i>Cedrela</i>	<i>Cordia</i>
Leaves, 1995	2.33 (0.07)	2.79 (0.05)	3.32 (0.04)	0.14 (0.01)	0.17 (0.01)	0.20 (0.03)
Leaves, 1996	1.85 (0.19)	2.34 (0.14)	2.59 (0.19)	0.17 (0.01)	0.26 (0.01)	0.27 (0.01)
Branches, 1995	0.67 (0.05)	0.53 (0.04)	0.73 (0.12)	0.11 (0.01)	0.12 (0.02)	0.20 (0.02)
Branches, 1996	0.45 (0.05)	0.64 (0.07)	0.75 (0.03)	0.10 (0.01)	0.17 (0.01)	0.26 (0.01)
Petioles (or rachises), 1995	*	0.97 (0.07)	1.38 (0.04)	*	0.23 (0.01)	0.23 (0.003)
Petioles (or rachises), 1996	*	0.96 (0.04)	1.42 (0.26)	*	0.38 (0.01)	0.32 (0.05)
Trunks, 1995	0.20 (0.02)	0.35 (0.05)	0.38 (0.05)	0.07 (0.01)	0.07 (0.003)	0.11 (0.001)
Trunks, 1996	0.32 (0.04)	0.35 (0.03)	0.45 (0.00)	0.08 (0.01)	0.10 (0.01)	0.14 (0.02)
Fine roots, 1995 [†]	0.69	0.88	0.69	0.20	0.46	0.18
Fine roots, 1996	0.82 (0.07)	0.74 (0.04)	0.83 (0.02)	0.24 (0.01)	0.29 (0.08)	0.11 (0.001)
Coarse roots, 1995	0.21 (0.01)	0.47 (0.02)	0.53 (0.04)	0.04 (0.01)	0.13 (0.02)	0.14 (0.01)
Coarse roots, 1996	0.25 (0.03)	0.42 (0.06)	0.55 (0.05)	0.05 (0.01)	0.21 (0.04)	0.15 (0.02)
Leaf Litter, 1995–1996	1.36 (0.02)	1.47 (0.09)	1.77 (0.09)	0.09 (0.001)	0.12 (0.01)	0.19 (0.02)
Branch litter, 1995–1996	0.63 (0.12)	0.73 (0.01)	1.16 (0.12)	0.05 (0.01)	0.06 (0.003)	0.11 (0.01)

* *Hyeronima* petioles were included with branches.

[†] Fine root samples from the three replicate blocks were combined prior to tissue nutrient analysis in 1995.

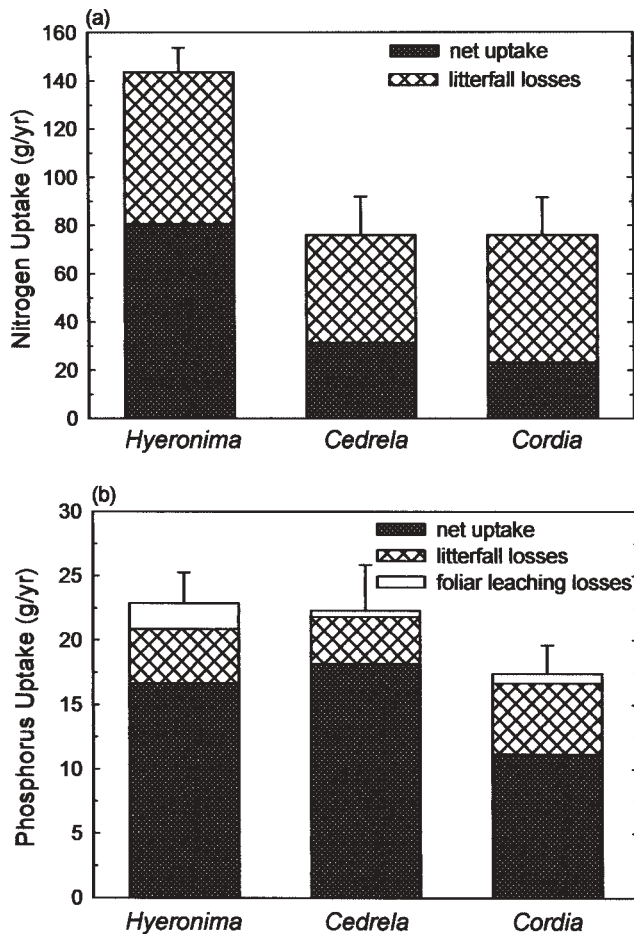


Figure 1. Total uptake of (a) nitrogen and (b) phosphorus by average individuals of the three species. Values are means (standard errors) of trees in three blocks. Foliar leaching losses of nitrogen are too small to show at this scale.

Hyeronima canopies was longer than in canopies of *Cedrela* ($P = 0.04$), although there was no difference between *Hyeronima* and *Cordia* ($P = 0.42$), or between *Cordia* and *Cedrela* ($P = 0.12$). Mean residence time of P in *Hyeronima* canopies, on the other hand, was longer than in canopies of *Cedrela* and *Cordia* ($P = 0.004$; Table 3).

Nutrient use efficiency calculated as the product of nutrient productivity and mean residence time of nutrients in the canopy yields the ratio of productivity to litter nutrients. Although this is not equivalent to the more holistically defined nutrient use efficiency (the ratio of total productivity to total nutrient uptake), the two terms are related because the

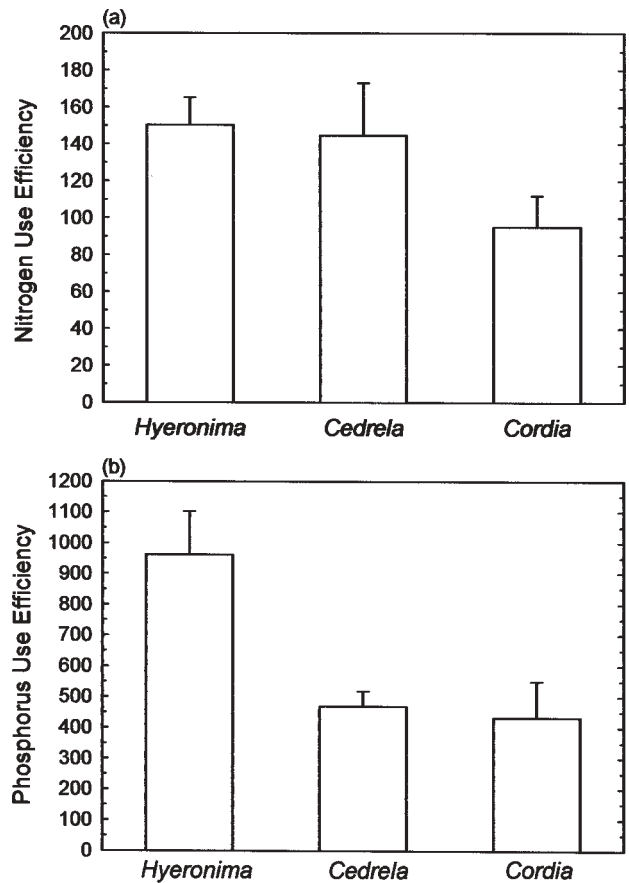


Figure 2. Use efficiency of (a) nitrogen and (b) phosphorus for average individuals of the three species. Nutrient use efficiency is the ratio of net primary productivity to total nutrient uptake. Values are means (standard errors) of trees in three blocks.

numerator, productivity, is common to both terms, and the denominators of the two terms are correlated. Nutrient use efficiency calculated as the product of nutrient productivity and mean residence time of nutrients in the canopy differed significantly among species with respect to both N ($P = 0.001$; Table 3) and P ($P < 0.0001$; Table 3).

Discussion

Nutrient Use Efficiency

Whole-tree nutrient use efficiency of the three species studied, with respect to both N (95–150) and P (433–962),

Table 3. Nutrient productivity (NPP / mean standing stock of foliar nutrients), mean residence time of nutrients (mean standing stock of foliar nutrients / rate of nutrient return to the soil as litter), and use efficiency (calculated as nutrient productivity \times mean residence time of nutrients) of nitrogen and phosphorus. Values are means (standard errors) of three blocks. Different letters indicate significant differences among species at $P = 0.05$.

Species	Nitrogen			Phosphorus		
	Nutrient productivity ($\text{g g}^{-1} \text{ yr}^{-1}$)	Mean residence time (yr)	Nutrient productivity \times mean residence time (g / g)	Nutrient productivity ($\text{g g}^{-1} \text{ yr}^{-1}$)	Mean residence time (yr)	Nutrient productivity \times mean residence time (g / g)
<i>Hyeronima</i>	343.9 a (39.6)	1.05 a (0.11)	352.9 a (14.4)	4,291.3 a (196.8)	1.23 a (0.07)	5,240.2 a (104.9)
<i>Cedrela</i>	365.9 a (25.9)	0.65 b (0.09)	234.5 b (15.4)	4,176.1 a (259.4)	0.69 b (0.08)	2,835.4 b (144.7)
<i>Cordia</i>	169.1 b (45.2)	0.92 ab (0.11)	146.9 c (23.3)	2,108.8 b (522.1)	0.72 b (0.08)	1,429.3 c (226.2)

Table 4. Whole tree use efficiency of nitrogen and phosphorus. Included for comparison are values of aboveground nutrient use efficiency obtained from studies in plantations of fast-growing species from a tropical (Puerto Rico), a subtropical (the lower Himalaya), and a temperate (Wisconsin) site. Values are g biomass/g nutrient.

Location	Source	Species	Age (yr)	Nitrogen use efficiency	Phosphorus use efficiency		
Costa Rica	This study	<i>Hyeronima alchorneoides</i>	4.5	150	962		
		<i>Cedrela odorata</i>	4.5	145	469		
		<i>Cordia alliodora</i>	4.5	95	433		
Lower Himalaya, India	Lodhiyal, et al. 1995	<i>Populus deltoides</i>	5.0	160	1,379		
		Puerto Rico	Wang et al. 1991	<i>Casuarina equisetifolia</i>	5.5	357	1,428
				<i>Albizia procera</i>	5.5	222	1,111
				<i>Eucalyptus robusta</i>	5.5	345	833
				<i>Leucaena leucocephala</i> K8	5.5	128	1,111
				<i>Leucaena leucocephala</i> P.R.	5.5	153	1,250
Wisconsin, USA	Son & Gower 1991	<i>Quercus rubra</i>	26.5	320	1,800		
		<i>Larix decidua</i>	26.5	480	3,750		
		<i>Pinus strobus</i>	26.5	140	1,500		
		<i>P. resinosa</i>	26.5	135	950		
		<i>Picea abies</i>	26.5	135	750		

was fairly low when compared with a number of other fast-growing species (Table 4). *Cordia*, in particular, had relatively low N and P use efficiencies; *Hyeronima* N and P use efficiencies, though low, were comparable to other species; and *Cedrela* N use efficiency was comparable to that reported for other species though its P use efficiency was lower than that reported for other species. The low nutrient use efficiencies we measured very likely reflect the fertile soils at the study site, and the adaptation of the species studied to those fertile soils (cf. Bridgman et al. 1995, but see Grubb 1989).

In its most aggregated form, nutrient use efficiency is the ratio of productivity to nutrient uptake. It is useful to examine those two components to determine whether similar nutrient use efficiencies result from similar values of each variable, or whether they result from wide ranges of values that yield similar ratios. Net primary productivity of the three species at age 4.5 yr ranged from about 11 to 32 Mg ha⁻¹ yr⁻¹. These values are toward the high end of the range compared with other fast-growing tropical species. For example, Lugo et al. (1988) reported aboveground NPP between 1.6 and 29.8 Mg ha⁻¹ yr⁻¹, with a median value of about 12 Mg ha⁻¹ yr⁻¹, for a number of plantation species from across the tropics.

Nutrient uptake is the sum of nutrient accrual and nutrient returns to the soil via litterfall and leaching from the crown. By age 4 yr, the species had accrued 225–301 kg/ha of N and 43–59 kg/ha of P. These values are comparable to values of N accrued (180–410 kg/ha), but lower than values of P accrued (50–80 kg/ha P) by different native tree species of the same age grown on less fertile soils close to our site (Montagnini and Sancho 1994). The differences are due to differences in nutrient concentrations (but not biomass) measured by Montagnini and Sancho (1994).

Losses of nutrients in litterfall are determined by rates of tissue turnover and the proportion of nutrients resorbed prior to abscission. Of the three species, *Cordia* had the highest litter nutrient concentrations. This was due, in part, to its high foliar nutrient concentrations, and in part to its relatively low nutrient resorption (about 37 and 24% for N and P, respectively) compared to the other two

species (about 50 and 40% for N and P, respectively; Hiremath 2000). Across a broad spectrum of species and biomes, average proportions of foliar N and P resorbed range from 40 to 60% (Chapin and Kedrowski 1983, Medina 1984), although extreme resorption values of up to 80% of P (by some mangrove species; Lugo 1998) and 90% of N (by species of larch; Gower and Richards 1990) have been reported.

Returns of N to the soil via leaching from the crowns were small: in the range of 0.1 to 0.5 kg ha⁻¹ yr⁻¹. Other studies have estimated annual N leaching losses of the order of 5.0 (Hölscher et al. 1998) to 6.9 kg ha⁻¹ yr⁻¹ (with a range of 0.5 to 22.1 kg ha⁻¹ yr⁻¹; Cole and Rapp 1981). Although we did not measure organic N in rainfall, stemflow, or throughfall, leaching from the crown constitutes such a negligible fraction (<0.6%) of total N uptake that even a four-fold increase in the estimate of N leaching losses would not substantially alter the calculation of total N uptake, and consequently, of N use efficiency. Our estimates of P leaching losses, unlike those of N losses, were higher than most values reported elsewhere: 1 to 3 kg ha⁻¹ yr⁻¹, compared with 0.5 (with a range of 0.1 to 1.9 kg ha⁻¹ yr⁻¹; Cole and Rapp 1981) to 0.8 kg ha⁻¹ yr⁻¹ (Hölscher et al. 1998).

We find, then, that although NPP varied at least four-fold among the species, and uptake of both N and P varied at least threefold, the ratio between the two, in the case of N (i.e., N use efficiency), is reasonably consistent, as described by a straight line (Figure 3a, $r^2 = 0.65$, slope = 140.1, $P = 0.01$). Moreover, the line has a decidedly positive slope, indicating an increase in NPP with increasing uptake: *Hyeronima*, with high values of both uptake and NPP, is clustered around the upper reaches of the relationship, *Cedrela* toward the middle, and *Cordia* at the lower end. Thus, very different values of NPP and uptake yield similar values of use efficiency. In the case of P (Figure 3b), the two axes appear to be unrelated (i.e., there is no response of NPP to additional uptake).

Mechanisms

Nutrient use efficiency is an index combining productivity and uptake, each of which involves multiple vari-

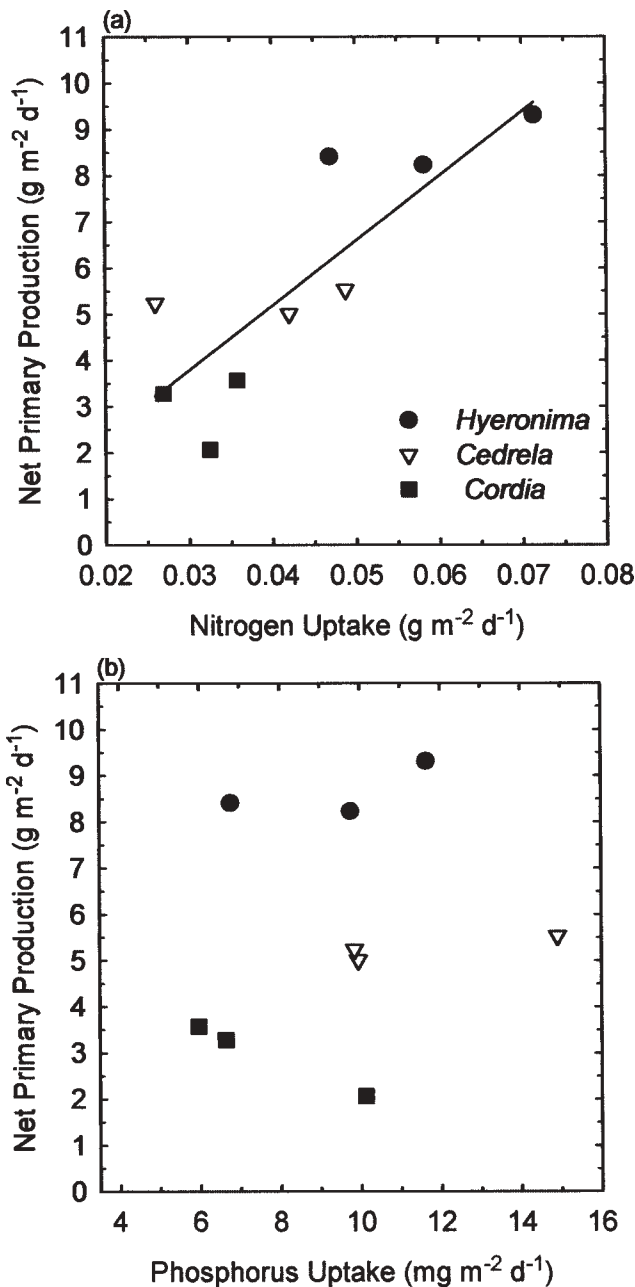


Figure 3. Relationships of net primary productivity to (a) nitrogen and (b) phosphorus uptake for the three tree species. Nutrient use efficiency is the ratio between these two variables, i.e., the slope if defined by a straight line.

ables. To understand the mechanisms underlying measured nutrient use efficiency, it is useful to disaggregate those components of nutrient use efficiency still further into nutrient productivity (i.e., productivity over nutrient standing stock) and mean residence time of nutrients (i.e., nutrient standing stocks over uptake) (Berendse and Aerts 1987). Nutrient use efficiency measured as the product of nutrient productivity and mean residence time of nutrients yields the ratio of productivity to litter nutrients.

Nutrient productivity ranged from about 169 to 365 g biomass [g N]⁻¹ yr⁻¹ and from about 2109 to 4291 g biomass [g P]⁻¹ yr⁻¹ for *Cordia* and *Hyeronima*, respectively (Table 3). These values of nutrient productivity are comparable to values of canopy N use efficiency (120–

420 g biomass [g N]⁻¹ yr⁻¹), though higher than values of canopy P use efficiency (400–1600 g biomass [g P]⁻¹ yr⁻¹), estimated by Harrington et al. (1995) for *Metrosideros* along an elevational gradient in Hawaii. Mean residence times of nutrients in the canopy (0.65–1.05 yr for N, 0.69–1.23 yr for P) were low compared to other forest ecosystems (e.g., about 2 yr and 9 yr for deciduous and evergreen forests, respectively; values calculated from Cole and Rapp 1981).

An important point emerges from examining plant resource use characteristics in this manner. Contrary to the proposition that there are inevitable tradeoffs between selection for high nutrient productivity and long residence times of nutrients (Berendse and Aerts 1987), the three species we studied span the possible outcomes: *Hyeronima* consistently had high nutrient productivity and a long residence time of both N and P, whereas *Cordia* had low nutrient productivity and intermediate to low nutrient residence time. *Cedrela* alone demonstrates possible tradeoffs in the selection for these different suites of characteristics, with high nutrient productivity and short nutrient residence times. Thus, N and P use efficiency calculated as the product of nutrient productivity and nutrient residence time (i.e., productivity/litter nutrients) followed the pattern *Hyeronima* > *Cedrela* > *Cordia*. This pattern was correlated with nutrient use efficiency measured for the three species (i.e., productivity/nutrient uptake).

A combination of high nutrient productivity and longer nutrient retention, as observed in the case of *Hyeronima*, indicates an ability for high productivity per unit of nutrient taken up as well as an ability to tolerate infertile soils. In contrast, high nutrient productivity in the absence of long nutrient retention, as in the case of *Cedrela*, may indicate an ability for high productivity per unit of nutrient taken up, but only on fertile soils. The observed distributions of these species support this idea: *Hyeronima* persists in competitive environments, growing slowly, but it can also grow very rapidly when resource availability is high (Clark and Clark 1992); *Cedrela*, on the other hand, occurs on fertile floodplain soils. It is possible that the high nutrient productivity of *Hyeronima* we observed is a phenotypic response to the high fertility of the site, although this is contrary to other studies that demonstrate a decrease in nutrient productivity in response to increased fertility (Aerts and de Caluwe 1994; Vázquez de Aldana and Aerts 1997). The relatively short mean residence times of N and P in *Cordia* argue for high nutrient productivities in this species. As with *Hyeronima*, the low nutrient productivity observed in *Cordia* may be a phenotypic response to soil fertility—but in this case a decrease in nutrient productivity with a decrease in fertility. Of the three species, *Cordia* showed very high productivity in the initial year or two of the experiment, but was the first of the three to manifest relative N limitation (as inferred from decreased foliar N to P ratios [Koerselman and Meuleman 1996; Hiremath 1999]), as N was sequestered in plant biomass and soil N supplies declined. This again, agrees

with the observed distribution of *Cordia*, which readily colonizes abandoned pastures but grows very slowly on infertile soils (Butterfield 1994). Thus, there are different ways to arrive at a given nutrient use efficiency, and those different mechanisms have important implications for interpreting relationships between trees and sites.

Applications

Nutrient use efficiency at the whole-plant level is an important consideration when attempting to understand species' distributions in natural communities. Individuals that use resources more efficiently may be at an advantage on infertile soils, a factor that might contribute to the pattern of species occurrence in patchy environments (Rundel 1982, Schlesinger et al. 1989). For example, evergreens, with their greater tissue longevity, are often credited with greater nutrient storage and recycling (Monk 1966, Waring and Schlesinger 1985, p. 175–176, Schlesinger et al. 1989, Aerts 1995). Such species often occur on infertile soils, as exemplified by the natural distribution of *Hyeronima*. On the other hand, species that have high tissue and nutrient turnover are able to achieve rapid growth on fertile soils, where nutrients are readily available, but do poorly on infertile soils and are likely to be out-competed by other species, as exemplified by the natural distribution of *Cordia*.

One component of nutrient use efficiency, within-plant nutrient recycling, has feedbacks to nutrient cycling at the ecosystem level (Hobbie 1992). Plants that recycle a large proportion of their nutrients internally are less dependent on uptake from the soil to meet subsequent nutrient requirements. Such plants may be the species of choice on impoverished soils, or in long-rotation forestry systems in which nutrient exports in harvest do not exceed the slow replenishment of soil fertility by weathering, bulk deposition, and biotic fixation of N₂. Furthermore, tighter within-plant nutrient cycling leads to tighter within-system nutrient cycling (Vitousek 1984), and this reduces the likelihood of nutrient losses from the system via leaching (Shaver and Melillo 1984).

A species' nutrient use efficiency is also an important consideration in managed systems (Ewel and Hiremath 1998). Human activity is increasingly turning to inherently infertile soils and to soils that have been impoverished due to previous land-use practices. In the tropics, the area under forestry plantations has more than trebled since the early 1980s, and although much of this expansion has been on infertile soils, chemical fertilizers are seldom an economically viable management option (Brown et al. 1997). Two objectives must be considered: one is to achieve productivity on infertile soils in the short term; the other is to sustain both productivity and soil fertility in the long term. Nutrient use efficiency, with its implications for productivity and soil fertility, is therefore a potentially important criterion in species selection when designing forestry or agroforestry systems, and when designating land use. As a process that is under substantial control at the species level, nutrient productivity should be an im-

portant selection criterion in the breeding programs of perennial plants, just as it has been for grains (Dambroth and El Bassam 1990). Perennial plants offer the additional attraction of affording an opportunity for genetic improvement in nutrient use efficiency through nutrient retention, a process of little consequence in annual plants.

Although nutrient use efficiency can be a very useful index, there are a number of processes, not all of which are independent, whereby similar values can be achieved, thereby masking the fundamental mechanisms of potential importance. In some cases it is one or more components of the index—productivity, nutrient contents of tissues, and nutrient residence times—that reveal most about differences in species' potential productivity across gradients of soil fertility. It is those fundamental components that merit attention if we are to understand patterns of natural distribution and focus artificial selection on traits crucial to achieving the best possible matches between species and sites.

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